



## Factors affecting home range size of feral cats: a meta-analysis

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**Abstract:** Managing invasive species requires knowledge of their ecology, including distribution, habitat use, and home range. In particular, understanding how biotic and abiotic factors influence home range can help with pest management decision-making, as well as informing native species management. Feral cats, self-sustaining cat populations that live independently of people, have caused numerous extinctions and continue to adversely affect native species globally. Managing feral cat populations requires spatially explicit knowledge to enable strategic deployment of management or monitoring devices, understand where native species are most likely to be at risk, and to mitigate the spread of cat-vectored diseases such as toxoplasmosis. Here, we present a meta-analysis of factors that influence feral cat home range size including land use types, differing levels of land use heterogeneity, and numbers of competitors. Male feral cats had larger home ranges than females, but effects of season, competitors, habitat heterogeneity, or land use on feral cat home range were not statistically significant, possibly due to high variability (male cat home range: 22.1 to 3232 ha; female cat home range: 9.6 to 2078 ha). This may reflect the fact that cats are generalists and are able to exploit any opportunity. Thus, we recommend that these factors and others, such as prey availability and composition, should be included in future research, so that the variability in home range size can be better understood. Improved understanding is vital for improving feral cat management in ecosystems where cats have been introduced.

**Keywords:** *Felis catus*, feral cat, invasive species, home range size, meta-analysis, pest animal management

### Introduction

Feral cats (*Felis catus*; defined as self-sustaining cat populations that live independently of people *sensu* Doherty et al. 2015a) occur globally, having been introduced to all continents except Antarctica (Lepczyk & Duffy 2017). They inhabit a diverse range of ecosystems, including urban areas (Mirmovitch 1995; Normand et al. 2019), deserts (Moseby et al. 2009; Johnston et al. 2014), forests (Gillies et al. 2007; Harper 2007) and agricultural landscapes (Langham & Porter 1991; Hansen et al. 2018), and cause biodiversity losses (Medina et al. 2011; Woinarski et al. 2011; Doherty et al. 2015b). Cats also transmit diseases such as *Toxoplasma gondii* to domestic animals like sheep (*Ovis aries*) (Buxton et al. 2007; Dempster et al. 2011), native species such as the North Island kākā (*Nestor meridionalis*), kererū (*Hemiphaga novaeseelandiae*), the North Island brown kiwi (*Apteryx mantelli*) (Howe et al. 2014), and even aquatic species such as Hector's and Māui dolphins (*Cephalorhynchus hectori hectori* and *C. h. mau*) are known to be affected (Roberts et al. 2021). The impact of feral cats on native biodiversity has prompted several eradication and management programmes in areas where they

have been introduced (Algar et al. 2020; Capizzi 2020; Lohr & Algar 2020). Understanding feral cat behaviour, habitat use and movement can increase the success of management by enabling strategic placement of control and monitoring tools (Robley et al. 2008; Moseby et al. 2009; Bengsen et al. 2012). Home range is a key behavioural metric for strategic deployment of devices for management such as placement of traps, baits or monitoring devices required per unit area to optimise detection; however, there is a lack of knowledge about factors that potentially affect cat home range size, such as landscape heterogeneity.

Home range is the area within which an animal moves while carrying out its normal activities such as mating, caring for young, foraging or hunting (Burt 1943). Home range sizes vary among individuals of a species due to a range of factors (McLoughlen & Ferguson 2000), including sex (Bengsen 2016), age (Cederlund & Sand 1994), body size (McNab 1963), season (Mayer et al. 2019), population density (Bengsen 2016), food availability (Saputra et al. 2017), predators (Picardi et al. 2019) and competitors (Mazzamuto et al. 2017). A global analysis showed that feral cat home range was influenced by sex (males having larger home ranges than females), body

size (larger cats have larger home ranges), population density (denser populations associated with smaller home ranges), and productivity of the environment (productive environments associated with smaller home ranges) (Bengsen et al. 2016). Although productivity can give us an indication of feral cat home range size, land use is a more direct way for managers to target specific areas for prioritising feral cat management. For managers, productivity is not likely to be a practical metric for implementation of feral cat management. Feral cats favour structurally complex habitat and use linear features as corridors for movement (Doherty et al. 2015a), so habitat heterogeneity and land use type could affect feral cat home range size. For example, McGregor et al. (2015) showed that cats had smaller home ranges when there was more riparian vegetation present. However, no studies have explicitly examined the influence of landscape heterogeneity on feral cat home range size.

We used a meta-analysis to investigate how variation in home range size estimates for feral cats is affected by: (1) sex, (2) season, (3) the presence or absence of competitors, and (4) habitat heterogeneity and land use. We predicted that: (1) males would have larger home range sizes than females because cats have a polygynous mating system and males move over larger areas to maximise the number of matings (Sandell 1989); (2) cats would have larger home ranges during the breeding season because they would be searching for mates (Sandell 1989); (3) the presence of interspecific competitors would be associated with larger home ranges because of the increased pressure on resources requiring a larger area to find sufficient prey and shelter (Glen & Dickman 2005; Molsher et al. 2017); and, (4) greater levels of landscape heterogeneity would be associated with smaller home ranges because of increased resources and potential hunting opportunities (Tews et al. 2004; Bengsen et al. 2012; Bevanda et al. 2015; McGregor et al. 2015).

## Methods

We collected feral cat home range data by searching the databases Scopus and Web of Science Core Collection (1900 to present) for published studies of feral cats and their home

ranges. We used combinations of the following search terms: ‘feral’, ‘unowned’, ‘*Felis catus*’, ‘cat’, and ‘home range’, ‘spatial use’, ‘movement pattern’, ‘territory’ and ‘utilisation distribution’. Feral cats were defined as being unowned with their needs not explicitly met by humans. Differentiating between stray and feral cats can be challenging as cats can be considered on a continuum between owned and feral (Bassett et al. 2020). Therefore, studies of feral cats in urban environments were included, although authors often noted that the cats were frequenting rubbish dumps and were possibly receiving supplemental food from other human sources. Additional studies found within cited reference lists were added, as well as publicly available theses and reports. Studies specifically researching stray cats or owned cats were excluded. Studies were also excluded if we were not able to determine their location on a map (six studies), if the quality of the satellite imagery viewed in a geographic information system (GIS) meant that the landscape could not be classified (two studies), if they did not use either very high frequency (VHF) or global positioning system (GPS) movement telemetry (two studies), or did not separate the male and female data (one study). Only home range data from adult individuals that had not been desexed were included.

A range of variables were extracted from each study, including the geographic location, season, and sex (Table 1). We determined if competitors were present or absent from a site using information given in the published study or by determining what other animals commonly occur in the area based on iNaturalist records (iNaturalist 2019).

For each study, we recorded which potential predictors of home range were significant ( $\alpha < 0.05$ ). These predictors included demographic factors such as sex, age, and weight, whether the animal was feral or domestic, population density, season, habitat, whether home range was estimated during the day or night, and competitor relative abundance. The land use of each study site was also recorded. These included agricultural land, agricultural land with forests, agricultural land with woodlands and heath, arid, braided riverbed, crops with forest, forest, grassland, grassland with shrubs and woodland, heath, shrub, shrub and grassland, shrub and woodland, urban,

**Table 1.** Definitions of factors that can affect cat home range included in the meta-analysis.

Factor	Definition in model
Land cover	The principal habitat type within a 314 km <sup>2</sup> area of the study (determined by a 10 km buffer around a GPS coordinate given by the study or a central point of the stated study area). These included: Developed – any infrastructure / Forest – continuous / Forest – diffuse / Forest – sparse / Shrubs – continuous / Shrubs – diffuse / Shrubs – sparse / Grassland / Pond/River/Lake / Rock/Gravel/Sand / Crops
Competitor Index	Mammalian predators: present or absent
Season	If it was possible to identify the season in which data were collected, the study was classed into one of two seasons: non-breeding (data collected in autumn and winter) or breeding (spring and summer). If seasonal classification was not possible they were grouped as unclassified.
Home range estimators	100% Minimum convex polygon (MCP) / 95% MCP / 100% Kernel density estimate (KDE) / 95% KDE
Habitat	Principal components (PC) PC1: Braided riverbeds mainly comprising gravel/rock/sand and river/pond/lake and grassland PC2: Urban to peri-urban environments typified by developed infrastructure and crops PC3: Landscapes with varying levels of forest compared to varying levels of shrubs PC4: Landscapes with high levels of continuous shrubs and lower levels of diffuse shrubs
Habitat heterogeneity	Shannon’s Index: calculation based on the proportion of each of the different habitat types in each of the landscapes

urban and crops, urban with crops and forest, woodland, and woodland with heath.

### Home Range Estimation Method

Many studies used multiple methods of home range estimation (Appendix S1 in Supplementary Materials); however, for the meta-analysis we only used the estimation method that was common to most studies to allow for comparison. For example, 100% minimum convex polygon (MCP) was the most common home range estimation method, so if a study had used this method, then the 100% MCP results were used for our analysis. The second most common estimation method was 95% MCP, so if a study had not used 100% MCP but had used 95% MCP then this metric was used. The third most common method was 95% kernel density estimate (KDE), with one other method, 100% KDE, being included in one study. These values were then classified as the home range.

### Season

Due to a low number of studies recording data in autumn ( $n = 2$ ) and spring ( $n = 2$ ), and many studies collecting data across seasons, the seasonal data were combined where possible into a breeding (spring and summer) and a non-breeding (autumn and winter) season. Data that could not be classified as either breeding or non-breeding were grouped as unclassified.

### Land cover

We categorised land cover by creating 10 km buffers to give an area of 314 km<sup>2</sup> around GPS coordinates given by each study (or the midpoint of a study area) (Bengsen et al. 2016). We excluded studies where inadequate information was provided to locate the study area geographically. We manually delineated land cover types using aerial imagery at a scale of 1: 20 000 and calculated the percentage of each land cover type (Table 1). These were chosen as the main land cover types present in the study areas (Table 1). To quantify habitat heterogeneity, Shannon's Index using the natural logarithm was calculated using the proportions of each land use type within the buffer area using the *vegan* package (Oksanen et al. 2018).

A principal components analysis was conducted using the proportions of each land use type to reduce the number of land use variables. We included the first four principal components (PCs) (Table 1) in subsequent modelling because each explained more than 10% of the total variation. We also considered whether the study had been carried out on an island or on the mainland. Studies were classified as islands if they were conducted on sites surrounded by water (excluding the North and South Islands of New Zealand, Tasmania, and mainland Australia).

### Competitor index

Only 8 studies were undertaken in study locations where competitors were absent (Appendix S1) and the variation in home ranges among these studies was high, ranging from 19 to 2083 ha (Appendix S2). These studies were all based on offshore islands from Australia ( $n = 2$ ), New Zealand ( $n = 3$ ), Mexico ( $n = 1$ ), Northern Mariana Islands ( $n = 1$ ), and South Africa ( $n = 1$ ). In studies where competitors were present, competing species included stoats (*Mustela erminea*) and ferrets (*M. putorius furo*) in New Zealand, foxes (*Vulpes vulpes*) and dingoes (*Canis dingo*) in Australia, and coyotes (*Canis latrans*), mongooses (*Herpestes javanicus*) or foxes in North America and Europe. Animals were considered to be competitors if they shared common prey.

### Statistical Analysis

Of the 50 studies found in the literature search, we included 39 in the analysis (Appendix S1). To minimise multicollinearity in the meta-analysis modelling, Pearson's correlations and two-way analysis of variance (ANOVA) and tabulation (contingency tables) were used to test for relationships among the explanatory variables. No strong, significant correlations were observed (correlations were all less than 0.6 and/or  $P < 0.05$ ), so all variables were included in the subsequent meta-analysis modelling. Home ranges were log-transformed to meet normality assumptions (Viechtbauer 2010). Home range estimators were split into: (1) home range and (2) core area, and a regression was conducted using the *metafor* package (Viechtbauer 2010) to determine if there were significant differences between the estimation methods before conducting further analysis. We were unable to conduct a meta-analysis using the core area which was defined as 50% MCP or KDE because only a small number of studies had calculated this ( $n = 11$ ), so analyses proceeded using home range estimations ( $n = 39$ ).

A mixed effects meta-analysis was conducted where the home ranges (response variable) were regressed against season, sex, competitor presence or absence, Shannon's diversity index of habitat heterogeneity, land use (PC1, PC2, PC3 and PC4) as fixed effects, with a unique code for each study as a random effect using the *metafor* package (Viechtbauer 2010). An intercept-only model, a model with each individual factor and home range estimation method as factors, and a full model were compared using Akaike information criterion corrected for small sample size (AICc). The home range estimator was included as a factor because there were significant differences between results of 100% MCP and 95% MCP. All analyses were conducted using R version 3.6.1 (R Core Team 2019).

## Results

### Study locations

The 39 reviewed studies were from six continents, the majority being from Australia ( $n = 15$ ) and New Zealand ( $n = 11$ ) (Fig. 1). Of the remainder, most were from the Americas (USA = 9, Mexico = 1), and one each from Northern Mariana Islands, Italy, and South Africa. For the most part, the studies included in the analysis were carried out with the aim of improving feral cat management (31 studies), although five studies were for the purposes of disease management, while six studies specifically tracked feral cat home range as part of a bait efficacy study or post bait application (Appendix S3).

The majority of studies were in mixed agricultural-forest ( $n = 7$ ), forest ( $n = 5$ ) or woodland ( $n = 4$ ). Most studies were observational and simply measured the home range size of each cat. The effect of sex on home range was tested across all land cover types. Males were found to have significantly larger home ranges in agricultural, agricultural-forest, braided riverbed, forest, shrub, urban, urban-crops, urban-crops-forest, shrub-grassland, and woodland habitats (Fig. 2). The effect of cat weight had also been tested in nine studies across several land cover types (woodland, forest, heath, agriculture, shrub, grassland, urban) but significantly influenced home range size in only two studies from a woodland environment (Fig. 2). The effect of prey abundance had only been analysed in grassland and woodland (one study in each land cover) and was not significant in these cases. The effect of competitor abundance

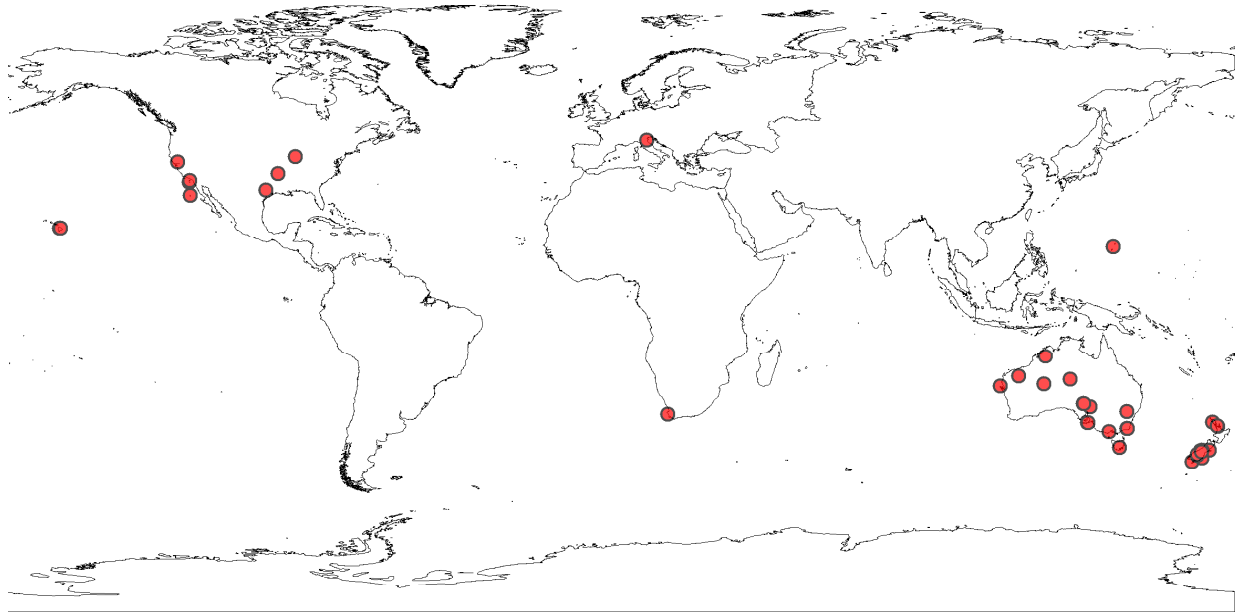


Figure 1. Map of the world showing the location of all the included studies ( $n = 39$ ).

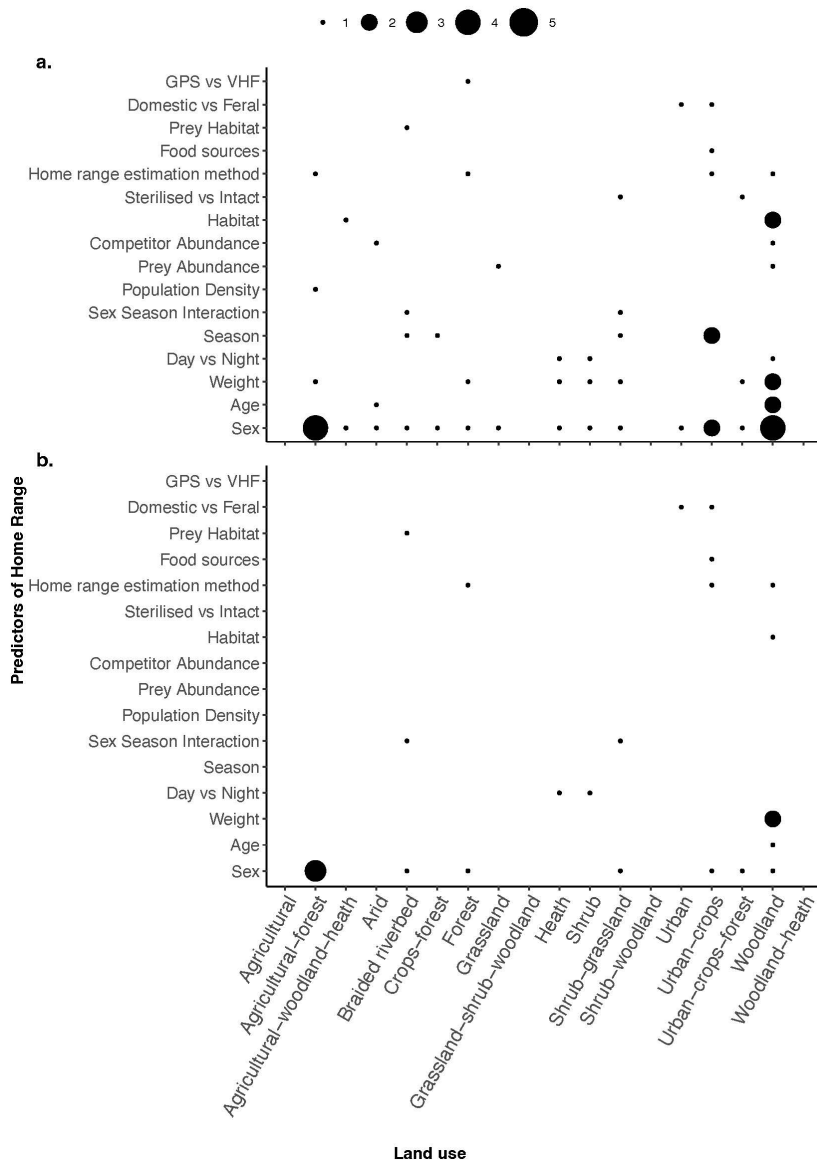


Figure 2. The relative number of studies that analysed (a) and determined to be significant at  $P < 0.05$  (b) the effects of different predictors on home range size across the different land cover types studied (Agricultural ( $n = 1$ ), Agricultural-forest ( $n = 7$ ), Agricultural-woodland-heath ( $n = 1$ ), Arid ( $n = 3$ ), Braided riverbed ( $n = 3$ ), Crops-forest ( $n = 1$ ), Forest ( $n = 5$ ), Grassland ( $n = 1$ ), Grassland-shrub-woodland ( $n = 2$ ), Heath ( $n = 1$ ), Shrub ( $n = 1$ ), Shrub-grassland ( $n = 3$ ), Shrub-woodland ( $n = 1$ ), Urban ( $n = 3$ ), Urban-crops ( $n = 2$ ), Urban-crops-forest ( $n = 1$ ), Woodland ( $n = 4$ ), Woodland-heath ( $n = 1$ )). The total number of studies included was 39.

had been tested in an arid and a woodland environment (one study in each land cover) and was not found to be significant.

**Influence of biotic factors**

*Male and female home range sizes*

Female feral cats had significantly smaller home ranges than males ( $\beta = -1.00$ , S.E. = 0.49,  $P = 0.041$ ; Table 2; Fig. 3). Male cats had home ranges from 22.1 to 3232 ha and female cats from 9.6 to 2078 ha.

*Season*

There were 24 studies with home range sizes that were not classified by season (Appendix S4). Most of the studies that could be classified were done in cooler months when the cats

were unlikely to be breeding. These studies had home ranges varying from 43 to 3232 ha, while the breeding season had ranges from 92.2 to 2093 ha. Given the low sample size (breeding:  $n = 7$  and non-breeding:  $n = 16$  studies), high variability in the seasonal data was unsurprising and there was no significant difference between the breeding and non-breeding seasons ( $\beta = -0.11$ , SE = 0.87,  $P = 0.899$ ; Table 2; Appendix S4).

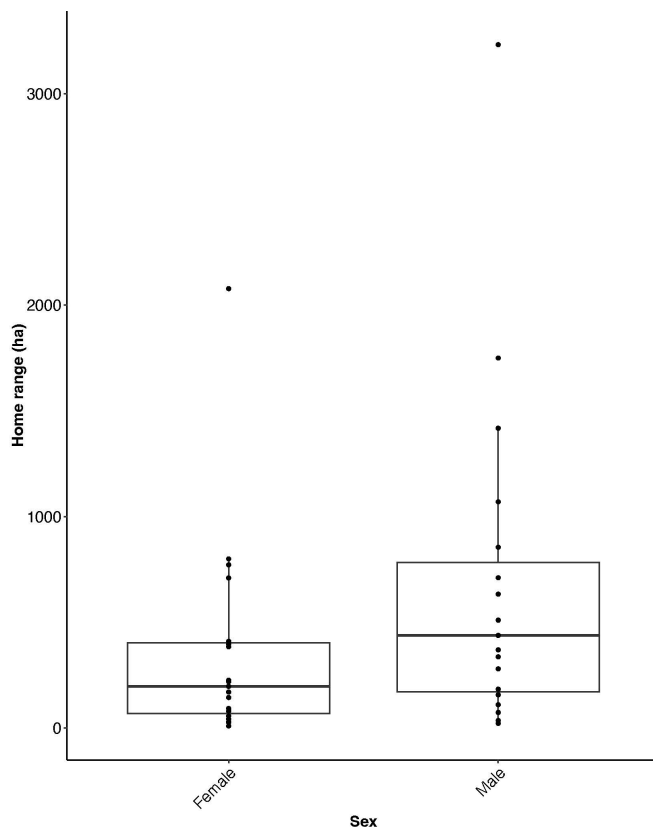
*Competitor presence*

No significant difference was found between home ranges in areas with and without competitors ( $\beta = 0.75$ , SE = 0.65,  $P = 0.245$ ; Table 2; Appendix S2).

**Table 2.** Results from the comparison of mixed effects models with the number of parameters (K), log likelihood (logLik), the deviance, small sample size corrected Akaike’s information criterion values (AICc), the change in AICc relative to the best model ( $\Delta AICc$ ), McFadden’s pseudo R-Squared ( $R^2$ ), Akaike weight ( $w_i$ ).

Models	K	logLik	deviance	AICc	$\Delta AICc$	$R^2$	$w_i$
Sex*+ Home Range Estimator	5	-120.90	18.76	255.19	0.00	0.04	0.32
Null	1	-126.23	29.41	256.64	1.45	0.00	0.15
PC1 + Home Range Estimator	5	-122.03	21.01	257.44	2.25	0.03	0.10
Competitors Present or Absent + Home Range Estimator	5	-122.26	21.46	257.89	2.70	0.03	0.08
Home Range Estimation and Shannon's Index	5	-122.39	21.73	258.15	2.97	0.03	0.07
PC3 + Home Range Estimator	5	-122.50	21.94	258.37	3.18	0.03	0.07
Island or Mainland + Home Range Estimator	5	-122.83	22.61	259.04	3.85	0.03	0.06
PC4 +Home Range Estimator	5	-122.94	22.82	259.25	4.06	0.03	0.05
PC2 +Home Range Estimator	5	-122.97	22.89	259.32	4.13	0.03	0.04
Season + Home Range Estimator	6	-122.58	22.11	261.03	5.84	0.03	0.04
Full Model	13	-118.35	13.64	272.61	11.58	0.06	0.02

\*indicates that the factor was significant in that model ( $P < 0.05$ )



**Figure 3.** Male and female feral cat home range sizes for each of the studies included in the analysis ( $n = 39$ ) using a range of home range estimation methods, 100% MCP ( $n = 22$ ), 95% MCP ( $n = 13$ ), 100% KDE ( $n = 1$ ), 95% KDE ( $n = 3$ ), and data collected from across all seasons; non-breeding ( $n = 14$ ), breeding ( $n = 8$ ) and unclassified ( $n = 29$ ).

### *Habitat heterogeneity*

There was wide variability in habitat heterogeneity, as measured by Shannon's Diversity Index; however, no significant relationship was observed with home range size ( $\beta = -0.39$ ,  $SE = 0.30$ ,  $P = 0.197$ ; Table 2; Appendix S5). The number of habitat types within study areas ranged from 1 to 11 (median = 5).

Only 12 of the 39 studies were conducted on islands, ranging in size from 125 to 10 432 500 ha (median = 43 086 ha). The home ranges of cats on these islands ranged from 19–2083 ha (median = 246 ha) and there was no significant difference in home range size found between studies on an island compared to the mainland ( $\beta = -0.34$ ,  $SE = 0.53$ ,  $P = 0.523$ ; Table 2; Appendix S6).

All four components explained a total of 71% of the variation in the land use data and could be used to broadly differentiate the different land use types. Lower PC1 values characterised braided riverbed environments in New Zealand, while PC1 values around zero were associated with arid or semi-arid land cover in Australia (percentage variance explained 25%; Appendix S7). Lower PC2 values represented studies with higher levels of developed land and crops while larger PC2 values represented studies with greater proportions of diffuse shrubs (percentage variance explained 17%; Appendix S7). Higher values on PC3 represented studies with varying levels of sparse, diffuse and continuous forest, whereas low values on PC3 represented landscapes with high levels of continuous or diffuse shrubs (percentage variance explained 15%; Appendix S7). PC4 showed that studies with high values represented environments with high levels of continuous shrubs and low levels of diffuse shrubs (percentage variance explained 11%; Appendix S7). There were no significant relationships between home range size and any of the principal components ( $P > 0.05$ ; Table 2; Appendices S8–11).

### **Predictors of feral cat home range size**

From the mixed effects meta-analysis modelling, none of the models performed substantially better than the null model ( $\Delta AICc < 2$ ), indicating that, for this dataset, sex, season, and habitat variables were not good predictors of feral cat home range.

### **Discussion**

We show that, although there was a high level of variation in feral cat home range sizes, males had a significantly larger home range size than females. However, no significant differences were found between seasons, habitats, or studies with and without competitors present, suggesting there is no real effect of these predictors on home range. However, the high levels of variation in home range size in feral cats found in our study and others (e.g. Moseby et al. 2009; Bengsen et al. 2012), in addition to the small sample sizes of studies, large differences in study environments and climates, and significant bias toward studies from Australia and New Zealand, could all have contributed to the lack of explanatory power of the meta-analysis model. However, if general patterns in cat home range size are to be discerned, future research should emphasise large sample sizes, consistent and comparable data collection methods, and study designs that distinguish between male and female animals, and account for variation in seasonality and landscape factors. Bengsen et al (2016)

found that larger cats have larger home ranges, and that cats living in more productive habitat have smaller home ranges. Our results suggest that it may be difficult to make further generalisations about what influences home range size of feral cats. Recent research on vertebrate pests suggests that individual-level behavioural variation or "personalities" are likely to play a role and effective management requires taking this into account (Garvey et al. 2020).

There was no effect of habitat type or heterogeneity on home range size. Our result, that habitat type and heterogeneity were not important for home range size, was consistent with previous studies; even when home range differences between different habitats have been directly tested, no significant differences were detected (Bengsen et al. 2012). However, although our results did not show any difference in feral cat home range size related to land cover type or the diversity of the landscape, cats have been shown to prefer habitats that are more structurally complex within their home range (Doherty et al. 2015a). Several studies could not be included in this review due to insufficient information in the paper or a lack of suitable aerial imagery to determine land cover. We cannot rule out that these issues, alongside the high level of variation among cat home range sizes both among and within studies, could have contributed to the lack of effect of habitat observed. Reviewed studies were also biased towards mixed land cover of agriculture and forest, forest, and arid habitats. Several studies assessed land cover within home ranges (Moseby et al. 2009; Strang 2018), but very few have examined the influence of land use at the landscape scale (Bengsen et al. 2012). Feral cat management, particularly trap placement, could be improved with a better understanding of how different habitat types and their configuration are likely to affect home ranges; this is particularly true in environments with changing land cover. The connectivity of the environment could potentially affect feral cat home range size as cats have shown a preference for moving through thicker vegetation cover (Moseby et al. 2009), riparian plantings (McGregor et al. 2015), and along linear features (Doherty et al. 2015a). Further research should test whether this preference is due to greater availability of resources (e.g. food) within those features or due to the reluctance of cats to move through an open landscape. Land cover changes, such as reforestation could also affect habitat use, home range sizes and the way cats move around the landscape, by providing movement barriers or corridors. Future research should consider not only how home range size differs among habitat types, but also how animal behaviour changes. This would provide crucial information for management, such as where devices should be placed, the size of area that should be covered, and whether management practices need to be adapted with changes in environment.

We found no difference in home ranges between islands or mainland areas even though 'island syndrome' can affect animals' morphology, ecology and behaviour (Blondel 2000; Meiri et al. 2005; Cuthbert et al. 2016). Islands can be small in area with scarce resources. Conversely, some islands have a concentration of food resources; for example, due to resource subsidies from marine systems (e.g. Fukami et al. 2006), or the presence of naive prey, such as nesting sea birds or turtles (Hilmer et al. 2010; Ratcliffe et al. 2010; MacLeod et al. 2020). Factors such as prey availability and the level of competition for that prey are likely to influence home range size on islands and this can be crucial for planning pest management on islands.

Competitor species composition differs widely throughout the world, potentially affecting the level of competitive pressure

on feral cats. Although small effects have been observed in some studies (e.g. Moseby et al. 2009), it is likely that competitors can suppress feral cats in some systems (Brook et al. 2012; Kennedy et al. 2012; Moseby et al. 2012). In many island environments, there are no other mammalian predators that can compete with cats (e.g. Harper 2007; Bengsen et al. 2012). In countries such as New Zealand, where the feral cat is the apex predator, its competitors are meso-competitors, such as stoats and ferrets (Norbury et al. 2013; Garvey et al. 2016). In contrast, foxes and dingoes in Australia are competitively dominant over cats (Brook et al. 2012; Moseby et al. 2012; Wysong et al. 2020). North America and Europe have a range of potential competitors such as coyotes and foxes (Phillips et al. 2007; Horn et al. 2011; Shamooin et al. 2017). Due to lack of data available for this review, we were unable to look at relative abundance of competitors; rather, they were classified as present or absent, and there were only eight studies where competitors were absent. Ideally, relative numbers of each competitor or predator species would be documented, and the relative interaction strengths estimated. For example, Strang (2018) investigated the effect of intra-specific competition by measuring changes in feral cat home range after a reduction in population density. Removal of male feral cats led to increased home range sizes of remaining males (Strang 2018).

Future research should also consider the effect of changes in competitor populations, especially if there is the potential for meso-predator or competitor release following pest control (Ritchie & Johnson 2009). Direct and indirect effects are likely to be complex and could occur in Australia with fox control (Mahon 2009) and in New Zealand with the planned “Predator Free New Zealand” programme to eradicate mustelids (Russell et al. 2015). For example, a study that directly measured feral cat home range before and after the removal of foxes (Molsher et al. 2017) observed a weak relationship with age, whereby older cats increased their home ranges following fox removal (Molsher et al. 2017).

Further research on how prey abundance affects feral cat home range size is an important research gap highlighted by this review; prey effects were investigated directly in only four studies and were not measured in a way that was comparable across studies. Invasive predator species freed from biotic constraints of their native habitats can be driven by bottom-up processes (Osenberg & Mittelbach 1996; Russell & Kaiser-Bunbury 2019). In bottom-up driven systems, prey abundance can limit predator populations (Cruz et al. 2013; Norbury 2017) and thus, prey are likely to have an important effect on home range size and habitat use by feral cats (Fitzgerald & Karl 1986). Critically, where prey numbers were reduced experimentally in one study, feral cats dispersed greater distances from their range centre (Norbury et al. 1998). This demonstrates the importance of prey as a potential influence on feral cat behaviour and movement. Other studies did not find a significant relationship between home range size and rabbit (*Oryctolagus cuniculus*) population density (Molsher et al. 2005). Quantifying when and why food availability is a determining factor on home range is critical for decision making in pest management, particularly if key prey species are being controlled. For example, rabbit population management could impact the way feral cats use the landscape. Understanding this and being able to predict changes in feral cat movement are important for feral cat control and for understanding how feral cat movement could impact native species (Courchamp et al. 2000).

Managers need to be aware of the high individual variability

of feral cat home range size when applying research results to feral cat control. Male home ranges are significantly larger than those of females on average, so the sexes should always be distinguished in home range studies. We also recommend that any future work determining feral cat home ranges also measures factors that could influence home range size, such as prey relative abundances.

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## Data availability

The data and code from this article are openly available at <https://github.com/cnot147/Feral-cat-home-range-meta-analysis-code>.

## Author contributions

CMN conceived the idea, data collection, conducted the data analysis and wrote the manuscript. MCS, ASG, BSC and HLB developed the idea, wrote, and edited the manuscript.

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## Supplementary material

Additional supporting information may be found in the supplementary material file for this article:

**Appendix S1.** List of studies that looked at feral cat home range size with the country where the study was carried out, the data collection methods, the data analysis methods, sample size (Females: Males), climate, if competitors are present in the environment, if prey information was provided by the study and if the study was included in our meta-analysis

**Appendix S2.** Feral cat home range sizes where competitors were present or absent ( $n = 39$  studies) using a range of home range estimation methods, 100% MCP ( $n = 22$ ), 95% MCP ( $n = 13$ ), 100% KDE ( $n = 1$ ), 95% KDE ( $n = 3$ ), data collected from across all seasons; non-breeding ( $n = 14$ ), breeding ( $n = 8$ ) and unclassified ( $n = 29$ ) and for male ( $n = 47$ ) and female ( $n = 46$ ) feral cats.

**Appendix S3.** The stated aim of each of the studies included in the analysis

**Appendix S4.** Feral cat home range for when cats were likely to be in breeding or not, or when it was not possible to be classified for each of the studies included in the analysis ( $n = 39$ ) using a range of home range estimation methods: 100% MCP ( $n = 22$ ), 95% MCP ( $n = 13$ ), 100% KDE ( $n = 1$ ), 95% KDE ( $n = 3$ ), and for males ( $n = 16$  [Non-breeding], 7 [Breeding], 24 [Unclassified]) and females ( $n = 15$  [Non-breeding], 7 [Breeding], 24 [Unclassified])

**Appendix S5.** Feral cat home range for the Shannon's Diversity Index ( $n = 39$  studies) using a range of home range estimation methods, 100% MCP ( $n = 22$ ), 95% MCP ( $n = 13$ ), 100% KDE ( $n = 1$ ), 95% KDE ( $n = 3$ ), data collected from across all seasons; non-breeding ( $n = 14$ ), breeding ( $n = 8$ ) and unclassified ( $n = 29$ ) and for male ( $n = 47$ ) and female ( $n = 46$ ) feral cats. The diversity index was calculated based on land use heterogeneity.

**Appendix S6.** Feral cat home range sizes either on islands ( $n = 12$  studies) or the mainland ( $n = 27$  studies) using a range of home range estimation methods, 100% MCP ( $n = 22$ ), 95% MCP ( $n = 13$ ), 100% KDE ( $n = 1$ ), 95% KDE ( $n = 3$ ), data collected from across all seasons; non-breeding ( $n = 14$ ), breeding ( $n = 8$ ) and unclassified ( $n = 29$ ) and for male ( $n = 47$ ) and female ( $n = 46$ ) feral cats.

**Appendix S7.** The loadings of each of the land cover variables for each of the principal components. PC1, PC2, PC3 and PC4 were included in the model.

**Appendix S8.** Feral cat home range for PC1 ( $n = 39$  studies) using a range of home range estimation methods, 100% MCP ( $n = 22$ ), 95% MCP ( $n = 13$ ), 100% KDE ( $n = 1$ ), 95% KDE ( $n = 3$ ), data collected from across all seasons; non-breeding ( $n = 14$ ), breeding ( $n = 8$ ) and unclassified ( $n = 29$ ) and for male ( $n = 47$ ) and female ( $n = 46$ ) feral cats

**Appendix S9.** Feral cat home range for PC2 ( $n = 39$  studies) using a range of home range estimation methods, 100% MCP ( $n = 22$ ), 95% MCP ( $n = 13$ ), 100% KDE ( $n = 1$ ), 95% KDE ( $n = 3$ ), data collected from across all seasons; non-breeding ( $n = 14$ ), breeding ( $n = 8$ ) and unclassified ( $n = 29$ ) and for male ( $n = 47$ ) and female ( $n = 46$ ) feral cats

**Appendix S10.** Feral cat home range for PC3 ( $n = 39$  studies) using a range of home range estimation methods, 100% MCP ( $n = 22$ ), 95% MCP ( $n = 13$ ), 100% KDE ( $n = 1$ ), 95% KDE ( $n = 3$ ), data collected from across all seasons; non-breeding ( $n = 14$ ), breeding ( $n = 8$ ) and unclassified ( $n = 29$ ) and for male ( $n = 47$ ) and female ( $n = 46$ ) feral cats

**Appendix S11.** Feral cat home range for PC4 ( $n = 39$  studies) using a range of home range estimation methods, 100% MCP ( $n = 22$ ), 95% MCP ( $n = 13$ ), 100% KDE ( $n = 1$ ), 95% KDE ( $n = 3$ ), data collected from across all seasons; non-breeding ( $n = 14$ ), breeding ( $n = 8$ ) and unclassified ( $n = 29$ ) and for male ( $n = 47$ ) and female ( $n = 46$ ) feral cats

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