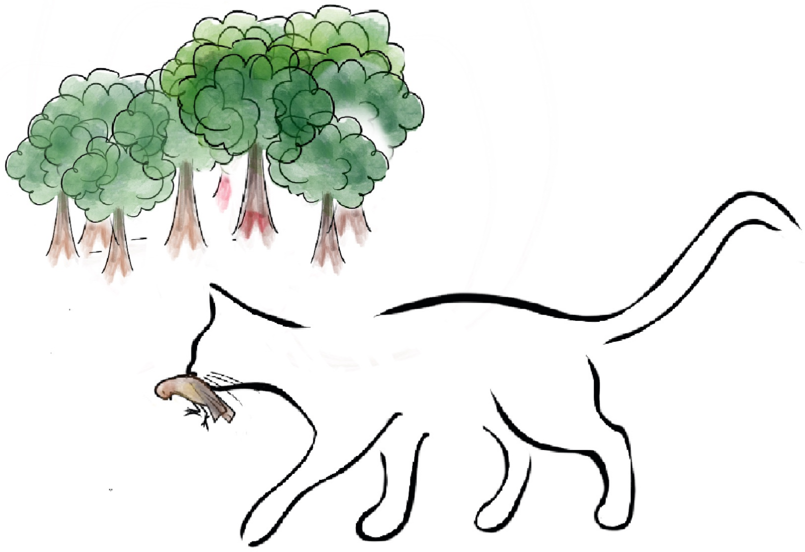
Ecology and management of predation of wildlife by domestic cats

Submitted by Martina Cecchetti, to the University of Exeter as a thesis for the degree of Doctor of Philosophy in Biological Sciences, December 2020.



I certify that all material in this thesis which is not my own work has been identified and that any material that has previously been submitted and approved for the award of a degree by this or any other University has been acknowledged.

(Signature)........Martina Cecchetti........

"…there is no animal that, in the course of its centuries-old association with man, has altered so little as the cat. There is some truth in the assertation that the cat, with the exception of some luxury breeds, such as Angoras, Persians and Siamese, is no domestic animal but a completely wild being. Maintaining its full independence it has taken up its abode in the houses and outhouses of man, for the simple reason that there are more mice there than elsewhere….the appeal of the cat lies in the very fact that she has formed no close bond with him [man], that she has the uncompromising independence of a tiger or a leopard while she is hunting in his stables and barns; that she still remains mysterious and remote when she is rubbing herself gently against the legs of her mistress or purring contentedly in front of the fire. The purring cat is, for me, a symbol of the hearthside and the hidden security which it stands for."

Konrad Lorenz
'So kam der Mensch auf den Hund', 1949

Abstract

1.The domestic cat shares a longstanding history with humans. Depending on the ecological and cultural contexts in which it lives, it can be classified as an invasive species, feral animal, pest-controller and companion animal. Cat behavioural plasticity and adaptability to all ecosystems is mainly related to the retention of hunting behaviour, the management of which is a source of social controversies. Pet owners are often opposed to common hunting management strategies, due to safety concerns or limits imposed upon what they perceive as natural feline behaviours. Conversely, wildlife conservationists often advocate cat confinement as cats pose a threat to wild animal populations. A better understanding of cat hunting behaviour and novel management strategies that recognise both views are required for ameliorating these conflicts.

2. The retention of hunting behaviour by cats is an underexplored issue. Through a literature review, I identified drivers and facilitators of hunting behaviour, and the available measures to reduce impact of cats on wild fauna through population-level and individual-level strategies. Hunting is driven by evolutionary constraints mainly related to an obligate carnivorous diet. Lethal approaches are considered indispensable for cat eradications from islands and large-scale population control. Enrichment has the potential to be a successful approach for reducing hunting in pet cats.

3. Confinement and collar-mounted devices reduce prey killed by domestic cats, but owner uptake of those is low. With a before-after-control-impact design trial, I found that, alongside conventional approaches, the novel enrichment measures of provision of high-meat content, grain-free food and introduction of daily object play reduced numbers of prey items brought home by 36%, and 25% respectively. Such approaches reduce hunting motivation, rather than impeding hunting, and are likely to find more support among cat owners concerned about welfare implications of other interventions.

4. The number of prey items brought home represents only a proportion of the total prey killed by cats, but other prey is eaten. I used Bayesian stable isotope mixing models (BSIMMs) to estimate contributions of wild and provisioned foods to diets of cats, analysing whiskers of cats that depredate wild animals. I also determined whether common deterrents and novel interventions affect the relative importance of wild prey in cats' diet. Wild prey was discernible from

provisioned pet foods, indicating that cat diets consisted primarily of provisioned foods and wild animals contribute a low proportion. Fitting cats with a BirdsBeSafe collar cover further reduces consumption of wild prey. I concluded that hunting wild prey is likely to address some micronutrients requirements, or behavioural motivations.

5. Cat owners express safety concerns regarding their cats' roaming behaviour. Cats are also a threat to wild fauna when roaming outside. I investigated the spatial ecology of cats that were both free to roam and partially confined by owners, and whether intervention measures for reducing predation also affect cat spatial behaviour. Cat home range size and roaming behaviour are affected by outdoor access. Cats fitted with a bell, provided with high-meat content food and subjected to object play increased time cats were located at home (Bell +29%; Food +20%; Play +24%). The most effective approach for reducing roaming remains confinement, whether partial or permanent.

6. Cat personality has been hypothesised to affect between-individual variation in hunting behaviour. I tested whether variation in the 'Feline Five' personality factors (scored by owners) allowed discrimination between cats that bring home prey and those that do not, and whether variation in number of prey returned is related to personality scores. Cats returning home prey were perceived by owners to be high in 'extraversion' or low in 'neuroticism'. Variation in number of prey returned was not affected by any of the personality factors. Assessing behavioural needs through characterisation of individual personality has the potential to enhance approaches for managing hunting by cats.

7. Domestic cats have retained hunting behaviour, which may satisfy behavioural motivational needs and/or nutritional requirements. The novel strategies proposed for reducing hunting in pet cats broaden the approaches owners can adopt while accommodating their diverse perspectives on cat husbandry. A better understanding of the analytical components making the food successful in reducing hunting motivation is advised, particularly for improving environmental sustainability of pet food. Hunting management can be enhanced by designing solutions that consider both the wild and the domestic sides of cats, leading to successful results for conservation.

Acknowledgements

It has been hard and extraordinary. This journey has changed me deeply, both as scientist and as person. I would like to thank my supervisors Robbie McDonald and Sarah Crowley for their guidance, patience (remarkable during my escapes to Linosa), and for having invested in my capacities and ideas. We have done something really ambitious and what's incredible it is we succeeded. You have taught me that self-control, hard work and perseverance always give good outcomes.

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Author's declaration for co-authored manuscripts

Chapters 2,3,4,5 and 6 have been published, accepted, submitted or written for publication as co-authored academic papers. I developed the direction and research design for Chapters 2,3,4,5 and 6 in conjunction with Robbie McDonald (RM) and Sarah Crowley (SC). The experiment in Chapters 3,4,5 and 6 was conducted in conjunction with SC.

For Chapter 2, I conducted the literature review.

For Chapter 3, I organised, processed and analysed the data with advice from Cecily Goodwin (CG).

For Chapter 4, I collected and analysed cat whiskers and dietary samples. Holly Cole and Jenni McDonald collected additional cat foods and carried out lipid extraction. I conducted the isotopic data analyses with guidance from Stuart Bearhop and advice from CG.

For Chapter 5, I collected tracking data. Then, I analysed the data with advice from Luca Nelli and Jared Wilson-Aggarwal.

For Chapter 6, personality item scores for additional cats were obtained from the 'Small Cat Project' study by Jenni McDonald. I analysed all the data.

I wrote all the manuscripts, then amended and revised them in response to comments, suggestions and advice from RM and SC and other co-authors, except for Chapter 3 which was written in conjunction with RM.

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Chapter 1
Introduction

Chapter 1: Introduction

Domesticated species

Over the past 20,000 years humans have formed commensal and domestic relationships with a wide range of animals for various reasons: as livestock and working animals, and more recently as household pets and companions (Zeder 2012a). Domestication is a gradual process, a continuous transition that produces modifications in physiology, morphology and behaviour of the domesticates, which all share the common trait of being tolerant of people (Driscoll et al. 2009b). Domestication is considered a rare process (Irving-Pease et al. 2018) which requires specific conditions to occur (Vigne et al. 2011) but which has had profound cultural impacts on human society (Zeder 2012a). Current thinking emphasizes domestication as a mutualistic relationship between human and animals (Zeder 2012a; Larson & Fuller 2014), at least initially. Certain behavioural characteristics can make particular taxa or individuals better disposed to domestication than others. Favourable traits are grouped into five main categories: social structure (e.g. large gregarious group with hierarchical group structure); sexual behaviour (e.g. promiscuous mating system); parent-young interactions (e.g. female accepts young soon after parturition or hatching); feeding behaviour and habitat choice (e.g. omnivorous); and responses to humans (e.g. readily habituated) (Hale 1969; Price 1984; Zeder 2012b).

The ways in which domestic animals have become integrated into human societies can be grouped into three broad scenarios. In the commensal pathway, wild animals were first attracted to elements of the human constructed niche, gradually establishing a commensal relationship which, over time, mutated into a closer social or economic bond and led eventually to a full domestic relationship (Zeder 2012b). In the prey-pathway, wild animals were firstly exploited for their meat and skins before humans took control over breeding and herd management, in order to maintain a constant supply of the resource (Zeder 2012b). In the directed pathway, humans applied their acquired knowledge of breeding and management of domesticates to capture wild animals and intentionally bring them under increasing levels of human control (Zeder 2012b). Today’s most popular companion animals, the dog and the cat, were both likely to have travelled into domestication along the commensal pathway.

The dog was the first domesticated animal; the earliest skeletal dog remains are dated to the end of Pleistocene, around 16-17,000 years ago, largely preceding the emergence of the agriculture (Larson et al. 2012; Thalmann et al. 2013). Based on genomic evidence, domesticated dogs descend from several distinct lineages of Pleistocene wolves which possibly emerged in different geographical areas (Skoglund et al. 2015; Frantz et al. 2016). Larson and Fuller (2014) proposed a sequenced process in which Pleistocene progenitor wolves went from following mobile hunter-gatherers to commensalism, becoming a separate ecotype that is adapted to the human niche and eventually domesticated through human selective breeding. Another view sustains that fearless but docile progenitor wolves became attached to the anthropogenic refuse associated with human camps, where they may have become accustomed to humans and have served as guards (Wilkins et al. 2014). Eventually these individuals gave rise to the early domesticated dogs that were then employed to working in other tasks, like hunting (Pitulko & Kasparov 2017).

The earliest close connection between human and cats is dated around 11,000-10,500 years ago (Vigne et al. 2012), considerably later than the domestication of dogs. The cat descends from both the Near Eastern and Egyptian populations of *Felis silvestris lybica* (Ottoni et al. 2017). Wildcats *Felis silvestris* have a series of ecological and behavioural traits that make them less than ideally suited to domestication, among these a narrow, carnivorous diet, and a solitary and territorial nature (Bradshaw et al. 1996). It is widely accepted that interactions between cats and humans started as a commensal relationship, in which wildcats were drawn to early human agricultural villages to prey on rodents attracted to grain stores (Driscoll et al. 2009a; Driscoll et al. 2009b; Zeder 2012b; Larson & Fuller 2014). Cats seen killing infesting rodents would have probably been appreciated as self-sustaining pest controllers (Krajcarz et al. 2020) and may have conferred advantages on individual people tolerating them (Crowley et al. 2020a). The value of domestic cats as predators played a significant part in their global spread, as they were employed for rodent control on trade ships and in the storehouses of emerging civilisations (Ottoni et al. 2017). Over time, cats developed an increasing dependency on anthropogenic resources for food and shelter, and behavioural adaptations to the human environment and the proximity of humans, culminated in their partial domestication (Crowley et al. 2020a;

Krajcarz et al. 2020). However, modern domestic cats are still remarkably similar to their ancestors, in terms of genetics, physiology and behaviour, making them unusual among domesticated species (Ottoni et al. 2017).

Domestication of plant and animal species for food, labour and companionship has revolutionised human life, mainly by creating new varieties of plants and animals that, under the protection of humans, could live in almost all environments around the world. However, it also led to the expansion in populations and ranges of domesticates and agricultural economies across the Mediterranean basin, causing a series of human environmental impacts due to the complete replacement of endemic island faunas by imported mainland fauna (Zeder 2008). Furthermore, the close relationships between domesticates and humans created atypical invasion routes and opportunities for these species to establish in novel areas and return to their wild state as feral animals (Gering et al. 2019b).

Domestic animals as feral or invasive species

Domestication is not always a one-way process. When domestic animals are unattended, abandoned, or poorly managed, they can become independent from human care and roam freely (Bonacic et al. 2019), threatening ecosystems and indigenous species. In these contexts, they are often referred to as feral populations, and, where they have detrimental impacts, as invasive species. Feralization is not a mere reversal of domestication, but rather it is complex and shaped by the varied histories of feral populations and novel selection pressures (Gering et al. 2019a).

Bonacic et al. (2019) recently described the various ecologically and economically negative impacts of feral domestic animals throughout the different stages of feralization in rural ecosystems (Figure 1.1). One deleterious effect arising from the presence of feral animals is disease transmission to wild fauna. For example, feral dogs in Chilean urban areas are rarely vaccinated against nonhuman pathogens and can facilitate disease spread to native carnivores (Acosta-Jamett et al. 2015). Moreover, zoonotic diseases, such as rabies, typhus, and toxoplasmosis, can flow between feral animals and human populations. Feral animals also alter community structure, such as that caused by feral ungulates overgrazing and trampling vegetation (e.g. sheep on Santa Cruz island, Klinger et al. 2002); alter nutrient cycle depleting soil nutrients (e.g. feral pigs in Hawaii, Long et al. 2017) and establish predator-prey relationships with existing species (e.g. feral cats, Marra & Santella 2016). Additionally, feral animals can compete with native taxa, as with feral horses that lead native ungulates in the Western United States to avoid water sources when are present (Hall et al. 2018).

Apart from the multiple effects of feral taxa on invaded ecosystems, managing feral domestic animals can present many obstacles. As feral domesticated species are closely associated with human societies, and often highly valued in other contexts, human attitudes with respect to feral domestic animal control and management tend to diverge from attitudes regarding the control of wild alien species (Gering et al. 2019b). Conceptually, and often practically, it is difficult to completely dissociate feral populations from domesticated individuals (Crowley et al. 2020a).

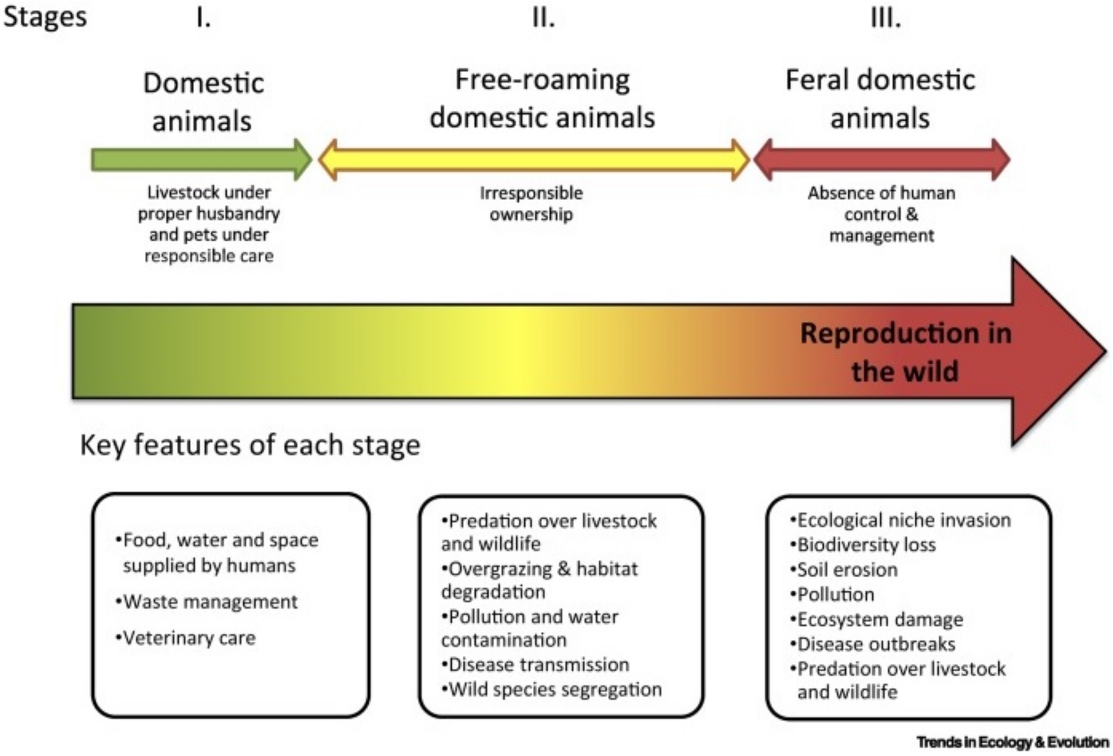


Figure 1.1. Stages of feralization and its effects on rural ecosystem and biodiversity. Figure from Bonacic et al. (2019).

Invasive species

Humans have traded and transported plants and animals for millennia, and two crucial moments in biological exchanges were the end of Middle Ages (Preston et al. 2004) and the beginning of the Industrial Revolution when international trades across all the countries increased as a consequence of highways, railways and steamships (Findlay & O'rourke 2009). Thus, species have reached distant places where they would otherwise have negligible opportunities to land naturally. Taxa introduced outside of their natural range, whether intentionally or unintentionally, by human agency are commonly referred to as alien species (IUCN 2000), and invasive species, when they have negative ecological, economic or social impacts (Mooney 2005). They differ from pest species, which primarily impact agricultural values (Russell et al. 2017). Biological invasion is considered one of the five top drivers of global biodiversity loss, ultimately leading to the homogenisation of world's fauna and flora (Baiser et al. 2012), and their consequences represent a huge cost to human societies worldwide. The environmental impact of invasive species ranges from affecting single species to having repercussion across entire ecosystems. There are examples of invasive species altering the course of evolution in endemic species, by competitive exclusion, niche displacement, hybridization and introgression, and predation, eventually leading to extinction (Mooney & Cleland 2001). Invasive species can drastically alter ecosystem structure and function by precipitating 'invasional meltdown' (Simberloff & Von Holle 1999), in which numerous introductions facilitate one another's success, causing extensive changes to species compositions and interactions.

Invasive species also have a large impact on the economy and public health of human communities. Economic impacts arise from loss of potential output (e.g. reduction in the survival, fitness or production of crops, or fisheries) and direct costs incurred as efforts to reduce impacts, including control and eradication (Neill & Arim 2011). Also, human health is affected in multiple ways, for example when the invasive species is a pathogen itself, or a vector for a native or exotic pathogen. Finally, the invasive species can provoke changes in ecosystems that favour outbreak of native and exotic pathogens. Today, globalisation is contributing to increasing the pathways, frequency and speed of invasions, with the total number of invasive species increasing worldwide (Seebens et al. 2017, 2018). This rise is linked to the expansion of global trade, specialisation in production, and increased connections to previously isolated locations (Seebens et al. 2018). Climate change is also contributing by opening new pathways for introductions and expansion of already introduced species (Medlock & Leach 2015).

Undoubtedly, invasive species have greater and disproportionate impacts upon biodiversity, agriculture, economy, health and culture on islands, when compared to continents (Reaser et al. 2007; Bellard & Jeschke 2016). In particularly, island ecosystems are vulnerable to newly introduced species because they generally have relatively low species diversity, simplified trophic webs, empty niches, high rates of endemism, and often naïve native species (Vitousek 1988; Williamson 1996). It is estimated that the introduction of mammalian predators has caused the extinctions of many populations and species of oceanic island birds (Atkinson 1996; Blackburn et al. 2004), that had evolved in the absence of such predators and lack appropriate anti-predator defences.

Management of invasive species and conflicts

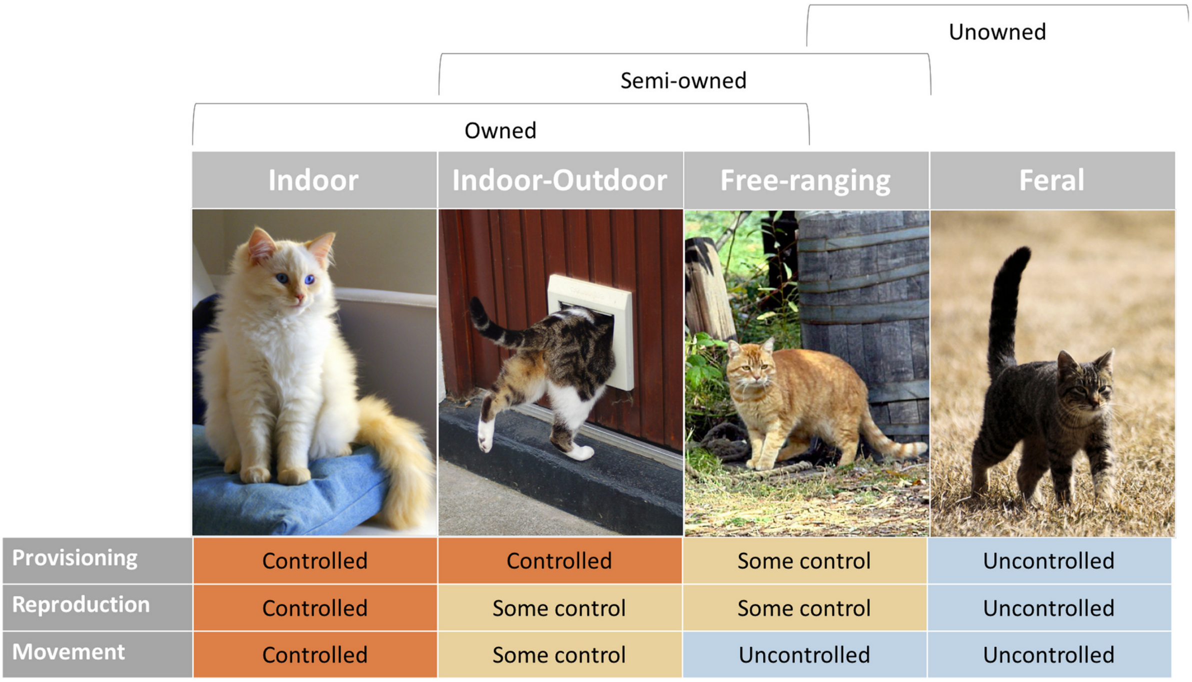
In order to address the vast and diverse negative impacts arising from invasions, a series of activities in environmental policy and practice, implemented at geographic and political levels have been introduced and contribute to invasive species management (ISM) (Simberloff et al. 2013). Management involves a series of strategies, primarily according with time since the species has been introduced, that span from prevention (information, regulation and legislation, quarantine measures) through early detection (interception, monitoring and surveillance, removal), to active management (eradication, containment, control) (Simberloff et al. 2013). Despite the importance of ISM projects, they are often the cause of social conflicts stimulating debates about achievability, efficiency, social fairness, and ethical implications (Crowley et al. 2017). ISM often involves contentious strategies and methods, including restriction of trade freedoms, extensive use of chemical and biological control agents, and large-scale culling of sentient and/or valued species (Crowley et al. 2017).

Human perceptions of nature and the environment are essential to shaping the outcomes of environmental management and conservation strategies (Shackleton et al. 2019). One of the factors influencing people's perceptions, attitudes and behaviours toward the management of an invasive species is its charisma, referring to characteristics and behaviour of a species that inspire positive responses in humans (Shackleton et al. 2019; Jarić et al. 2020). Some animal traits are known to contribute to charisma, including body size, coloration, furry coat, peculiar appearance, neotenic features and sentience (Beever et al. 2019; Shackleton et al. 2019). For example, feral populations of cats and dogs are especially likely to be considered charismatic and this charisma can and historically has contributed to these species' establishment, through public support and provisioning of resources (e.g. feeding) (Allen 2018; Jarić et al. 2020). Considering invasive species' charisma is crucial in planning effective management strategies and address educational programmes for raising people's awareness of their impacts, particularly when it comes to invasive species that otherwise share a long history of association with humans via domestication.

The domestic cat

Cats have a near-global distribution, occurring on all continents except Antarctica and on hundreds of islands (Long 2003), and in many human societies their primary role has become companionship. The domestic cat is characterised by high behavioural plasticity and can quickly transition from being a companion animal, to an invasive, feral state, being able to survive independently from human assistance (Bradshaw et al. 1999). Their flexibility is mainly related to the retention of hunting behaviour, which permits them to kill prey efficiently. The reasons underpinning the retention of a fully functional genetic repertoire for hunting, also retained in well-fed pet cats, are not still fully understood (see Chapter 2).

Cats can be classified in relation to human control over provision of food, control of reproduction and control of movement (Crowley et al. 2019) (Figure 1.2.), where self-sustaining feral cats are not subjected to any human controls. When food resources are available (intentionally or accidentally), feral cats can also congregate into colonies, which in some societies are actively managed by volunteer 'caretakers' who may also provide for their sterilization (Crowley et al. 2019). "Indoor-outdoor" cats have closer relationships with individuals who provide food and shelter, and owners may also control reproduction and/or cat movement (e.g. keeping cats in overnight). Finally, indoor cats are those kept exclusively inside and fully depend upon human assistance (Figure 1.2).



	Indoor	Indoor-Outdoor	Free-ranging	Feral
Provisioning	Controlled	Controlled	Some control	Uncontrolled
Reproduction	Controlled	Some control	Some control	Uncontrolled
Movement	Controlled	Some control	Uncontrolled	Uncontrolled

Figure 1.2. Different categories of cat ownership and husbandry practices in relation to human control over provisioning, reproduction, and movement. Figure from Crowley et al. (2019).

All cats that have access to the outdoor environment represent a threat to wildlife, through predation, indirect effects, diseases and hybridisation. On the other hand, while the outdoor environment provides welfare benefits to the cats, in turn it can also negatively impact their welfare.

Predation of wildlife

Feral cats are dietary generalists feeding on many types of native and introduced prey species, with their diet composition usually affected by prey fluctuations (Nogales & Medina 2009; Bonnaud et al. 2011b). In delicate island ecosystems, feral cats are thought to be a major driver of biodiversity loss, contributing to the extinctions of insular endemic birds, mammals and breeding seabirds (Medina et al. 2011). Consequently, cats are listed as one of the world’s 100 worst invasive alien species (Lowe et al. 2000).

However, the adverse ecological impacts of domestic cats on biodiversity are not limited to islands (Loss & Marra 2017). On mainlands (continents and large islands, such as Australia and the UK), free-roaming cats are sustained at high densities through subsidised food and veterinary care provided by people, so their survival is no longer dependent upon prey fluctuations and availability. While it is more difficult to quantify precisely the impact of free-roaming cats on prey populations in mainland settings, they are considered responsible for killing large numbers of wild animals. At a national level, for example, free-roaming domestic cats are estimated to kill between 100 and 350 million birds per year in Canada (Blancher 2013). In Australia, they are estimated to kill an average of 377 million birds per year (Woinarski et al. 2017). In the United States, it was estimated that 1.3–4.0 billion birds, 6.3–22.3 billion mammals, 258–822 million reptiles and 95–299 million amphibians are killed by free-ranging domestic cats each year (Loss et al. 2013). Factors that may influence owned cats' predation rates and species caught, other than the location of their home, include the cats' age and condition, the extent they are fed and cared for, the use of anti-predation devices, the time of day cats are allowed outside, and the time of year (Woods et al. 2003; Kays & DeWan 2004; van Heezik et al. 2010; Silva-Rodriguez & Sieving 2011; Krauze-Gryz et al. 2017).

Indirect effects on prey populations

Cats can also have a series of indirect effects on prey populations, through disturbance, or fear induced by the cats' appearance, presence or scent. Fear effects adversely influence the foraging, space use and reproduction of impacted species populations (Freeberg et al. 2016). Fear effects may even exercise an even greater influence on prey populations than predation itself (Loss & Marra 2017). Modelling by Beckerman et al. (2007) suggested that even when urban songbird predation mortality from domestic cats is as low as 1%, fear effects from those same cats might reduce bird abundance by 95%.

Diseases

Domestic cats can additionally impact wildlife through disease transmission. A broad range of vertebrates can be affected by cat-transmitted diseases like toxoplasmosis, rabies or feline leukaemia (Gerhold & Jessup 2013). An explanatory example of cat disease impact is the death of five members of endangered puma, the Florida panther *Puma concolor*, caused by an outbreak of feline leukaemia virus which was traced back to a single domestic cat in Florida (Brown et al. 2008). Cat diseases are not limited to the members of the family Felidae, but can be contracted by other mammals, for instance significant mortality from toxoplasmosis has been documented for marsupials, neotropical primates and even marine mammals (Gerhold & Jessup 2013).

Hybridisation

Hybridisation is another conservation issue caused by domestic cats mating with wildcats *Felis silvestris* (Beaumont et al. 2001). Hybridisation and introgression of domestic animal genes can result in the extinction of native species both directly and indirectly. It can lead to 'genetic swamping', where interbreeding with domestic cats produces hybrid populations in which no remaining individuals can properly be described as the native, wild cat species (Todesco et al. 2016).

Negative impacts of free-roaming on cat welfare

When cats are free to roam outside, they can interact with other companion animals or wildlife (Loyd et al. 2013a), increasing the possibility of transmission of parasites and diseases. Relevant, readily transmissible infections include the feline leukaemia virus (FeLV) and feline immunodeficiency virus (FIV). Both can be transmitted through bite wounds and FeLV can also be transmitted through more casual contact, such as mutual grooming. Similarly, outdoor cats are more susceptible to parasites, like helminths, fleas and ticks. Diseases and parasites can kill cats, or cause temporary or permanent injuries (Tan et al. 2020).

Road traffic accidents are another major hazard for free-roaming cats, causing the death of the cat or inflicting extensive damage to organs or extremities which can develop into acute or chronic long-term health consequences. One study examined causes of death in cats brought into a Canadian veterinary clinic, and found that trauma was the cause of 39% of sudden deaths in cats, with 87% of those cases due to motor vehicle accidents (Olsen & Allen 2001). The same study reported cat trauma fatalities caused by dog bites. In some regions, another source of concern is predation *of* cats by wild predators, such as coyotes (Lukasik & Alexander 2011).

Despite these risks, in many countries a substantial proportion of owned cats are permitted to roam freely, in order to carry out pest control duties or natural feline behaviours, like, travelling, exploring and hunting. Cat owners believe that exhibition of natural behaviours can be best expressed in the outdoor environment, overcoming the dangers the cats possibly face outdoors (Crowley et al. 2020b).

Conflicts over cat management

The detrimental effects on wildlife caused by free-roaming cat populations have led to the design and adoption of various management strategies ranging from lethal methods for controlling unowned cat populations to the use of deterrents, like belled collars, and restrictions upon outdoor access for owned cats (see Chapter 2). However, the perceptions of conservationists who primarily value wildlife and those of cat lovers who primarily value cat welfare, have not converged around any unanimously accepted solutions, aggravating social conflicts and uncertainty in how to address the cat problem (Peterson et al. 2012).

One example of a public conflict around feral cat management plays out in North America, where the strategy of trap-neuter-return is the subject of a long-standing and increasingly polarised public debate between activists supporting and those opposing it (Peterson et al. 2012; Loss et al. 2018). In contrast, in Australia, cats are more widely recognised as predators of native wildlife (Hall et al. 2016a), and even if the management of predation by feral cats remains controversial (Farnworth et al. 2014), it is more generally considered a necessity (Doherty et al. 2017). In some states, the management of owned domestic cats is regulated by law (e.g., Western Australia Cat Act 2011). Although support for registration and night confinement of cats is relatively high, there is nevertheless resistance to permanent confinement and bans on cat ownership (Travaglia & Miller 2018).

A clear legal position on the problem is indicated by Trouwborst et al. (2020). They reviewed the impact of free-roaming cats on wildlife and the obligations of governments around the world to respond to international conservation agreements which require the adoption and implementation of policies aimed at preventing, reducing or eliminating impacts of free-ranging cats, particularly by removing feral and other unowned cats from the landscape and restricting the outdoor access of owned cats. They recognised that interests of cat owners (and caretakers) and the perceived interest of domestic cats themselves explain why many authorities have failed to take effective action to address the threats posed by free-ranging cats to date, however, they argue that from a legal perspective such factors provide little justification for not complying with international environmental law. This is another example of strongly-held views surrounding cat management, and one that is unlikely to help reduce conflict. Indeed, implementing or enforcing laws, without gaining social acceptance of the reasoning for this, or public understanding of the problems presented by free-roaming cats, would likely lead to lack of compliance or active protest (Crowley et al. 2017).

Defining alternative management solutions to those that already exist for the control of unowned cat impacts upon wildlife is a major challenge, also because management of feral cats can frequently be controlled by local authorities and individual-level solutions are obviously not feasible. However, given that pet cats are an important and beneficial part of many people's lives, the most productive approach to these problems is to identify, and then advocate for, cat husbandry practices that maintain or improve cat welfare, protect wildlife, and allow people the pleasure of owning a cat (Hall et al. 2016a).

The cat situation in the UK

The United Kingdom is home to ~ 10.9 million pet cats (PDSA 2020), and in 1995 the estimated feral cats were 813,000 (Harris et al. 1995). Levels of cat ownership are highest in urban areas, with some locations having more than 100 individuals per km^2 (Baker et al. 2008; Thomas et al. 2012). The UK has a high rate of cat sterilisation, >90% (Thomas et al. 2012), compared to around 80% in the USA (Chu et al. 2009) or 43% in parts of Italy (Slater et al. 2008).

Restrictions upon cat roaming behaviour by keeping cats inside at night or confined to the owners' property are very unpopular among cat owners in the UK (Hall et al. 2016a; Crowley et al. 2019). Predation studies, based on numbers of prey brought home suggest that pet cats are responsible for killing an estimated number of 55 million birds and 119 million mammals per year (Thomas et al. 2012). One study estimated that owned cats, in a 5-month survey period, brought home 57 million mammals, 27 million birds and 5 million reptiles and amphibians (Woods et al. 2003). Some studies additionally identified that predation of various bird species at study sites in the United Kingdom was so severe that the studied populations are likely to act as ‘sinks’, requiring immigration from areas with fewer cats to persist (Baker et al. 2008; Thomas et al. 2012).

To quantify predation of wildlife by cats, studies have largely relied upon numbers of prey brought home, which are considered to be an underestimation of the overall scale of predation on wild populations. Typically, only a fraction of hunted prey is brought back to the house or the farm, for instance 18-23% (Loyd et al. 2013b; Seymour et al. 2020) or 10% (Krauze-Gryz et al. 2019). Thus, when estimating the impact of cats on a broader scale, a correction factor is usually applied (Loyd et al. 2013b; Seymour et al. 2020). Additionally, through the use of animal-borne cameras, researchers have discovered that part of such captures can be eaten or part left in the place of capture (Loyd et al. 2013b; Seymour et al. 2020). These cameras, called ‘kitty-cams’, themselves present a series of limitations, as they might represent an impediment to the usual cat hunting activities, and the analysis of data requires going through long hours of recording, potentially limiting the sample size of cats involved in a study. Thus, we need to better understand the relationship between hunting and prey consumption in pet cats and also to develop additional methods for studying their diets. The number of prey items brought home and recorded by householders is an index representing the minimum number of animals killed by cats and it is adequate when measuring the effects of a deterrent (e.g. a bell) on rates of predation (Woods et al. 2003). Between-individual variation in number of prey items returned can also be controlled for, by adopting a before-after-control-impact design making paired observations of the same individual before and after the application of a specific intervention. There is great variation between individual cats in numbers of prey brought home, with most bringing home few or no prey (Woods et al. 2003; Baker et al. 2005; Thomas et al. 2012). Nevertheless, even if the individual rate or predation is low, the cumulative impact of cats living at high density may be critical (Baker et al. 2005; Sims at al. 2008; Kays et al. 2020).

Despite the evidence, cat owners rarely perceive a strong individual responsibility for preventing or reducing predation by their pets (Crowley et al. 2019). For this, in the UK, any regulatory interventions in cat ownership or management aimed solely at the reduction of predatory behaviour would contrast with widely held societal values and could place unnecessary restrictions on owners whose cats either do not hunt or are valued as pest-controllers (Crowley et al. 2019). However, many owners are not pleased by the prey brought home by their cats and show interest in effective ‘cat-friendly measures for reducing such behaviour’ (Crowley et al. 2019, 2020b). Cat owners exhibit diverse perspectives regarding the management of domestic cat roaming and hunting behaviours, with different priorities that provide insight into the likely effectiveness of engaging these people with different management options for dealing with their cats’ impacts on wildlife (Crowley et al. 2020b). It is therefore important to offer multidimensional strategies to owners, compatible with their priorities, that in turn will bring direct or indirect benefits to wildlife. For instance, strategies that can modify cat roaming behaviour might help in reducing hunting while also improving cat safety, and so are likely to be highly valued by owners. While interventions that directly interfere with cat hunting success already exist (e.g. belled collars), it is also desirable to design interventions that aim to confer to the cat the same physiological and behavioural rewards that result from its hunting activities.

Thesis aims and outline

In this thesis, I apply ecological research methodologies to explore the ecology of predation of wildlife by domestic pet cats, and I test novel management strategies identified with reference to current knowledge of feline physiological needs and behavioural requirements.

This ecological framework intersects with a simultaneously developed framework for social aspects of the problem, led by Dr Sarah Crowley, and both approaches come together into a larger project called “Cats, cat owners and wildlife”. This wider project recognises that the relationship between domestic cats, people and wildlife is a complex, shared problem and that cat owners are a key interest group, central to any effort to minimise cat predation. The social aspects of the project have so far been framed in three published papers: Crowley et al. (2019) investigate cat owners’ perceptions of their pets’ behaviour, responsibilities for its management and mitigation strategies; Crowley et al. (2020a) propose a novel ‘companion animal ecology’ for an interdisciplinary approach to domestic cat management; and Crowley et al. (2020b) characterise five perspectives held by cat owners on roaming and hunting behaviour of their pets.

The specific aims of my research, presented in this thesis, are to:

1. Explore the drivers and facilitators of hunting in domestic cats, and give an overview of the management strategies available and adopted for reducing cat populations and impact on wildlife.
2. Test the efficacy of novel management strategies for reducing the numbers of prey captured and brought home by domestic cats and to compare them to the efficacy of popular deterrents. This will help to understand whether persistence of hunting behaviour in pet cats is driven by physiological or behavioural needs that are not met by the provisioned diet and/or in the home environment and whether non-invasive strategies represent a valid alternative to measures that inhibit hunting behaviour.
3. Evaluate the use of stable isotope analysis as tool for studying domestic cats' diet and reliance on wild prey, and test whether any of the common deterrents and novel management strategies could reduce cat consumption of wildlife. This will help to validate the use of stable isotope analysis as non-invasive method for studying the diets of pet cats that depredate wildlife, and understand whether cats are addressing any shortfall in macronutrient/micronutrient consuming wild prey. Furthermore, it will give deeper insights into the relationship between hunting motivation and prey consumption.
4. Investigate the spatial behaviour of cats and determine whether common deterrents and novel strategies can influence home range and movements within it. This will help to understand the extent to which cats roam for addressing hunting motivation. Furthermore, it will enable assessment of the implications of roaming behaviour for cat welfare, as valued by cat owners.
5. Explore cat personalities and their influence on cat predatory behaviour. This will help to understand whether high between-individual variation in cat hunting behaviour is determined by specific personality profiles. Furthermore, this will allow to identify the potential for application of targeted predation management strategies that better suit individual cats.

Following this general introduction as Chapter 1, the thesis is arranged into five chapters (2-6), structured as a series of self-contained academic papers, each of which has its own introductory and discussion sections; it concludes with a general discussion as Chapter 7. Each of the Chapter 2-6 addresses one of the five aims outlined above.

For Chapter 2, I conducted a literature review to explore the drivers and facilitators of cat predatory behaviour and management strategies. I identified two hunting drivers, (evolutionary origins and diet) and three facilitators (early-life history, personality and environment). Based on the findings of this review, I decided to test novel management strategies focused on cat diet requirements and reproduction of natural feline behaviours in the home environment.

In Chapter 3, I experimentally tested the effectiveness of a range of techniques designed to reduce the number of prey brought home by pet cats. I tested popular deterrents (a belled collar and BirdsBeSafe collar cover) alongside novel management strategies (provisioning of high-meat content food, delivery of food through a puzzle feeder and dedicated playtime with toys).

In Chapter 4, I investigated the diets of domestic cats through stable isotope analysis of their whiskers and of putative prey items. In this chapter, I explore cat reliance on wild prey and pet foods provided by owners. I also investigate any changes in consumption of wild prey, attributable to the introduction of common deterrents and novel management strategies.

In Chapter 5, I documented the spatial ecology of cats using GPS trackers. I investigated variations in cat home range size and spatial movements within it, including the proportion of time spent inside the house in response to the introduction of common deterrents or novel management strategies.

In Chapter 6, I classify cat personalities and investigate possible relationships between personality and cat predation rates.

My thesis concludes with a general discussion, where I synthesise the key findings and the contribution of this thesis to the comprehension of the ecology of cat predation of wildlife and evidence for the benefits of novel management strategies that reduce hunting rates without directly restricting cat behaviour.

Chapter 2

Drivers and facilitators of hunting behaviour in domestic cats and options for management

Chapter 2: Drivers and facilitators of hunting behaviour in domestic cats and options for management

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Abstract

Domestic cats *Felis catus* are distinct from other domesticated animals because their phenotype and genotype are relatively unchanged. While they live with people as pets or pest-controllers, they retain capacity for survival independent of human support and readily persist as feral animals. Most cats retain some propensity to express hunting behaviours, even if hunting is not required for nutrition. In some settings, depredation by cats is a threat to biodiversity conservation, leading to attempts to mitigate their impacts.

We characterise drivers and facilitators of the hunting behaviour of domestic cats: evolutionary origins, diet, life-history, personality and environment. Hunting is driven particularly by evolutionary constraints and associated physiological and nutritional requirements. Proximate causes of variation in hunting behaviours relate to prey availability, husbandry and degree of domestication, while early life-history and personality play further roles.

We review cat management approaches in terms of effectiveness, feasibility and welfare. Amongst lethal, large-scale methods of population control, poisoning is most frequently used in cat eradications from islands. Because poisoning is challenged on welfare grounds, euthanasia is used at smaller scales, and in inhabited, mainland settings. Non-lethal approaches, primarily surgical sterilisation, are favoured by cat advocates but entail challenging logistics and scale. In attempts to inhibit predation of wild species by pet cats, owners restrict outdoor access, and use collar-mounted devices, including bells, sonic devices, collar covers and bibs. Other individual-level interventions, such as dietary and behavioural enrichment, some of which may improve cat welfare, have potential, but effects on hunting remain untested.

Understanding and managing the hunting behaviour of cats are complex challenges. We highlight drivers and facilitators of this behaviour, representing starting points for formulating solutions that might be acceptable to cat owners and wider groups of people who value cat welfare, while also being effective for wildlife conservation.

Introduction

Relationships between domestic cats *Felis catus* and people have evolved over millennia (Serpell 2014). Conflict among people about cats is prevalent in some societies, where human populations have been crudely divided into those who value cats as companions and pest-controllers, and those who value wildlife and are concerned about cats as predators and invasive pests (van Heezik 2010; Marra & Santella 2016; Loss et al. 2018). Although vibrantly expressed in contemporary debate, this duality in popular characterisations of cats and their impacts is associated with a more fundamental tension between natural selection for predatory independence in the wild, and artificial selection for affectionate dependence in companion animals (Crowley et al. 2020a).

Cat populations encompass degrees of domestication, varying from one individual to another, as well as with local ecological and cultural conditions (Turner & Bateson 2014). Arguably, complete domestication, consisting of high-level dependence and anthropogenic control of breeding, is apparent only in some pedigree breeds (Bradshaw et al. 1999). Several terminologies are used to describe the degree of domestication of individual cats and, to some extent, their populations, primarily based on their degree of dependence upon humans: Bradshaw et al. (1999) define pedigree, pet, semi-feral, feral, and pseudo-wild cats, while Sparkes et al. (2013) distinguish household, stray or abandoned, street or community, and feral cats. The lack of a uniform definition is clear, for example, in the varying use of the term 'feral', in different countries. In New Zealand and on other islands where cats are perceived as invasive, feral refers to cat populations living and breeding in a wild state (Farnworth et al. 2010). By contrast, in the USA, feral refers to abandoned, stray or unowned cats (Loyd & Hernandez 2012). We follow our earlier classification (Crowley et al. 2020a) of domestic cats, according to the degree of human "ownership" and the degree of human control over food provisioning, reproduction and movement. By this classification, for example, feral cats are unowned and not subject to control of provisioning, reproduction or movement. The domestic cat retains a behavioural repertoire that makes some individuals very successful when living independently of people, and all cat populations show a degree of genotypic and phenotypic flexibility that enables them to move between states within a few generations, or even within a lifetime Bradshaw et al. (1999). Cats' abilities to hunt are among the most important characteristics that have been maintained throughout their evolution, and it underpins their ability to survive in diverse ecosystems. For example, in island ecosystems, feral cats hunt for survival and are major threats to biodiversity (Medina et al. 2011; Palmas et al. 2017). On islands, impacts of cats are amplified, relative to continental areas, due to the evolution of endemic prey species in the absence of terrestrial predators (Bonnaud et al. 2012; Woinarski et al. 2017). Currently, cats on islands are most often characterised as pests, perhaps ironically, given that most were introduced to such islands to control rodent pests (Driscoll et al. 2009a).

Estimations of the scale of killing by cats suggest that, when abundant, they can be responsible for large numbers of wild animal deaths (Lepczyk et al. 2003; Woods et al. 2003; Blancher 2013; Loss et al. 2013; B. P. Murphy et al. 2019). Determining the relative importance of compensatory (Møller & Erritzøe 2000; Baker et al. 2005) and additive (van Heezik et al. 2010) effects of predation by cats on prey populations remains a challenge, but Loss and Marra (2017) gathered considerable evidence of indoor-outdoor, free-ranging and feral cats affecting continental vertebrate populations. Beyond their direct effects, cats are implicated in indirect, sub-lethal effects (Beckerman et al. 2007), including reduction of parental care and facilitation of nest predation (Bonnington et al. 2013), competition (Pavey et al. 2008) and disease transmission (Honnold et al. 2005; Eymann et al. 2006).

Numerous caveats notwithstanding, prey animals brought home by owned cats are tangible evidence that some individuals remain proficient hunters. Owned cats no longer need to hunt for survival, though instinct may mean they still feel such a need. The factors affecting variation in hunting are less well understood. Bradshaw et al. (1999) suggested three factors that may have acted to ensure that cats can switch between independence, commensalism and symbiosis with people: “1) the probability that diets provided by people were [until the 1980s] unlikely to meet their nutritional requirements; 2) the small number of generations that have elapsed since domestication began, and 3) the historical dual role of cats as pest controllers and companions”. Extending from these three factors, we have reviewed a broad literature and identified a range of potential drivers and facilitators of hunting behaviour in cats. We define hunting behaviour as all behaviours forming part of finding and killing live prey, rather than its scale or impact. We organised our review into five factors: evolutionary origins, diet, early life-history, personality and environment (Table 2.1), that either drive or facilitate hunting behaviour. We then reviewed approaches to mitigating any effects of predation by cats of wildlife, and indicated their effectiveness, feasibility and welfare implications. We cover cats as owned, companion animals (pets), and as semi-owned and unowned animals. For domesticated species, and for few more so than cats, human-animal relationships are profound. Management can therefore be as much a social as a biological challenge, and the social aspects of cat management merit their own review. We suggest that a better understanding of hunting behaviour in cats could support the development of, and inform debates about, approaches to management. We hope that some of these might open ways for collaboration between advocates both for cats and for wildlife.

Methods

We searched web of science and google scholar, using terms including: cat, *Felis catus*, domestic, feral, hunting, diet, predation, behaviour, personality, ontogeny, nutrition, evolution, management and invasive species. We assessed books on cats and their biology. We followed articles cited by and citing the located literature.

Drivers and facilitators of hunting behaviour

Evolutionary origins

Felis catus is a member of the order carnivora and family Felidae, and descends primarily from near-eastern wildcats *Felis silvestris lybica* (Driscoll et al. 2007). The history of domestic associations began ~10000 years ago, when it is thought the species became increasingly commensal and cats’ hunting abilities were appreciated by humans as a means of controlling rodent populations in food stores (Driscoll et al. 2009a; Table 2.1). Both near-eastern and Egyptian cat lineages have contributed at different times to the worldwide gene pool of domestic cats (Ottoni et al. 2017). Domestication has been a long-term process, where frequent and long-range translocations by people facilitated mixture between geographically distant populations (Ottoni et al. 2017). Unlike the domestic dog *Canis familiaris*, which has undergone strong artificial selection, the domestic cat remains largely a product of natural selection (Driscoll et al. 2009b). It remains morphologically (Yamaguchi et al. 2004), physiologically and behaviourally similar in most respects to its progenitor: a solitary, territorial and obligate carnivore that kills several small animals per day (Bradshaw 2006, 2016). The very recent history of 'true' domestication, beginning perhaps as little as ~200 years ago, means that domestic cats effectively remain genetically 'wild' (Tamazian et al. 2014). Few genomic alterations in domestic cats are attributable to domestication, excepting genes affecting memory, fear-conditioning and reward learning (Montague et al. 2014). Domestic cats have retained the genetic basis for effective hunting (Bradshaw 2006), including sensory traits such as a broad hearing frequency range, high visual acuity and accentuated vomeronasal capacity (Montague et al. 2014). Critically, in relation to augmented impacts upon prey, cats maintain separation between hunting motivation and prey consumption (Leyhausen et al. 1956) and do not necessarily eat what they kill. Adamec (1976) observed that hungry cats would leave palatable food in order to kill live prey, but would then return to provisioned food. This is likely to increase food input by providing for multiple kills when opportunities arise (Adamec 1976; Macdonald & Rogers 1984), and surplus killing has been documented in feral (McGregor et al. 2015) and owned cats (Loyd et al. 2013b).

Diet

Domestic cats are obligate carnivores in terms of nutrient requirements, ingestion, digestion and metabolism (Bradshaw et al. 1996; Table 2.1). The narrow carnivory expressed by all Felidae, and their nutritional peculiarities (Macdonald & Rogers 1984) relate to ancestral loss of metabolic enzymes, including those involved in synthesis of vitamin a, prostaglandin, taurine and arginine. In the feline genome, genes implicated in lipid metabolism are enriched (over-represented among differentially expressed genes), further indicating adaptation to obligate carnivory (Cho et al. 2013). Cats’ requirement for high-protein diets derives from lack of regulation of aminotransferases in dispensable nitrogen metabolism and urea cycle enzymes (Rogers et al. 1977; Rogers & Morris 1980; Morris 2001). Similarly, the requirement for dietary niacin is related to picolinic carboxylase activity (Suhadolnik et al. 1957), while requirements for vitamin d relate to 7–dehydrocholesterol–Δ7–reductase activity (Morris 2001). Unlike in kittens, there is no dietary requirement for carbohydrates in adult cats (Macdonald & Rogers 1984).

The nutrients cats require are all found in wild prey. Dietary analyses of feral cats show that among wild foods, they mainly eat small mammals, with smaller contributions from birds, herpetofauna and insects, and take multiple small meals of high protein content per day (Bonnaud et al. 2007; Medina & Nogales 2008; Faulquier et al. 2009; Ozella et al. 2016). While some owned cats fed from birth on nutritionally complete food are characterised as ‘fussy’, in exhibiting neophobia towards novel foods (Bradshaw et al. 2000), others exhibit catholic diets. Cats modify their prey preferences to support a balanced diet (Bradshaw 2006), and dietary diversity in feral and free-ranging cats is maintained by (anti-apostatic) selection of rarer food items (Church et al. 1994; Bradshaw et al. 2000). Maintaining dietary diversity appears to be an adaptive means of addressing specific nutritional demands. Many owners feed their cats once or twice a day, sometimes giving more than their cats can eat in a single meal (Kaufman et al. 1980). When owned cats have *ad libitum* access to food, they eat 7-20 small meals daily (Mugford 1977), more closely resembling wild-type feeding patterns, hence feeding other than *ad libitum* might prompt more frequent hunting.

Over the last half-century, cats’ requirements for specific nutrients have been increasingly well understood, and since the 1980s improvements have been implemented by pet food manufacturers. Owned cats can, in principle, now rely on human provisioning to obtain a ‘balanced’, ‘complete’ diet. Nevertheless, commercial pet food bears little resemblance to natural prey, having lower energy density and different sensory properties (Bradshaw 2006). Moreover, because natural prey is high in protein and scarce in carbohydrates, and most cat foods are rich in starches, it has been speculated that high-carbohydrate pet foods could be detrimental for cat health (Verbrugghe & Hesta 2017). Outdoor access

(Defauw et al. 2011) and taking wild prey are protective of urinary tract disease, and this effect interacts with dry food provision, leading to hypotheses that cats fed a high proportion of dry food might seek alternative, wild prey (Jones et al. 1997). Direct provision by people of any food to cats is a very recent attribute of domestication and, with the even more recent advent of complete diets, selection is likely to have favoured maintaining hunting ability to obtain essential, but otherwise scarce, nutrients. The specific dietary requirements of cats, together with variation in the quality, quantity and availability of wild and provisioned foods, are therefore likely to be significant drivers of variation in hunting behaviour and predation rates.

Early life-history

The early development of kitten behaviour plays an important role in forming adult behaviour, individuality and sociability towards humans ('friendliness'; McCune et al. 1995; Ahola et al. 2017; Table 2.1). In the wild, kittens are introduced to hunting by their mother creating situations in which they hone hunting skills (Bateson 2000). Kittens tend to follow maternal prey choices, and young cats acquire skills through social learning (Kuo 1930). Adult cats are better able to catch particular prey if they had experience of that prey as kittens, but being more skilful in catching one prey does not engender a general improvement in hunting skills (Caro 1980a). Life-history shapes individuality in hunting technique and prey specialisation, and this has gained attention as a means of focusing management upon 'problem individuals' (Dickman & Newsome 2015; Moseby et al. 2015; Swan et al. 2017).

Similarities between hunting and playing behavioural sequences suggest that play behaviours are linked to hunting skill. Play is not, however, required for developing basic elements of hunting behaviour. At 11 weeks, cats reared in social isolation showed normal predatory responses when presented with prey-like stimuli (Thomas & Schaller 1954) and early-life object play does not affect adult predatory skills (Caro 1980b). However, play and hunting behaviour both increase towards the end of weaning, alongside declining social play, suggesting that this change characterises impending independence from the natal environment (Bateson & Barrett 1978). Owners can engage their cats in various forms of interactive object play, with wands, fishing toys, laser pointers, balls, etc.

Such play involves the reproduction of elements of the predatory sequence, and different types of play might conceivably be associated with development of prey preference or specialisation, which can impose a pressure on small populations of prey species (Scrimgeour et al. 2012). Contact in early life influences cats' tolerance of people; 'friendliness' towards humans is genetically influenced, but experientially determined during socialisation at 2-12 weeks (Turner et al. 1986; McCune 1995). Lack of association with humans would produce cats that are less suited to being pets, and more likely to be self-reliant foragers, whether by hunting or by exploiting foods accidentally or deliberately provided by humans.

Personality

Individual cats exhibit remarkable variation in hunting rates and strategies (Kays & DeWan 2004; Tschanz et al. 2011; Thomas et al. 2012; Loyd et al. 2013b: Table 2.1). Such marked individual variation is a key element of cat personality, where personality refers to differences in behavioural patterns, consistently expressed across multiple contexts, that distinguish one animal from others of similar sex, age or class (Lowe & Bradshaw 2001). Individual behavioural differences are well described in cats (McCune 1995) and a personality structure has been developed for captive Scottish wildcats *Felis silvestris grampia* (Gartner & Weiss 2013b). Building on the wildcat study, Litchfield et al. (2017), in a study involving almost 3000 owned cats, determined that personality profiles map across 'the feline five' (comparable with the 'Big Five' human personality traits; Digman 1990): neuroticism, extraversion, dominance, impulsiveness and agreeableness. Cats exhibiting certain of these personality types, perhaps most likely low neuroticism (boldness, leading to travelling, exploring), or high extraversion (curiosity, leading to boredom; Litchfield et al. 2017), would potentially be more interested in hunting wild prey, but there has not yet been any investigation of personality and hunting.

Links between personality and coat colour and pattern have been proposed. Tricoloured cats (calicos, tortoiseshells) are perceived to be more intolerant and aloof, while ginger and bicoloured cats are considered to be particularly friendly (Delgado et al. 2012; Stelow et al. 2016). Associations between coat pattern and personality are weak, however, suggesting little association between genes influencing coat and behavioural phenotypes. An exception is apparent for ginger cats, which exhibit greater interest in prey (Wilhelmy et al. 2016). This might also align with their relative abundance in rural areas, and suggests links between the genetic underpinnings of behavioural variation among coat polymorphisms (Garcia 1990; Pontier et al. 1995).

Environment

Different environments provide varying availabilities and diversities of food, in terms of species, abundance, accessibility and prey animals' avoidance of predation (Table 2.1). Cats are generally considered to be opportunistic hunters that are adaptable to seasonal fluctuations in prey abundance (Krauze-Gryz et al. 2017), and this is particularly evident on islands populated by feral cats that tolerate variation in the availability of non-native and native prey (Genovesi et al. 1995; Nogales & Medina 2009; Bonnaud et al. 2011a; Ozella et al. 2016). Island endemic species are especially vulnerable to predation by cats (Fitzgerald 1988), and when breeding seabirds are present, they become important secondary prey (after introduced mammals, Bonnaud et al. 2011b; Keitt et al. 2002).

Feral cats are widely established in continental areas characterised by high diversity of wild prey species. In addition to wild prey, feral cats take food accidentally or deliberately provided by humans (Bradshaw et al. 1999). Provisioned populations are less regulated by fluctuations in wild prey, leading to hyperpredation, as their densities may exceed local, 'natural' carrying capacity (Courchamp et al. 2000).

For owned, free-ranging cats, their lifestyles, hunting motivations and opportunities are affected by their husbandry and location in urban or rural ecosystems. Cats living on farms, and many of those in rural environments, are kept for their ancestral role as rodent controllers, and their survival relies on prey availability. Indeed, some farmers have believed that keeping cats undernourished makes them better hunters (Tabor 1983). Hungry cats do hunt more (Kays & DeWan 2004; Silva-Rodriguez & Sieving 2011), and hunger can reduce attachment to their residence (Fitzgerald & Turner 2000). In contrast, owned urban cats are generally well-fed, and survival and density vary independently of wild prey availability (Thomas et al. 2014). Differences in the composition of prey brought home in rural and urban areas probably reflect local prey availability, driven by differences in land use. The diets of cats on farms exhibit temporal variation according to seasonal variability in small mammal populations, while bird captures are more frequent among urban cats, reflecting the relative abundance of resident garden birds (Kauhala et al. 2015; Krauze-Gryz et al. 2017). This might alternatively reflect variation in the tendency to keep owned cats in urban areas inside at night, when small mammals are more active (Woods et al. 2003), and wider ranging by rural cats (Hanmer et al. 2017). Densities of cats in urban areas are high, and increase with housing density, imposing local pressure on prey populations (Baker et al. 2005; Sims et al. 2008; Thomas et al. 2012). Social factors and environmental characteristics influence densities of urban cats, particularly unowned cats. In New Zealand, residential areas with higher human density and a high deprivation index host greater numbers of aggregations of unowned cats (Aguilar & Farnworth 2012, 2013).

Table 2.1. Summary of drivers and facilitators of hunting behaviour in cats and their biological implications.

Driver/facilitator of hunting		Biological implications
Evolutionary origins	*Felis silvestris lybica*: • Obligate carnivore • Solitary hunter • Territorial predator catching multiple prey items per day	*Felis catus*: • Obligate carnivore • Solitary hunter • Surplus killing
Diet	• Hypercarnivorous (obligate carnivore) • Able to regulate calorific intake	• Unable to synthesise essential nutrients found in wild prey • High protein requirement • No requirement for carbohydrates in adults • Predation may address deficiencies
Early life-history	• Kitten introduced to hunting by the mother	• Mother influences kitten prey preferences • Adult prey specialisation
Personality	• Individual behavioural variation	• Individual variation in hunting rates and strategies
Environment	• Availability and diversity of food sources • Purpose of cat ownership • Cat motivational state for hunting	• Islands: feral cats hunt for survival; endemic species susceptible • Mainland: feral cats exploit anthropogenic food, populations not closely regulated by prey availability • Farms: free-roaming cats as pest controllers kept hungry to maximise hunting; subject to prey fluctuations • Urban areas: free-roaming pet cats, independent of prey availability

Management approaches

Numerous approaches to management have been advocated and adopted for reducing the direct and indirect effects of cats upon wildlife. This is an extensive topic, with particularly detailed and valuable accounts for Australia (Doherty et al. 2017; Woinarski et al. 2019) and the USA (Marra & Santella 2016; Loss et al. 2018). We outline what each management approach involves, its effectiveness, feasibility in different environments and implications for cat welfare. We have identified five categories of approach (Figure 2.1; Table 2.2): lethal control, non-lethal control (largely involving control of reproduction), inhibition (involving various devices and deterrents), access management, and enrichment (involving improvements to welfare, health and nutrition).

Lethal control

Lethal control is considered to be indispensable for predator eradication on islands (Russell et al. 2016). For cats, lethal control methods include trapping (cage traps, paw traps, leg-hold-traps), hunting with dogs, shooting, poisoning and introducing diseases (Nogales et al. 2004; Tables 2.2, 2.3). Up to October 2020, feral cats have been eradicated from 107 islands, while 19 attempts have failed (DIISE 2020), reportedly due to lack of planning, inappropriate methods and failure of local support (Campbell et al. 2011). Each eradication employed combined methods, but all successful programmes relied upon poisoning. The most widely used toxicant for cats is sodium fluoroacetate (1080), though its extreme toxicity and risks of non-target and secondary exposure (Eisler 1995) have led to restrictions on use. Para-aminopropiophenone (PAAP) has been developed and successfully tested in New Zealand as a more humane toxin that targets carnivores, including cats (Murphy et al. 2007).

Trapping and shooting can complement chemical controls, and applying multiple, independent methods appears to be essential for the control of residual individuals (Nogales et al. 2004). With intense effort and favourable terrain, trapping may facilitate eradication from small islands. Otherwise, cage traps are used in capture for euthanasia, sterilisation or live removal (Hanson et al. 2010), or when non-target casualties, including of owned cats, are unacceptable. Captured feral cats may be killed by shooting, lethal injection or carbon dioxide gas (Rocamora & Henriette 2015), though the latter is associated with welfare concerns (Simonsen et al. 1981). Trapping (particularly leg-hold trapping) causes injuries to non-target animals, posing ethical concerns, especially for threatened species (Surtees et al. 2019). Shooting is a labour-intensive method, preferentially applied in small areas, or in targeting problematic, or residual, individuals (Moseby et al. 2015).

The biological control of cats has primarily been through introductions of feline viruses. Feline panleukopenia virus was successfully applied in eradication campaigns on Marion Island, Indian Ocean, and Jarvis Island, South Pacific Ocean (Nogales et al. 2004).

Some highly effective lethal methods, including biological control and some toxicants, are markedly inhumane, due to the severity of distress or pain experienced before death (Table 2.3). Symptoms of 1080 include disorientation, uncoordinated movements, vocalisations and vomiting. Cats become lethargic and immobile for several hours before death, which occurs up to 24 hours after exposure (Eason & Frampton 1991). By comparison, PAPP is considered relatively humane; it causes death by methaemoglobinaemia, resulting in central nervous system anoxia, rapid loss of consciousness and rapid death (Eason et al. 2010). Viral infections compromise welfare over extended periods. Sickness due to feline parvovirus is associated with pain, high fever, lethargy, vomiting, severe bloody diarrhoea, discharge and dehydration. More humane methods in lethal control are shooting and euthanasia, which provide more rapid, less painful deaths, though prolonged containment in traps compromises welfare.

Cat eradications generally bring major direct benefits to island faunas (Jones et al. 2016), and further permit the restoration of native taxa locally extirpated by cats (Algar et al. 2020). However, unexpected trophic cascades arising from cat removal can be environmentally and economically costly. On Little Barrier Island, New Zealand, cat removal resulted in reduced breeding success of Cook’s petrel *Pterodroma cookii* due to increased predation by rats R*attus* spp. (Rayner et al. 2007). On Macquarie Island, Pacific Ocean, cat eradication precipitated a trophic cascade leading to rapid landscape and ecosystem changes, due to increased rabbit *Oryctolagus cuniculus* populations (Bergstrom et al. 2009).

On inhabited islands, human residents often contribute directly to unowned cat populations by not sterilising their cats and by abandoning unwanted kittens and adults (Medina et al. 2016), so regulation of owned animals is required to eradicate unowned cats. Regulatory measures include: sterilisation, identification, registration and control of importation (Nogales et al. 2013). Such measures are being implemented on Ascension Island, South Atlantic Ocean, under a “Dogs and Cats Ordinance”, with fines for non-compliance. In strict campaigns, such as on Balta Island, Galápagos Islands, owning cats, as companion animals, is prohibited, and existing pets were translocated or euthanised (Campbell et al. 2011). In continental areas, eradication of feral cats is difficult because of the challenges of using toxins in human settlements. Consequently, the most common lethal method used for reducing populations in settled areas is trapping and euthanasia (Tan et al. 2017).

Non-lethal control

Non-lethal control approaches aim for reduction in cat numbers over several years (Levy et al. 2003). Control of reproduction can be achieved through surgical methods (neutering of males and females; spaying of females) or non-surgical methods (contraceptives; Table 2.2). Surgical procedures are carried out via trap-neuter-return (TNR), trap-neuter-relocate (to farms, sanctuaries, or to the mainland in the case of islands) and variants. Controlling cat populations via TNR is possible, but requires sterilisation rates of 51%-94% (Andersen et al. 2004; Schmidt et al. 2009; McCarthy et al. 2013). Intensive TNR and adoption of socialised cats and kittens can reduce colony size (by around 31%), improve welfare and reduce cat intake to shelters (Levy et al. 2014; Tan et al. 2017; Spehar & Wolf 2018), and can markedly reduce ‘preventable’ cat deaths (Boone et al. 2019). TNR has also proven comparable, in cost terms, to lethal control by trapping, but with benefits in terms of reduced complaints about cats and impoundments of cats (Hughes et al. 2002). The inefficiency of TNR for managing large populations has generated disapproval among conservation organisations (Longcore et al. 2009; Loss & Marra 2017). The approach requires intense effort and often relies on volunteers, so sustaining control and assessing outcomes are problematic (Robertson 2008) over anything more than small geographic areas (Crawford et al. 2019), e.g. A university campus of 5.7 km^2 (Levy et al. 2014) and a docklands area of 0.8 km^2 (Spehar & Wolf 2017). Moreover, the ecological benefits derived from neutering campaigns are uncertain (Guttilla & Stapp 2010) and there are no scientific studies of the effect of sterilisation on predation.

Of non-surgical methods, a promising avenue is immunocontraception, which, in principle, induces long-term or permanent sterility after a single treatment. In principle, it is less costly, less technically demanding and less invasive than surgery (Levy et al. 2011). GonaCon is a gonadotropin-release hormone vaccine that was tested on laboratory cats and provides effective fertility control over multiple years with a single dose. However, granulomatous masses at the injection site were observed in 33% of treated cats two years after injection (Levy et al. 2011). Unfortunately, tests of a safer, modified vaccine, showed that a single dose of GonaCon did not provide contraception for a sufficient proportion of female cats living under colony conditions (Fischer et al. 2018). Thus, although the approach is promising, no immunocontraceptive for cats are yet available.

Inhibition

Various devices and deterrents have been developed and commercialised to reduce predation (Tables 2.2, 2.3). Fitting owned cats with a collar with a bell has diverse outcomes, with no effects on predation rates in Australia (Barratt 1997), but significant reduction in prey returns by 50%, at least in the short-term, in the UK (Ruxton et al. 2002; Nelson et al. 2005) and New Zealand (Gordon et al. 2010). Woods et al. (2003) found that bells were associated with lower reported rates of predation on mammals, but not birds, speculating that birds relied on visual cues to avoid predators. Over the long-term, cats may compensate for any hunting handicap arising from wearing a bell by modifying hunting strategies (Nelson et al. 2005). CatAlert (Willana Life Sciences), a collar-mounted sonic warning device, reduces prey rates by 38% for mammals and by 51% for birds (Nelson et al. 2005). CatBib (www.catgoods.com) is a ‘pounce protector’ bib attached to a collar, which, in a single trial, stopped 81% of cats catching birds, 33% catching herpetofauna and 45% catching mammals (Calver et al. 2007). BirdsBeSafe (www.birdsbesafe.com) is a brightly coloured collar cover that reduces bird-killing [0.72 birds per year with BirdsBeSafe and 5.56 without (Willson et al. 2015); 0.44 birds per month with BirdsBeSafe and 1.89 without (Pemberton & Ruxton 2019)]. Cats wearing rainbow-patterned BirdsBeSafe showed a greater reduction than those wearing the collar covers with other patterns in the number of prey with colour vision (birds and herpetofauna) brought home (Hall et al. 2015). All such device trials acknowledge a reliance on numbers of animals brought home by cats as a proxy for the frequency of killing, which camera studies suggest is likely to be an underestimate (Loyd et al. 2013b).

Irrespective of their successes in reducing killing, inhibitory devices may not prevent indirect effects on prey populations. Moreover, cat owners seem reluctant to use inhibitory measures to reduce hunting, especially when conservation benefits do not accord with their priorities for cat welfare (Hall et al. 2016a; Harrod et al. 2016; Crowley et al. 2019, 2020b).

Access management

Owners can eliminate or reduce hunting opportunity by restricting cats' access to the outdoors, by keeping them indoors at night, or at dawn and dusk when birds are most active (Table 2.2). Owners variously see confinement as beneficial in reducing the risk of fighting, theft and road accidents or as detrimental to cat welfare or to pest control functions, if nocturnal confinement reduces capture of target rodents or non-native species (Crowley et al. 2019; Linklater et al. 2019; Crowley et al. 2020b). Other available options for controlling cat outdoor access are exclusion fencing, cat patios ('catios', e.g. ProtectaPet), leash or harness walks and tie-outs (Tan et al. 2020). Fencing is, however, primarily used to prevent incursions by feral cats to protected areas, and use in Australia and New Zealand is widespread and effective (Moseby & Read 2006). Fenced exclusion zones have been also established in urban habitats (e.g. Zealandia in Wellington, Mulligans Flat in Canberra). Cat exclusion zones have also been proposed in rural areas, and in protected areas close to human settlements (Metsers et al. 2010).

Enrichment

Enrichment implies an improvement in animal welfare, measurable in terms of increased lifetime, reproductive success or health, through modifications of environment or husbandry (Newberry 1995; Ellis 2009). Enrichment approaches for owned and semi-owned cats that might affect hunting of wildlife, by affecting stimuli relating to nutrition, foraging and hunting, include: reproducing natural foraging behaviours, hiding food, using 'puzzle' feeders, and engaging cats in play simulations of hunting sequences (Ellis 2009; Table2.2). Direct nutritional enrichment might also involve manipulations of the frequency of feeding, food quantity, quality and content, to ensure provision of essential nutrients (Bloomsmith et al. 1991). Given the specificities of cat nutritional requirements outlined above, this avenue holds particular research potential for reducing any motivations for hunting deriving from nutritional deficiency, not least because of the apparent disconnect between motivation and prey consumption (Leyhausen et al. 1956). Indoor environments can be enriched by physical modifications (cat trees, scratching posts, hiding places), and provision of appropriate feeding, drinking, toileting and rest areas (Ellis et al. 2013). Dedicated playtime keeps cats active, resulting in a reduction of common behavioural problems (Strickler & Shull 2014). Little research has been undertaken to investigate the link between environmental or nutritional enrichment and hunting rates. Providing litter boxes and hiding places was significantly associated with reduced numbers of prey brought home by indoor-outdoor cats (Escobar-Aguirre et al. 2019), thus it may be the case that enhancing the cat's environment and overall wellbeing leads to variation in hunting activities, opening the possibility to adopt beneficial interventions as novel management approaches.

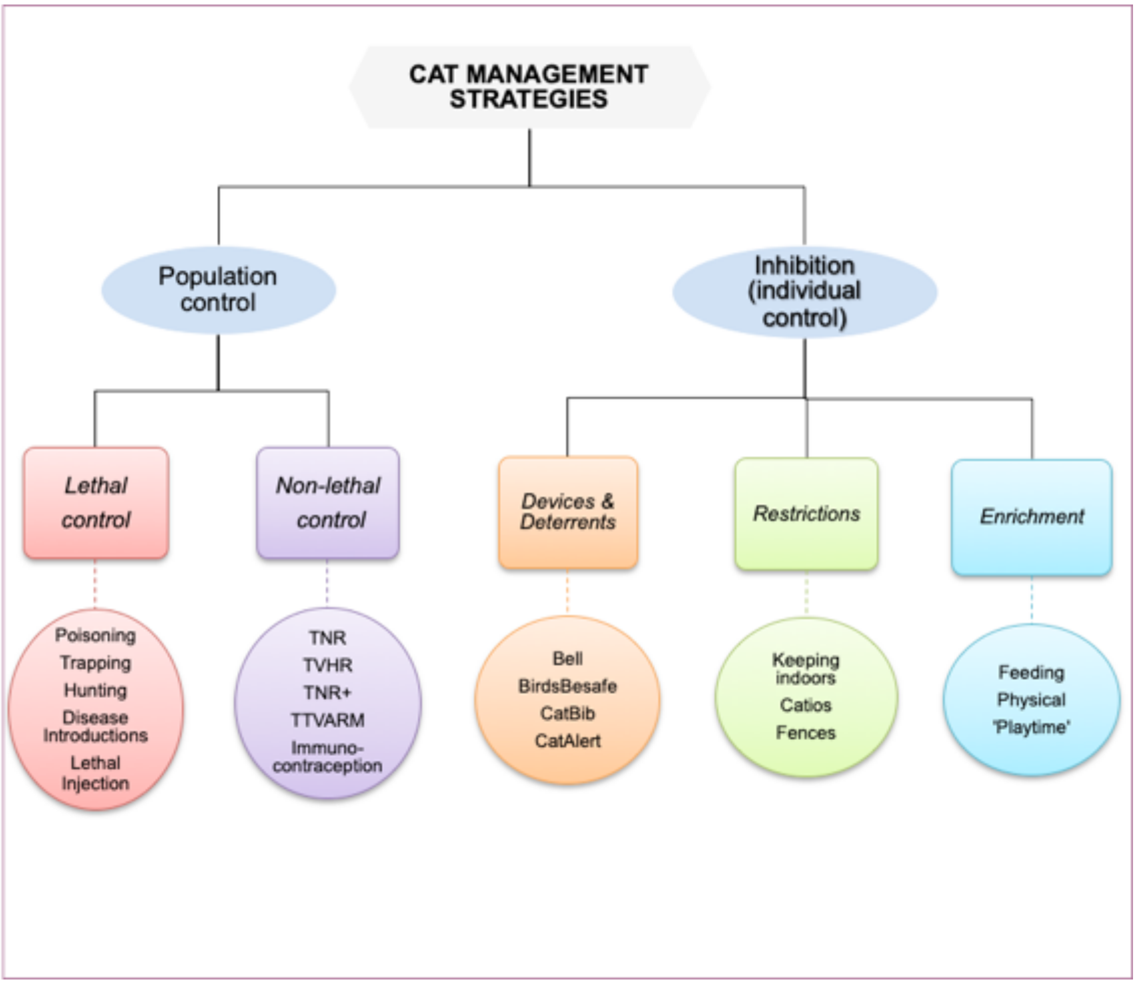

Figure 2.1. Schematic showing management approaches for cat populations and individuals. Non-lethal approaches to population control are largely based on Trap-Neuter-Return (TNR) and variants thereof, including: Trap-Vasectomy-Hysterectomy-Return (TVHR), TNR with removal of kittens for adoption (TNR+), trap-test-vaccinate-alter-return-monitor (TTVARM).

Table 2.2. Summary of management approaches for reducing predation of wildlife by cats, through cat population control and individual interventions (tick=applied, cross=not generally applied).

Management approaches		Feral cats		Free-ranging owned cats		
		Islands	**Mainland**	**Islands**	**Farms**	**Urban areas**
Lethal control	Poisoning	✓	✗	✗	✗	✗
	Shooting	✓	✓	✗	✗	✗
	Disease introduction	✓	✗	✗	✗	✗
	Trapping then shooting	✓	✗	✗	✗	✗
	Trapping then injection	✓	✓	✓	✓	✓
Non-lethal control	Trap-Neuter-Return and variants	✗	✓	✓	✓	✓
	Immunocontraception	✗	✗	✓	✓	✓
Devices and deterrents	Bell	✗	✗	✗	✗	✓
	BirdsBeSafe (brightly coloured collar cover)	✗	✗	✗	✗	✓
	CatBib	✗	✗	✗	✗	✓
	CatAlert (Sonic warning device)	✗	✗	✗	✗	✓
Access management	Indoors at sunrise and dusk	✗	✗	✓	✗	✓
	Indoors	✗	✗	✓	✗	✓
	Fence	✓	✓	✗	✗	✗
	Cat enclosures (Cat patio, Catio)	✗	✗	✗	✗	✓
Enrichment	Feeding	✗	✗	✗	✗	✓
	Physical	✗	✗	✗	✗	✓
	Object play (Playtime)	✗	✗	✗	✗	✓

Table 2.3. Summary of methods used in lethal population control of cats

Lethal method	Time to death	Modes of action	Welfare implications
Toxin: Sodium fluoroacetate (1080)	24 hours	Interferes with cellular energy production, inhibition of tricarboxylic acid cycle	Disorientation, vocalisations and vomiting, immobile for several hours before death
Toxin: Para-aminopropiophenone (PAPP)	37-246 minutes	Causes methaemoglobinaemia (elevated blood methaemoglobin)	Central nervous system anoxia and lethargy, rapid loss of consciousness and rapid death
Biocontrol: Feline panleukopaenia virus	2-10 days	Infects and kills growing and dividing cells (bone marrow, intestines, foetus). Fall in white blood cells.	Loss of appetite, avoidance and inactivity, pain, fever, lethargy, vomiting, diarrhoea, discharge and dehydration
Direct killing: trapping, hunting, shooting/euthanasia	Related to time elapsed before euthanasia; death occurs within seconds/minutes	Euthanasia (central nervous system)	Stress during time of latency in trap

Conclusions

Domestic cats are abundant and near-ubiquitous predators. Whether they are feral or are indoor companions, modern cats display the inherited influence of their wild ancestors on morphology, physiology and behaviour. The most apparent elements of this evolutionary legacy relate to feeding, comprising their obligate hypercarnivorous diet, solitary hunting activity, and feeding patterns. Marked between-individual variation in hunting behaviour is likely to be part of cat personality, though it seems difficult to link it to other phenotypic traits. Environment and opportunity have powerful impacts on both frequency and effectiveness of hunting behaviour by cats.

In response to the actual and perceived impacts of cats upon wild prey populations, various management approaches have been adopted to control cat populations and hunting behaviour: lethal control methods, non-lethal control methods that tend to stabilise densities but rarely reduce them, and devices, deterrents and restrictions that use inhibition and access restrictions with the aim of reducing the success of hunting by cats. Enrichment remains largely untested as a means of reducing hunting, but indications of association between environment and hunting behaviour suggest the potential of this approach.

Few researchers have highlighted the drivers of the retention of hunting behaviour or have attempted to reduce predation rates by working with strategies that relate to or build on their evolutionary origins. Hunger increases cats' motivation for both play (Hall & Bradshaw 1998) and predatory behaviour, suggesting that play and predation share common elements (Biben 1979; Hall & Bradshaw 1998). Being an obligate carnivore implies requirements for high protein, associated with high activity of nitrogen catabolic enzymes and loss of metabolic enzymes or pathways involved in the synthesis of essential nutrients. In nature, strict nutritional requirements are addressed by a diet consisting of animal prey (Bradshaw 2006). With the advent of commercial pet food manufacture, owners can, in principle, provide a complete diet to their cats, which fulfils their macronutrient, micronutrient and amino acid requirements. Nevertheless, some nutrients may be diminished or lost during manufacturing, some foods rely on plant protein sources, potentially compromising bioavailability of amino acids (Kanakubo et al. 2015), and some brands do not meet all micronutrient recommendations (Davies et al. 2017; Brunetto et al. 2019). Thus, we accord with (Bradshaw et al. 1999) that a selective advantage of retaining wild behaviours, arose from "the probability that diets provided by people were unlikely to meet their nutritional requirements". We hypothesise that variation in diet quality, as well as quantity (Silva-Rodriguez & Sieving 2011), has the potential to drive between-individual variation in hunting by provisioned cats. Enhancing the quality of nutrition of the world's owned cats therefore merits further investigation as a means of addressing predation of wildlife by domestic cats, while also improving cat health and welfare.

Chapter 3

Provision of high meat content food and object play reduce predation of wild animals by domestic cats *Felis catus*

Chapter 3: Provision of high meat content food and object play reduce predation of wild animals by domestic cats *Felis catus*

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Abstract

Predation by domestic cats *Felis catus* can be a threat to biodiversity conservation (Medina et al. 2011; Loss & Marra 2017; Murphy et al. 2019) but its mitigation is controversial (Crowley et al. 2020a). Confinement and collar-mounted devices can impede cat hunting success and reduce numbers of animals killed (Cecchetti et al. 2020), but some owners do not wish to inhibit what they see as natural behaviour, perceive safety risks associated with collars or are concerned about device loss and ineffectiveness (Crowley et al. 2019, 2020b). In a controlled and replicated trial, we tested novel, non-invasive interventions that aim to make positive contributions to cat husbandry, alongside existing devices that impede hunting. Households where a high meat protein, grain-free food was provided, and households where 5-10 minutes of daily object play was introduced, recorded decreases of 36% and 25%, respectively, in numbers of animals captured and brought home by cats, relative to controls and the pre-treatment period. Introduction of puzzle feeders increased numbers by 33%. Fitting BirdsBeSafe collar covers reduced numbers of birds captured and brought home by 42%, but had no discernible effect on mammals. Cat bells had no discernible effect. Reductions in predation can be made by non-invasive, positive contributions to cat nutrition and behaviour that reduce their tendency to hunt, rather than impede their hunting. These measures are likely to find support among cat owners who are concerned about the welfare implications of other interventions.

Introduction

Depending on the ecological and cultural context in which domestic cats live, they are variously perceived as pets, pests or pest controllers, leading to intense social debates about cat management (Crowley et al. 2020a). Their adaptability to diverse environments, with and without human support, is connected to retention of hunting behaviour from their wild ancestor *Felis silvestris lybica,* to which they are physiologically and behaviourally close (Bradshaw 2006). The abundance of cats is associated with ecological impacts that are particularly severe in island ecosystems (Medina et al. 2011). While there is debate about the extent to which cat predation is compensatory or additive to natural mortality, high densities of cats have been convincingly linked to detrimental effects on vertebrate populations at continental scales (Loss & Marra 2017; Murphy et al. 2019). In addition to any direct impacts of predation, cat presence can indirectly affect avian productivity, through reductions in nest provisioning rates and increases in nest predation by other predators (Bonnington et al. 2013), which could markedly affect bird abundances where cat densities are high (Beckerman et al. 2007). Unless their cats are kept as pest controllers, owners rarely consider killing wild animals to be desirable (Crowley et al. 2019, 2020b). To reduce killing, owners might completely or partly restrict outdoor access, or attempt to inhibit or impede hunting with collar-mounted devices, such as bells, collar covers and bibs, with varying success (Nelson et al. 2005; Calver et al. 2007; Pemberton & Ruxton 2019). Cat owners vary in their use of such measures: roaming and hunting are often seen by owners as a natural component of cat behaviour; the measures might, or might be perceived to, adversely affect cat welfare or safety; and cats may reject collars (Crowley et al. 2019). Moreover, while these measures might successfully impede hunting, they do not repress the cats' instinct, tendency or desire to hunt.

The behaviours and perspectives of cat owners are clearly central to the problem of cat management. Permanent confinement of cats would eliminate depredation of wildlife, perhaps excepting commensal rodents. As effective as it might be in principle, permanent confinement is unpopular among cat owners in many societies, including the U.K., where outdoor access is considered by owners to be critical to cat welfare (Crowley et al. 2019, 2020b) and New Zealand, where containment to enclosures and 24-hour confinement were among the measures least likely to be adopted by owners (Linklater et al. 2019). In developing effective advocacy, there is a trade-off between effectiveness in principle and scale of uptake in practice. Prioritizing behaviours that are likely to be widely adopted by cat owners is likely to lead to more effective advocacy. Eventually, if adopted behaviours mitigate the problem, this would lead towards more effective conservation actions and incremental change in societal norms (Linklater et al. 2019).

Methods

Recognising the importance of cat welfare to cats and their owners, we tested whether novel, non-invasive dietary and behavioural interventions, that would ostensibly benefit cats, might reduce killing, not by impeding hunting but by reducing the cats' tendency to hunt. We recruited cat owners whose cats regularly hunted and killed wild animals and brought them back to the house. With a before-after-control-impact design, we evaluated two existing inhibitory measures: equipping collars with a BELL, or with a BirdsBeSAFE collar cover; alongside three novel measures: provision of food in a 'PUZZLE' feeder; provision of grain-free FOOD in which meat was the principal source of protein; and 5-10 minutes daily object PLAY; plus a CONTROL group (Figure 3.1). Our response variables were the total numbers of prey animals, and of mammals and birds separately, captured and brought home by cats living in the same household and recorded by householders. When the trial ended, we surveyed participants about their intention to continue using their assigned interventions. *For more details on methods, see STAR Methods*.

Results

219 households in southwest England, owning 355 cats, completed the 12-week trial (Table 3.1). Relative to the CONTROL and pre-treatment period, total numbers of animals per cat were significantly reduced in households in the FOOD (-36%, p<0.001) and PLAY (-25%, p=0.016) treatments (Figure 3.1; Table 3.2). Conversely, households in the PUZZLE treatment recorded significantly increased numbers (+33%, p=0.009). BELL and SAFE treatments had no discernible effects on total prey. For mammals only, FOOD (-33%, p=0.002) and PLAY (-35%, p=0.002) reduced numbers, PUZZLE increased numbers (+49%, p=0.002), but BELL and SAFE had no discernible effects. For birds only, FOOD (-44%, p=0.032) and SAFE (-42%, p=0.047) reduced numbers, but BELL, PLAY and PUZZLE had no discernible effects.

Of the survey respondents, 16 of 30 (53%) from BELL, 7 of 33 (21.2%) from SAFE, 13 of 40 (33%) from FOOD, 13 of 41 (32%) from PUZZLE, and 29 of 38 (76%) from

PLAY treatment groups reported that they planned to continue with the intervention (Table 3.3). Respondents from the SAFE and BELL groups reported cat discomfort and loss of collars as reasons for discontinuing use. Low intention to continue in the PUZZLE group was primarily attributed to cat disinterest, and in the FOOD group to low palatability of the wet, but not the dry, food.


A
B
C
D
E
F

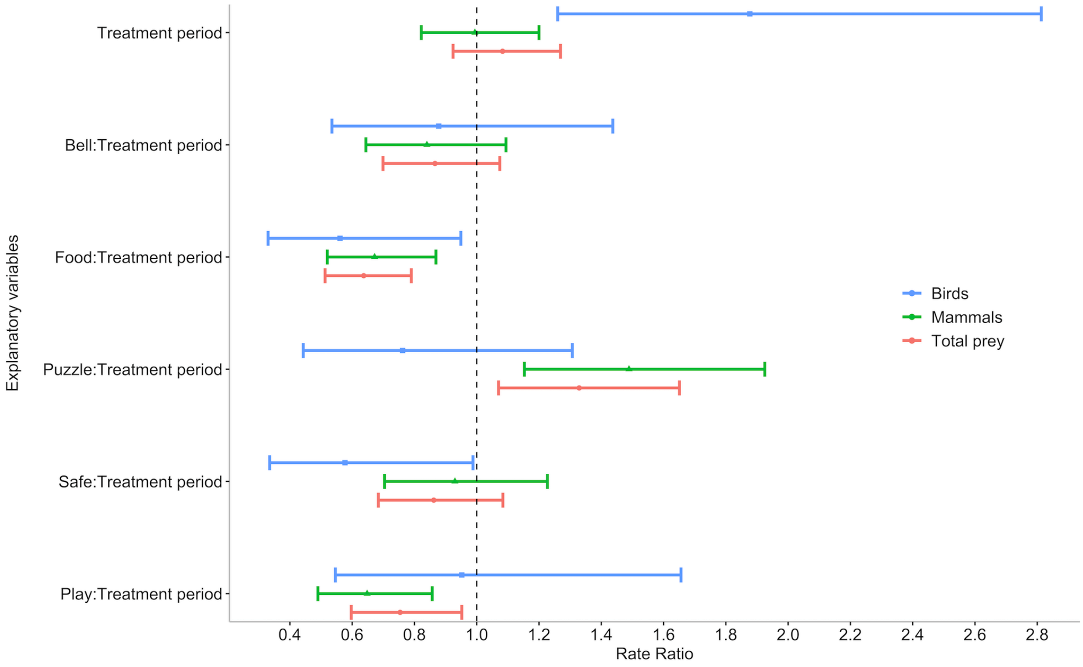
Treatment period
Bell:Treatment period
Food:Treatment period
Puzzle:Treatment period
Safe:Treatment period
Play:Treatment period
Explanatory variables
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2
2.4
2.6
2.8
Rate Ratio
Birds
Mammals
Total prey

Figure 3.1. (Previous page) Effects of treatments applied to domestic cats to reduce the numbers of wild animals killed, brought home and recorded by householders. A. BELL: a collar mounted ‘standard’ cat bell, B. FOOD: in which cats are provided with a high-quality, commercially available food that was high in meat protein content and lacked grain, C. PUZZLE: provision of existing dry foods in a standard, commercially available puzzle feeder, D. SAFE: a BirdsBeSafe® collar cover, E. PLAY: in which cat owners engaged in object play with their cats, using a ‘fishing’ toy (illustrated) and a ‘mouse’ toy for a minimum of five minutes per day, and F. CONTROL: in which owners only recorded the numbers of wild prey brought home every day. Comparisons of the effects of treatments are based on analysis of numbers killed during the treatment period, relative to the control group and the pre-treatment period. The main effect of treatment period reflects seasonal increase in wild bird availability. Rate ratios are shown with 95% confidence intervals.

Table 3.1. Summary of sample sizes in treatment groups and wild animal prey brought home by domestic cats and recorded by households in pre-treatment and treatment periods. Owners living in 456 households with a total of 753 cats signed up to take part in the trial. After allocation to treatment groups and cleaning of data, a total of 219 households and 355 cats were included in the analyses. Median recording effort was 49 days (Interquartile range = 46-49 days) in the pre-treatment period and 34 days (IQR=28-35) in the treatment period. Treatments were: BELL, in which cats were fitted with a collar-mounted ‘standard’ cat bell; SAFE, in which cats were fitted with a BirdsBeSafe® collar cover; FOOD, in which cats were provided with a high-quality, commercially available food that was high in meat protein content and lacked grain; PUZZLE, in which cats were provided existing dry foods in a standard, commercially available puzzle feeder; PLAY, in which cat owners engaged in object play with their cats for a minimum of five minutes per day; and CONTROL, in which owners only recorded the numbers of wild prey brought home every day. Note that these are raw data as recorded and analyses incorporate duration of recording and other covariates.

Treatment group	N households	N cats	Period	Mammals	Birds	Reptiles	Amphibians	Insects	Unidentified	All prey
Bell	33	56	Pre-treatment	316	92	23	2	22	31	486
			Treatment	175	96	9	1	1	16	298
Food	39	66	Pre-treatment	418	79	28	0	5	46	576
			Treatment	188	57	5	0	3	18	271
Puzzle	38	51	Pre-treatment	278	64	8	4	8	27	389
			Treatment	253	55	7	0	8	16	339
Safe	31	50	Pre-treatment	267	76	23	3	12	19	400
			Treatment	146	48	13	2	3	6	218
Play	46	65	Pre-treatment	318	51	3	1	1	24	398
			Treatment	129	55	3	1	2	12	202
Control	32	67	Pre-treatment	267	43	14	2	6	29	361
			Treatment	185	55	7	2	3	19	271
Total	219	355		2940	771	143	18	74	263	4209

Table 3.2. Summary of analyses of variation in the numbers of wild animal prey brought home by domestic cats and recorded by households. Model outcomes are summarised as the estimated regression parameters (Est.) with standard errors (SE), rate ratios (RR) and 95% confidence interval (95% CI), and p-values from a generalised linear mixed model, where the interaction between treatment and period is the term of interest. Descriptions of the effects in terms of reductions or increases in animals killed are derived by exponentiating the estimate of the effect, to obtain the Rate Ratio (RR), and the corresponding percentage decrease in the rate is given by ([RR-1]*100%). Estimated variance in total prey explained by the fixed and random variables was 0.87 (R^2c= 0.87), as well as in mammals (R^2c= 0.87), while in birds is 0.58 (R^2c= 0.58).

	All prey					**Mammals**					**Birds**				
	Est.	(SE)	RR	(95% CI)	p	Est.	(SE)	RR	(95% CI)	p	Est.	(SE)	RR	(95% CI)	p
Intercept	-2.327	(0.153)			<0.001	-2.724	(0.184)			<0.001	-4.600	(0.224)			<0.001
Bell	0.422	(0.213)	1.53	(1.00-2.33)	0.048	0.241	(0.257)	1.27	(0.76-2.12)	0.349	0.892	(0.291)	2.44	(1.38-4.34)	0.002
Food	0.442	(0.205)	1.56	(1.04-2.33)	0.031	0.442	(0.246)	1.52	(0.94-2.49)	0.085	0.668	(0.287)	1.95	(1.11-3.44)	0.020
Puzzle	0.319	(0.208)	1.38	(0.91-2.08)	0.126	0.254	(0.250)	1.29	(0.78-2.12)	0.310	0.805	(0.292)	2.24	(1.26-3.99)	0.006
Safe	0.341	(0.217)	1.41	(0.92-2.16)	0.117	0.302	(0.261)	1.35	(0.81-2.27)	0.247	0.938	(0.296)	2.55	(1.43-4.59)	0.002
Play	0.124	(0.201)	1.13	(0.76-1.69)	0.537	0.200	(0.241)	1.22	(0.76-1.97)	0.406	0.195	(0.296)	1.22	(0.68-2.18)	0.511
Treatment period	0.080	(0.080)	1.08	(0.92-1.27)	0.319	-0.006	(0.095)	0.99	(0.82-1.20)	0.950	0.629	(0.204)	1.88	(1.26-2.81)	0.002
Bell:Treatment period	-0.144	(0.109)	0.87	(0.70-1.07)	0.186	-0.175	(0.113)	0.84	(0.64-1.09)	0.191	-0.130	(0.252)	0.89	(0.54-1.44)	0.606
Food:Treatment period	-0.451	(0.109)	0.64	(0.51-0.79)	<0.001	-0.400	(0.130)	0.67	(0.52-0.87)	0.002	-0.578	(0.269)	0.56	(0.33-0.95)	0.032
Puzzle:Treatment period	0.285	(0.110)	1.33	(1.07-1.65))	0.009	0.400	(0.129)	1.49	(1.15-1.93)	0.002	-0.271	(0.276)	0.76	(0.44-1.31)	0.326
Safe:Treatment period	-0.149	(0.116)	0.86	(0.86-0.68)	0.200	-0.072	(0.140)	0.93	(0.70-1.23)	0.604	-0.550	(0.276)	0.58	(0.34-0.99)	0.047
Play:Treatment period	-0.282	(0.117)	0.75	(0.60-0.95)	0.016	-0.433	(0.140)	0.65	(0.49-0.86)	0.002	-0.050	(0.283)	0.95	(0.55-1.65)	0.862

Table 3.3. Summary of participant feedback and uptake related to Participant Feedback. At the end of the study, participants were surveyed about the interventions they trialled. They were asked whether they intended to keep using the intervention once the trial had finished, and for comments on the intervention they trialled. This table includes responses from households whose cats may not have been included in the final analysis, e.g. owners of cats in the puzzle group who never used the puzzle feeder.

	n respondents	Will keep using intervention (%)	Will not keep using intervention / not sure (%)	Positive feedback summary	Negative feedback summary
Bell	30	16 (53.3)	14 (46.7)	Cat behaviour not affected by collars; perceived reduction in hunting	Cat discomfort with collars (scratching, efforts to remove); loss of collars
Food	40	13 (32.5)	27 (67.5)	Cats readily ate food; perceived reduction in hunting	Cats refused, or initially refused, wet food
Puzzle	41	13 (31.7)	28 (68.3)	Cats ate more slowly; cats engaged with puzzle feeder	Cats disinterested in, or became bored of, puzzle feeder
Safe	33	7 (21.2)	26 (78.8)	Cat behaviour not affected by collars; perceived reduction in hunting	Cats had difficulty grooming; owners disliked collar appearance
Play	38	29 (76.3)	9 (23.7)	Cats engaged well with toys; owners enjoyed increased interaction	Cats lost interest in toys

Discussion

Domestic cats are valued companion animals and owners tend to prioritise their perceived framings of cat welfare over any potential hazard cats might present to wildlife (Crowley et al. 2019, 2020b). The fulfilment of cats' physiological and behavioural requirements has not previously been considered important for managing hunting behaviour (Cecchetti et al. 2020), yet our study has shown that modifications to diet, and behavioural enrichment with object play, both affect cats such that they capture and bring home significantly fewer wild animals.

Our study is consistent with the theory that some cats may hunt more because they are stimulated to address some deficiency in their provisioned food (Cecchetti et al. 2020). We are not, however, able to distinguish specific drivers of the beneficial effect of dietary change, since the trial food had multiple attributes that differed from most previous foods: freshly prepared meat was the primary source of proteins and the food lacked grains, rendered meat or meat meal. It is possible that the effect arises from augmentation of a specific micronutrient or amino acid, the availability of which has the potential to be increased in a targeted way, without necessarily increasing any wider environmental impacts of providing meat-rich diets to companion animals (Swanson et al. 2013). It is therefore desirable and feasible to evaluate the precise nature of the relationship between food contents and hunting behaviour in a blinded trial, with a view to targeting recommendations for owners and pet food manufacturers. As well as contents, palatability is important. While there were no apparent differences in effectiveness between wet and dry foods, 50% of survey respondents from the food group reported that their cats found the experimental wet, but not the dry, food unpalatable.

Reproduction of natural behaviours in the home environment is beneficial for pet cats (Ellis 2009). During hunting and play, similar behaviours are observed, and hunger increases both predation rate and play motivation in cats (Hall & Bradshaw 1998). Again, we have made an ostensibly positive intervention with the introduction of object play, associated with desirable reductions in hunting. Participant feedback indicated that most cats readily engaged with the toys, and that three-quarters of households planned to continue with regular play. Dietary and behavioural drivers of hunting may operate independently, and so it would be valuable to investigate potential additive effects of diet and play.

Increased predation in the PUZZLE treatment might be attributable to device novelty, insufficient training of owners and/or cats, or inability to easily access food and resulting hunger or frustration. For owners willing to equip their cats with collars, and are concerned about their cats hunting birds, the BirdsBeSafe collar cover was effective.

Given the value of applying a precautionary approach to this issue (Calver et al. 2011), reduction in killing by domestic cats is a positive step in most ecological settings. However, the degree of impact that cat predation has upon prey populations varies with ecological and human social context, as will the effectiveness of mitigation attempts. In areas of low cat density, reductions in individual killing are likely to bring greater benefits than in areas of dense human settlement, where cats live at their highest densities (Sims et al. 2008). Such conditions in some human residential areas mean that even reduced, individual predation rates may still result in considerable cumulative impacts (Kays et al. 2020). Similarly, reductions in individual killing might not suffice to mitigate impacts upon particularly vulnerable populations or species.

In managing predation by domestic cats, owner behaviour is as important as cat behaviour and so, to reduce killing by cats, management strategies need to be both effective and implemented by owners (Linklater et al. 2019). Positive interventions, aimed at benefiting cats and appealing to owners, can reduce cats' tendencies to hunt, and might therefore form the basis of a conservation win-win.

STAR Methods

Experimental model and subject details

This study worked with adult and juvenile (>6 months), male and female domestic cats *Felis catus* living as companion animals, as part of human households.

Cat owners were recruited through advertisements on broadcast, print and social media. During sign-up, owners completed a questionnaire for each cat in the household, regarding the cats' general characteristics (e.g. name, sex, breed), owners' perceptions of health and behaviour, feeding and roaming habits, frequency of hunting, and any ongoing management strategy adopted for reducing hunting. To test owner willingness and continuity in recording for the study duration we set the first two weeks as surveillance weeks. Power analysis based on a pilot study and on previous experimental studies suggested we had 80% power of detecting a statistically significant reduction of >67% in numbers of animals returned to the household, over a period of three weeks with a sample of 40 cats that regularly captured and brought home wild animal prey. Allowing for drop out, our target sample per treatment was 70 cats. We selected households in which at least one prey item had been brought home during two weeks of preliminary surveillance. Owners not selected for inclusion in the intervention study kept recording prey but were not included in formal analyses.

The study protocol was approved by the ethics committee of the University of Exeter, College of Life and Environmental Sciences, Penryn Campus (Reference CORN000181). The project also received specialist veterinary guidance and the protocols was approved by an independent Project Advisory Group, comprising feline veterinary, behavioural and welfare specialists. Owners provided informed written consent.

Method details

Basis of treatments

It has been hypothesised that the selective basis for domestic cats retaining hunting behaviour relates to the probability that diets provided by people have, at times, been unlikely to meet cat nutritional requirements in their entirety (Bradshaw et al. 1999). Cats are obligate carnivores with an absolute requirement for high levels of protein as the source of nitrogen and essential amino acids, and no essential requirement for carbohydrates (Macdonald & Rogers 1984). They are incapable of synthesizing some essential nutrients that are readily available in their wild prey (Macdonald & Rogers 1984). Among their nutritional peculiarities, cats have an absolute requirement for high protein diets, many water-soluble B vitamins (e.g. niacin), vitamin A, vitamin D, arginine, taurine, methionine, cysteine and some essential fatty-acids (Macdonald & Rogers 1984; Morris 2001). Nutritional deficiencies can have severe implications: arginine deficiency causes hyperammonaemia and severe uraemia and may lead to death within few hours (Morris & Rogers 1978), while taurine deficiency causes central retinal degeneration (Hayes et al. 1975) and leads to cardiac abnormalities (Schaffer et al. 2016). An important aspect in characterising cat foods is protein quality, evaluated in terms of digestibility and the relative abundance and bioavailability of amino acids. Bioavailability of dietary amino acids is the proportion of ingested dietary amino acids that is absorbed, and renders them potentially suitable for metabolism or protein synthesis (Batterham 1992). The protein components of pet foods can comprise both animal and plant sources, though it is recognised that, compared to animal protein sources, plant protein sources have lower digestibility (Neirinck et al. 1991; Kanakubo et al. 2015), with lower bioavailability (Zafalon et al. 2020) and a less complete profile of amino acids (Donadelli et al. 2019). Adult cats fed on a meat meal as protein source had higher apparent nitrogen absorption and retention, as well as higher dry matter digestibility, when compared to a corn gluten meal-based diet (Funanba et al. 2005). Cats fed plant-based diets in which protein content is provided largely by soybean had lower plasma concentrations of taurine (Hickman et al. 1992; Kim et al. 1995) and such diets are also associated with arginine shortage (Gray et al. 2004; Zafalon et al. 2020). Consequently, while essential taurine is found in animal proteins, it must be supplemented when plant sources are used in the diet.

The advent of pet food manufacturing has allowed cat owners to feed their cats with an ostensibly “complete” (providing adequate amounts of all the required nutrients) and “balanced” (the nutrients are present in the correct proportions) diet. Guidelines for pet food companies in countries of the European Union are established by Fédération Européenne de l’Industrie des Aliments pour Animaux Familiers (FEDIAF). This Federation provides guidelines for complete and complementary pet foods, to ensure adequate concentrations of macronutrients, micronutrients and amino acids for a daily ration to satisfy cat energetic and nutrient requirements. However, detailed examination of the composition of common commercial pet foods has revealed inconsistency in their provision of some essential elements (Gosper et al. 2016; Zafalon et al. 2020) and some commercial foods do not meet all the nutrient minima, compared to dietary requirements, in terms of fatty acids, amino acids, and minerals (Zafalon et al. 2020). Domestic cats have a target macronutrient intake of 52% of total energy from protein, 36% from fat and 12% from carbohydrates (Hewson-Hughes et al. 2011). Instead, some pet food diets contain much higher proportions of energy content from carbohydrates (minimum 26% of energy from carbohydrates), which limits further food intake and creates a shortfall in protein and fat intake (Gosper et al. 2016), potentially leading cats to seek those nutrients elsewhere. Moreover, dry foods have higher carbohydrate content than wet foods because of the starches used as binding agents, making aspects of target intake for some cat macronutrients attainable only through provision and consumption of wet food (Hewson-Hughes et al. 2013). Production of pet foods has a substantial environmental impact, stemming in particular from the use of meat (Swanson et al. 2013). Cats require specific nutrients but not necessarily specific sources for these nutrients. Detailed analytical examination of meat foods might provide insights into their chemical and nutritional attributes that influence hunting behaviour. This would allow manufacturers to refine their composition without necessarily adding to environmental impacts.

To reduce adverse signs of stress in cats and to ensure their behavioural needs are met, as well as to address common pathologies like obesity and diabetes mellitus, various behavioural enrichment strategies have been evaluated (Buffington et al. 2006) and are advocated by animal welfare organisations (Ellis et al. 2013). These have included the use of ‘puzzle feeders’ designed to mimic instincts for pursuit of food, while object play with toys engages cats in a pseudo-predatory activity (Ellis et al. 2013). A complete hunting sequence in domestic cats involves seeking prey, stalk, chase, manipulate, kill and consume (Fitzgerald & Turner 2000) and playing and hunting activities increase with hunger, suggesting a shared motivational basis (Fitzgerald & Turner 2000). A lack of physical and mental stimulation in the home environment might therefore increase the time that companion animal cats spend outside, with associated increases in hunting, and the possibility that behavioural enrichment might reduce hunting and killing.

There are several collar-mounted devices that aim to inhibit hunting success that have been previously tested. BirdsBeSafe is a colourful collar cover that works as a visual warning, increasing the visibility of cats to potential prey animals with colour vision. It exhibits pronounced effectiveness in reducing killing of birds (Barratt 1997; Hall et al. 2015; Pemberton & Ruxton 2019) and, more generally, prey with good colour vision, including herpetofauna (Hall et al. 2015). The BirdsBeSafe is variably effective in affecting killing of mammals (Hall et al. 2015; Willson et al. 2015), as might be expected given their lack of colour vision and tendency to be more nocturnal. Studies on collars equipped with bells have reported divergent outcomes, with no effects on predation rates in Australia (Paton 1991; Barratt 1997), but a significant (by around 50%) reduction reported in UK (Ruxton et al. 2002; Nelson et al. 2005). In our earlier, observational study (Woods et al. 2003), we found that cats fitted with bells tended to bring back fewer mammals but found no difference in numbers of birds.

Experimental design

The trial was carried out from 20th March to 21st June 2019. Participants were required to remove any existing device that potentially interfered with cat hunting activity immediately before entry to the trial. The trial followed a before-after-control-impact (BACI) design. Before interventions were applied, owners recorded all prey brought home by cats for a pre-treatment period of seven weeks (20th March to 9th May). There then followed a transition period of one week (from 10th to 16th May) during which owners introduced their cats to the intervention to which they were assigned. After this, owners applied the intervention for a treatment period of five weeks (17th May to 21st June). All cats in the same household were treated in the same way, except when one of the cats was exclusively kept indoors. The experimental unit for the trial was therefore the household.

The six treatment groups were: BELL, where cats were fitted with a quick-release reflective collar (Kittygo, Wink Brands, UK) to which a single cat bell was attached; SAFE, where the same quick-release collar was fitted with a rainbow-patterned BirdsBeSafe® (www.birdsbesafe.com) collar cover; FOOD, where owners provided cats with a commercial, grain-free food in which protein was predominantly derived from meat sources (Lily's Kitchen Everyday Favourites paté multipack 8x85 g as wet food; and Lily's Kitchen Delicious Chicken as dry food); PUZZLE, in which owners provided their cats with dry food in puzzle feeders (PetSafe SlimCat interactive toy and food dispenser); PLAY, in which owners spent at least 5 minutes per day dedicated time playing with their cats, with a 'fishing' toy (Cat Dangler Pole Bird) and a 'mouse' toy (Kong refillable feather mouse toy, with the catnip replaced with bubble wrap); and CONTROL with no intervention, where owners were required to not make any changes to management of their cats, but were asked to keep completing prey records.

All food and equipment was provided by the project and was sent, with detailed guidance for the introduction of the treatment. For the BELL and SAFE interventions, detailed instructions were provided to ensure safe fitting and monitoring of the collar. In the case of households where cats exhibited prolonged intolerance of the collar, owners removed the collar and continued with prey recording but were excluded from further analysis. For the FOOD intervention, the food was purchased at wholesale price by the project from the manufacturer and shipped directly to the household. Food was presented in the same manner and quantities as the regular food, including relative proportions of wet and dry food. The new food gradually replaced regular food over the seven-day transition period (presenting a small amount of new food mixed with the normal food, then shifting the quantities until only the new food was provided). Owners were requested to monitor their cat and notify the research team if the cat refused the new food. In four households where cats exhibited complete aversion, the households continued recording but were excluded from analysis. Following the conclusion of the study, owners were provided with a further week's supply of food, to enable gradual transition back to regular food. The trial was not blinded, and owners in the FOOD group might have introduced recording bias. For the PUZZLE group, the puzzle feeder was introduced gradually over several days, following a procedure set by Dantas et al. (2016). Cat treats (Lily's Kitchen Little Lovelies Delicious Chicken) were initially provided to increase cat motivation and, as the cat became more adept at using the puzzle feeder, owners could replace treats with the normal dry food. Part of the cats' normal daily ration of dry food was used in the ball (i.e. the ball did not become an additional source of food). The holes in the feeder were adjustable. It was initially put on an 'easy' setting. As cats became more familiar, the difficulty of the puzzle was increased, and an increasing proportion of the normal dry food was provided using the feeder. By the end of the transition week, cats received their entire daily dry food ration from the puzzle feeder. In the PLAY group, owners were provided with play guidance, to slowly move the 'fishing' toy away from their cat, allowing it to stalk and/or ambush it, and then provide the 'mouse' toy filled with bubble wrap to be caught and manipulated (catch, bite and kick) in order to reproduce a complete hunting sequence. Toys were removed when not in use, both to maintain their value to cats and for safety reasons. Play duration per day was 5-10 minutes, after which adult cat motivation in playing tends to reduce as a consequence of habituation

(Hall et al. 2002). It is therefore unlikely that the modest duration of object play affected the availability of time that cats might have spent outdoors. Because of the importance of CONTROL group owners to the study, we encouraged their active participation with a final gift consisting of a small pack of cat food, and a discount voucher for future food orders.

Prey recording and basis of response variables

The main response variables were the numbers of animal prey items brought home and recorded by the owners. Cat owners regularly uploaded prey records online, using a unique participant number, identifying the cat responsible for the kill, where possible, or entering "unknown" in case of uncertainty in a multiple cat household, date of finding the item, animal type (mammal, bird, reptile, amphibian, insect or unidentified in case of prey remains), species (an identification guide was available for facilitating species identification), whether prey was alive or dead, and comments.

A limitation of this and similar studies (Paton 1991; Barratt 1997; Ruxton et al. 2002; Woods et al. 2003; Nelson et al. 2005; Hall et al. 2015; Willson et al. 2015; Pemberton & Ruxton 2019) relates to using the numbers of prey brought home by cats as a proxy for the numbers of animals they kill. Two studies (Loyd et al. 2013b; Seymour et al. 2020) that have equipped domestic cats (n = 16 and 18 cats, respectively) with cameras ("KittyCams"), found that 9 of 39 (23%) and 11 of 62 (18%) prey items were brought home, while the remainders were left or eaten *in situ.* Similarly, direct observation of hunting by tracked indoor-outdoor cats (n = 12 cats) and of hunts resulting in kills (n = 4 kills), when compared to prey records, suggest that householders might record around 30% of the prey killed (Kays & DeWan 2004). Notwithstanding the scale of these studies, they are consistent in their findings. Therefore, it is probable that some of the cats in our study killed and ate some of their prey while away from home, or killed and left them *in situ*, and so returned a proportion of their total kills to the household for recording. However, our study design accounts for this unquantified variation in multiple ways: 1. It is not quantified in the three observational studies (Kays & DeWan 2004; Loyd et al. 2013b; Seymour et al. 2020), but it is likely there is between-individual variation in the tendency of cats to bring home prey. We have accounted for this by adopting a before-after-control-impact design, whereby between-cat and temporal variation are controlled-for, by making paired observations of the same individuals before and after implementation of the treatment, and analysing variance by period and by treatment group, including a control. 2. Not accounting for all the animals killed by cats is a critical bias in quantifying the totality of killing by domestic cat populations and their impact upon prey populations (Loss et al. 2013; Kays et al. 2020). However, our study is of the effect of interventions on the relative frequency of prey returns and we do not extend our findings to the impact of killing upon prey populations. Hence our study is not subject to this bias. Rather, we work on the basic premise that any killing of wild animals by domestic cats is, in general, ecologically and socially undesirable (Crowley et al. 2019, 2020b) and that any reduction is beneficial. The same factor, i.e. cat abundance, that means their impacts can be locally and regionally substantial, also means that even small *per capita* reductions in killing are likely also to reduce substantially the total numbers killed. 3. In recognising *a priori* the constraints upon directly observing killing by cats, we recruited households where their cats had a track record of bringing home animals they had killed. While this represents a sample that is biased towards the tendency to bring home prey, which we note above is problematic for impact assessment, this bias is not relevant to our interventions. We have only to assume that the tendency to bring home prey is randomly distributed with respect to any potential impact of our interventions upon hunting and killing. 4. An alternative experimental approach would be to equip cats with cameras or to track them directly during hunts, as in the studies above (Kays & DeWan 2004; Loyd et al. 2013b; Seymour et al. 2020), and then to implement our treatments. This more direct approach to quantification of predation has promise, though there are clear challenges of scale. Our power analysis suggested a necessary sample in the hundreds of cats that regularly killed prey, whereas previous camera studies were an order of magnitude smaller. More importantly, perhaps, equipping cats with collar-mounted cameras is itself a moderately invasive intervention, along similar lines to collar covers and bibs. Thus, the means of observation likely affects the observation. Also, the premise of three of our treatments is that they are non-invasive and are not dependent on collaring. This would further increase the challenges of scale, as camera deployment would itself require incorporation as a level in a factorial design. 5. Our aim is to use the numbers of animals brought home as a proxy, to test the effect of our interventions on the numbers of animals killed. An alternative hypothesis is that our interventions did not affect the numbers of animals killed, but instead affected the numbers of animals brought home while the killing continued unabated. We acknowledge that this alternative hypothesis cannot wholly be excluded with our design but we consider this to be a much less parsimonious explanation. In our longstanding study quantifying wildlife predation by cats (Woods et al. 2003), we addressed this point: A proxy for the number of animals killed is adequate for a specific purpose “if we can assume that it is the cat's ability or inclination to capture prey that is influenced by the factors being investigated and not its inclination to bring prey home. That is, it seems safe to assume that by wearing a bell a cat's ability to catch a mouse may be affected, but not the cat's tendency then to bring the mouse home.”

The project team sent participants a weekly email prompt to provide data and to confirm ongoing participation using an update form. Participants inserted dates on which they were unable to record prey brought home by the cat (e.g. holidays) and dates on which the intervention was likely ineffective, for example if the bell or collar had been lost. In case of collar loss, a replacement was supplied and re-fitted as soon as possible and days on which cats were not wearing collars were excluded from the analysis. Overall, 15 households presented this problem with a median of 4 days excluded (IQR = 2.5-5.0 days) from the analysis. Two households reported cats not tolerating trial collars at all and these did not continue with the study.

Participant feedback

Owner participation was encouraged through project Facebook pages, in which they could share their ongoing experience with other members of the same group of treatment, and through a series of in-person workshops held in different regions throughout the trial. We collected feedback on the owners’ experiences of trialling the interventions through the weekly update forms, and conducted a short survey at the end of the trial, in which we asked participants whether they planned to carry on using their assigned interventions. Details of uptake and a summary of feedback for each intervention are provided in Table S3. For some cats, collars appeared to be a source of discomfort, causing cats to scratch the area and try to remove them. Nine owners reported that BirdsBeSafe collars prevented cats from grooming effectively, an issue also identified in a previous study (Hall et al. 2015). Some owners additionally reported disliking the appearance of the collars, stating they looked ‘silly’ or ‘ridiculous’. Post-trial intent to continue with the FOOD intervention was limited by around 50% of owners reporting that the cats disliked the wet food provided; this is not considered to have affected trial outcomes, as cats continued to eat the wet food and the majority ate mixed diets of wet and dry foods. Cats who completely rejected the food were excluded from the analysis. Post-trial intention to continue with the PUZZLE feeder depended on cat engagement with the device, with some owners reporting cats becoming bored or disinterested. Cat engagement with puzzle feeders may rely on appropriate introduction and training, which could improve uptake and reduce frustration caused by cats' inability to access food. Post-trial intention to continue with object PLAY was high (76%), with owners reporting both engagement with, and sometimes solicitation of, play from cats, and their own enjoyment of the measure.

Quantification and statistical analysis

All statistical analyses were conducted in R (R Development Core Team 2018). Our response variables were the total numbers of prey animals, and separately the numbers of birds and of mammals, captured and brought home by cats living in the same household and recorded by householders. The numbers of prey caught by multiple cats in the same household were combined, because prey could not in every case be confidently attributed to an individual cat. Households in which cats did not experience the intervention, for example where one of the cats was intolerant of a collar or diet change, were excluded from analyses. Records of prey brought home during the transition week were excluded from the analyses. In the treatment period, daily prey records were excluded from analysis if the cats in the house were not all following the treatment on that day (e.g. one of them had lost the collar, or owners were not using the puzzle feeder). Sampling 'effort' was calculated for each household as the total number of days when owners were active in recording prey, during the pre-treatment and treatment periods.

To analyse variation in the total numbers of prey brought home by cats as a function of treatment, a generalised linear mixed effect model with a Poisson error distribution and log link was used. Fixed factors were treatment (six levels, comprising five interventions and the control group), and period (pre-treatment and treatment). The effect of treatment was tested by the interaction term (treatment*period). To incorporate the dependency among observations of cats living in the same household, household identification number was a random variable. To adjust the value of the dependent variable by the number of cats in each house and owner recording effort, an offset for number of cat surveillance days was used (log(n_cats*effort)). The proportion of variance in the dependent variable explained by the model was expressed as a conditional R^2 (R^2c) value incorporating fixed and random effects. Model assumptions were verified by using the package DHARMa (Hartig 2019). Descriptions of the effects in terms of reduction or increase in rates of animals killed are derived by exponentiating the estimate of the effect, to obtain the Rate Ratio (RR) and the corresponding percentage decrease in the response rate ([RR-1]*100%).

To test for a possible effect of the novelty of the trial food driving any effects of dietary changes, as opposed to the food content, we conducted a secondary analysis of the daily prey brought home by cats in the FOOD group during the treatment period. We tested whether records of animals killed and brought home tended to increase as the duration of the trial increased. We fitted a generalised linear mixed effect model with a Poisson error distribution and log link. Day of observation was a fixed quadratic term. Household identification number was a random variable. To adjust the value of the dependent variable by the number of cats in each house, an offset was used (log(n_cats)). Model fit was verified using the package DHARMa (Hartig 2019). We found no significant effect or trend arising from day of trial ($p = 0.845$).

Chapter 4

Contributions of wild and provisioned foods to the diets of domestic cats that depredate wild animals

Chapter 4: Contributions of wild and provisioned foods to the diets of domestic cats that depredate wild animals

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Abstract

Predation of wildlife by domestic cats *Felis catus* presents a threat to biodiversity conservation in some ecological contexts. The proportions of wild prey captured and eaten by domestic cats and thus the contributions of wild prey to cat diets are hard to quantify. This limits understanding of any impacts of cats may have on wild animal populations and confound analyses of the effects of interventions aimed at reducing wildlife killing.

We used stable isotope analyses to quantify the contributions of wild and provisioned foods to the diets of domestic cats kept as companion animals and which frequently captured wild prey. We tested the effects of treatments aimed at reducing killing upon stable isotope ratios of cat whiskers and, where treatments had significant effects, we estimated variation in the contributions of wild prey to cats' diets before and during treatment. We evaluated bells, BirdsBeSafe collar covers, provision of food in a 'puzzle feeder', provision of food in which meat was the principal source of protein, object play and a control group.

As expected, cat diets consisted primarily of provisioned foods, though the contribution of wild animals to the diets of these cats, all of which regularly caught wild animals, was low (cat food ~96%, wild animals ~3–4%). Compared to the pre-treatment period and control group, cats with a BirdsBeSafe collar cover, exhibited significant reduction in nitrogen stable isotope ratios in their whiskers and consumed less wild prey, most likely attributable to effective inhibition of hunting, particularly for birds. Fitting cats with a BirdsBeSafe collar cover, therefore, reduced both returns of wild birds and consumption of wild prey.

While multiple interventions can significantly affect the numbers of wild animals that cats capture and return home, the remarkably small dietary contributions made by wild animal prey mean dietary change is harder to discern. Domestic cats rely almost exclusively on food provided by people even when they

frequently kill wild animals. This suggests that the hunting behaviour of domestic cats may be driven by behavioural motivations, or by a need to address micronutrient requirements, but is unlikely to alter macronutrient intake.

Introduction

Predation of wild animals by domestic cats *Felis catus,* in combination with their global distribution and abundance, constitutes a hazard for the conservation of biodiversity in a range of ecological contexts. In particular, cats living on islands are often considered to be invasive, non-native species that are responsible for the decline, extirpation and, in some cases, extinction, of endemic species (Medina et al. 2011). In continental areas, while the relative importance of compensatory (Møller & Erritzøe 2000; Baker et al. 2005) and additive (van Heezik et al. 2010) mortality due to predation by cats remains in debate, a growing body of evidence has identified the substantial direct and indirect impacts that owned and unowned free-ranging cats have on populations of some threatened vertebrates (Loss & Marra 2017) and upon the welfare of the animals they capture (Baker et al. 2018).

Although the relationship between cats and humans extends some 10,000 years into both species' histories, domestication of cats has progressed less completely than for other widely domesticated species (Driscoll et al. 2009a; Driscoll et al. 2009b). Retention of a full behavioural repertoire for hunting (Bradshaw et al. 1999; Bradshaw 2006) means that cats are adaptable to diverse ecosystems, and are able to live independently of human care and food provision. Hunger is a key driver in hunting, indeed hungry cats hunt more than well-fed cats (Kays & DeWan 2004). However, hunger, in a broad sense, is not the only reason for expression of hunting behaviour. Some free-ranging cats, kept as companion animals and regularly fed by people, frequently capture wild animals and bring them back, alive and dead, to the human household (Woods et al. 2003; Blancher 2013; Loss et al. 2013; Murphy et al. 2019). Some cats are more proficient and prolific hunters than others (Kays & DeWan 2004; Tschanz et al. 2011), with most domestic cats probably catching few or no prey (Churcher & Lawton 1987; Baker et al. 2005). Even if the individual frequency of killing is low, however, the cumulative impact of locally high densities of cats may be severe (Baker et al. 2005; Sims et al. 2008; Thomas et al. 2012). It has been suggested that the number of animals brought home by cats is not a reliable means of estimating the numbers of animals they kill (Loyd et al. 2013b; Seymour et al. 2020), and this remains a key uncertainty in determining rates of predation and the impact of cat predation upon prey populations. Consequently, for studies of predation rates, coupling surveys of prey returns with other methods of dietary analysis has been advocated (Krauze-Gryz et al. 2012).

Stable isotope analysis of consumer and prey tissues can offer an effective means of quantifying variation in the composition of predator diets (Crawford et al. 2008). In broad terms, ratios of the abundance of stable isotopes of carbon, ^{13}C to ^{12}C, reported as $\delta^{13}C$, in consumer tissues vary in relation to the relative importance of primary carbon sources and reflect gradients from terrestrial to marine systems or, within terrestrial systems, the relative importance of production stemming from, among other things, differences in photosynthetic metabolism (such as C3 versus C4 plants). The ratios of ^{15}N to ^{14}N, reported as $\delta^{15}N$, are serially enriched by consumers and therefore can broadly reflect the consumer's trophic level. Many manufactured pet foods contain high proportions of maize *Zea mays*, a C4 plant, and its derivatives, resulting in high values of $\delta^{13}C$ (Jahren & Kraft 2008; Newsome et al. 2015). In temperate regions, isotope ratios of provisioned foods are therefore likely to differ from those of wild animals that feed in natural food webs, where producers are predominantly C3 plants (Farquhar et al. 1989). Stable isotope analyses of feral cats' diets have identified reliance on high proportions of anthropogenic food items (Cove et al. 2018; Maeda et al. 2019). For cats kept as companion animals, however, a recent study (McDonald et al. 2020) found that stable isotope analysis of cat hair had little power to discern the proportions of cat diet comprised of wild prey or pet foods. This was mainly due to high variability in isotope ratios in pet foods, including variation among batches of the same variety, though their study also relied on small numbers of museum specimens to sample wild foods, rather than locally-collected wild animals (McDonald et al. 2020).

Cat owners rarely appreciate killing of wild animals by their cats (Crowley et al. 2019, 2020b) and some owners attempt to reduce their cats' hunting success through collar-mounted devices like bells, collar covers and bibs (Ruxton et al. 2002; Nelson et al. 2005; Calver et al. 2007). Such devices have been proven to be effective in reducing numbers of animals captured and brought home, but are characterised by low uptake by cat owners for various reasons, ranging from perceiving cat hunting as natural, albeit undesirable, behaviour (Crowley et al. 2019), to safety and welfare concerns linked to wearing a collar (Lord et al. 2010).

The persistence of hunting by domestic cats kept as companion animals and which are generally and regularly provisioned with food, suggests there may be physiological or behavioural needs that are not completely met in their environment and/or their provisioned diets. Hunting is a multi-faced behaviour affected by a series of drivers, including cat evolutionary constraints, idiosyncratic nutritional physiology and early life behaviour (Cecchetti et al. 2020). Predatory behaviours can be expressed independently from hunger, and even well-fed cats hunt, or engage in pseudo-predatory play with their owners (Hall & Bradshaw 1998b; Ellis et al. 2013). Cats have evolved as obligate carnivores with an absolute requirement for high intake of protein, as the source of essential amino acids and nitrogen, many water-soluble B vitamins (e.g. niacin), vitamin A, vitamin D, arginine, taurine, methionine, cysteine and some essential fatty-acids (Macdonald & Rogers 1984; Morris 2001). Such specific requirements would be fulfilled by eating wild prey. Bradshaw et al. (1999) advanced the hypothesis that retention of hunting behaviour in cats that are provisioned with food, could be linked to some nutritional inadequacy in the diets provided by people, particularly before the advent of commercial pet food manufacturing, and the adherence to standardised, “complete” and “balanced” diets. Detailed examination of the composition of widely available commercial pet foods has recently revealed inconsistency in their provision of some essential elements (Gosper et al. 2016; Zafalon et al. 2020) and in their macronutrient composition (Hewson-Hughes et al. 2011). Furthermore, the protein in pet foods can be derived from both animal and plant sources. Plant protein sources have lower digestibility (Neirinck et al. 1991; Kanakubo et al. 2015), lower bioavailability (Zafalon et al. 2020) and a less complete profile of amino-acids (Donadelli et al. 2019) than animal proteins. Therefore, it is possible that domestic cats that hunt wild prey are attempting to address some nutritional shortfall, though their success in so doing will clearly depend on successfully hunting, killing and ultimately consuming their prey.

Our aim was to improve understanding of the factors that might drive domestic cats, that are kept as companion animals and are fed regularly, to hunt wild prey.

We sought to understand the importance of wild foods to the diets of cats that regularly captured wild prey, and to ask whether this prey likely contributed to the cats' macro- or micro-nutritional needs. We analysed the diets of domestic cats through stable isotope analysis of cats' whiskers and of samples of wild animal prey and provisioned foods. We worked exclusively on owned cats living as companion animals that frequently captured wild animals and returned them to their households. We were able to discern provisioned commercial pet foods from wild prey and thereby to quantify the cats' relative reliance on food provided by owners and on wild foods obtained by hunting. Finally, we determined whether intervention measures that we have shown elsewhere (Cecchetti et al. in press) to affect significantly the numbers of animals killed and brought home, further affect the relative importance of wild prey in cats' diets.

Materials & Methods

Ethical statement

The study protocol was approved by the ethics committee of the University of Exeter, College of Life and Environmental Sciences, Penryn Campus (References CORN001673 and CORN000181). The project also received specialist veterinary guidance and the protocols was approved by an independent Project Advisory Group, comprising feline veterinary, behavioural and welfare specialists. Owners provided informed written consent.

Participant recruitment and sample collection

As part of a larger experimental study (Cecchetti et al. in press), cat owners whose cats regularly captured wild animals and brought them back to the house were recruited through social, broadcast and print media. Participants completed an online questionnaire regarding their cat, comprising details of sex, age, breed, health status, feeding and outdoor access (access outdoors restricted at night or unrestricted), frequency of hunting and ongoing management strategies adopted for reducing hunting.

More details of the experimental trial of interventions to reduce numbers of animals killed by cats are reported in Cecchetti et al. (in press). Briefly, the trial was conducted from 20th March to 21st June 2019. Participants were required to remove any existing device that potentially interfered with cat hunting activity before entry to the trial. Before interventions were applied, owners recorded all prey brought home by cats for a pre-treatment period of seven weeks (Period 1: 20th March to 9th May). There followed a transition period of one week (from 10th to 16th May) during which owners introduced their cats to the intervention to which they were assigned. After this, owners applied the intervention for a treatment period of five weeks (Period 2: 17th May to 21st June). All cats in the same household were treated in the same way. The six treatment groups were: **Bell**, where cats were fitted with a quick-release reflective collar (Kittygo, Wink Brands, UK) with a bell attached; **Safe**, where the same quick-release collar was fitted with a rainbow-patterned BirdsBeSafe (www.birdsbesafe.com) collar cover; **Food**, where owners provided cats with a grain-free food in which protein was predominantly derived from meat sources (Lily's Kitchen Everyday Favourites paté multipack 8x85g as wet food; and Lily's Kitchen Delicious Chicken as dry food); **Puzzle**, in which owners provided their cats with dry food in puzzle feeders (PetSafe SlimCat interactive toy and food dispenser); **Play**, in which owners spent at least 5 minutes per day dedicated time in object play with their cats, with a 'fishing' toy (Cat Dangler Pole Bird) and a 'mouse' toy (Kong refillables feather mouse toy, with the catnip replaced with bubble wrap, to provide an auditory stimulus); and **Control** with no intervention, where owners were required to not make any changes to management of their cats, but were asked to keep completing prey records.

From the experimental sample of 70 cats per treatment group, we selected a subset of 15-20 cats per treatment for detailed analysis of diets, based on owner willingness and household location to facilitate sample collection. We clipped one of the cats' whiskers at the beginning and one at the end of the trial to represent periods before and during treatment. Whiskers were stored in a paper envelope in ambient conditions.

To sample wild prey, cat owners were asked to collect and freeze the prey items brought home by their cats. Prey items were collected by the project team and stored at -80ºC. Owners provided cats with a diversity of pet food brands, varieties and flavours. There is great variability in the isotope ratios of commercial pet foods, both among and within brands and varieties (~6‰ in both δ^{13}C and δ^{15}N; McDonald et al.2020). Our aim was to quantify the relative importance to cats of provisioned versus wild foods, and the contributions of individual pet foods were harder to estimate, given within-brand variance. Therefore, our approach was to obtain a representation of the total isotopic space from which the ratios of all brands and varieties of provisioned foods could be sampled in stable isotope mixing models. We did this by determining the isotope ratios of a large sample (n = 172) of commercial foods, across brands and varieties. In the first collection, made from June to December 2017, owners of 106 cats specified the brand and variety of the food (n = 112) they had given their cats. Dry food samples (n = 61) were sent in by post, while wet foods (n = 51) were purchased according to the owners' specifications (see McDonald et al. 2020 for more details). In the second collection, made in February 2018, we collected from owners a further 29 samples of wet food and 31 of dry foods (n = 60 samples).

Recording of wild animals captured and brought home

Cat owners recorded the animals that were captured and brought home to the household. They regularly uploaded records online, identifying the cat responsible for the capture, where possible, or entering "unknown" in case of uncertainty in a multiple cat household, date of finding the item, animal type (mammal, bird, reptile, amphibian, insect or unidentified in case of indistinct remains), species (an identification guide was provided for facilitating species identification), whether the animal was alive or dead, and other observations.

Whisker growth rates

Whiskers generally grow continuously and so the basal section of whiskers sampled at the beginning of the study represented diet prior to the intervention, while the basal section of the whisker sampled at the end of the trial represented diet during and towards the end of the trial intervention period. To estimate the growth rate and thereby the approximate time interval represented by different whisker lengths, the owners of nine domestic cats were recruited for a biomarker feeding experiment. The cats were fed with their usual wet food (or their preferred food, e.g. tuna) mixed with a dose of 25 mg/kg (cat weight) of Rhodamine B, which, after ingestion, is incorporated into keratinous tissues, leaving a distinctive band detected under a fluorescence microscope (Fisher 1999). Dosing was undertaken twice, one week apart. After a minimum of three weeks, one whisker per cat was clipped and examined under a fluorescence microscope. Growth rate (mm per day) was calculated by measuring the distance between the two fluorescent bands, dividing it by the time span between the two doses (seven days).

Stable isotope analysis

A small section of muscle from all wild and provisioned foods was freeze-dried at -90º for 24-48 hours, then ground using a pestle and mortar. 0.6-0.8 mg of the resulting powder was weighed out and placed in tin capsules. Cat whiskers were rinsed in distilled water, wiped and placed in an envelope and freeze-dried at -90º for 24 hours. For each whisker, total weight and total length were measured. Each whisker was divided into one or more sections based on its total weight, with the basal section of the whisker representing the most recent period of whisker growth. Each section was cut into pieces of <1 mm using a scalpel and enclosed in tin capsules. The minimum sample weight was 0.35 mg and maximum 0.85 mg.

Masses of the stable isotopes of carbon and nitrogen and ratios of C:N were quantified using elemental analysis isotope ratio mass spectrometry using a Sercon Integra-2 EA-isotope ratio mass spectrometer at University of Exeter, and a Thermoquest EA1110 elemental analyser linked to a Europa Scientific 2020 isotope ratio mass spectrometer at Elemtex Ltd, Cornwall, UK. Stable isotope ratios were expressed as δ values in ‰ (parts per mil), the ratio of heavy to light isotopes, relative to the isotopic ratios of an international standard for each element: the Vienna Pee Dee Belemnite (VPBD) for $\delta^{13}C$ and atmospheric N_2 for $\delta^{15}N$. In both instances, samples were scale-corrected using USGS40 and USGS41 standards, with additional internal standards of bovine liver (University of Exeter and Elemtex Ltd) and alanine (University of Exeter only). Averaging across standards and laboratories, estimated precision was 0.08‰ ± 0.01 (1 standard deviation ± standard error) for $\delta^{13}C$ and 0.11‰ ± 0.02 for $\delta^{15}N$.

Handling of lipids

Lipids are depleted in ^{13}C, relative to proteins and carbohydrates (resulting in more negative $\delta^{13}C$), and variation in lipid content among organisms or among tissues introduce considerable bias into analyses of variation in $\delta^{13}C$. Such bias increases with lipid concentration (Post et al. 2007), which for these purposes can be approximated by C:N ratio. For terrestrial animals showing C:N ratios higher than 4, a mathematical correction is recommended (Post et al. 2007) and we mathematically corrected the $\delta^{13}C$ ratios of wild food sources (mean C:N = 3.6, SD = 0.2, range = 3.2–4.7) applying the equation:

$$\Delta\delta^{13}C = -3.44 + 1.00 * C{:}N \text{ ratio}$$

Our initial analyses found that provisioned, commercial cat foods had considerably higher and more variable C:N ratios (mean C:N = 8.7, SD = 2.0, range = 4.4–13.4) than wild foods, and did not show a strong or a linear relationship between $\delta^{13}C$ and C:N ratio ($r^2 = 0.06$). Therefore, we did not apply the Post et al. (2007) correction to $\delta^{13}C$ of provisioned cat foods. Rather, we chemically extracted lipids, following the method used by (Chouvelon et al. 2011), from a sample of 105 cat foods (n dry foods = 56, n wet foods = 49) and regressed $\delta^{13}C$ before and after extraction, deriving the equation:

$$\delta^{13}C_{after} = -3.76 + 0.83 * \delta^{13}C_{before} \; (r^2 = 0.71),$$

which was then applied as a correction to the $\delta^{13}C$ values of all provisioned cat foods.

Trophic Discrimination Factors

The processes of ingestion, digestion and assimilation by consumers are associated with a shift in isotopic ratios, the magnitude of which is often referred to as discrimination, fractionation or enrichment (Inger & Bearhop 2008). Trophic Discrimination Factors (TDFs) quantify the offset in stable isotope ratios between consumers and their food, and are a requirement of dietary reconstruction methods based on stable isotope mixing models (Healy et al. 2018). There are few reference values for means or variance in TDFs for modern domestic cats available in the literature. McDonald et al. (2020) provide TDFs for diet to hair of +1.9‰ for $\delta^{15}N$ and +2.6‰ for $\delta^{13}C$, derived from a single indoor-only cat. Maeda et al. (2019) report mean TDFs for diet to hair of +2.8‰ (SE 0.1‰) for $\delta^{15}N$ and +2.3‰ (SE 0.3‰) for $\delta^{13}C$, derived from shelter cats (n = 14; Y. Watari, pers. comm.). Among wild felids, Parng et al. (2014) quantified TDFs for diet to hair for

1 African lion *Panthera leo*, 3 bobcats *Lynx rufus*, 1 Canada lynx *L. canadensis and* 2 mountain lions *Puma concolor*, all held in captivity. For species where TDFs are not described in detail, it is possible to infer TDFs from species where they have been empirically determined using Bayesian phylogenetic regression approaches, that incorporate details of tissue types and feeding ecology (SIDER; Healy, 2018). However, the nutritional state, feeding ecology and macronutrient intake of wild felids, on which such an approach would be based, are very different from those of domestic cats. Aside from this, our main concern was that domestic cats are regularly fed with foods of diverse origins and highly variable macronutrient composition and derivation. Therefore, we determined diet to whisker TDFs directly using a sample of 10 domestic cats that were exclusively kept indoors and were fed on known foods. We clipped a whisker from each cat and sampled every food provided in the past three months. We calculated the mean difference between the averaged individual isotopic signature of all sections of the whisker and the averaged isotopic values of provisioned foods for both δ^{13}C (after correction for lipids) and δ^{15}N.

Statistical analyses and isotope mixing models

All statistical analyses were conducted in R (R Development Core Team 2018). Cats that did not successfully complete the trial, and cats that had only one whisker clipped, were excluded from analyses.

ANOVA, followed by post-hoc Tukey's pair-wise tests, was used to quantify isotopic variation amongst food sources. Food sources were then grouped according to their broad origins (wild prey and provisioned cat foods) and the similarity of their isotope ratios. We then used Bayesian isotopic mixing models with uninformative priors to estimate the relative contributions of wild and provisioned food source groups to cat diets in the pre-treatment and treatment periods for the overall cat population using the package 'SIMMR' v.0.3 (Parnell et al. 2010). Models were built with 3 Markov chains with a burn-in of 50,000 and 1,000,000 iterations. Gelman diagnostics were used to check model convergence.

To test whether cats' diets were affected by experimental treatments that we had shown (Cecchetti et al. in press) were effective in reducing the numbers of animals captured and brought home by cats, we analysed variation in δ^{13}C and δ^{15}N of individual cats as a function of experimental treatment, using two general linear mixed models. Fixed factors were treatment, period (pre-treatment and treatment), age class (6 months to 5 years and 6 years to 15 years), sex, and outdoor access (restricted or unrestricted). The effect of treatment was tested by a treatment*period interaction term. Cat identity was set as a random effect. The significance of the interaction term was evaluated by comparing models with and without the interaction term, using ANOVA. Where a treatment was found significantly to affect variation in $\delta^{13}C$ or $\delta^{15}N$ of the treated cats, we estimated and compared the contributions of the food source groups to the diets of the cats subject to that treatment and the control group, before and during treatment, using Bayesian stable isotope mixing models as described above. Estimates of diet composition at the level of treatment group should be viewed as a means of gauging the relative importance of food sources, rather than deriving precise estimates, due to the increased influence of uninformative priors in the models with lower numbers of observations (Swan et al. 2020).

Results

Whiskers were sampled from 90 cats. 82 cats were included in analysis of the diet of the whole cat population in the pre-treatment period because instrument process errors during analysis led to the exclusion of samples from 7 cats and a further cat was excluded because its diet was reported to be based primarily on fish. 57 cats were included in analysis based on individual prey returns because 25 cats were excluded because prey items could not reliably be attributed to individual cats living in multiple cat households. Six cats did not complete the experimental trial, and so 76 cats were included in analyses of variation in $\delta^{13}C$ and $\delta^{15}N$ and of the effect of treatments on wild prey consumption: 9 in Bell, 15 in Food, 10 in Puzzle, 13 in Safe, 14 in Play and 15 in the Control group.

During the pre-treatment period, the median number of prey items brought home per cat (n = 57 cats) was 4 (Interquartile range = 2–8) and the median prey return rate was 0.13 items per day (IQ range = 0.06–0.21) of recording effort (median = 37 days). During the treatment period, the median number of prey items brought home per cat (n = 58) was also 4 (IQ range = 2–8) and the median prey return rate was 0.11 items per day (IQ range = 0.06–0.25) of recording (median = 36 days).

232 wild animal prey items were analysed. Insects were not included as they contributed to a very small proportion of the biomass of wild prey captured and brought home by cats. It was not possible to discern potential food sources to the species level on the basis of stable isotope signatures, but two broad groups of wild animals could reliably be discriminated: 1) herbivorous mammals (n = 64), comprising rabbits *Oryctolagus cuniculus*, field voles *Microtus agrestis* and bank voles *Myodes glareolus* and 2) omnivorous and carnivorous vertebrates, comprising shrews *Sorex* spp., wood mice *Apodemus sylvaticus*, rats *Rattus norvegicus*, birds and herpetofauna (n = 168). These two groups differed in their mean $\delta^{13}C$ ratios (-24.9 ± 1.3‰ and -28.6 ± 1.4‰) but were similar in their $\delta^{15}N$ ratios (6.6 ± 1.6‰ and 6.04 ± 1.5‰; Figures 4.1, 4.2).

167 provisioned cat foods were analysed and their $\delta^{13}C$ values corrected for lipid content. Two groups of provisioned cat foods, dry (n = 90) and wet (n = 77), differed in their mean $\delta^{13}C$ ratios (dry = -23.7 ± 1.53‰, wet = -25.2 ± 1.23) but were similar in their $\delta^{15}N$ ratios (dry = 3.98 ± 1‰, wet = 4.03 ± 0.8‰) (Figure 4.2). These four food source groups (two wild prey and two cat food groups) differed significantly from one another in $\delta^{13}C$: (ANOVA $F_{3,395}$ = 171.9, p<0.001) and $\delta^{15}N$ ($F_{3,395}$ = 115.9, p<0.001). Critically, wild and provisioned foods were distinct in their ratios of $\delta^{15}N$, while within each of wild and provisioned foods, the two source groups were distinct in their ratios of $\delta^{13}C$ (Figure 4.2).

Three whiskers displayed two fluorescent bands, with an average growth rate of 0.48 mm/day (range 0.45-0.52 mm/day). Given the mean length of cat whiskers was 65 mm (range 37-118 mm), this corresponds to approximately 135 days of growth, such that analysis of the average whisker reflects cat diet over a period of around 4.5 months. The mean length of the basal section was 12.9 mm, corresponding to approximately 27 days.

Trophic discrimination factors calculated from nine indoor cats (one was excluded from analysis as its diet was fish-based) were 2.92‰ (SD 1.27‰) for $\delta^{13}C$ and 1.90‰ (0.72‰) for $\delta^{15}N$.

In both periods, cat diets consisted almost entirely of provisioned cat foods (Figure 4.2; Table 4.1). In the pre-treatment period, dry cat food was estimated to comprise 79.0% of cat diet (95% Credible Interval 69.4–88.0%) and wet cat food comprised a further 17.0% (95% CI 7.4–27.1%); while herbivorous mammals comprised 1.4% (95% CI 0.3–3.7%), and omnivorous and carnivorous vertebrates comprised 2.3% (95% CI 0.6–5.1%) (Figure 4.2c). Cat diets overall were similar during the treatment period: Dry cat food comprised 77.5% (95% CI 68.2–86.4%) and wet food comprised 18.7% (95% CI 9.3–28.5%), while herbivorous mammals accounted for 1.3% (95% CI 0.3–3.5%), and omnivorous and carnivorous vertebrates for 2.1% (95% CI 0.6–4.7%).

Variation in $\delta^{15}N$ was significantly affected by the treatment*period interaction (ANOVA comparison of models, χ^2 = 11.6, p=0.04). Cats equipped with a BirdsBeSafe collar cover showed reductions in $\delta^{15}N$, when compared to the control group and pre-treatment period (effect size for $\delta^{15}N$ = 0.92, 95% CI 0.86–0.99, p = 0.02). Older cats (age class 6–15 years) showed higher $\delta^{15}N$ ratios (effect size = 1.08, 95% CI 1.03–1.13, p<0.001). The total variance explained by the model (R^2c) was 0.67. There was no effect of any of the other interventions upon variation in $\delta^{15}N$. There was no effect of any interventions upon variation in $\delta^{13}C$.

In the BirdsBeSafe treatment group, consumption of omnivorous and carnivorous vertebrates was estimated to be 11.3% (95% CI 2.0–31.1%) in the pre-treatment period but was reduced to 4.7% (95% CI 0.9–14.1%) during the treatment period (Figure 4.3). Consumption of herbivorous mammals was estimated to be 4.7% (95% CI 0.9–14.3%) in the pre-treatment period and was similar at 3.6% (95% CI 0.7–10.8%) during the treatment period. In the Control group, consumption of omnivorous and carnivorous vertebrates was estimated to be 3.0% (95% CI 0.7–8.3%) in the pre-treatment period, and was unchanged at 2.9% (95% CI 0.6–8.4%) during the treatment period. Similarly, consumption of herbivorous mammals was estimated to be 2.8% (95% CI 0.6–7.9%) in the pre-treatment period, and was unchanged at 2.7% (95% CI 0.6–7.8%) during the treatment period.

Table 4.1. Estimates of the composition of domestic cat diets from Bayesian stable isotope mixing models, based on analysis of cat whiskers and four putative food source groups of wild and provisioned foods. Diet composition was estimated for the whole population of cats, before (pre-treatment) and during (treatment) an experimental evaluation of interventions aimed at reducing killing of wild animals.

Food source group		Pre-treatment period **(n = 82 cats)**		Treatment period **(n = 76 cats)**	
		Median	95% credible interval	Median	95% credible interval
Provisioned cat foods	Dry cat foods	0.790	(0.694-0.880)	0.775	(0.682-0.864)
	Wet cat foods	0.170	(0.074–0.271)	0.187	(0.093-0.285)
Wild animal foods	Herbivorous mammals	0.014	(0.003–0.037)	0.013	(0.003–0.035)
	Omnivorous and carnivorous vertebrates	0.023	(0.006–0.051)	0.021	(0.006–0.047)

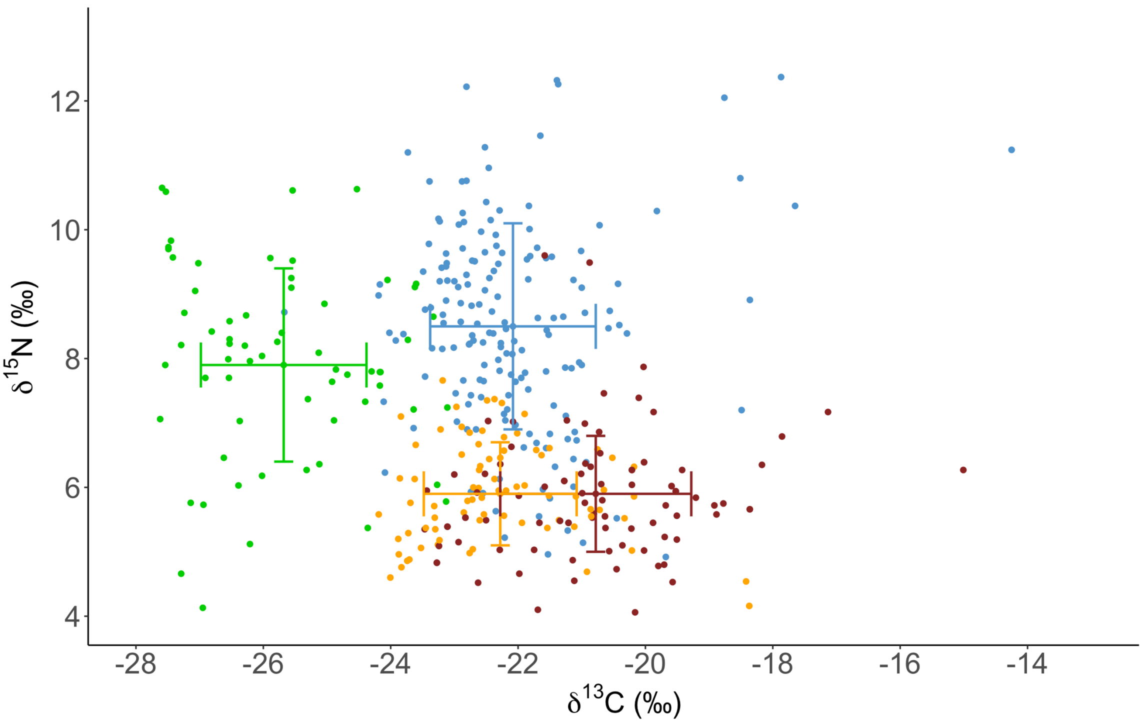

Figure 4.1. Carbon and Nitrogen stable isotope ratios of potential food sources for domestic cats. Dots represent individual samples belonging to four putative food source groups: two provisioned cat food groups (orange= wet foods; brown = dry foods) and two wild animal food groups (Green = Herbivorous mammals; Blue = Omnivorous and carnivorous vertebrates). $\delta^{13}C$ and $\delta^{15}N$ values are parts per mil. Bars indicate the mean ± standard deviation for each group.

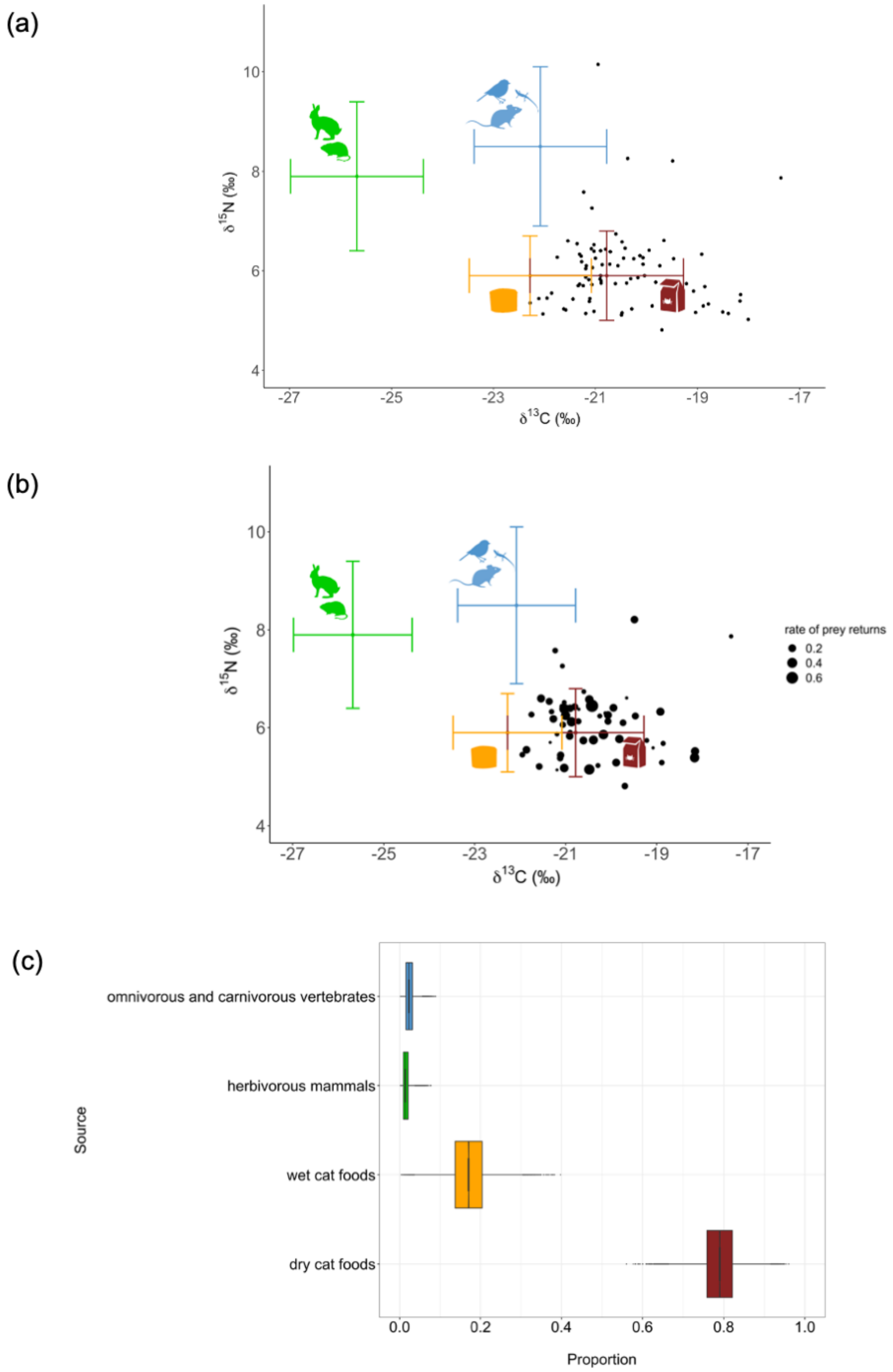
(a)
10
8
6
4
δ15N (‰)
-27
-25
-23
-21
-19
-17
δ13C (‰)
(b)
10
8
6
4
δ15N (‰)
-27
-25
-23
-21
-19
-17
δ13C (‰)
rate of prey returns
0.2
0.4
0.6
(c)
omnivorous and carnivorous vertebrates
herbivorous mammals
wet cat foods
dry cat foods
Source
0.0
0.2
0.4
0.6
0.8
1.0
Proportion

Figure 4.2. (Previous page) Estimates of the composition of the diets of free-ranging domestic cats determined by stable isotope analyses of cat whiskers and of putative food sources. (a) Stable isotope ratios (δ^{13}C and δ^{15}N) of basal sections of whiskers sampled from domestic cats (n = 82) in the pre-treatment period, and of their putative food source groups. Stable isotope ratios for cats are shown as black dots and for food source groups as the mean ± standard deviation, adjusted upwards by the Trophic Discrimination Factors. (b) Stable isotope ratios as in a) but where the sizes of the dots are scaled by the rate of prey returns during the surveillance period, for individual cats (n = 57) where prey items could reliably be attributed to individuals. The rate of prey returns is given by the number of prey brought home divided by the number of days of recording (c) Estimates from Bayesian stable isotope mixing models of the proportional contributions of wild foods (herbivorous mammals; omnivorous and carnivorous vertebrates) and pet foods (dry, wet foods) to cat diets (n = 82). Each box represents the 25th and 75th percentiles and whiskers represent 1.5 times the interquartile range.

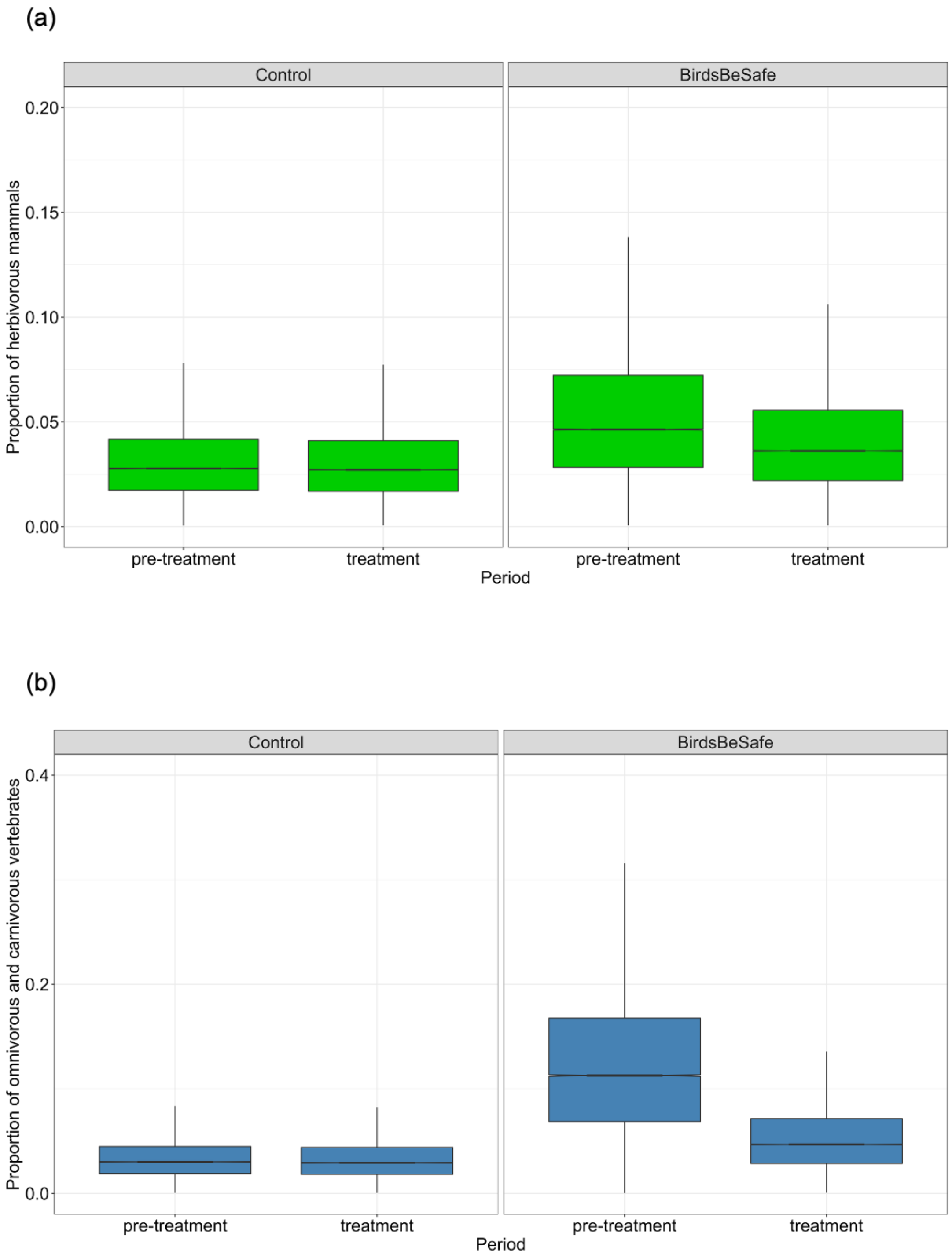

Figure 4.3 Estimates of the proportional contributions of wild foods (a) herbivorous mammals and (b) omnivorous and carnivorous vertebrates to the diets of cats equipped with BirdsBeSafe collar covers and a Control group. Estimates are from Bayesian stable isotope mixing models of the composition of the diets of the whole sample of cats in the treatment and control groups, in the pre-treatment and treatment periods.

Discussion

Domestic cats that regularly capture and kill wild animals nevertheless rely almost entirely on commercial pet foods provided by their owners. Among our sample of cats, all of which regularly captured and killed wild animals, they tended overall to consume relatively small amounts of the wild foods they caught. Where anthropogenic foods are available, free ranging, owned domestic cats clearly rely predominantly on them, suggesting that hunting and killing wild prey does not substantially contribute to the gross protein or energetic requirements of such cats. Rather, provisioned foods subsidise the cats, enabling hunting that might have potentially deleterious consequences for vulnerable species or ecosystems (Cove et al. 2018; Maeda et al. 2019).

Cats are obligate carnivores, requiring high levels of protein as the source of nitrogen and essential amino acids (Macdonald & Rogers 1984). The animal and plant proteins used in manufacturing commercial cat food differ in various aspects. Animal proteins are highly digestible by cats and are characterised by greater bioavailability of amino acids, relative to plant proteins (Funanba et al. 2005; Kanakubo et al. 2015; Donadelli et al. 2019). Whilst industry bodies (Fédération Européenne de l'Industrie des Aliments pour Animaux Familiers) provide specific guidelines to meet nutritional requirements of cats, some commercial pet foods have been found not to meet all the minimum requirements for some fatty acids, amino acids, and minerals (Davies et al. 2017; Brunetto et al. 2019; Zafalon et al. 2020). On this basis it has been proposed that some cats may hunt more because they are stimulated to seek additional or diverse food items to compensate for some aspects of deficiency in the food they are provided within the household. Our study suggests, however, that while some cats may be stimulated to hunt in this way, the contribution that wild prey then makes to such cats' diets is very small, relative to provisioned food. It is therefore possible that despite hunting to address some need, this need may not be being addressed by hunting. Alternatively, if cats lack some micronutrient, it may be that even low levels of wild prey consumption suffice.

Because of the relatively recent domestication of the cat, it has retained many behavioural traits of its wild progenitor, amongst them the separation between hunting motivation and prey consumption (Leyhausen et al. 1956), not necessarily eating what is killed, and surplus killing when opportunities arise (Adamec 1976; Macdonald & Rogers 1984). Some cats tend to eat their prey *in situ* while others bring it to a safe place to eat immediately or later (Loyd et al. 2013b; Seymour et al. 2020), and the human household is likely to represent such a place for most owned, domestic cats. Possible explanations for the disparity between the frequency of capturing and bringing prey home and the relative importance of wild prey consumed by cats might be: a) that once home, cats might be distracted by highly palatable provisioned food and eat it in preference to the wild prey or b) that cats may have the intention of consuming their prey later (Niewold 1986), but in many cases the owner removes it before it can be partly or wholly consumed. Cats have retained a similar behavioural repertoire to that of their wild ancestors (Bradshaw 2006), and killing might be strongly driven by such inherited instincts and not necessarily by specific attempts to address nutritional needs (Bradshaw et al. 1999). Killing prey can also be facilitated by owner husbandry and the degree of domestication of the cat, and by the environment where the cat lives, which determines the availability and diversity of potential prey (Cecchetti et al. 2020).

In our wider study, provisioning of high meat-protein food and object play led cats to capture and return wild prey with significantly reduced frequency (Cecchetti et al. in press). By contrast, use of a ‘puzzle’ feeder increased numbers of animals captured and returned, perhaps associated with insufficient training and inability to access food and resulting hunger (Cecchetti et al. in press). While these interventions significantly affected returns of wild prey by these domestic cats, their effects on consumption of the prey they captured could not be discerned in this study. Instead, variation in the assimilated mass of wild prey was, in most cases, random with respect to treatment, both for interventions that reduced and increased prey capture rates.

The BirdsBeSafe collar cover was the exception. This device effectively inhibits hunting success, particularly hunting of birds, by making cats more visible to their prey (Pemberton & Ruxton 2019). In our broader study (Cecchetti et al. in press), fitting this device reduced the capture and return of birds by 42% (albeit with large variation in individual responses: 95% confidence interval 1–66%), but had no significant effect on returns of mammals. Our analysis of the diets of a subsample of this treatment group suggests that when wearing the collar covers, central estimates of the relative importance of omnivorous vertebrates, the food source group that included birds, in these cats' diets fell from 11.5% to 4.3%. Fitting cats with a BirdsBeSafe cover collar therefore reduces both the frequency of capture and return of birds, and the consumption of a wild prey group that includes birds. For owners that are content to equip their cats with collars and collar-mounted devices, the BirdsBeSafe can be validated as an effective means of reducing the capture and consumption of wild birds, but not mammals. Some owners and animal welfare organisations, however, express reservations about fitting their cats with collars, stemming from concern about welfare, safety or collar loss and cost (Lord et al. 2010) and so this measure may not be a general solution to depredation of birds by cats.

Our study confirms that stable isotope analysis of cats' whiskers and potential foods can be a useful approach to estimating the contributions of broad categories of wild and provisioned foods to the diets of free-ranging domestic cats. The stable isotope ratios of $\delta^{13}C$ and $\delta^{15}N$ of cat foods and wild prey differed markedly, though at the scale at which we were operating, individual prey species were not distinguishable. We were able to discern two wild and two provisioned food sources: herbivorous mammals; omnivorous and carnivorous vertebrates; wet cat food and dry cat food. It was nonetheless disappointing not to be able to discriminate wild birds, which are of particular conservation concern, from wild mice and rats, which tend to be considered pests. Some greater resolution in dietary analyses might be achieved by sampling and quantifying both wild and provisioned food inputs at the level of individual cat or household, though the substantial between-batch variation in isotope ratios of provisioned foods would require such monitoring to be exhaustive in detail. Resolution might also be improved with greater understanding of variation among individual cats and, perhaps more importantly, among food sources, in affecting trophic discrimination factors. Our analysis of 9 individuals highlighted relatively large between-individual variation in estimates of this offset between food and consumer (coefficient of variance = 43% for $\delta^{13}C$ and 38% for $\delta^{15}N$). Our mixing models incorporated this uncertainty, and we are confident of the robustness of our distinction between the broad groupings of wild and provisioned foods. However, this between-individual variation is consistent with bulk analysis of food isotope ratios not fully reflecting the bioavailability to cats of macronutrients in commercial foods. Commercial foods have high and variable C:N ratios and dry foods, in particular, contain high proportions of plant sugars and starches, including from distinctive C4 plants, much of which may be indigestible to cats. These would, however, substantially affect $\delta^{13}C$ ratios, and the offset between food and consumer tissues. To address this possibility, compound-specific isotope analytical approaches would allow the distinction of the nutritional importance of the diverse components of cat dietary intakes.

In conclusion, domestic cats living as companion animals rely almost exclusively on provisioned cat foods, even when they regularly kill wild prey. If provisioned cats hunt to address some nutritional deficiency, what they kill is unlikely to alter macronutrient intake. Hunting might nevertheless address some micronutrient requirement or behavioural motivation. Our studies together suggest that cat motivation for hunting and returning prey can be markedly reduced, even though domestic cats eat only relatively small amounts of wild prey, and further highlight the disconnect between hunting, capturing and then eating wild prey and the motivations for these behaviours.

Chapter 5

Night-time confinement of domestic cats reduces roaming and interventions to reduce capture of wild prey increase time cats spend at home

Chapter 5: Night-time confinement of domestic cats reduces roaming and interventions to reduce capture of wild prey increase time cats spend at home

Abstract

Roaming behaviours in free-ranging domestic cats *Felis catus* increase their exposure to hazards to their health and welfare. Hunting by cats can also be a hazard to biodiversity conservation and to wild animal welfare. Management approaches that attempt to mitigate risks arising from cat roaming and hunting behaviours are often controversial. Confinement of pet cats can be unpopular with owners, but might bring benefits in terms of reduced exposure to hazards. Similarly, approaches to reducing hunting might have the potential to bring benefits to cats by reducing roaming.

We investigated variation in roaming behaviours among cats that were continuously free to roam or partially confined by their owners. Using an experimental design, we tested whether interventions aimed at reducing predation by cats also affected their spatial behaviour. We tested relationships between spatial behaviour and rates of prey capture and return to the household. We tracked cats living as companion animals in southwest England and which regularly captured and returned wild prey. We evaluated cat bells, BirdsBeSafe collar covers, provision of food in a ‘puzzle feeder’, provision of grain-free food in which meat was the primary source of protein, object play and a control group.

72 cats completed the 12-week trial in Spring 2019. Cats wore GPS collars for at least 5 days in both pre-treatment and treatment periods. Cats’ home ranges were small ($AKDE_{95}$; median = 1.51 ha, inter-quartile range = 0.76–2.38). Cats that were continuously free to roam outside travelled greater distances from home and had home ranges 75% larger than those of cats with restricted outdoor access at night. Older cats tended to have smaller home ranges and to move less than younger cats. None of the treatments intended to reduce predation significantly affected cat roaming distances, though multiple treatments increased the number of times cats were located at home (Bell +29%; Food +20%; Play +24%).

Whilst cat owners might use some of the interventions effectively to reduce hunting. to reduce their cat's roaming and associated exposure to outdoor hazards, the most effective approach, although unpopular, remains confinement, whether partial or continuous.

Introduction

Domestic cats *Felis catus* that live as companions in human households, but which have access to the outdoors are exposed to multiple hazards that can negatively affect their health and welfare. Roaming behaviours increase risks of cats contracting viral (e.g. FeLV) and parasitic (e.g. *Toxoplasma*) infections (Chalkowski et al. 2019), of being injured or killed in road traffic accidents (Olsen & Allen 2001; Rochlitz et al. 2001), and of being attacked by wildlife (Lukasik & Alexander 2011) or dogs (Olsen & Allen 2001). Cats with outdoor access are at greater risk of getting lost and contributing to feral cat populations (Tan et al. 2020). Moreover, outdoor cats can be considered a nuisance to human neighbours (Toukhsati et al. 2012) and can carry a variety of zoonotic infections (Teutsch et al. 1979).

Predatory cats also present a hazard for wild animal welfare (Baker et al. 2018) and direct and indirect hazards for biodiversity conservation. Some, but not all, domestic cats can be prolific hunters (Woods et al. 2003; Baker et al. 2005; Thomas et al. 2012). Cats reach their highest densities in urban areas (Baker et al. 2008; Sims et al. 2008), with correspondingly high national population estimates. For example, there were estimated to be 10-11 million pet cats in the U.K. in 2011 (Murray et al. 2015) and 90 million cats in the USA in 2013 (Loss et al. 2013). Because of their abundance, the numbers of wild animals killed by domestic cats can be great (Lepczyk et al. 2003; Woods et al. 2003; Blancher 2013; Murphy et al. 2019), with cumulative adverse effects on prey populations at local (Baker et al. 2005; Baker et al. 2008; Sims et al. 2008; Thomas et al. 2012) up to continental scales (Blancher 2013; Loss et al. 2013; Woinarski et al. 2017; Murphy et al. 2019). In some ecological contexts, the direct (Medina et al. 2014) and indirect (Beckerman et al. 2007; Bonnington et al. 2013) effects of cats can therefore be detrimental for biodiversity conservation (Doherty et al. 2016).

Assessments of the relationships between cat spatial behaviour and wildlife depredation have previously shown ambiguous results. Variation in home range size did not influence numbers of prey caught (van Heezik et al. 2010), though cats with larger home ranges returned greater diversity of prey items (Morgan et al. 2009). A recent study by Kays et al. (2020) revealed that pet cats generally have remarkably small home ranges (mean = 3.6 ha, SD = 5.6 ha, n = 876), but high numbers of prey animals killed per unit area (14.2–38.9 prey items ha^{-1} yr^{-1} per cat). The patterns and extent of roaming in domestic cats are influenced by a variety of factors: Sex, with male cats having larger home ranges than females (Hall et al. 2016c; Kays et al.2020); reproductive status, with intact male cats having larger home ranges than neutered males (Kays et al. 2020; Ferreira et al. 2020); age, older cats having smaller ranges than younger cats (Hervías et al. 2014; Hall et al. 2016c; Kays et al. 2020); and urbanisation, with urban cats having smaller ranges than rural cats (Wierzbowska et al. 2012; Kitts-Morgan et al. 2015; Hall et al. 2016c; Hanmer et al. 2017; Kays et al. 2020).

Owners regularly express concern about the hazards to which roaming outdoors exposes their pets, and some are also concerned about their cats' impacts on wildlife (Crowley et al. 2019, 2020b). In order to limit these risks, approaches like keeping cats indoors, or using enclosures such as cat patios (catios), have been suggested. However, owners may perceive such permanent confinement as an impediment to expression of what they see as natural feline behaviours (Tan et al. 2017; Crowley et al. 2019). Partial curfews tend to be more acceptable to owners, with nocturnal mammals being the main beneficiaries of night-time confinement of cats (Woods et al. 2003), while nocturnal or crepuscular confinement, particularly in warmer months, is recommended when most wild species are active and in their reproductive periods (Mori et al. 2019). Some previous studies have shown that cats with unrestricted outdoor access roam significantly further at night than during the day (Metsers et al. 2010; Thomas et al. 2014), while others found no differences (van Heezik et al. 2010; Hanmer et al. 2017). Similarly, whether a cat was kept in at night or allowed to roam freely all the time had no impact on home range size (Hall et al. 2016b).

Other strategies proposed for reducing the numbers of prey killed by cats include collar mounted devices, such as bells, collar covers and bibs, that inhibit or impede cat hunting. Such devices have each been shown to be at least partly effective in reducing numbers of prey brought home (Ruxton et al. 2002; Nelson et al. 2005; Calver et al. 2007). The collar-mounted pounce protector CatBib (Cat

Goods Inc., 2000) and the BirdsBeSafe® collar cover (Birdsbesafe LLC, 2009) have been found not to reduce cat home range size (Hall et al. 2016c). Again, cat owners vary in their acceptance or application of such measures for several reasons, but not using them is likely because purported benefits do not override owners' priorities for, and perceptions of, cat welfare (Calver et al. 2013; Harrod et al. 2016; Hall et al. 2016a; Crowley et al. 2019). Finding approaches that lead to a reduction in roaming behaviour might find greater acceptance by owners.

Cats are obligate carnivores with strict nutritional requirements (Macdonald & Rogers 1984). Some commercial pet foods appear not to provide some essential elements (Gosper et al. 2016; Zafalon et al. 2020) and macronutrients (Hewson-Hughes et al. 2011). Furthermore, the proteins in pet foods can be derived from both animal and plant sources, but plant proteins have lower digestibility (Neirinck et al. 1991; Kanakubo et al. 2015), lower bioavailability (Zafalon et al. 2020) and a less complete amino-acid profile (Donadelli et al. 2019) than animal proteins. Cats also have specific behavioural needs, and encouragement of physical activity and reproduction of natural feline behaviour in the home environment is important for preventing negative states such as boredom and frustration (Tan et al. 2020). Behavioural enrichment strategies include object play with toys that engages cats in a pseudo-predatory activity (Ellis 2009; Ellis et al. 2013), and use of 'puzzle feeders' (Dantas et al. 2016) that require cats to be more engaged in food acquisition. The nutritional and behavioural needs of cats prompted our testing of novel management strategies for reducing motivation for hunting, rather than impeding hunting success. We have shown (Cecchetti et al. in press) that provisioning of food with high meat protein content, and object play, decreased numbers of prey brought home and recorded by householders by 36% and 25% respectively, while puzzle feeders increased numbers of prey returned by 33%.

We analysed variation in domestic cat spatial behaviours and whether this related to the numbers of prey captured and brought home by domestic cats that regularly caught wild animals. We evaluated the effects upon spatial behaviour of conventional measures used to reduce prey capture and retrieval rates, i.e. bells and BirdsBeSafe collar covers, as well as novel dietary and behavioural interventions, high meat content food, food delivery though the use of a puzzle feeder, and object play. If these management strategies for predation could be shown also to affect cat roaming behaviour, they could offer additional options for cat owners seeking to reduce their cats' exposure to multiple outdoor hazards, as well as reducing the exposure of wildlife to the direct and indirect hazards presented by cats.

Materials & Methods

Ethical statement

The study protocol was approved by the ethics committee of the University of Exeter, College of Life and Environmental Sciences, Penryn Campus (Reference CORN000181). The project also received specialist veterinary guidance and the protocols was approved by an independent Project Advisory Group, comprising feline veterinary, behavioural and welfare specialists. Owners provided informed written consent.

Participant recruitment

The tracking trial was part of a larger experimental study aimed at testing the efficacy of measures to reduce predation of wildlife by cats (Cecchetti et al. in press). Cat owners whose cats regularly killed wild animals and brought them back to the house were recruited through social, broadcast and print media. Participants completed an online questionnaire regarding their cat's sex, age and breed, health and behavioural status, feeding habits, access to outdoors, frequency of hunting, and ongoing management strategies adopted for reducing hunting. To test owner willingness and continuity in recording for the study duration we set the first two weeks as surveillance weeks. We selected households in which at least one prey item had been brought home and recorded during these two weeks of preliminary surveillance. From the experimental sample of 70 cats per treatment group, we selected a subset of 10-20 cats per treatment for detailed analysis of spatial movements, based on owners' willingness to track their cats, and household proximity to the University to enable frequent checks and the possibility of replacing the tracker in case of loss (Figure 5.1). Pets were equipped with a quick release collar and a GPS unit 'iGotU GT120' (4.4 x 2.7 x 1.3 cm, 26 g, Mobile Action Technology, Taiwan) with a fix schedule of 1 fix per 15 minutes, for at least 5 days during both the pre-treatment and treatment periods. The location accuracy of this GPS logger was considered sufficient for this study, with average location errors of approximately 10 metres (Morris & Conner 2017), and with knowledge of the speed at which a specific study animal is able to travel, erroneous locations can be identified and removed, based on improbable travel distances given time between locations (Morris & Conner 2017; Hanmer et al. 2017; Kays et al. 2020). However, some studies employing the same GPS units have detected an increased number of error locations in urban areas (Hanmer et al. 2017) and when cats were indoors, resulting in a cloud of points within 30 m of the house (Hanmer et al.2017; Kays et al.2020).

Prey recording

Cat owners recorded the animals that were killed and brought home to the household. They regularly uploaded prey records online, identifying the cat responsible for the returned item, where possible, or entering “unknown” in case of uncertainty in a multiple cat household, date of finding the item, animal type (mammal, bird, reptile, amphibian, insect or unidentified in case of indistinct remains), species (an identification guide was provided for facilitating species identification), whether prey was alive or dead, and other comments.

Experimental interventions

More details of the experimental trial of interventions to reduce numbers of animals killed are reported in Cecchetti et al. (in press). Briefly, the trial was carried out from 20th March to 23rdJune 2019, comprising a pre-treatment period of 7 weeks, followed by a transition week during which owners introduced their cats to the intervention to which they were assigned and a treatment period of five weeks. Cats were tracked for at least five days before and during treatment. The six treatment groups were: **Bell**, with cats fitted with a quick-release reflective collar (Kittygo, Wink Brands UK) and a bell attached; **Safe**, where the same quick-release collar was fitted with a rainbow-patterned BirdsBeSafe (www.birdsbesafe.com) collar cover; **Food**, where owners provided cats with a food in which protein was predominantly derived from meat sources (Lily’s Kitchen Everyday Favourites paté as wet food; and Lily’s Kitchen Delicious Chicken as dry food); **Puzzle**, in which owners provided their cats with dry food in puzzle feeders (PetSafe SlimCat interactive toy and food dispenser); **Play**, in which owners spent at least 5 minutes per day dedicated time playing with their cats, with a ‘fishing’ toy (Cat Dangler Pole Bird) and a ‘mouse’ toy (Kong refillable feather mouse toy, with the catnip replaced with bubble wrap); and **Control** with no intervention, where owners were required to not make any changes to management of their cats.

Analytical methods

All statistical analyses were conducted in R (R Development Core Team 2018).

Spatial behaviour

Prior to analysis, tracking data were filtered to remove inaccurate fixes on the basis of unrealistic speed and distance travelled (threshold value for maximum speed/ distance travelled was 100 m/min corresponding to 1.5 km/15 min and for removing 'spike' locations, the speed angle threshold was set to 15 m/min (225 m in 15 m; Recio & Seddon 2013) through the function 'ddfilter' in the 'SDLfilter' package (Shimada et al. 2012). Home and core ranges were calculated using autocorrelated kernel density estimates (AKDE) from continuous-time movement models (Fleming et al. 2015). Models were fit using the 'ctmm' package (v0.5.10) following procedures set out by Calabrese et al. (2016). Variograms were used to check the autocorrelation structure of each individual's movement data. Individuals were excluded from home range analyses if there was no asymptote in the variogram, suggesting the individual had not been monitored for long enough, or was exhibiting non-range-resident behaviours (e.g. range expansion or dispersal). Movement models were fitted using maximum likelihood, and model selection was determined on the basis of the Akaike information criterion (AIC). Once the models were selected, the 95% AKDE ($AKDE_{95}$) and the 50% AKDE ($AKDE_{50}$) were calculated (Figure 5.2).

Variation in the home range sizes of cats in the pre-treatment period was analysed using a linear model. We only used $AKDE_{95}$ in this analysis as $AKDE_{50}$ was highly correlated (rho = 0.94; $p<0.01$). Log_e-transformed $AKDE_{95}$ was the response variable and age, sex, number of tracking days to control for sampling effort and human settlement type (city, town or village) were explanatory variables. We did not distinguish diurnal and nocturnal fixes as some of the cats were confined at night, instead we included outdoor access as a predictor variable in the analysis (unrestricted or restricted at night). Not all cat owners were able to report their cats' exact ages in years, thus age class (6 months to 5 years, and 6 to 15 years) was used in the analysis as a categorical variable. To explore any relationships between numbers of prey brought home and home range size, we used a generalised linear model with a negative binomial structure. Explanatory variables were $AKDE_{95}$, age class, outdoor access, sex and settlement type, while number of days of prey recording was set as an offset to account for sampling effort. Cats living in households with >1 cat where owners were not able reliably to attribute prey records to an individual, were excluded, as were cats with no prey return records in the pre-treatment period.

Model selection adopted an information theoretic approach based on the value of AIC (Burnham & Anderson 2002). A difference in AIC (ΔAIC) of <2 was used to select the top model set and to obtain the model-averaged coefficients of predictor variables, and to rank them according to their predictive importance (∑w). To check for collinearity in the final models, we calculated the variance inflation factors (VIF, Zuur et al. 2010).

In order to understand if any treatment had an effect on home range size, we fitted a general linear mixed model (GLMM) using package lme4. Fixed factors were treatment (six levels), and period (pre-treatment and treatment) and the effect of the treatment was tested by the treatment*period interaction term. Other explanatory variables: sex, age class, outdoor access and settlement type, were included, based on the model averaging results of the model run in the pre-treatment period. Individual cat was fitted as a random term. Because we were interested in the effect of the interaction term, the model was compared to a model with no interaction term through ANOVA. The proportion of variance explained by the selected model was expressed as conditional R^2 (R^2_c).

Maximum distance from home, distance travelled and time at home

In addition to size of home and core ranges, we evaluated three further measures of cat spatial behaviour: daily maximum distance from the house, daily distance travelled, and daily time at home. To estimate these, polygons of the owners' houses were drawn in QGIS (Figure 5.2). Daily maximum distance travelled from the home polygon was measured from the edge of the home polygon to the furthest point at which a cat was detected on each day. Daily distance travelled was calculated as the sum of distances from one fix to the next, over a 24-hour period from midnight to midnight. The time the cat spent at home was defined as the number of active fixes within the home polygon. This was likely an estimate of the minimum, as it excluded the time for which the logger was unable correctly to locate the animal within the home building.

Variations in the spatial variables in the pre-treatment period were analysed using three separate models. In all models, age class, sex, outdoor access and settlement type were explanatory variables. Individual cat was a random factor to account for repeated daily observations. Specifically, we ran two GLMMs with $\log_e$-transformed maximum distance from home and $\log_e$-transformed daily distance travelled as the response variables. The third model of variation in time at home was a GLMM with a Poisson error structure. Models of daily distance travelled, and time spent at home included the $\log_e$-transformed number of daily fixes as an offset to account for logger recording success. Model selection and averaging were carried out following the same procedure as described above for home range and prey returned.

The effects of treatments on variation in these spatial variables was evaluated running three separate models in which the main effects were: treatment (six levels) and period (pre-treatment and treatment). The effect of treatment was tested by the interaction term (treatment*period). Other explanatory variables: sex, age class, outdoor access and settlement type were included based on the model averaging results of the model run in the pre-treatment period. Model selection was carried out as above, with comparison of models with interaction terms by ANOVA. Again, the proportion of variance explained by the selected model was expressed as conditional R^2 (R^2_c).

For all models where the dependent variable is $\log_e$-transformed, effect sizes are expressed in the result section, or reported in tables, by exponentiating the estimates of the fixed effects. For negative binomial model we refer to these as Odds Ratios (OR), while for Poisson models, as Rate Ratios (RR). Corresponding percentage of increase or decrease in times at home is derived by ([RR-1]*100%).

Correlations between explanatory variables were investigated prior to all analyses using Spearman's rank correlation tests, and correlated variables were precluded from appearing in the same models.

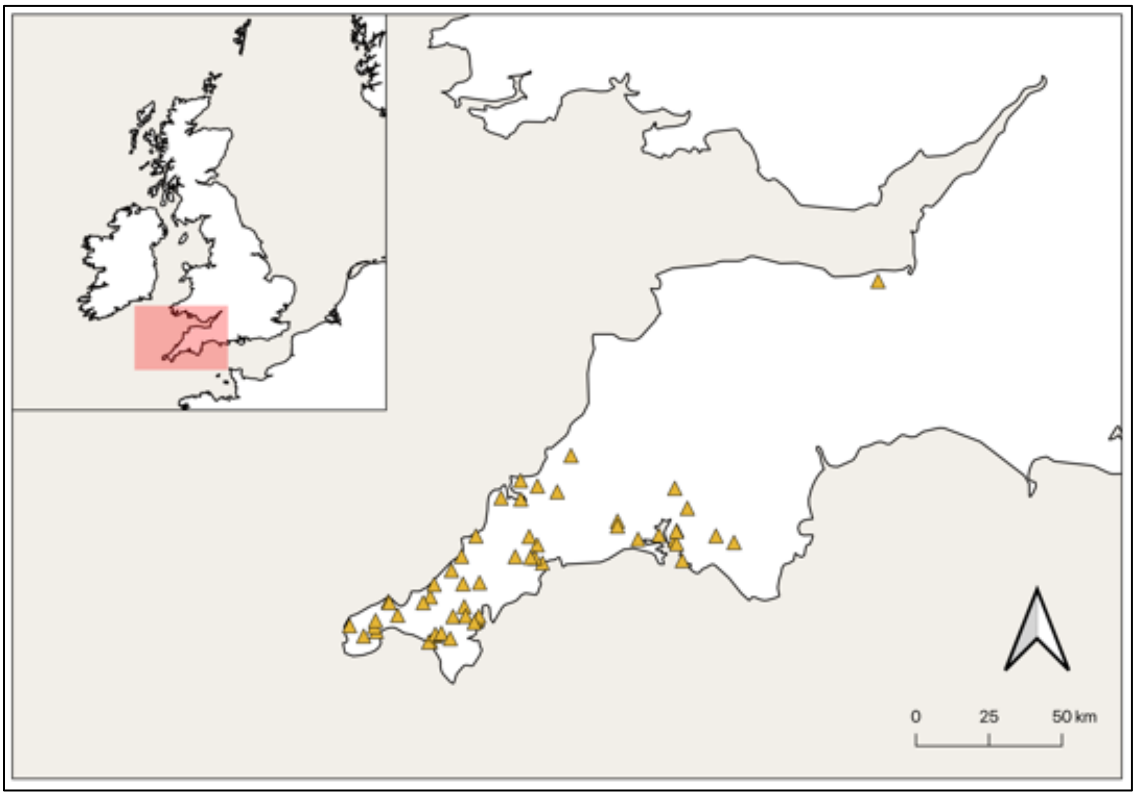

Figure 5.1. Locations of the households in southwest England in which domestic cats were tracked.

Figure 5.2. Representative map showing the house polygon, core range, home range and the fixes recorded by the GPS unit for one of the cats in the trial.

Results

82 cats completed the 12-week trial and generated usable tracking data for at least 5 days. 10 cats were excluded from analyses; nine because they had variograms that did not level off (in one or both periods), and one with an exceptionally large home range ($AKDE_{95}$ = 17.3 ha) that had particular influence on the analyses, thus a total of 72 cats were included in analyses (Table 5.1). In the pre-treatment period, mean deployment was 8.9 days (SE mean = 0.2 days), while in the treatment period mean deployment was 7.5 days (SE = 0.1 days). 59 cats (82%) had unrestricted access to the outdoors, and 13 (18%) had their access restricted at night.

Overall, the cats' median home range ($AKDE_{95}$) was 1.51 ha (interquartile range = 0.76–2.38 ha), median core range ($AKDE_{50}$) was 0.20 ha (IQR = 0.10–0.33 ha), median daily maximum distance from home was 89 m (IQR = 55–138 m), median daily distance travelled was 884 m (IQR = 543–1353 m), median daily times at home was 3 (IQR = 1–5), and median number of daily fixes was 33 (IQR = 22–42).

Outdoor access had the greatest, and a significant, influence on variation in home range size, indicating that cats that were free to roam tended to have larger home ranges (median = 1.79 ha, IQR = 0.99–2.48 ha), than those for which outdoor access was restricted at night (median = 0.74 ha, IQR = 0.55–1.41 ha) (Table 5.2). Age class and sex had less influence, but suggested that older and female cats tended to have smaller home ranges (Table 5.2). Number of days of tracking had an even lower predictive power, but indicated that an increase in number of days of deployment was associated with increased estimates of home range size. Human settlement type had no influence on cat home range size.

In the pre-treatment period, six cats brought home no prey, so were excluded from the analysis investigating the relationship between prey returned and home range size. In households owning multiple cats, few owners could unequivocally attribute prey records to a specific individual cat and so the number of cats dropped to 34 individuals. None of the variables had a strong effect, but greater home range sizes were associated with increased number numbers of prey captured and brought home by cats and restricted outdoor access at night was associated with reduced prey numbers. Older cats tended to bring home fewer prey items (Table 5.3). Human settlement type and cat sex did not influence the numbers of prey brought home by cats.

Outdoor access had a strong and significant influence on variation in the daily maximum distance from home, indicating that cats that were free to roam tended to go further (median = 97 m, IQR = 60–147 m), than those with restricted access at night (median = 60 m, IQR = 43–104 m) (Table 5.2). Age class had a similar predictive power, indicating that older cats had maximum distances that were shorter (median = 85 m, IQR = 46–137 m) than younger cats (median = 100 m, IQR = 64–146 m). Sex had less influence, but suggested that female cats travelled shorter distances from home (median = 80 m, IQR = 52–112 m) than males (median = 101 m, IQR = 57–158 m) (Table 5.2). Human settlement type had no influence on maximum distance from home.

Similarly, for daily distance travelled, outdoor access and age class had the greatest effects. Cats that were free to roam travelled longer distances (median = 974 m, IQR = 573–1387 m) than those confined at night (median = 799 m, IQR = 514–1114 m). Older cats travelled less (median = 800 m, IQR = 476–1310 m), than younger ones (median = 1027 m, IQR = 660–1386 m). Males travelled longer distances (median = 1006 m, IQR = 580–1430 m) than females (median = 865 m, IQR = 546–1240 m).

None of the considered variables had a strong effect on time spent at home, though cats with access restrictions and older cats were likely to be found at home more frequently (Table 5.3).

Cat home range ($AKDE_{95}$) was not affected by any of the treatments (ANOVA comparison of models, $\chi^2 = 4.26$, $p = 0.51$). R^2_c for the model with no interaction term was 0.76. Treatments had no effect on daily maximum distance from home (ANOVA comparison of models, $\chi^2 = 7.98$, $p = 0.16$). R^2_c for the model with no interaction term was 0.40. Daily distance travelled was not affected by any of the treatments (ANOVA comparison of models, $\chi^2 = 4.30$, $p = 0.51$). R^2_c for the model with no interaction term was 0.44. However, treatments significantly affected the time cats spent at home (ANOVA comparison of models, $\chi^2 = 11.09$, $p = 0.04$). When compared to the control group and the pre-treatment period, cats were located at home significantly more frequently during the treatment period when they were fitted with a bell (rate ratio = 1.29, 95% CI = 1.04–1.58, p = 0.02), provisioned with a grain-free high meat-protein content food (RR = 1.20, 95% CI = 1.00–1.44, p = 0.04) and engaged in object play (RR = 1.24, 95% CI = 1.06–1.56, p = 0.01). Overall, during the treatment period the time cats spent at home was significantly decreased (RR = 0.80, 95% CI = 0.70–0.90). The R^2_c for the model was 0.51.

Table 5.1. Summary of cat ranging behaviour and measures of roaming in a trial of measures aimed at reducing cat predation of wildlife. Measures are summarised for the different treatment groups in the pre-treatment and treatment periods. Home range is the 95% autocorrelated density estimate (AKDE$_{95}$). Core range is the 50% autocorrelated density estimate (AKDE$_{50}$). Time at home is the daily number of times the cats were located inside the house polygon. Median and inter-quartile ranges (25%-75%) are provided for each parameter.

Treatment	Number of cats	Period	Home range AKDE$_{95}$ (ha)	Core range AKDE$_{50}$ (ha)	Daily maximum distance from home (m)	Daily distance travelled (m)	Times at home (active fixes in the house polygon)
Control	17	pre-treatment	2.23 (1.41-2.65)	0.28 (0.16-0.37)	110 (65-167)	1040 (578-1630)	2 (1-6)
		treatment	2.39 (1.64-3.06)	0.35 (0.25-0.42)	113 (67-186)	985 (576-1448)	2 (1-5)
Bell	10	pre-treatment	1.07 (0.49-1.96)	0.17 (0.07-0.26)	77 (42-111)	663 (343-1310)	2 (1-5)
		treatment	0.94 (0.69-1.46)	0.14 (0.09-0.24)	65 (41-98)	585 (284-957)	2 (0-4)
High meat-protein food	15	pre-treatment	1.82 (0.91-2.32)	0.23 (0.13-0.40)	94 (54-137)	943 (564-1363)	3 (1-5)
		treatment	1.52 (0.84-3.14)	0.25 (0.11-0.41)	79 (57-146)	895 (564-1367)	2 (1-5)
Puzzle feeder	8	pre-treatment	2.17 (0.99-2.38)	0.19 (0.13-0.26)	83 (62-151)	853 (515-1170)	3 (1-6)
		treatment	1.51 (0.70-2.03)	0.22 (0.09-0.28)	88 (52-140)	713 (443-1238)	3 (1-4)
BirdsBeSafe collar cover	11	pre-treatment	1.00 (0.57-1.98)	0.13 (0.07-0.28)	89 (59-149)	1061 (717-1329)	3 (1-6)
		treatment	1.09 (0.61-1.78)	0.17 (0.08-0.22)	72 (52-122)	823 (618-1202)	2 (1-4)
Object play	11	pre-treatment	1.10 (0.87-1.65)	0.12 (0.10-0.18)	78 (51-114)	890 (619-1258)	4 (2-7)
		treatment	1.48 (0.75-2.07)	0.17 (0.11-0.21)	91 (60-121)	912 (635-1432)	3 (2-6)
Total	72	pre-treatment	1.48 (0.79-2.36)	0.18 (0.10-0.31)	90 (54-143)	918 (561-1357)	3 (1-6)
		treatment	1.54 (0.76-2.40)	0.22 (0.09-0.34)	85 (55-133)	850 (518-1318)	2 (1-5)
		overall	1.51 (0.76-2.38)	0.20 (0.10-0.33)	89 (55-138)	884 (543-1353)	3 (1-5)

Table 5.2. Summaries of multi-model inference analyses of variation in domestic cat home range size, daily maximum distance from home and daily distance travelled in pre-treatment period. Categorical explanatory variables originally included in all the models were: Outdoor access (baseline-unrestricted), Age class (6-15 years), Sex (male), and Settlement type (city). VIF: variance inflation factors, Estimates: full model-averaged coefficients for explanatory variables, SE: standard error of the coefficient, ∑w: sum of Akaike's weights, N: number of models containing the explanatory variable, Effect size (95% CI): Exponential of estimates and 95% confidence interval.

	VIF	Estimates	SE	∑w	N	Effect size (95%
Home range size (AKDE$_{95}$)						
Outdoor access	1.04	0.56	0.25	1	4	1.75 (1.05-2.90)
Age class	1.03	-0.07	0.15	0.28	1	0.93 (0.69-1.26)
Sex	1.01	0.03	0.11	0.19	1	1.04 (0.83-1.29)
Days of tracking	1.02	0.02	0.09	0.15	1	1.02 (0.86-1.21)
Daily maximum distance from home						
Outdoor access	1.03	0.37	0.15	1	2	1.45 (1.09-1.93)
Age class	1.03	-0.24	0.11	1	2	0.79 (0.63-0.98)
Sex	1.00	0.13	0.13	0.64	1	1.14 (0.88-1.47)
Daily distance travelled						
Outdoor access	1.04	0.26	0.09	1	2	1.30 (1.09-1.56)
Age class	1.04	-0.20	0.07	1	2	0.82 (0.72-0.94)
Sex	1.00	0.11	0.07	0.59	1	1.07 (0.92-1.25)

Table 5.3 Summaries of multi-model inference analyses of variation in prey returned home and time at home in pre-treatment period. Number of prey brought home is the number of individual items brought home and recorded by owners; median recording effort was 49 days (IQR= 48.25-49 days). Time at home is the number of fixes within the house polygon; median number of total daily fixes was 33 (IQR= 22-42). Categorical explanatory variables originally included in both models were: Outdoor access (baseline-unrestricted), Age class (6-15 years), Sex (male), and Settlement type (city). VIF: variance inflation factors, Estimates: full model-averaged coefficients for explanatory variables, SE: standard error of the coefficient, ∑w: sum of Akaike's weights, N: number of models containing the explanatory variable, Odds Ratio (95% CIs): Exponential of estimates and 95% confidence intervals, applied to negative binomial model. Rate Ratio (95% CIs): Exponential of estimates and 95% confidence intervals, applied to Poisson model.

	VIF	**Estimates**	**SE**	**∑w**	**N**	**Odds Ratio (95% CIs)**
Number of prey brought home						
$AKDE_{95}$	1.06	0.07	0.09	0.45	3	1.07 (0.89-1.29)
Outdoor access	1.05	0.12	0.24	0.37	3	1.13 (0.65-1.97)
Age class	1.03	-0.14	0.28	0.29	3	0.87 (0.65-1.42)
						Rate Ratio (95% CIs)
Time at home						
Age class	1.03	0.08	0.13	0.24	1	1.02 (0.88-1.18)
Outdoor access	1.03	-0.10	0.17	0.23	1	0.98 (0.81-1.17)

Discussion

Management of pet cats is often a controversial issue. Cat owners tend to prioritise cat welfare (Crowley et al. 2019; Linklater et al. 2019; Crowley et al. 2020b) and may avoid management interventions that they believe would constrain what they perceive as natural feline behaviours. Other people, primarily concerned about wildlife conservation, strongly advocate keeping cats indoors. Complete confinement clearly eliminates the exposure of wildlife to the hazard of predation by cats and the exposure of cats to hazards encountered outside the home. Despite the reduction in risks to wildlife and to cats arising from confinement, restricting cat roaming behaviour by keeping them partially or permanently confined remains unpopular amongst cat owners in some societies, particularly in the U.K. (Crowley et al. 2019, 2020b). This is culturally variable (Hall et al. 2016a) and the incidence of permanent confinement of pet cats ranges from 35% to 60% (Patronek et al. 1997) in mainland USA, compared to <10% in the UK (Sims et al. 2008) and in Australia (Lilith et al. 2006). This may be related to a perception of greater risks to outdoor cats in the USA, including predation of cats by wildlife (Hall et al. 2016a).

Many cat owners are dismayed by their cats' hunting, and express interest in effective 'cat-friendly' measures to reduce this (Crowley et al. 2019; Linklater et al. 2019; Crowley et al. 2020b). Some mitigation of the risks to wildlife is offered by the use of interventions that can contribute to reducing hunting success. However, uptake of collar-mounted devices by owners generally remains low, due to perceived risks associated with cat safety, device loss and doubts about efficacy (Crowley et al. 2019). Interventions that both reduce the exposure of wildlife to the hazards presented by the cats and the exposure of cats to environmental hazards encountered while roaming, might offer opportunities to increase owner action to reduce depredation of wildlife, even where this was not their primary motivation.

In terms of the spatial extent of cat ranging, our study showed that home ranges of pet cats are remarkably small (Kays et al. 2020). In common with other studies, cat home ranges decreased with age (Hall et al. 2016c; Kays et al. 2020; Castañeda et al. 2019), and were slightly larger in males than females (Kays & DeWan 2004; Thomas et al. 2014). Human settlement type had no influence upon cat spatial behaviour in this study, probably because the towns and villages where the cats in this study lived might all be considered relatively low housing density. As expected, cat home ranges were 75% larger when cats were free to roam outdoors (Metsers et al. 2010; Thomas et al. 2014), similarly maximum distance travelled from home was 45% further and daily distance travelled 30% greater, suggesting that even intermittent confinement of cats would substantially reduce cat roaming. We have also shown that free-roaming cats returned slightly (13% but with high uncertainty) more prey than those restricted at night.

Unfortunately, our study has shown that neither existing management approaches (bells, BirdsBeSafe collar covers), nor the novel approaches (food, object play, puzzle feeders), were effective in reducing cat home range size, maximum distance from home, or daily distance travelled. However, number of times the cats were located at home dropped by around 29% when equipped with a bell, 20% when provided with grain-free high meat protein content food and 24% when engaged in object play. In our associated experimental study, (Cecchetti et al. in press), cats subjected to the dietary and object play treatments brought home significantly fewer prey items, while the use of the puzzle feeders resulted in an increase in number of prey brought home by cats. No discernible effects were detected in the numbers of prey returned by cats with the bell treatment, while cats fitted with the BirdsBeSafe collar cover returned markedly fewer birds.

Cats are obligate carnivores, with a requirement for high levels of protein and no requirement for carbohydrates (Macdonald & Rogers 1984). Animal protein and plant proteins in pet foods vary in terms of bioavailability, digestibility and amino acid profiles (Kanakubo et al. 2015; Zafalon et al. 2020). Although specific guidelines for pet foods are provided, some commercial foods do not meet all the nutrient minima, in terms of fatty acids, amino acids, and minerals (Zafalon et al. 2020). It might be the case that fulfilment of physiological needs afforded by the provision of a new food with high meat-protein content reduced the motivation not just for hunting but also roaming outside, consequently reducing the exposure of wildlife to the direct and indirect hazards presented by cats.

Cat behavioural enrichment within the home has previously been shown to be beneficial for reducing stress, behavioural problems and common diseases in indoor pet cats (Ellis et al. 2013). During hunting, play behaviours are commonly observed (Biben 1979) and hunger increases both predation rate and play motivation in cats (Hall & Bradshaw 1998). Because cats are ‘ambush predators’, and spend large parts of their hunting excursions watching and stalking their prey, it might be that increasing the frequency and regularity of time spent in object play and opportunities for exercising natural behaviours in the home environment can reduce motivation to go outside, again reducing the exposure of wildlife to the direct and indirect hazards presented by cats.

Explaining the effect of bells is harder, though it might be the case that the cat experiences some discomfort or disruption to behaviour, leading it to spend less time mobile and consequently more time inside the house.

We used the same measure of time spent at home before and during treatments and so our paired comparison, alongside a control group, means the effects observed are robust to the likely negative bias in our estimates of time cats spent inside the house. Nevertheless, the reliability of GPS loggers to obtain fixes inside buildings is limited and future investigations might better quantify time spent at home by complementing GPS with additional devices, such as directional transponder systems fitted on cat flaps.

Conclusions

The numbers of prey captured and brought home by cats can be reduced through the use of collar-mounted devices, or through the provision of high meat content food or object play. The same management approaches increase the time cats spend at home, but did not substantially affect their roaming behaviour. Owners wishing to mitigate any risks to their cats associated with their roaming behaviour therefore have limited options. Keep their cats indoors, at least at night, is the best way to reduce the extent of their roaming. High meat protein content food and object play, as well as fitting a bell, increase the time cats spend at home. Owners are able to enrich the home environment if they are concerned about cat aversion to confinement or about restricting cat natural behaviours. Ellis et al. (2013) provide exhaustive guidelines on feline environmental needs and lay out a framework for a healthy environment, ranging from providing hiding places (e.g. cardboard boxes) to opportunities for play and predatory behaviour (e.g. hiding food). Nevertheless, cats that are used to having unregulated outdoor access may struggle to adapt to a life of partial or complete confinement indoors

(Hubrecht & Turner 1997). A pragmatic solution in such cases might be the use of outdoor enclosures, with enrichment by objects that enable the cat to hide, play and exercise (Ellis et al. 2013).

Chapter 6

Personality profiles distinguish domestic cats that capture and bring home wild animal prey

Chapter 6: Personality profiles distinguish domestic cats that capture and bring home wild animal prey

Abstract

In some ecological contexts, predation of wildlife by domestic cats *Felis catus*, combined with their global abundance, is a threat to biodiversity conservation. The predatory behaviour of domestic cats shows remarkable between-individual variation. Many free-roaming cats living as companion animals bring home few or no prey, while others are prolific killers and likely contribute disproportionately to any impacts upon wild animal populations. Recent work has identified five personality factors for cats (“The Feline Five”). We tested whether variation in scores for these five factors allowed discrimination of cats that captured and brought home wild prey and was related to variation in numbers of recorded prey. We recruited owners of domestic cats kept as companion animals in southwest England. Owners completed a questionnaire assessing their cats’ behavioural traits, and recorded prey items brought home by their pets. Cats that hunted and brought home wild prey scored high for ‘extraversion’ or low for ‘neuroticism’, compared to cats that did not bring home wild prey. However, variation in the numbers of prey captured and brought home by hunting cats was not affected by scores for any of the personality factors. Assessing behavioural needs through characterisation of individual personality has the potential to enhance approaches for managing hunting by cats, including approaches that do not compromise cat welfare and effectively reduce predation. For example, extraverted cats can be stimulated and encouraged in physical activity through object play in the home environment decreasing hunting motivation. Cat owners might also be more inclined to adopt strategies that better suit their perceptions of their cat’s personality.

Introduction

Domestic cats *Felis catus* have one of the largest geographical distributions amongst terrestrial carnivores (Baker et al. 2010). Their close relationship with humans has allowed them to reach almost every corner of the globe, including remote islands where they have had significant impacts upon the conservation status of multiple endemic species (Medina et al. 2011). In continental areas, owned and unowned domestic cats also have significant direct and indirect effects upon threatened prey populations (Loss & Marra 2017). The most common approach to attempting to decrease any impacts of feral or stray cats on island wildlife is to eradicate them or to reduce their population size (Cecchetti et al. 2020). Both can be achieved through the use of various methodologies, including lethal and non-lethal methods, that differ in their feasibility, efficacy and welfare implications (Cecchetti et al. 2020). However, in many cases, attempts to reduce populations might nevertheless fail to reduce predation sufficiently. This may, in part, be attributable to the disproportionate predation pressure inflicted by a minority of specialised hunters (Moseby et al. 2015) or problem individuals (Swan et al. 2017). Prey specialization has been detected in cats and attributed to cat sex, age, size and to variation in the personality of individuals (Dickman & Newsome 2015). Thus, approaches to the identification of problem individuals and more targeted approaches to their removal from the population have been advocated (Dickman & Newsome 2015; Wilhelmy et al. 2016).

Individual animals often behave in ways that distinguish them from others of their species. Behavioural patterns can distinguish one animal from others of same sex, age or class (Lowe & Bradshaw 2001), and when such differences are consistently expressed over time, they can be referred to as 'personalities' (Gosling 1998). Among free-roaming pet cats, there is remarkable individual variation in terms of hunting success and strategies (Kays & DeWan 2004; Tschanz et al. 2011; Thomas et al. 2012; Loyd et al. 2013b) and this may also be attributable in part to cat personality. Despite being fed by people, some free-roaming pet cats still kill wild animal prey, and some frequently bring them back to the human household (Lepczyk et al. 2003; Woods et al. 2003; Blancher 2013; Loss et al. 2013; Murphy et al. 2019). Most domestic cats catch few or no prey (Churcher & Lawton 1987; Baker et al. 2005) but a minority are much more proficient and prolific hunters (Kays & DeWan 2004; Tschanz et al. 2011).

Many cat owners perceive their cats as members of their family (Salman et al. 1998), and so, perhaps unlike feral cats on islands, removal of problematic individuals to benefit wildlife is not socially desirable and does not constitute a feasible approach to owned cat management. Confinement indoors or within enclosures, offers an alternative approach, and is often strongly advocated by wildlife conservationists (Mori et al. 2019). However, cat owners often perceive permanent confinement as an impediment to cats expressing their owners' conceptions of natural feline behaviours (Tan et al. 2017; Crowley et al. 2019). Similar perspectives and motivations compromise the uptake of other strategies that inhibit cat hunting, such as collar-mounted devices, including bells, collar covers and bibs (Calver et al.2013; Hall et al. 2016a; Harrod et al. 2016; Crowley 2019). Such devices have each been shown to be at least partly effective in reducing numbers of prey brought home (Ruxton et al. 2002; Nelson et al. 2005; Calver et al. 2007). Recently, examination of the nutritional and behavioural needs of cats has prompted testing of novel management strategies for reducing cats' motivations for hunting (Cecchetti et al. in press). Provisioning of a cat food with high meat protein and low-grain content, and engaging cats in object play, decreased numbers of prey brought home by cats and recorded by householders by 36% and 25% respectively (Cecchetti et al. in press).

Some management strategies might suit some cats because they better align with individual aspects of their hunting behaviour, or their preferences for and specialisation upon particular prey types (Dickman & Newsome 2015). For example, Moseby et al. (2015) advanced the hypothesis that some cats with specific hunting preferences or acuities could be less vulnerable to trapping or baiting. For pet cats, it might also be that some management approaches better suit the owner's perception of the cat's personality, or indeed the owner's own personality (Finka et al. 2019). Tailoring approaches for reducing predation that suit the personality profile of hunter cats, and welfare needs, might therefore find greater acceptance by owners.

The individuality and distinctiveness of cats are strongly apparent to their owners, and can reliably be measured with owner assessments (Gartner & Weiss 2013a). Litchfield et al. (2017) assessed 52 behavioural traits of 2802 cats, rated by their owners. They identified five personality factors, referred to as 'the Feline Five': *Neuroticism* involves being insecure, anxious, fearful of people, suspicious and shy; *Extraversion* includes high scores for traits like active, vigilant, curious, inquisitive, inventive, and smart; *Dominance* reflects bullying, dominant and aggressive to other cats; *Impulsiveness* reflects impulsive, erratic and reckless; and *Agreeableness* includes being affectionate, friendly to people, and gentle (Litchfield et al. 2017). It was suggested that accurate assessment of pet cat personality might help owners to manage individual cats through solutions that optimise their welfare. For example, cats with high scores for extraversion (associated with curiosity, leading to boredom) may need more complex environmental enrichment to avoid boredom in the house (Litchfield et al. 2017). Thus, cats exhibiting this personality type, and most likely low neuroticism (boldness, leading to travelling, exploring) (Litchfield et al. 2017), might also be more interested in hunting wild prey.

To our knowledge there have so far been no investigations of any relationship between cat personality, as perceived by owners, and cat predatory behaviour. Our study investigates whether scores attributed to the Feline Five personality factors could distinguish the personalities of hunting from non-hunting cats, and then explain variation between hunting cats in the numbers of prey captured and brought home.

Methods

Participant recruitment

Cat owners were recruited through social, broadcast and print media across southwest England in two exercises, one carried out in 2017 as part of the ‘Small Cat Project’ a collaborative initiative to further the understanding of domestic cats and community views on their ownership and management; and the other in 2019 as part of an intervention study aimed at testing the efficacy of common and novel management strategies to reduce predation of wildlife by domestic cats (Cecchetti et al. in press). In the first study, cat owners completed a main questionnaire divided into three sections: information on the individual cat (including demographics, outdoor behaviours, hunting, diet and owners' perception of hunting behaviour), on the owner-cat relationship and on owner demographics. A subset of cats (n = 96) in this first study also underwent a GPS tracking study, in which the numbers of prey captured and returned home were recorded over a two-week period. The second study was heavily focused on involving owners whose cats regularly killed wild animals and brought them back home. At the beginning of the intervention trial, participants completed an online questionnaire regarding their cat, comprising details of sex, age, breed, health and behavioural status, feeding and roaming habits. For this study, we selected households in which at least one prey item had been brought home and recorded during two weeks of preliminary surveillance. Cat owners recorded the animals that were killed and brought home to the household for five weeks, before any intervention took place. They regularly uploaded prey records online, identifying the cat responsible for the kill, where possible, or entering “unknown” in case of uncertainty in a multiple cat household, date of finding the item, animal type, species (an identification guide was provided for facilitating species identification), whether prey was alive or dead, and other comments (including days on which they were home or not).

For both studies, cat owners completed a personality questionnaire on their cats based on The Cat Tracker Project Questionnaire (Litchfield et al. 2017), a 52-item measure of domestic cat personality. The survey included specific definitions alongside each item to ensure a uniform understanding of the terms among participants, who were asked to rate the extent to which their cat demonstrated each personality trait along a seven-point Likert scale ranging from ‘not at all’ to ‘very much so’. In the second study, four items (independent, individualistic, eccentric and vocal) that had been excluded from analyses by Litchfield et al. (2017) because they did not contribute to their factor structure, were not recorded in the questionnaire, resulting in scores for 48 of the 52 items. This also helped in reducing questionnaire length, which had been highlighted as a possible limitation of the study (Litchfield et al. 2017).

Statistical analyses

All analyses were conducted using R (R Development Core Team 2018).

Personality factor scores were created for each cat, using the item loadings derived from factor analysis in Litchfield et al. (2017). The salient item loadings for each factor were multiplied by the Likert scale score for each of the 48 survey items for each cat. The resulting values were then summed together to create factor scores for individual cats on all factors of the ‘Feline Five’. For each personality factor, scoring quantiles were categorised into Low (includes score values <25% quantile); Typical (>= 25% and < 75% quantile); and High (>= 75% quantile).

All cats with one or more prey records during the surveys were classified as hunters, while those that did not return any prey were classified as non-hunters (1 when hunter, 0 otherwise). However, some cats that hunt wild prey are less likely to bring home their prey and more likely to eat them *in situ* or leave them in the place of capture (Loyd et al. 2013b; Seymour et al. 2020). Thus, we may incorrectly misclassify some hunting cats as non-hunters and so any observed effects are likely to be underestimates of true relationships between personality and hunting behaviour. We used five generalised linear models (GLMs) with binomial distributions to investigate whether being a hunter, or not, could be ascribed to any of the ‘Feline Five’ personality factors (Neuroticism, Extraversion, Dominance, Impulsiveness, Agreeableness). Fixed effects were the score obtained in each of the personality factors (continuous variable), age class (two levels: 6 months to 5 years, and 6 years to 16 years) and sex. Recording effort was calculated for each cat as the total number of days when owners were active in recording prey and was included as an offset (log(effort)).

The proportion of variance in the dependent variable explained by each model was expressed as Tjur’s R^2 (or coefficient of determination) using the package ‘performance’ (Lüdecke et al. 2020). The models were validated by calculating the percentage of correct classification (CC) and area under curve ROC analyses.

To analyse variation in the total numbers of prey brought home by cats as a function of any of the five personality factors, generalised linear models with a negative binomial distribution and log link were used on the subset of hunter cats, defined as above. Fixed effects were the scores obtained in each of the personality factors (treated as a continuous variable), age class, and sex. Effort was included as an offset, as above.

Results

In the first recruitment, 96 cats completed the survey and had their prey returns recorded. 10 cats were excluded from analyses as owners neglected to score one or more behavioural traits. In the second recruitment, owners of 154 cats completed the personality test. Ten cats were excluded because of missing scores on one or more behavioural traits. Of the 144 cats left, the owners of 76 cats reliably attributed prey items to individual cats and reported their days of recording. Thus, a total of 162 cats (73 females, 89 males) were included in the analyses. 95 cats were between 6 months and 5 years old, and 67 cats between 6 and 16 years (Table 6.1).

The median score for Neuroticism was -2.50 (IQR = -9.35–6.98), for Extraversion was 21.79 (IQR = 17.35–25.34), for Dominance was 9.41 (IQR = 4.61–14.19), for

Impulsiveness was 2.57 (IQR = 0.42–5.62), and for Agreeableness was 10.75 (IQR = 6.83–12.81). 30% of young cats (0.5–5 years) were rated highly for Extraversion (scores >= 25.34 and <= 32.37) while only 18% of older cats received high scores in the same factor (Table 6.1). 32% of young cats were also rated highly for Impulsiveness (scores >= 5.62 and <= 12.21) against 16% of older cats (Table 6.1), indicating that young cats are perceived as impulsive and erratic. 36% of females were scored highly for Neuroticism (scores >= 6.98 and <= 26.11), and so were perceived as more anxious, fearful of people and other cats, compared to males, of which only 15% were accorded high scores for this factor (Table 6.1).
65 cats brought home no prey in a median number of 16 days of recording and were categorised as non-hunters. 97 cats brought home more than one prey item (median = 3 prey; IQR= 1-9) in a median number of 42 days of recording (IQR= 16–49). 40% of non-hunters were rated highly for Neuroticism (scores >= 6.98 and <= 26.11) and low for Extraversion (scores >= 4.62 and < 17.35), while 34% of hunters was scored low for Neuroticism (scores >=-18.75 and <-9.45) and 32% scored highly for Extraversion (Table 6.1, Figure 6.1).

All binomial models performed better (lower AIC) without the variable sex, which was consequently excluded from later analyses. The binomial model including scores for Extraversion among the fixed effects, showed that for one unit increase in the Extraversion score, the odds of being classified as a hunter increased by a factor of 1.08 (95% CI = 1.03–1.12, $p < 0.001$). The model showed 74% correct classification and AUC of 0.80, Tjur's R^2 was 0.15. Conversely, the binomial model including scores for Neuroticism among the fixed effects, showed that for one unit increase in Neuroticism score, the odds of being classified as a hunter decreased by a factor of 0.95 (95% CI = 0.93–0.98, $p < 0.001$). The model showed 68% of CC and AUC of 0.78, Tjur's R^2 was 0.16.

When considering only cats that brought home at least one prey item during the observation period, variation in the numbers of prey captured and brought home was not influenced by scores for any of the personality factors (Figure 6.2). In all models, age class had a significant effect. Older cats tended to bring home fewer prey when compared to younger cats (in all models, cats in the older age class (6–16 years) brought home around 50% fewer prey items, compared to cats of 0.5–5 years).

Table 6.1. Descriptive statistics of distribution of the domestic cat population in age range, sex, type categories, and respective distribution into the five personality factors. For each personality factor, scoring quantiles were categorised into Low (includes score values >=0% and <25% quantiles); Typical (includes score values >= 25% and < 75% quantiles); and High (includes score values >= 75% and <= 100% quantiles). Specifically, for Neuroticism- Low: >= -18.75 and < -9.35, Typical: >-9.35 and <6.98, High: >= 6.98 and <= 26.11; for Extraversion - Low: >= 4.62 and < 17.35, Typical: >17.35 and <25.34, High: >= 25.34 and <= 32.37; for Dominance- Low: >= -0.87and <4.46, Typical: >4.40 and <14.19, High: >= 14.19and <= 25.63; Impulsiveness- Low: >= -4.42 and <0.42, Typical: >0.42 and <5.62, High: >= 5.62 and <= 12.21; Agreeableness - Low: >= -4.62 and <6.83, Typical: >6.83 and <12.81, High: >= 112.81 and <= 15.81. Number of cats and relative percentage falling into each score quantile is reported. L= Low; T= Typical; H= High.

			PERSONALITY FACTORS														
			Neuroticism			**Extraversion**			**Dominance**			**Impulsiveness**			**Agreeableness**		
		N	**L**	**T**	**H**	**L**	**T**	**H**	**L**	**T**	**H**	**L**	**T**	**H**	**L**	**T**	**H**
Age class	0.5-5	95	25	46	24	24	42	29	25	49	21	21	44	30	20	51	24
			26%	48	25%	25%	44%	30%	26%	52%	22%	22%	46%	32%	21%	54%	25%
	6-16	67	16	34	17	17	38	12	16	31	20	20	36	11	21	29	17
			24%	51%	25%	25%	57%	18%	24%	46%	30%	30%	54%	16%	31%	43%	25%
Sex	M	89	26	48	15	18	49	22	24	41	24	21	46	22	18	45	26
			29%	54%	17%	20%	55%	25%	27%	46%	27%	24%	52%	25%	20%	51%	29%
	F	73	15	32	26	23	31	19	17	39	17	20	34	19	23	35	15
			20%	44%	36%	31%	42%	26%	23%	53%	23%	27%	47%	26%	31%	48%	20%
Type	Non-hunter	65	8	31	26	27	28	10	16	29	20	15	33	17	20	31	14
			12%	48%	40%	41%	43%	15%	25%	45%	31%	23%	51%	26%	31%	48%	21%
	Hunter	97	33	49	15	14	52	31	25	51	21	26	47	24	21	49	27
			34%	50%	15%	14%	54%	32%	26%	53%	22%	27%	48%	25%	22%	50%	28%

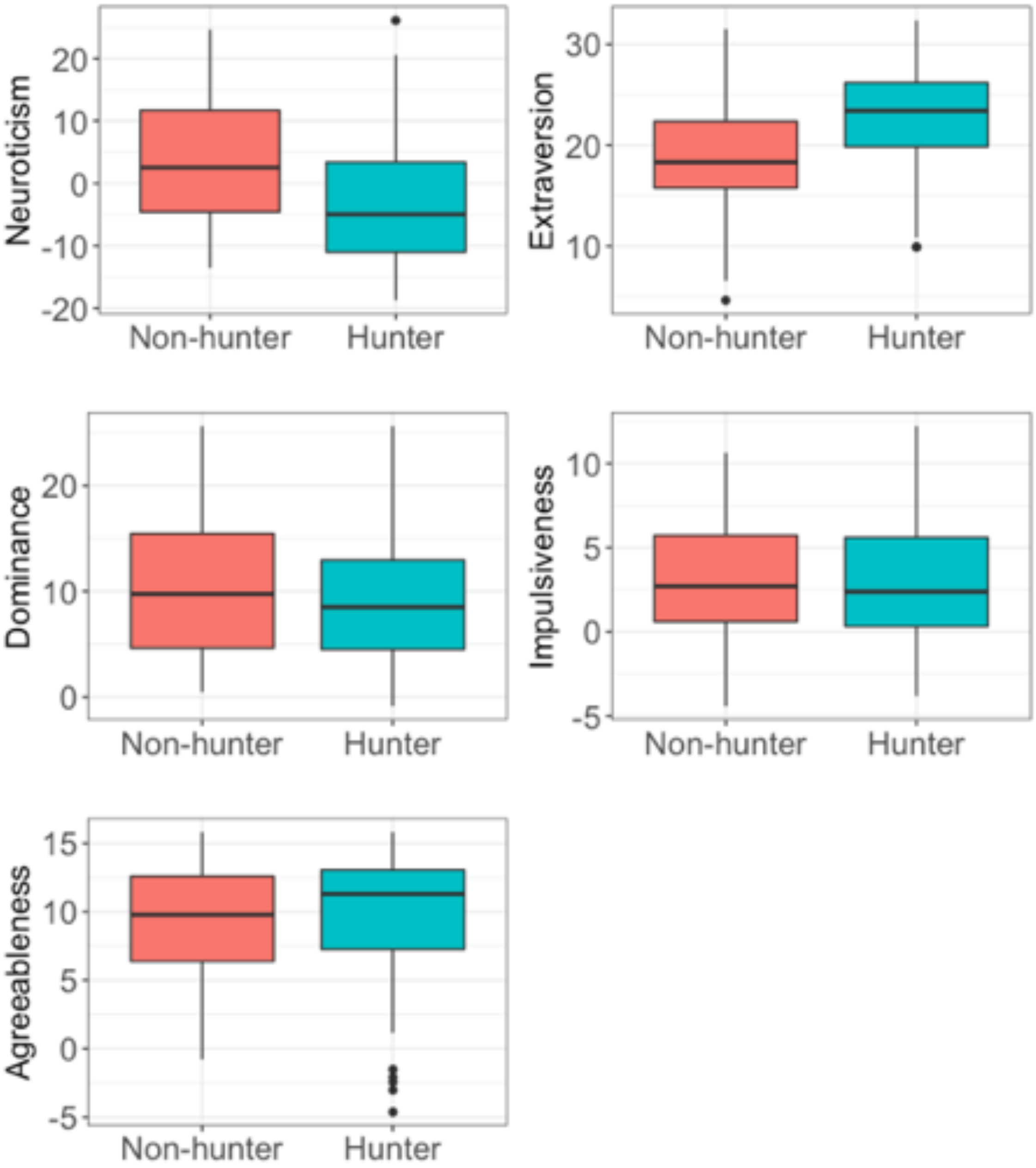

Figure 6.1. Summary scores for the Feline Five personality types in non-hunting (no prey brought home, n = 65) and hunting (at least one prey brought home, n = 97) cats. Each box represents the 25th and 75th percentiles and whiskers represent 1.5 times the interquartile range. Black dots represent outliers.

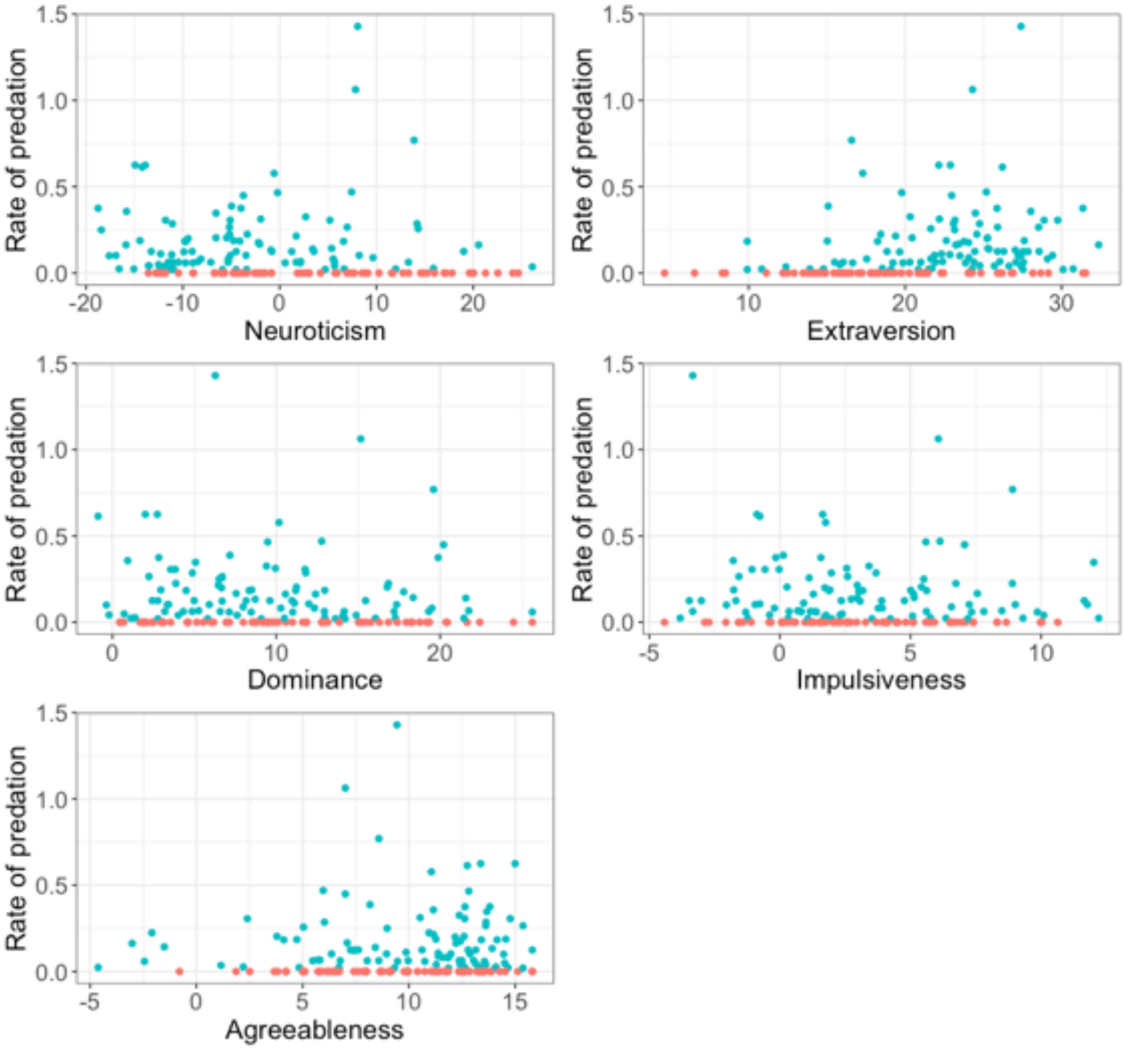

Figure 6.2. Scatterplots illustrating variation in non-hunting cats' scores (pink dots) and hunting cats' scores (light blue dots) for the Feline Five personality types and the rate of predation of wild animals. Rate of predation is the number of prey captured and brought home and recorded by householders, divided by owner recording effort in days.

Discussion

Scores for two of The Feline Five personality types, Extraversion and Neuroticism, as rated by cat owners, discriminated hunting from non-hunting cats. Specifically, cats that hunted and brought home wild animal prey were characterised by higher scores in Extraversion or lower scores in Neuroticism. However, none of the personality factors affected variation in numbers of prey brought home by hunting cats, which instead was largely influenced by cat age, with younger cats bringing home more prey compared to older cats (van Heezik et al. 2010). Hunting by domestic cats is a complex and multifaceted behaviour affected by evolutionary constraints, nutritional requirements, and environmental variation, providing opportunities for varying access to prey (Cecchetti et al. 2020). Standardising such diverse factors in order effectively to evaluate the variance in scale of killing attributable to personality is therefore challenging. However, the scale of killing was clearly not important in profiling cats, and owners were neither asked to rate their cats' personality based on their hunting habits, nor was the survey framed around specific personality traits associated with predation. Nevertheless, the habit of returning home prey was sufficient to make owners perceive differently the personality profiles of hunter and non-hunter cats, probably associating this behaviour with the individual attributes of the cat. A limitation of this study relates to the use of number of prey brought home as approximation of total killing. Indeed, around 20-30% of killed prey is left or eaten *in situ* by domestic cats (Kays & DeWan 2004; Loyd et al. 2013b; Seymour et al. 2020). Thus, variation in prey brought home might not represent a good metric for detecting any influence of personality on hunting behaviour. For the same reason, our classification of hunter/non-hunter may have been subject to misclassification and been different if the non-hunters were observed for longer.

These findings can be framed in the context of cat welfare and management strategies for reducing predation of wildlife. To reduce adverse signs of stress in cats, meet their behavioural needs and to address some common pathologies such as obesity and diabetes mellitus, various behavioural enrichment strategies are recommended (Buffington 2002; Buffington et al. 2006; Ellis 2009). Hunting cats that showed higher scores for Extraversion or lower scores for Neuroticism are most likely to benefit from being stimulated and encouraged in physical activity, and by opportunities to reproduce natural feline behaviour in the home environment. The most common behavioural enrichment strategies include object play with toys that engages cats in a pseudo-predatory activity, and feeding enrichment, for example hiding food, and the use of puzzle feeders (Ellis 2009; Ellis et al. 2013). Management approaches to reduce predation that are focused on feline personality might bring benefits to cat welfare, reduce hunting motivation, and find greater support amongst cat owners, who express interest in effective 'cat-friendly' measures to reduce predation upon wildlife (Crowley et al.

2019; Linklater et al. 2019; Crowley et al. 2020b). Alternatively, owner perceptions of cat personality related to behavioural repertoire, might also explain aversion towards the adoption of some commonly advocated mitigation measures, like permanent confinement (Tan et al. 2017; Crowley et al. 2019), which can be perceived as particularly limiting for highly extraverted cats (Litchfield et al. 2017).

Cat personality can influence both the applicability of management approaches and their effectiveness. Among the emerging explanations for the low uptake by owners in the use of collar-mounted devices are a lack of acceptance by cats and perceived inefficacy at preventing hunting (Crowley et al. 2019). Extraverted or neurotic cats might be particularly likely to exhibit reluctance to wear a collar, and/or collar mounted devices (e.g. bell).

Future studies could be focused upon identifying predation management strategies that might suit specific cat personality profiles and thereafter testing to investigate whether tailored approaches differentially affect predatory behaviour. Effectiveness could be diagnosed in terms of reduction in number of prey returned home coupled with observational studies during hunting excursion (e.g. Dickman & Newsome 2015), as well as through evaluation of changes in owner perception of their cats' behaviour.

Chapter 7

Discussion

Chapter 7: Discussion

Domestic cats share a long-standing history with humans, developed and diversified over thousands of years through a dynamic symbiosis (Zeder 2012a). Nevertheless, compared to other domesticates, they have developed only a few small physiological and behavioural changes from their ancestors, which they still markedly resemble (Driscoll et al. 2009b; Ottoni et al. 2017). While the mutualistic association with humans might have started in favour of proficient hunting activities as pest-controllers, today this legacy is imposing negative pressure on wild animal populations, generating social conflicts. The dual status of the species as both wild predator and domestic companion underpins the division amongst cat advocates, who primarily recognise the domestic side of cats, and wildlife advocates, who focus on their wild side and consequent ecological threats (Crowley et al. 2020a).

In this thesis, I have attempted to tackle the issues related to management of predation upon wildlife by free-roaming domestic cats kept as pets, through a better understanding of the retention of hunting behaviour and enlarging the spectrum of options cat owners might adopt for reducing hunting success, directly or indirectly. Particularly, I have sought to apply an understanding of owners' views, which are often overlooked, to design novel management strategies which reduces hunting motivation without imposing behavioural constraints.

Why do pet cats still hunt?

While hunger is one of the key drivers of hunting, well fed pet cats are still motivated to engage in hunting activities. **Chapter 2** highlights that hunting is driven by evolutionary constraints and the associated hypercarnivorous diet. For instance, cats have an absolute requirement for high levels of protein as source of nitrogen and amino acids (Macdonald & Rogers 1984). During their evolution they have lost the ability to synthetise some essential nutrients, like vitamin A, many water-soluble B vitamins, vitamin D, taurine, arginine and some essential fatty acids (Macdonald & Rogers 1984), which can be found in their wild prey (Bradshaw 2006). Among the management strategies reviewed, enrichment implies an improvement in feline welfare, and is consistent with many strategies aimed at reproducing natural foraging behaviours and engaging cats in play simulations of hunting sequences. Nevertheless, the potential of such strategy had never been tested as means for reducing hunting. Consequently, in **Chapter 3** I attempted to reduce predation rates by working with strategies built upon cats' strict dietary constraints, and on enrichment strategies. The effects of both the provision of high-meat content food and daily object play on the numbers of prey returned suggests that hunting might be related to the need to satisfy some nutritional shortfalls or behavioural motivations. However, stable isotope analysis of cats' whiskers carried out in **Chapter 4** shows that pet cats that regularly kill and bring back prey nevertheless rely almost entirely on pet foods; the low proportion of wild animals consumed seems likely to satisfy micronutrient or amino acid requirements more than macronutrients. This would confirm the already demonstrated inadequacy of some commercial pet foods in meeting all the minimum requirements for some fatty acids, amino acids and minerals (Davies et al. 2017; Brunetto et al. 2019; Zafalon et al. 2020). Hunting might alternatively be disconnected from the eating motivation, as killing might be predominantly driven by strong inherited instincts (Bradshaw et al. 1999) (**Chapter 2**). **Chapter 5** introduces the possibility that cats which feeding/behavioural needs are addressed spend more time at home, and consequently less in roaming activities. Finally, **Chapter 6** suggests that more extraverted cats or those low in neuroticism are likely to exhibit the behaviour of returning prey home. However, personality traits could not reveal further insights regarding the high between-individual variation in number of prey returned home.

Areas for future research

This thesis has identified promising new directions in the management of pet cats. Each driver and facilitator identified in **Chapter 2** represents a starting point for formulating new solutions that not only have the potential to reduce hunting motivation, but also, importantly, take into account cat owners' views, which is essential for effective management.

Following this thesis path, next steps could include research to:

i) Investigate the composition of high-meat content food to distinguish the analytical components that might reduce hunting motivation.

ii) Investigate the combined action of object play and high-meat content food in reducing hunting behaviour.

iii) Identifying predation management strategies that might suit specific cat personality profiles, and thereafter testing to investigate whether tailored approaches differentially affect predatory behaviour.

A broader spectrum of management strategies for reducing hunting and aligning with cat owner priorities

Cats are a ubiquitous and abundant species. Considering that any reduction in killing is a success, and provision of outdoor access is often considered a fundamental, or intrinsic component of cat husbandry (Crowley et al. 2020b), high-meat content food and object-play can be therefore advocated as effective management strategies for reducing killing, and potentially mitigating the pressure of cats on wild populations (**Chapter 3**). The strength and novelty of these strategies relies on reducing the tendency to hunt, rather than impeding hunting. Moreover, they do not involve any safety risks associated with wearing a collar, which often limits the uptake by owners of collar-mounted devices.

Cat owners have diverse perspectives towards the management of their cats' hunting (Crowley et al. 2020b). These novel strategies might be particularly appealing for some types of cat owners, or broaden the options for others. Both high-meat content food and object play suit "Tolerant guardians" who prioritise outdoor access as beneficial for cat welfare, but dislike hunting and express uncertainty over the effectiveness and welfare implications of common interventions (Crowley et al. 2020b). "Conscientious caretakers" prefer their cats to have outdoor access but are highly concerned about their effects on wild prey, particularly birds. They might be advised to use the BirdsBeSafe collar cover, which reduces bird captures and consumption (**Chapters 3 and 4**) and/or to provide high-meat content food (**Chapter 3**). There are few suggestions that can be made to "freedom defenders", a group that includes cat owners whose purpose of keeping a cat is to carry out pest controller duties, as reducing hunting would contradict the primary role of the cat (Crowley et al. 2020b). Nevertheless, should they want to safeguard birds from being captured, they can use the BirdsBeSafe cover collar. A completely opposite view characterises the "concerned protectors", who for safety reasons might be more willing to introduce partial (night-time) or permanent confinement, also bringing benefits to wildlife

(**Chapter 5**). Cat owners might fail to recognise their own cat as a proficient hunter for various reasons, among which the number of prey returned home, and the frequency at which they are delivered. Taking part in ‘citizen science’ studies like ours (**Chapter 3**) that required owners to record prey returned by cats on a daily basis, might be sufficient in helping them realising the existence of problems and inducing them to take action. This may be particularly influential with the “Lasseiz-faire landlords”, who are broadly unaware of the issues regarding cat hunting, but receptive in accepting collar-mounted devices if the problem is recognised. The habit of returning prey home also affects cat how personality profiles are perceived by owners (**Chapter 6**), possibly explaining aversion towards the adoption of permanent confinement, which can be considered particularly limiting for highly extraverted cats (Litchfield et al. 2017); owners of these cats are likely to prefer object play over any other hunting management strategy.

Indirect effects of cats on wildlife, and how these might be addressed by management strategies

The interventions proposed reduce numbers of prey brought home, which directly and positively reduces the direct mortality of wild prey. However, in some ecological contexts, such as urban areas where cats live at high densities (Sims et al. 2008), a reduction in killing might not be sufficient to overcome a more serious cumulative effect (Kays et al.2020), or to prevent severe impacts on vulnerable species.

Another issue of both novel and common predation management strategies is to what extent they can address the negative indirect effects that free-roaming cats have upon wildlife, including transmission of diseases, induction of fear effects, hybridisation and behavioural shifts (Medina et al. 2014). Wearing a belled collar, high-meat content food provision and object play all increase the time cats spend at home (**Chapter 5**), potentially reducing these indirect effects. However, much more effectiveness in reducing roaming activities is achieved by night-time confinement (**Chapter 5**), which, conversely does not reduce number of prey captured (Loyd et al. 2013b). Thus, it is particularly challenging to design management strategies with high efficacy in both reducing killing and indirect effect on wild populations, while still allowing cats to roam outside.

A further and broader environmental impact of domestic cats arises from the production and distribution of food, clothing, toys and other materials, which generate environmental loads that contribute to global warming and climate change (Di Cerbo et al. 2017). Of particular relevance is the dietary ‘ecological paw print’ (Martens et al. 2019), which measures how much biologically productive land is used for companion animals’ food consumption (Martens et al. 2019), and highlights the urgency for more sustainable production. Therefore, advising a high-meat content diet for cats could have much greater negative indirect impacts on wildlife than cats hunting *per se*. However, as briefly suggested in **Chapter 3**, and partially confirmed by the analysis of cats’ diet (**Chapter 4**), a detailed analytical examination of cat foods might provide insights into chemical and nutritional attributes that influence hunting behaviour, and pet food manufacturers could refine their products, adjusting food composition without necessarily adding more pressure to the environments for meeting a higher demand of meat. Enriching plant-based proteins would even make possible a partial or total replacement of animal proteins and lower greenhouse gas emissions (Westhoek et al. 2011), therefore supporting a more sustainable pet food industry, while meeting the nutritional requirements of cats.

A further solution could be opting for an alternative source of meat which disposes of the same protein quality in terms of bioavailability and digestibility as that of livestock animals, but whose footprint is lower. Domestic cats partially consume insects (Seymour et al. 2020) or bring them home (**Chapter 3**). In Australia, insects and invertebrates in general constitute almost 40% of animals consumed by stray cats (Woolley et al. 2020). There have already been advances in the use of insects in pet foods, and insect-based hypoallergenic foods are available for cats suffering from supposed or diagnosed food sensitivity, as well as insect-based snacks (Bosch & Swanson 2020). Multiple studies have evaluated aspects on nutritional quality of various insects’ species, but the impact of long-term feeding on the nutritional status and health in companion animals are still largely unexplored (Bosch & Swanson 2020).

Managing feral cats

While the promotion of hunting management strategies that fulfil behavioural/physiological needs might be universally applied to all owned domestic cats, there are obvious limitations when it comes to feral and invasive animals. Individual-based strategies can be adopted for owned cats living in the socio-cultural context of the UK and similar settings, but are not feasible for feral cats, which tend to be managed at population level (**Chapter 2**). The impact of feral cats is broadly recognised, particularly where they are considered invasive (e.g. Australia), and many countries have initiated feral cat control and eradication campaigns (Robertson 2008). From a human perspective, feral cats represent a slightly different side of domesticates and a special charisma (Jarić et al. 2020) attracts public support for their survival and population persistence (Allen 2018). Therefore, for successful population control, it is essential to engage interested and affected communities where the management needs to take place.

In Australia, feral cats are increasingly perceived as a major threat to the endemic wild fauna (Woinarski et al. 2017) and their management, including lethal methods, is mostly accepted by the public (Travaglia & Miller 2018). The clear distinction among feral, stray and pet cats has been considered a key success in implementing management strategies specific to each cat category (Deak et al. 2019). In other countries, like Europe and the USA, it is both conceptually and practically difficult to distinguish stray and feral cats. The terms stray and feral are often used interchangeably, and feral and stray cats live in mixed colonies, where they receive food and basic care from volunteer caretakers. This lack of clarity around the definition might also reflect the behavioural flexibility of cats, able to switch between states within few generations or even in the course of a lifespan (**Chapter 2**). This continuum may result in a failure to perceive feral cats as a threat to wild fauna and consequently, management is a greater source of public controversy (Loss et al. 2018). Thus, as in the case of pet cats, planning and implementing feral cat management programs depend on the culture of the location and it is vital to choose an approach that is socially acceptable and ecologically effective for the region (Stoskopf & Nutter 2004).

“Domestic-invasive species”, the importance of an interdisciplinary approach

The ecological role and social characterisation of free-roaming cats as invasive species in delicate ecosystems (e.g. islands) is proportionally appropriate to the generally severe impact they impose on wild endemic species (Medina et al.

2011). On the other hand, their global distribution and occurrence wherever humans are, reveals that their characterisation as domestic species is also appropriate to the close and longstanding relationship they have been sharing with us over millennia (Zeder 2012a). This juxtaposition of roles is reflected in several species that persist as both invasive and domesticated species and has clear bearing upon public perceptions and options for management. There is abundant evidence that introduced species cause negative ecological, economic and social impacts (Mooney 2005), nevertheless conflicts surrounded their management can be prolonged and destructive when histories, geographies, politics, knowledge, values and attachments of people to a species are overlooked (Crowley et al. 2017). Therefore, it is of particular importance when planning management strategies to consider the social context as much as the ecological one where the invasive species is located. Best practice will include engaging inclusively with relevant publics and local communities in management and to adopt communications strategies that promote dialogue and are able to respond to concerns (Crowley et al. 2017).

Since we have brought the wild into our human lives, we have not only shaped differently ecosystems but also our culture, and we cannot manage complex and multifaceted problems such as that of invasive species management applying the solely principles of ecology, but experts in social science, in geography and many other disciplines are required to act together to identify, refine and promoting more feasible management tools. The need for an interdisciplinary approach is particularly evident in relation to managing free-roaming cats and this project has successfully shown how when social aspects are considered and evaluated, they lead to beneficial contributions for the focus species, and wildlife.

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