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Review

A critical review of habitat use by feral cats and key directions for future research and management

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Abstract. Feral cats (*Felis catus*) have a wide global distribution and cause significant damage to native fauna. Reducing their impacts requires an understanding of how they use habitat and which parts of the landscape should be the focus of management. We reviewed 27 experimental and observational studies conducted around the world over the last 35 years that aimed to examine habitat use by feral and unowned cats. Our aims were to: (1) summarise the current body of literature on habitat use by feral and unowned cats in the context of applicable ecological theory (i.e. habitat selection, foraging theory); (2) develop testable hypotheses to help fill important knowledge gaps in the current body of knowledge on this topic; and (3) build a conceptual framework that will guide the activities of researchers and managers in reducing feral cat impacts. We found that feral cats exploit a diverse range of habitats including arid deserts, shrublands and grasslands, fragmented agricultural landscapes, urban areas, glacial valleys, equatorial to sub-Antarctic islands and a range of forest and woodland types. Factors invoked to explain habitat use by cats included prey availability, predation/competition, shelter availability and human resource subsidies, but the strength of evidence used to support these assertions was low, with most studies being observational or correlative. We therefore provide a list of key directions that will assist conservation managers and researchers in better understanding and ameliorating the impact of feral cats at a scale appropriate for useful management and research. Future studies will benefit from employing an experimental approach and collecting data on the relative abundance and activity of prey and other predators. This might include landscape-scale experiments where the densities of predators, prey or competitors are manipulated and then the response in cat habitat use is measured. Effective management of feral cat populations could target high-use areas, such as linear features and structurally complex habitat. Since our review shows often-divergent outcomes in the use of the same habitat components and vegetation types worldwide, local knowledge and active monitoring of management actions is essential when deciding on control programs.

Additional keywords: *Felis catus*, habitat selection, home range, introduced predator, invasive predator, predator control.

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Introduction

Invasive mammalian predators have caused or contributed to the decline and extinction of many species worldwide (Salo *et al*. 2007). Examples include the red fox (*Vulpes vulpes*) (Johnson 2006), mustelids (Mustelidae) (King and Moody 1982; Salo *et al*. 2010), rats (*Rattus* spp.) (Jones *et al*. 2008; Capizzi *et al*. 2014) and the domestic cat (*Felis catus*) (Medina *et al*. 2011; Duffy and Capece 2012). Humans have introduced the domestic cat to almost every region of the world and self-sustaining wild populations now exist in a wide variety of landscape types including deserts, forests and tropical to sub-Antarctic islands (Long 2003). Animals in these populations are generally termed ‘feral’, meaning that they are descended from domesticated ancestors but now exist in a free-living state with no direct dependence on humans. Feral cats are distinguished from ‘unowned’ cats (stray or semiferal) in that unowned cats remain dependent on humans for at least the incidental provision of resources such as food or shelter.

Feral cats are almost exclusively carnivorous and generally obtain most of their food resources by hunting live prey (Fitzgerald and Turner 2000). Feral cats are acknowledged as one of the world’s worst 100 invasive species (Lowe *et al*. 2000) and are thought to have been an important contributing factor to at least 14% of bird, reptile and mammal extinctions globally (Medina *et al*. 2011) and at least 16 mammal extinctions in Australia (Johnson 2006). Predation by feral cats can jeopardise conservation programs aiming to reintroduce native fauna into areas of their former range (Moseby *et al*. 2011; Potts *et al*. 2012), and cats can have non-lethal impacts on susceptible populations through competition, disease transmission, induced predator-avoidance behaviour and hybridisation (Daniels *et al*. 2001; Medina *et al*. 2014). Reducing the impacts of feral cats is a priority for conservation managers in Europe (Daniels *et al.* 2001; Sarmento *et al.* 2009), North America (Blancher 2013; Loss *et al.* 2013), Oceania (Medway 2004; Woinarski *et al.* 2011; Garnett *et al.* 2013) and islands worldwide (Keitt *et al.* 2002; Judge *et al.* 2012; Nogales *et al.* 2013).

Substantial effort has been invested in research and management to mitigate the impacts of feral cats in recent years (e.g. Hess *et al.* 2009; Moseby *et al.* 2009; Luna-Mendoza *et al.* 2011). Cats have been eradicated from 105 mostly small islands (IUCN SSC Invasive Species Specialist Group 2012), but unfenced mainland sites generally require sustained control efforts because cats have a high reproductive output and an aptitude for reinvasion (Read and Bowen 2001; Short and Turner 2005). The development of efficient and effective management programs for invasive predators such as feral cats usually requires reliable information about the spatial ecology of the subject species to inform management decisions such as the density at which control devices should be deployed (Goltz *et al.* 2008; Moseby *et al.* 2009) or the geographic scale of control operations (Mosnier *et al.* 2008). Information about habitat use is particularly important for maximising the rate at which pest species encounter control devices such as traps or poison baits (Recio *et al.* 2010; Bengsen *et al.* 2012), designing efficient monitoring programs (Pickerell *et al.* 2014), predicting the spatial distribution of an invasive species' impacts (Kliskey and Byrom 2004) or identifying native fauna populations that are most likely to be threatened by the invader (Gehring and Swihart 2003; Recio *et al.* 2014).

Given the growing recognition of the impact of feral and unowned cats and developments in the technology available to both monitor and control them (e.g. Algar *et al.* 2007; Recio *et al.* 2010; Bengsen *et al.* 2011), it is timely to review the state of knowledge on the habitat use patterns of cats across their broad global distribution. Here, we review experimental and observational studies conducted around the world over the last 35 years that aimed, at least in part, to examine habitat use by feral and unowned cats. The term 'habitat use', as used here, refers to the habitat components and vegetation types that an animal uses, whereas 'habitat selection' refers to the behavioural process that ultimately produce habitat use patterns, and is usually described as preference or avoidance of different habitat components or vegetation types (Johnson 1980; Hall *et al.* 1997). Our aim here is not to provide strict guidelines for research and management of feral cats because this is not feasible or useful, given their global distribution and the wide range of contexts in which they occur. Rather, we seek to establish a conceptual framework that will guide the activities of researchers and land managers in reducing feral cat impacts at a scale appropriate for useful management and research. Specifically, our aims are to: (1) summarise the current body of literature on habitat use by feral and unowned cats in the context of applicable ecological theory (i.e. habitat selection, foraging theory); (2) develop testable hypotheses to help fill important knowledge gaps in the current body of knowledge on this topic; and (3) build a conceptual framework that will guide the activities of researchers and managers in reducing feral cat impacts. Most of the available literature is on feral cats, rather than unowned cats, so we generally refer to them collectively as feral cats throughout.

Methods

We searched Web of Science and Scopus international databases for studies on habitat use by feral and unowned cats with combinations of the following keywords: feral cat, *Felis catus*, stray cat, semi-feral, free-living, habitat use, habitat selection, and home range. To these results, we added any additional studies on cat habitat use that we sourced from reference lists, book chapters and publically available theses. After removing duplicates, we also excluded studies that did not include a component on habitat use by *Felis catus*, and studies that did not include feral or unowned cats, resulting in a list of 27 studies published between 1979 and 2014 (Fig. 1).

The small number of studies available ($n = 27$) meant that a quantitative analysis of observed patterns was not possible. Instead, we examined habitat use within home-ranges and collated information for each study to describe survey methods, observed patterns of irregular habitat use (resulting from apparent habitat preferences or aversions), and any factors that were believed to be responsible for the observed patterns of habitat use. We classified these factors as one or more of the following: none; prey availability; intraguild predation/competition; shelter availability; or human resource subsidies. We also graded the ability of each study to identify those factors responsible for observed patterns using five levels: (1) supposition – no data or references to support contentions; (2) supposition based on casual observation of apparent coincidence, e.g. predators or prey more abundant in one habitat component, but supporting data are not provided; (3) supposition based on casual observation of apparent coincidence and supporting data provided; (4) manipulative study without experimental controls or replicates; (5) manipulative study with experimental controls and replicates.

To describe broad patterns in cat habitat use we recorded the frequency of studies where cats favoured or avoided the following seven broad habitat components within their home ranges: forest (~30–100% tree cover); woodland (~10–30%); shrub/heathland; grassland; riparian areas; infrastructure (farm buildings, urban and industrial areas); and agricultural land (fields, pasture, paddocks and crops). We did not include habitat components that fell outside of these groups and were reported in only one or two studies (e.g. mudflats, swales, refuse dumps, dunes) or habitat components that were too broad or ambiguous for classification (e.g. open areas, small and large remnant patches, adjacent slopes, steep slopes). We did not focus on intrahabitat use (e.g. microhabitats) because few studies recorded information at this resolution and we note that it is difficult to collect such fine-scale information for wide-ranging carnivores like feral cats. Some studies qualified for both avoidance and preference of one habitat component (e.g. favoured deciduous forest and avoided pine forest). These frequencies are for comparative purposes only, as we recognise that preference or avoidance of different habitats depends largely on the availability of other habitat components in a study landscape. All favoured or avoided habitat components are listed in Table 1 as they appear in the studies.

Results

Of the 27 studies reviewed, 74% were solely on feral cats and 11% were a mixture of feral, unowned and owned (pet) cats.

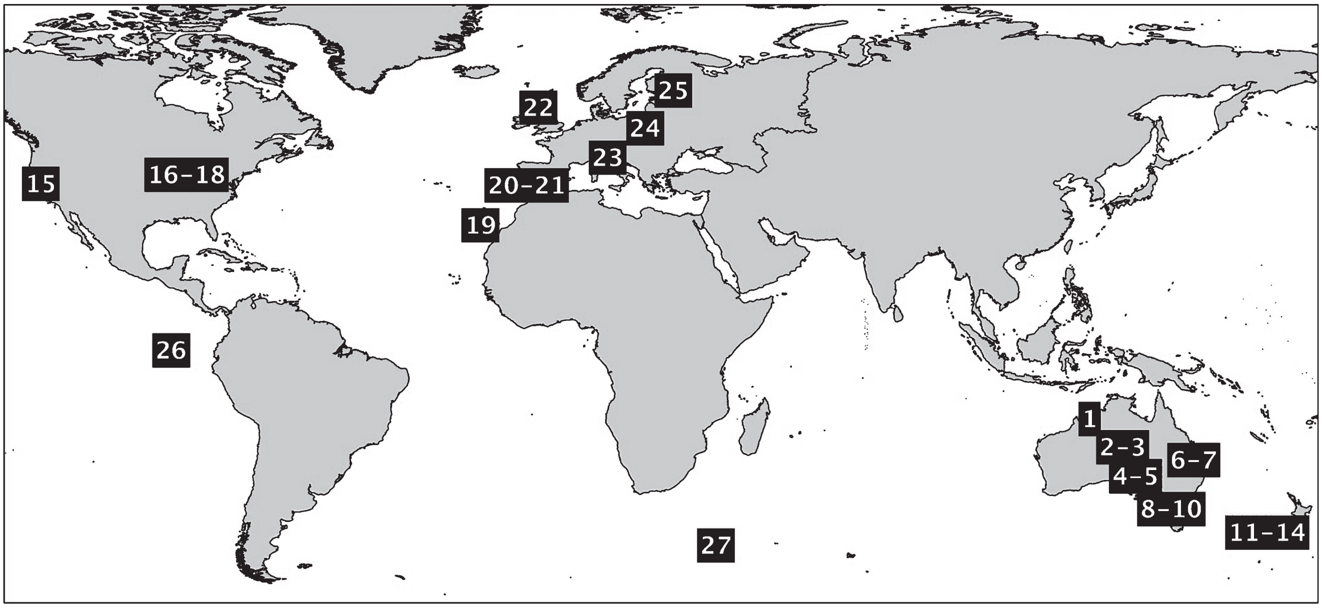

Fig. 1. World map showing the locations of the reviewed studies on habitat use by feral and unowned cats (*Felis catus*). Numbers refer to studies listed in Table 1.

We also included two studies where the group of study animals were a mixture of feral *Felis catus* and the closely related native *F. silvestris*, and two studies that were on unowned cats only. We treated Recio and Seddon (2013) and Recio *et al*. (2014) as a single study because they used the same dataset.

VHF or GPS tracking was used to study cat space use in 70% of studies, with sample sizes ranging from four to 32 animals (mean 13.8 ± 1.8, s.e.). Of the eight studies that did not track individual cats, three used tracking stations with visual or scent-based lures (active tracking stations), whereas the remaining studies used scat counts, visual surveys or passive tracking stations (Table 1). We assume that habitat use patterns identified in these studies represent the results of habitat selection within home ranges.

Patterns of habitat use

In all, 37% of studies were from Australia, 15% from New Zealand, 22% from the UK and Europe, 15% from the USA and one study each from the Galapagos Islands, Canary Islands and Marion Island (Fig. 1). Of the studies, 22% were conducted on islands and the rest were continental. Nine studies had temperate marine/maritime climates, five were Mediterranean, four were warm/hot summer continental, three each were arid or humid subtropical, two had a steppe climate and one had a tundra (sub-Antarctic) climate (Table 1). Around half of the studies (13) were conducted in a mixed landscape of native vegetation and agricultural land and/or urban areas, and the remainder (14) were conducted solely in vegetated/natural areas (Table 1).

The habitat components most commonly reported as being favoured by cats were infrastructure (26% of studies), riparian areas (22%), and agricultural land and shrub/heathlands (18.5% each; Fig. 2). The most commonly avoided habitats were agricultural land (26%) and grassland (11%; Fig. 2). Cats used a diverse range of habitats including but not limited to arid deserts, shrublands and grasslands, fragmented agricultural landscapes, glacial valleys, equatorial to sub-Antarctic islands, urban areas and a range of different forest and woodland types (Table 1). Use of linear features such as tree lines and road verges was recorded in four studies, all of which were conducted in mixed agricultural landscapes, and five studies suggested that feral cats exploit different habitat components to meet different activity requirements, such as hunting or resting.

Strength of inference

Overall, most studies provided weak or no data to support their perceptions about the factors driving habitat use by cats (78% Level 1 or 2) (Fig. 3). 19% of studies provided some data to support their inferences (Level 3), but only one study conducted a manipulative experiment (Level 5). 59% of studies posited that prey availability influenced cat habitat use, but only 20% of those studies provided data to support this idea (Fig. 3). 11% of studies suggested that human resource subsidies influenced cat habitat use and 37% suggested that shelter availability influenced habitat use, but only one provided supporting data (Fig. 3). Predation/competition was put forward as a determining factor by 26% of studies, around half of which provided data to support those inferences: three with data on variation in predator abundance or activity among habitat components and one study that undertook a landscape-scale manipulative experiment with controls and replicates. Five studies made no inferences as to the mechanisms influencing cat habitat use (Fig. 3).

Discussion

Feral and unowned cats occur in a wide range of biomes and climatic zones, within which individual cats may have access to a limited range of macrohabitat components or vegetation types. It is therefore not possible or useful to make

Table 1. Summary information for the 27 studies reviewed here on habitat use by feral and unowned cats (*Felis catus*)

Climates were categorised according to the Köppen-Geiger classification system (Wilkerson and Wilkerson 2010). GOF, goodness of fit; PCA, principal component analysis. Strength of inference rating: (1) supposition – no data or references to support contentions; (2) supposition based on casual observation of apparent coincidence e.g. predators or prey more abundant in one habitat component, but supporting data is not provided; (3) supposition based on casual observation of apparent coincidence and supporting data provided; (4) manipulative study without experimental controls or replicates; (5) manipulative study with experimental controls and replicates. Identification numbers for studies that contained a mix of feral, owned and unowned cats: 15, 23 and 24; a mixture of *F. catus* and *F. silvestris*: 20 and 21; and unowned cats only: 16 and 19. All other studies were conducted on feral cats only

Study #	First author	Year	Location	Climate	Landscape type	Survey type	Analysis	Favoured habitat	Avoided habitat	Hypothesised structuring factors	Strength of inference for structuring factors
1	McGregor	2014	Central Kimberley, Australia	Steppe	Tropical grasslands	GPS tracking	Discrete choice modelling and multimodel inference	Open areas, edges, recently burnt and/or grazed areas, riparian areas and water.	Higher elevations	Prey Predation/ competition	3 2
2	Edwards	2002	Northern Territory, Australia	Desert (arid)	Arid	Passive tracking station	Chi-square GOF	Mulga woodland	Grasslands	Prey Predation/ competition	2 1
3	Mahon	1998	Simpson Desert, Australia	Desert (arid)	Arid	Passive tracking station	Chi-square GOF	Dune crests	–	None	n.a.
4	Moseby	2009	Roxby Downs, Australia	Desert (arid)	Arid	GPS tracking	Compositional analysis	Dunes, creekline	Swales	Prey Shelter	2 2
5	Bengsen	2012	Kangaroo Island, Australia	Mediterranean	Mixed agricultural, island	GPS tracking	Chi-square GOF	Mixed shrub and woodland, woodlands	Low and medium woodlands, open paddocks	None	n.a.
6	Graham	2012	Queensland, Australia	Humid subtropical	Mixed agricultural	Active tracking station	Occupancy	Agricultural land, large remnant edges, roadside verge remnants	Interior of small and large remnant patches	Shelter	2
7	Molsher	1999	Lake Burrendong, Australia	Humid subtropical	Temperate woodlands	VHF tracking	Compositional analysis	Open woodland (landscape scale), grasslands (home-range scale)	Mudflats (both scales)	Prey Shelter Predation/ competition	2 2 5
8	Buckmaster	2012	Gippsland, Australia	Marine temperate	Tall forest	VHF and GPS tracking	Logistic regression	Creeklines	n.a.	Predation/ competition	2
9	McTier	2000	French Island, Australia	Marine temperate	Mixed agricultural, island	VHF tracking	Chi-square	Bushland, roadsides, buildings	Grasslands	Shelter Prey	2 2
10	Hutchings	2000	Angelsea Tip, Australia	Marine temperate	Refuse site, mixed	VHF tracking, spotlighting	Chi-square	Heathland (day), refuse dump (night)	Heathland (night), refuse dump (day)	Shelter Prey	2 2
11	Recio	2010	Tasman Valley, New Zealand	Maritime temperate	Glacial valley and riverbed	GPS tracking	Compositional analysis and Chi-square GOF	Mature riverbed	Adjacent slopes	Shelter Prey	1 2
12	Recio	2013 and 2014	Godley Valley, New Zealand	Maritime temperate	Glacial valley and riverbed	GPS tracking	Logistic regression	Shrub and pasture cover, lower elevations, bare ground on slopes	n.a.	Prey	3

13	Harper	2007	Stewart Island, New Zealand	Maritime temperate	Island	VHF tracking	Compositional analysis	Tall podocarp–broadleaf forest	Sub-alpine shrubland, alpine heath	Shelter Prey	3 3
14	Alterio	1998	Boulder Beach, New Zealand	Maritime temperate	Coastal, mixed agricultural	VHF tracking	Chi-square GOF	Ungrazed areas, dunes	Grazed areas, grasslands	Prey	2
15	Hall	2000	California, USA	Mediterranean	Mixed agricultural	VHF tracking	Chi-square GOF	Riparian, buildings	Annual crops, perennial crops	Shelter Prey	1 1
16	Gehring	2003	Indiana, USA	Hot summer continental	Mixed urban–agricultural	Active tracking station	Logistic regression	Higher canopy cover, lower ground cover, lower diversity of habitat, smaller patch area, greater human development, presence of corridors	Fields	None	n.a.
17	Horn	2011	Illinois, USA	Hot summer continental	Mixed urban–agricultural	VHF tracking	Compositional analysis	Grasslands, forests, industrial areas, row crops (summer only)	Row crops (autumn, winter)	Shelter Prey	2 2
18	Gehrt	2013	Chicago, USA	Hot summer continental	Mixed urban–natural	VHF	Euclidean distance-based selection ratios	Urban land	–	Predation/ competition	3
19	Medina	2007	Canary Islands, Spain	Mediterranean	Island	Scat survey	Kruskal–Wallis	None	None	Prey	2
20	Ferreira	2011	Portugal	Mediterranean	Mixed agricultural	VHF tracking	Compositional analysis	Farms, areas within 200 m of roads, smaller slopes	Steep slopes, areas >200 m from roads, native vegetation	Human resource subsidies. Predation/ competition	2 3
21	Lozano	2003	Iberian Peninsula	Mediterranean	Mountainous	Scat survey	PCA and regression	High rabbit abundance, scrub–pastureland mosaic, high scrub cover and shelter availability	n.a.	Shelter Prey	2 2
22	Daniels	2001	Scotland, UK	Maritime temperate	Highlands	VHF tracking	Compositional analysis	Woodland, stream edge	Pasture, heather	None	n.a.
23	Genovesi	1995	Italy	Humid subtropical	Mixed agricultural	VHF tracking	Chi-square GOF	Arboreal shelter belts, reed thickets, riparian vegetation	Open cultivated fields	None	n.a.
24	Krauze-Gryz	2012	Poland	Marine temperate	Mixed agricultural	Active tracking station	Occupancy	Forest	Open areas	Predation/ competition Human resource subsidies	3 2
25	Holmala	2009	Finland	Warm summer continental	Mixed agricultural	VHF tracking	Wilcoxon signed-rank test	Fields, open areas, young and mature deciduous forest	Mature pine and mixed forests	Human resource subsidies	2
26	Konecny	1987	Galapagos Islands, Ecuador	Steppe	Island	VHF tracking	Contingency table	Lava/shrub	–	Prey	2
27	van Aarde	1979	Marion Island, South Africa	Tundra (sub-Antarctic)	Sub-Antarctic island	Observation	*t*-tests	Coastal habitat types	Barren lava fields	Prey	2

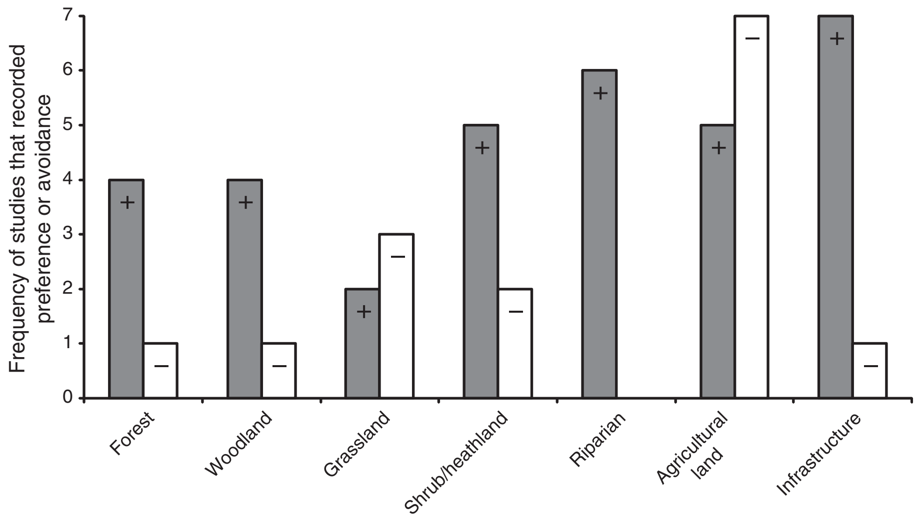

Fig. 2. Frequency of studies where cats favoured (grey bars with + symbol) or avoided (white bars with – symbol) seven broad habitat components: forest, woodland, grassland, shrub/heathland, riparian areas, agricultural land, and infrastructure.

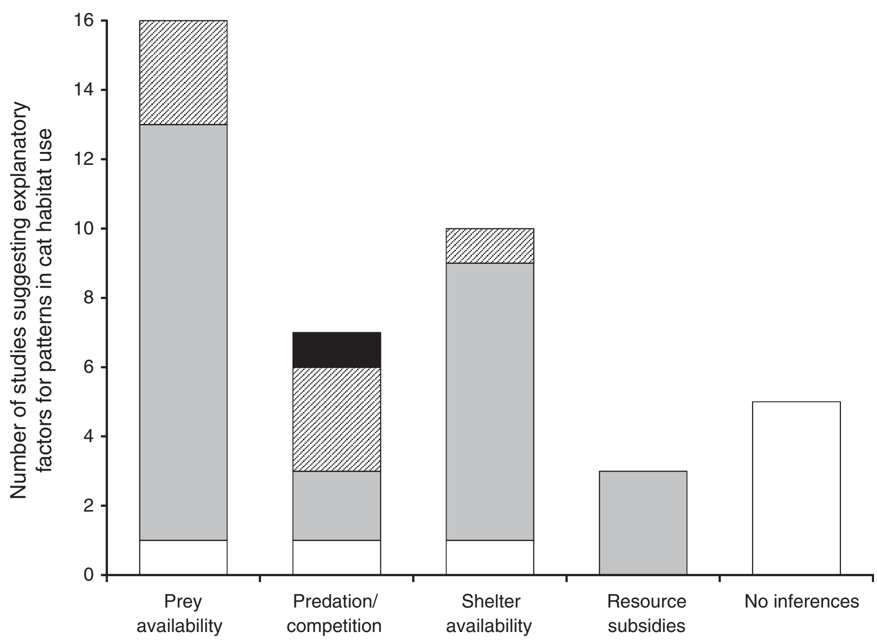

Fig. 3. Frequency of studies suggesting factors that may explain observed patterns in cat habitat use: Level 1 (solid white); Level 2 (solid grey); Level 3 (diagonal stripe); Level 5 (solid black). No studies were classed as Level 4.

broad generalisations about preferential use or avoidance of specific habitat components. However, the combined results of all studies suggest that feral cats generally favour structurally complex habitat components over simpler ones. For example, most studies showed that cats or their sign were more likely to be recorded in vegetation types characterised by a mixture of plant growth forms close to ground level, such as mixed shrublands and woodlands, than vegetation types characterised by an open or homogenous structure, such as mature pine forests or grasslands (e.g. Horn *et al*. 2011; Bengsen *et al*. 2012). Several studies also found that cats were more likely to be recorded at the edges of vegetation patches, or along linear features such as road verges or creeks that traversed patches, than in the patch interior (e.g. Gehring and Swihart 2003; Graham *et al*. 2012; Pastro 2013). Only three studies showed contradictory patterns, in which cats were more likely to be recorded in open country than in structurally complex vegetation. One study in northern Australia found that cats favoured areas characterised by open grass cover and suggested that this was probably due to increased hunting success (McGregor *et al*. 2014). However, that study only considered habitat use by moving cats and discarded data that were deemed to represent cats at rest. A further two studies from Europe found that cats were more likely to be recorded in open country around farm houses that supplied them with food than in native vegetation (Holmala and Kauhala 2009; Ferreira *et al*. 2011), although one of these did show a preference for patch edges over interior (Ferreira *et al*. 2011).

Most studies made inferences based on four mechanisms hypothesised to influence habitat use by feral cats: prey availability; shelter availability; predation/competition; and human resource subsidies. The hypothesised role of prey availability in structuring habitat use is supported by models of predator–prey habitat selection and optimal foraging theory (Pyke 1984; Mitchell and Powell 2004; Börger *et al*. 2008). Flaxman and Lou (2009) posited that predators preferentially use landscape elements associated with either high prey densities (‘prey tracking’), or with high densities of the prey’s resources (‘resource tracking’ – an indirect way of identifying where prey will occur). None of the studies experimentally tested these ideas, although one study (Recio and Seddon 2013; Recio *et al*. 2014) found that feral cat home ranges tended to be concentrated on habitat types characterised by high suitability for rabbits – their key prey species in the area. Intraguild predation and competition can also play a key role in structuring habitat use across a range of marine and terrestrial taxa (Polis and Holt 1992; Ritchie and Johnson 2009), and this may hold for feral cats where they occur with higher-order predators. For example, Molsher (1999) found that cats increased their use of open grasslands (which were thought to be more profitable foraging areas) after the density of foxes using those areas was reduced. Similarly, in an arid environment, Brawata and Neeman (2011) found that feral cats were more likely to be detected close to artificial watering points at sites where dingoes were subjected to lethal control, than at sites where they were not. Other studies have also found that cats were observed less frequently at sites where larger carnivores were more common (Brook *et al*. 2012; Krauze-Gryz *et al*. 2012; Lazenby and Dickman 2013). Temporal segregation between cats and larger carnivores also suggests that intraguild predators can influence the activity times of feral cats (Brook *et al*. 2012; Wang and Fisher 2013). The effect of intraguild predation on habitat use is closely linked with that of shelter availability. Meta-analysis has shown that prey experience less intraguild predation in more structurally complex habitats (Janssen *et al*. 2007), so shelter availability is likely to play a key role in providing feral cats with protection from larger predators, including humans. However, the cases recorded here of humans influencing cat habitat use were all in a positive direction, since all of those studies contained at least some unowned cats that were potentially fed by humans (Holmala and Kauhala 2009; Ferreira *et al*. 2011; Krauze-Gryz *et al*. 2012). Nonetheless, humans could also be considered an apex predator with potentially prohibitive effects on cat habitat use. Hutchings (2000) discussed the possibility of such an interaction for cats at a municipal refuse site, but no study investigated this in detail. Availability of shelter may also provide cats with protection from environmental stressors such as inclement weather (Harper 2007). In reviewing their own results and previous studies, Lozano *et al*. (2003) concluded that cats need two specific habitat types: closed habitats for shelter and resting, and open areas for hunting. In that study, the occurrence of ‘wild-living’ cats (feral *F. catus* and native *F. silvestris*) was positively related to scrub–pastureland mosaics and areas with high rabbit abundance, and microhabitats with high shrub cover and availability of shelter. Similar inferences were made in four other studies (Genovesi *et al*. 1995; Molsher 1999; Hall *et al*. 2000; Hutchings 2000), and we term this ‘behaviourally-stratified’ habitat use.

These general patterns of cat habitat use can be related to the known hunting behaviour of cats. Domestic cats are solitary hunters that rely mainly on sight and sound to detect their prey (Bradshaw 1992). Fitzgerald and Turner (2000) described two primary hunting techniques: ‘mobile’, whereby the cat moves around an area of habitat seeking out prey, and ‘stationary’, where the cat waits at a point of interest, such as the entrance to a rabbit burrow, and ambushes its prey upon appearance. These two techniques aren’t mutually exclusive and both rely heavily on stealth. The general pattern of feral cats using habitats with a mixture of vegetation cover at ground level is likely to improve hunting success by providing cats with a mixture of both cover and open areas in which they can observe, stalk and then ambush their prey. The ‘habitat heterogeneity hypothesis’ also predicts that, in many cases, these areas may support a greater diversity and density of potential prey than more homogeneous habitat components (Tews *et al*. 2004). Edge habitats, linear features, and riparian vegetation are similarly likely to improve hunting success. For example, Pastro (2013) found that feral cats were recorded more frequently at the ecotone between burnt and unburnt grasslands than in continuous areas of habitat. In this regard, dense homogeneous habitats where a cat’s visual detection ability would be compromised are likely to be unfavourable areas for hunting by feral cats. In contrast, McGregor *et al*. (2014) found that feral cats in tropical savannas actively chose areas with high prey abundance that had been recently burnt or grazed and posited that the reduced vegetation cover improved cats’ hunting success. In future, an improved understanding of how habitat use by feral cats is influenced by their hunting behaviour could be achieved by undertaking within-habitat analyses of vegetation composition. This might include consideration of patch structure, edge availability and cover continuity.

The strength of evidence available for factors explaining habitat use was generally low in the studies we examined, with 78% of cases providing little or no data to support their inferences. Most studies examined habitat use using radio-tracking and employed observational or correlative data on other variables to explain these patterns. These types of studies have poor inferential capabilities because they generally involve multiple confounding and interactive explanations for the observed patterns and are hence unable to demonstrate cause and effect. Additionally, few studies acknowledge the limitations of their conclusions. The strongest inferences are gained through ‘classical experiments’, i.e. those that employ treatment and nil-treatment areas and are replicated and randomised, or other types of experiments that lack either replication or randomisation

(Hone 2007). Only one study used this kind of approach (Molsher 1999).

Conceptual model

The low inferential capacity of the studies reviewed here also limits our ability to make generalisations about the mechanisms influencing habitat use by feral cats. However, by drawing on ecological theory and published literature on other medium-sized carnivores, we have been able to propose a conceptual framework for this topic. Such theoretical frameworks have been developed to explain predator–prey habitat use and dynamics (Polis and Holt 1992; Holt and Polis 1997; Heithaus 2001; Rosenheim 2004). For example, game-theoretic models predict that mesopredators should preferentially use habitat that reduces the risk of predation from apex predators, rather than habitat with high prey availability, when dietary overlap between the two predator levels is high and when the apex predators are efficient competitors (Heithaus 2001). Several studies of mammalian predators have reported results consistent with these predictions (Thompson and Gese 2007; Wilson *et al*. 2010), and the same might be expected for feral cats in many situations (e.g. Molsher 1999). However, cats also commonly occur as apex predators, particularly on islands (e.g. Rayner *et al*. 2007), in which case patterns of space use and habitat selection should largely be determined by resource availability (Heithaus 2001). Excluding humans, cats were the top predator in the six island studies reviewed here, and five of those studies asserted that prey and/or shelter availability determined cat habitat use. For example, on Stewart Island in New Zealand, Harper (2007) found that cats preferred to use podocarp–broadleaf forests where shelter from inclement weather was most available, and used the less protective and less preferred subalpine shrubland significantly more on dry days than on wet days.

We developed a conceptual model to explain patterns in cat habitat use (Fig. 4). The relationships that we discuss here warrant further examination, given the speculative nature of this model and the knowledge gaps that we have previously identified. We propose that ecosystem components that influence

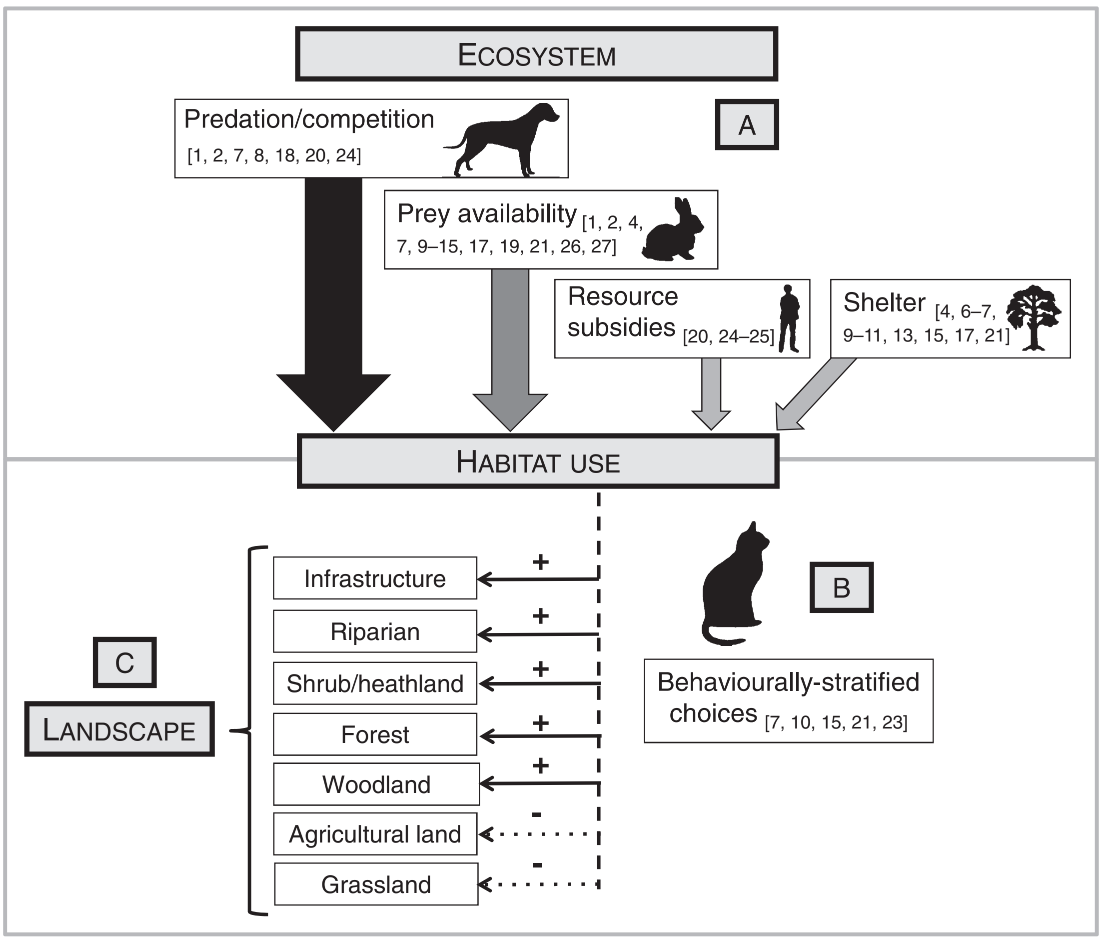

Fig. 4. Conceptual model to describe factors that can potentially influence habitat use by feral cats. Ecosystem components that influence habitat use are hierarchical (A), i.e. predators have a stronger influence than prey, but prey increases in importance where predators are absent. Habitat choices are behaviourally stratified (B) and broad habitat components that cats favour (+) or avoid (–) are nested in the landscape (C). Studies that provide support for or inferences regarding each component are listed using subscripts that correspond to study numbers in Table 1.

habitat use (A in Fig. 4: predators, prey, shelter and resource subsidies) are hierarchically structured, with predation/competition exerting the strongest influence, and other factors increasing in importance where predators are absent (Thompson and Gese 2007; Ross *et al*. 2012). We also expect that habitat choices are behaviourally stratified (B in Fig. 4), with dense habitats used for shelter and more open habitats used for hunting prey (Lozano *et al*. 2003). Broad vegetation types or habitat components that are generally favoured (but not exclusively) include infrastructure, riparian areas, shrub/heathland, forests and woodland, while agricultural land is generally avoided, as are grasslands to a lesser extent (but not exclusively) (C in Fig. 4).

To aid in validating this model, we developed testable hypotheses for further investigation: (1) higher-order predators with a high dietary overlap with feral cats and strong competitive ability will have spatially or temporally prohibitive effects on cat habitat use (Heithaus 2001; Wilson *et al*. 2010; Ross *et al*. 2012); (2) where higher-order predators exclude feral cats from using areas with optimal prey availability, removal of those predators will allow cats to expand their use of optimal prey habitat (Molsher 1999; Prugh *et al*. 2009; Ritchie and Johnson 2009); (3) prey and/or shelter availability will be the most important factors influencing cat habitat use where higher-order predators are absent (Heithaus 2001).

Key directions for future feral cat research and management

Because feral cats occur in a wide range of ecological contexts and show high variability in many population-specific traits, including those related to spatial ecology and habitat use, cat-management programs should be designed to account for site-specific conditions (Dickman *et al*. 2010; Doherty *et al*. 2015). Future research and management to ameliorate the damage caused by feral cats will benefit from an integrated conceptual framework that facilitates the identification, development and evaluation of site-specific management activities. Consequently, in Table 2 we provide a list of key directions that will assist conservation managers and researchers in better understanding and ameliorating the impact of feral cats at a scale appropriate for useful management and research, and we discuss these in detail below.

Apex predators may play an important role in structuring habitat use by feral cats in some cases, but additional research is needed to establish how the strength of this mechanism varies across a range of different systems. Interference competition can have spatially or temporally prohibitive effects on habitat use by cats (Molsher 1999; Krauze-Gryz *et al*. 2012) and, although untested, larger predators might therefore help exclude feral cats from areas inhabited by threatened prey species. Apex predators are declining across the globe (Ripple *et al*. 2014) and loss of top predators can lead to mesopredator release of cats and more intense impacts on native fauna (Crooks and Soulé 1999; Risbey *et al*. 2000), although it is often difficult to clearly attribute causation in mesopredator release studies (Prugh *et al*. 2009; Allen *et al*. 2012). Conservation managers should consider apex predators as a possible tool for ameliorating feral cat impacts (Letnic *et al*. 2012; Ritchie *et al*. 2012), but must also consider potentially conflicting social, economic and other biodiversity conservation concerns (Fleming *et al*. 2012).

Linear features are used by feral cats in fragmented production landscapes, and cats can benefit from fragmentation when native carnivores do not (Crooks 2002). The use of tree lines, road verges and other corridors suggests that control devices could be deployed in these areas to maximise their encounter rate by cats, and hence maximise the efficacy and efficiency of control or monitoring programs (Bengsen *et al*. 2012). However, roads may be less important in arid areas where vegetation contrasts are less extreme (Mahon *et al*. 1998; Read and Eldridge 2010). Since our review shows often-divergent outcomes in the use of similar habitat components or vegetation types worldwide, active monitoring and evaluation of expectations is essential for developing effective and efficient control programs. Also, given that prey availability appears to be an important determinant of cat habitat use, incorporating information on spatial and temporal variation in prey availability should benefit control programs (Christensen *et al*. 2013; Recio and Seddon 2013; Recio *et al*. 2014), particularly in situations where cats are the dominant predator.

Table 2. Key directions for future research and management that aims to understand and ameliorate the impact of feral cats

Management

- Incorporating information on spatial and temporal variation in prey availability should benefit control programs by enhancing the efficiency and effectiveness of control and monitoring activities.
- Control programs should consider the presence of higher-order predators and the effects they may have on habitat use by cats.
- Active monitoring of management actions is essential for the continual improvement of control programs and to ensure that effort is not wasted. Continual improvement may be best achieved by using an adaptive management framework that evaluates assumptions about habitat use by cats and the ability of control activities to impact on the population.

Research

- Research should use experimental approaches and ecological theory to develop and test hypotheses regarding predator–prey dynamics and intraguild interactions.
- The strongest evidence will be gained from replicated landscape-scale experiments where the densities of predators, prey or competitors are manipulated and then the response in cat habitat use is measured.
- As far as possible, studies should:
- Relate habitat use patterns of cats to variability in the abundance or activity of cat prey species and sympatric predators.
- Be conducted over temporal scales appropriate to the study's aims.
- Aim to examine habitat use by feral cats in landscapes that are poorly represented in the existing literature.

Our review has revealed that the standard of evidence available to explain patterns of cat habitat use is generally low. There is a risk that an accumulation of weak evidence will be mistaken for the existence of strong evidence. Given that a sound understanding of the habitat-use patterns of feral cats is often an important precursor to effective mitigation of their impacts, and that most of our current understanding is based on observational studies involving multiple confounding and interactive explanations for observed patterns, there is a clear need for more rigorous approaches to future studies. To adequately address the range of possible explanations, future studies should, where possible, use rigorous, experimental approaches and ecological theory to develop and test hypotheses regarding predator–prey dynamics and intraguild interactions. Also, studies should ideally incorporate information on spatial and temporal variation in the activity or abundance of cat prey species and sympatric predators (Dickman 1996) and be conducted over appropriate temporal scales to account for potential biases caused by changes in predator behaviour or prey and shelter availability (Cruz *et al*. 2013). The spatial and temporal scales needed for such experiments make them expensive and logistically difficult (Glen *et al*. 2007), although not impossible (e.g. Molsher 1999). Studies should also aim to examine habitat use by feral cats in landscapes such as rainforests, salt marshes and alpine habitats, which are poorly represented in the existing literature. An improved understanding of habitat use by feral cats is key to reducing their impact on native species across the globe.

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