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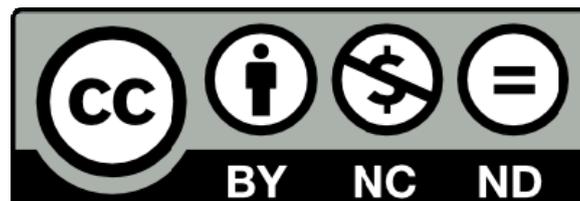
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Factors determining the home ranges of pet cats: A meta-analysis

Catherine M. Hall^a, Kate A. Bryant^a, Kathy Haskard^b, Taryn Major^b, Sarah Bruce^b, Michael C. Calver^{a,·}

^a Environment and Conservation Cluster, School of Veterinary and Life Sciences, Murdoch University, Murdoch, Western Australia 6150, Australia

^b Data Analysis Australia, PO Box 3258, Broadway, Nedlands, Western Australia 6009, Australia

Abstract

Roaming pet cats *Felis catus* are a significant conservation issue because they may hunt, harass and compete with wildlife; spread disease, interbreed with cats in feral populations, and hybridise with wild native felids. Studies of the roaming behaviour of pet cats are often hampered by modest sample sizes and variability between cats, limiting statistical significance of the findings and their usefulness in recommending measures to discourage roaming. We resolved these difficulties through meta-analyses of 25 studies from 10 countries involving 469 pet cats to assess the influence of sex, whether a cat was desexed and housing density on roaming. A complementary linear mixed models approach used data on 311 individual animals from 22 studies and was also able to assess the influence of age and husbandry practices on roaming. This restricted sample gave greater statistical power than the meta-analyses.

Meta-analyses found that: male pet cats had larger home ranges than females, desexing did not influence home range, and cats had larger home ranges when housing densities were low. The linear mixed models supported those results. They also indicated that animals ≥ 8 years old had smaller home ranges than younger cats. Cats fed regularly, provided with veterinary care and socialised with

humans had similar home ranges to cats living in association with households but not provided for in some of these ways. Short of confinement, there is no simple measure owners can adopt to reduce roaming by their cats and prevent the associated environmental problems.

Keywords: Pet cats; *Felis catus*; Wildlife protection; Home range

1. Introduction

Wandering pet cats (*Felis catus*) (those closely associated with a household providing food and other needs (Baker et al., 2010)) hunt wildlife (Baker et al., 2005; Kauhala et al., 2015), transmit diseases to people and wildlife (Lepczyk et al., 2015), compete with other predators (George, 1974), reduce the reproductive success of prey species by fear of predation (Beckerman et al., 2007) or causing prey to display defensive behaviour that attracts other predators (Preisser et al., 2005), reduce the genetic integrity of wild felids by hybridising (Beaumont et al., 2001), and contribute to feral populations by interbreeding or abandonment of kittens (Jongman, 2007). There are also concerns about unrestrained roaming because of risks to cat welfare (Egenvall et al., 2009; Loyd et al., 2013).

Research on relationships between the home ranges of pet cats and their impacts on wildlife give ambiguous results. Hansen (2010) and van Heezik et al. (2010) concluded that home range did not influence the number of prey caught, but Meek (2003) and Morgan et al. (2009) found a greater diversity of prey in pet cats with larger home ranges. Nevertheless, concern about pet cats entering nature reserves or remnant native vegetation led Lilith et al. (2008) and Metsers et al. (2010) to use data on roaming behaviour to recommend buffer zones around sensitive habitat to protect against cat incursions. Concern amongst owners fuels interest in commercial deterrents for predatory behaviour (Calver et al., 2007; Hall et al., 2015; Nelson et al., 2005; Willson et al., 2015), which might act in part by curtailing roaming behaviour (Hall et al., 2016b). Reduced roaming should also restrict opportunities for other problems such as disease transmission or encounters that could change prey behaviour through fear of predation, but we are unaware of relevant data.

Despite the uncertainty about the relationship between roaming and impacts on wildlife, under the precautionary principle the plausibility that restricting roaming might protect wildlife justifies attempts to reduce roaming while the uncertainty is resolved (Calver *et al.*, 2011). Surveys this century indicate that many owners are reluctant to confine their cats to protect wildlife (Grayson *et al.*, 2002; Hall *et al.*, 2016a; Lilith *et al.*, 2006; MacDonald *et al.*, 2015; Thomas *et al.*, 2012) but there might be other husbandry approaches such as desexing or confining only younger animals that might be more acceptable. A better understanding of the influence of factors such as age, desexing, sex, habitat variables such as housing density, and husbandry on roaming behaviour are important topics, because they might indicate practices owners could adopt or regulators could encourage to reduce roaming.

One of the primary difficulties in assessing influences on roaming behaviour is the substantial variation between individual cats (e.g. cats in Lilith *et al.* (2008) had home ranges (95% MCP) between 0.01 and 2.54 ha, while cats in Hall *et al.* (2016b) had home ranges (95% KDE) between 0.20 and 20.00 ha), causing difficulty in obtaining large enough sample sizes to reach statistically significant conclusions in the face of these variations. For example, several studies on pet cats report larger home ranges for males than females but no statistically significant difference between the two (Kays and DeWan, 2004; Lilith *et al.*, 2008; Morgan, 2002; Thomas *et al.*, 2014), while others do report a significant difference (Corbett, 1979; Liberg, 1980; Schär and Tschanz, 1982). Sample sizes, husbandry of cats, whether the animals were desexed or entire, and possible interactions between these factors might all influence findings. In sum, Kays and DeWan (2004) observed that influences on cat roaming are not well understood, both at the level of individual cat's characteristics such as sex and at the level of environmental factors such as housing density, although better understanding could improve management of cats for wildlife protection.

We sought to overcome these difficulties through meta-analyses of the available data, concentrating on the influence of sex, age, desexing, husbandry practices and housing density on home range. Based on the results, we offer suggestions for managing the roaming of pet cats.

2. Materials and methods

2.1. Selection of studies

We attempted to find every study that had analysed the home ranges of pet cats. In order to find studies we searched for key words (various combinations of pet, farm, domestic, cats, home range, roaming, wandering) in the Keywords + titles + abstracts in the journal database Scopus. All results were carefully checked for data on cat home range. Scopus does not claim to have complete data prior to 1996, so to locate earlier studies and grey literature such as theses we checked the reference lists of all the papers that either tested for cat home range or referred to studies that did. We continued to do this with any new papers until no new references were found. In the case of theses we attempted to contact the library of the relevant university if the thesis was unavailable online, but unfortunately some had been lost.

Estimates of home range are sensitive to variations in methods, especially the time periods involved and the density of location data. We included studies that used radio-tracking (17) or GPS collars (8) to determine home range. We excluded studies that used observational data only because cats could often not be seen, leading to underestimates of home range.

2.2. Study variables

We attempted to find the home range, living conditions (husbandry), age, sex, and breeding status (desexed or entire) for each individual cat in each study. Sometimes this was provided in text or in supplementary material, but for other studies we contacted the authors of the papers or found a relevant thesis with additional information. Information on individual cats was found for 22 of the 25 studies ultimately included.

We considered, but ultimately did not include, numerous other predictor variables including detailed descriptions of the habitat and more details on the study methods (e.g. GPS vs radio-tracking) because of considerable variation in the information reported and because including many predictor variables relative to sample size in statistical models risks overfitting (Anderson, 2008). Instead, we included

individual studies as a variable in analyses and regard habitat and methodological effects as part of the variability within studies.

2.2.1. Home range

For some papers only figures of the home ranges were provided and these were analysed with Assess 2.0 image analysis software (Lamari, 2015). Assess 2.0 was developed to determine the area of diseased tissue in plant leaves, so it is readily transferrable to measuring other irregular 2D shapes such as home range. In instances where multiple home ranges were provided for a single cat (e.g. nocturnal and diurnal home ranges or seasonal home ranges) the largest home range for each cat was chosen as a representation of the most extreme possible scenario. All home ranges, irrespective of whether or not authors had demonstrated that home range estimates had plateaued, were included because authors were not always clear on this point (an important reason for including individual studies as a random factor in analyses).

The home range data provided by each study varied in how they were recorded because preferred methods of determining home range have changed over time. They included 100% minimum convex polygons (100% MCP), 95% MCP and 95% Kernel density estimates (95% KDE). For analysis, a single measure of home range in hectares (HR in tables and equations) was defined which used the 95% KDE where available, with the 95% MCP or 100% MCP used where 95% KDE measurements were not given.

2.2.2. Living conditions

These embraced two variables: the husbandry methods used by owners and the housing density where the cats were living. On the basis of husbandry, we distinguished between pet cats and farm cats. Refining the definition of Baker et al. (2010), pet cats were those that belonged to a household and were fed at least daily. They received veterinary treatment when required and had a close relationship with their owners. In the included studies, they often lived in single-cat households and very rarely did more than three cats live in one household. Cats from the same household were sometimes related (i.e. sibling or parent/offspring), but were often living with unrelated cats. Farm cats lived on farms

and were usually kept to catch rodents in farm buildings. They were fed regularly (at least daily), but were unlikely to receive veterinary treatment and lived in farm buildings rather than the house. We chose to include farm cats because we wanted to determine if there were any differences in home range based on husbandry practices and not just housing density. Farm cats were also much less likely to be desexed and therefore sex differences and the effect of desexing could be better analysed. We did not include studies that analysed the home range of stray or feral cats that lived on farms unless they also included data for pet or farm cats. Farm cats tend to live in groups of related cats.

With regard to housing density, where possible cats were described qualitatively as rural (pet cats living in non-urban areas of low housing density), farm (rural cats not allowed access to human habitation but living on farm and regarded as owned) and urban (pet cats living in cities or their suburbs with higher housing density than rural). All classifications were based on the information provided by authors in text, which was mostly inadequate to quantify housing density more precisely. Housing density may actually function as a surrogate for cat density, but it can be measured more readily.

2.2.3. Age

It was decided that a categorical measure of age was sufficient for analysis purposes, because this allowed us to accommodate age ranges given in some papers. Cats were classified as “young” if < 2 years old, “adult” if at least 2 years old but < 8 years old and “mature” if at least 8 years old. Although an age in years wasn't provided for cats in either Macdonald and Apps (1978) (four cats) or Hansen (2010) (eight cats), both studies provided enough information to conclude that the cats were older than 2 years. These cats were included in the adult category.

2.2.4. Sex and breeding status

Cats were classed as male and female and as desexed or entire. If information on the sex of animals or desexed status was not given in the paper, this information was obtained directly from the authors where possible.

2.3. Statistical analysis

Taking the natural logarithm of home range resulted in data that were approximately normal with stable variance. Exploratory data analysis of studies with results from more than one type of home range measure showed that ratios of group means (e.g. males/females, mature/adult/young) were reasonably consistent across measurement types. This gave more confidence to combine data with different measurement types in the one analysis, since only the ratio matters when modelling log-transformed home range data.

We first determined the effects of factors of interest (sex, desexed status, and housing density) using meta-analyses. We also fitted linear mixed models to the unit level home range data (on the log scale), taking advantage of the individual data available from 22 of 25 relevant studies identified. These totalled 311 of 469 cats. Given the high proportion of cats with unit level data this complementary analysis was worthwhile because of its greater statistical power. Linear mixed models also permitted analysis of the effects of age and husbandry on home range. All analyses were carried out in the statistical package R version 3.1.2 (R Core Team, 2014).

2.3.1. Meta-analyses

We examined the study level data for suitability for performing a separate meta-analysis for each of the factors of interest: sex, desexed status, husbandry and housing density (Table 1). A study could only contribute to a meta-analysis if we could estimate the effect size of interest from it.

Only one study included both farm and pet husbandry, so we were unable to perform a meta-analysis for husbandry. For the remaining three factors (sex, desexed status and housing density), we collapsed the data within each relevant study by each factor in turn, to estimate the effect size for that factor.

Although housing density had three levels overall (urban, rural and farm), the three studies with complete housing density data and cats from more than one housing density factor only included urban and rural density, so only this difference could be tested in the meta-analysis. Barratt (1997) included both farm and pet cats, but it was unknown whether the pet cats came from urban or rural dwellings. Hence, Barratt (1997) was excluded from the housing density meta-analysis.

In cases where one factor level within a study had only one cat, the standard deviation for the other factor level within that study was used for both factor levels. Bradshaw (1992) was excluded from the analysis, because both rows had only one cat. Chipman (1990) was also excluded because no estimate of the home range standard deviation was available.

The treatment effect within each study was calculated using the weighted mean difference (WMD) method on the collapsed data. Random effects models were used, because data exploration showed evidence of heterogeneity between the studies. The DerSimonian and Laird method (DerSimonian and Laird, 1986) was used to estimate this between-study variation and incorporate it into the calculation of the common effect. Heterogeneity was assessed using both the I^2 measure of heterogeneity and Cochran's Q, with a 10% significance level because of the test's low power when the number of studies is small (Higgins et al., 2003).

Reporting bias (publication bias, selective outcome reporting or selective analysis reporting) was qualitatively examined through funnel plots (Sterne *et al.*, 2001; Sterne *et al.*, 2011 ; Sutton *et al.*, 2000). A statistical test for funnel plot asymmetry exists but is not recommended for meta-analyses with < 10 studies because of its low power. Funnel plot asymmetry does not necessarily indicate reporting bias if heterogeneity is present. Such asymmetry can also be caused by other factors such as poor methods (especially in small studies) or chance (Sterne et al., 2011).

When effect estimates are related to standard errors (as indicated by funnel plot asymmetry), the random effects estimate will give more weight to smaller studies than the fixed effects estimate. Hence random effects models are not always conservative. Sterne et al. (2011) recommend comparing fixed and random effects estimates when funnel plot asymmetry exists in a meta-analysis with between study heterogeneity.

2.3.2. Linear mixed models

Fixed effects were included in the initial model for study year, sex, desexed status, age, husbandry and housing density, as well as several two-way interactions with sex. Study year was included as a fixed effect because GPS monitoring tools were more commonly used in later studies and their

readings are thought to be more accurate than those of VHF monitoring of cats. Study was included as a random effect to account for the likely correlation between observations on cats from the same study. Random effects were estimated using residual maximum likelihood (REML). There is no universally agreed way of calculating the denominator degrees of freedom (DDF) for small sample inference in mixed effects models using REML (Kenward and Roger, 1997; Schaalje *et al.*, 2002). The approach taken by R's nlme package, which was used for this analysis, “coincides with the classical decomposition of degrees of freedom in balanced, multilevel ANOVA designs and gives a reasonable approximation for more general mixed-effects models” (Pinheiro *et al.*, 2010).

No study tested all levels of all factors of interest, so the study design was unbalanced. With such unbalanced designs, the order in which factors are added to the model affects the results. This means that multiple models are needed in order to fully explore the significance of various terms in the model. Consequently, F test p-values need to be interpreted with care.

Backwards elimination was used to select the best set of fixed effects terms for inclusion in the final model. A significance level of 5% was used. Once the model was selected, individual terms were tested by dropping each one in turn from the final model.

Predicted means and their standard errors were calculated for fixed effects significant at the 5% level. For these predicted means, 95% confidence intervals were calculated, with the means and confidence limits back-transformed to report them on the original measurement scale. In order to maximise the data available for model fitting, missing values for categorical age and housing density were coded as a separate category called “miss” and “UrbanRural”, respectively.

Models were initially fitted including housing density (urban/rural/farm), which combined both rural/urban density types with pet/farm husbandry. The “full” model included the terms: sex, desexed, categorical age (agecat), housing density (density) and study year as well as the two-way interaction terms sex:desexed, sex:agecat and sex:density.

Using backwards elimination, all two-way interaction terms and study year were removed because of lack of statistical significance ($\chi^2 = 0.42$ on 8 df, $p = 0.99$). The resulting model included the main

effects terms: sex, desexed, categorical age and housing density. However, within the housing density factor, urban cats were different to both rural and farm cats, while rural and farm cats were not significantly different from each other. We could conclude that cats from rural or farm areas had larger home ranges than pet cats from urban areas, regardless of their husbandry. Therefore we collapsed the housing density factor from the three levels of urban/rural/farm to the two levels urban/rural. A new variable was created, hereafter designated UR, that categorised all cats from the “farm” or “rural” categories of housing density as “rural” and all cats with unknown housing density (“UrbanRural” category) as “miss.”

For completeness, backwards elimination was performed starting from a “full” model that included the husbandry variable as well as the new UR variable. The “full” model included the terms: sex, desexed, agecat, husbandry, UR and study year as well as the two-way interaction terms sex:desexed, sex:agecat, sex:husbandry and sex:UR.

Using backwards elimination, all two-way interaction terms, study year, desexed and husbandry were removed because of lack of statistical significance ($\chi^2 = 2.95$ on 10 df, $p = 0.98$).

3. Results

3.1. Studies included and cat characteristics

We found 32 studies that had studied the home ranges of pet or farm cats and a summary of the main findings of these is provided in Online Appendix A. Seven of these studies were excluded for various reasons, leaving 25 studies that were selected for analysis (Online Appendix B). Subsets of these studies were used in specific analyses as described.

Pet cats ranged in age from 1.0 to 18.0 years old with a mean of 5.7 years (median 5) and 96% were desexed. Farm cats do not live as long as pet cats. Their ages ranged from 1.0 to 10.0 years old with a mean of 2.9 years (median 2). Farm cats were less likely to be desexed with only one (1%) desexed farm cat (Online Appendices A and B). Studies were included if the farm cats were fed at least once

per day although they primarily hunted for their food, often in the farm buildings. These cats are unlikely to receive veterinary treatment. Across the studies, farm cats vary in their affection to and treatment by humans, but in general they were wary of people and usually had to be trapped in order to be fitted with the radio or GPS collar.

3.2. Meta-analyses

3.2.1. Testing for a difference between male and female home ranges

Study level data from the 22 studies that tested for a difference in male and female cat home ranges were collapsed and a random effects meta-analysis was performed. Male cats had a home range around 1.88 times larger than female cats ($z = 4.92$, $p < 0.001$), with a 95% confidence interval 1.46 to 2.42 (Fig. 1).

There was evidence of heterogeneity between studies: Cochran's Q had a p-value < 0.001 ($Q_{21} = 56.41$) and the I^2 measure of heterogeneity indicated that around 63% of the total variation across studies was caused by heterogeneity rather than chance. Therefore, modelling study as a random effect was the preferred choice for these data.

Examination of funnel plots (Borenstein et al., 2009) showed slight asymmetry, possibly indicating weak publication bias arising from three studies. A bias-corrected estimate of differences in male and female home ranges supported the conclusion of a sex difference ($z = 3.26$, $p = 0.001$), but with smaller magnitude (1.60 times larger, 95% CI 1.21 to 2.12).

Since we had heterogeneity between studies and asymmetry of the funnel plot, we also performed a meta-analysis with study as a fixed effect. The results were consistent with the random effects model, with an estimated effect size of 1.68 (95% CI 1.46 to 1.93).

3.2.2. Testing for a difference between entire and desexed cat home ranges

Study level data from the six studies that tested for a difference in desexed and entire cat home ranges were collapsed and a random effects meta-analysis was performed. There was no evidence that entire cats have a different home range than desexed cats ($z = 0.42$, $p = 0.68$) (Fig. 2).

There was little evidence of heterogeneity between studies: Cochran's Q had a p-value of 0.19 ($Q_5 = 7.46$) and the I^2 measure of heterogeneity indicated that around 33% of the total variation across studies was caused by heterogeneity rather than chance. With only six studies included in this meta-analysis, it was not possible to assess symmetry with funnel plots.

We also performed a meta-analysis with study as a fixed effect. The results were consistent with the random effects model and showed no evidence that entire cats have a different home range than desexed cats ($z = 0.16$, $p = 0.87$).

3.2.3. Testing for a difference between urban and rural pet cat home ranges

Study level data from the three studies that tested for a difference in urban and rural housing density pet cat home ranges were collapsed and a random effects meta-analysis was performed. Pet cats from rural areas had a home range around 14.4 times as large as pet cats from urban areas ($z = 7.50$, $p < 0.001$), with a 95% confidence interval 7.2 to 28.8 (Fig. 3).

There was evidence of heterogeneity between studies: Cochran's Q had a p-value of 0.07 ($Q_2 = 5.43$), and the I^2 measure of heterogeneity indicated that around 63% of the total variation across studies was due to heterogeneity rather than chance. With only three studies included in the meta-analysis, it was not possible to assess symmetry with funnel plots.

We also performed a meta-analysis with study as a fixed effect. The results were consistent with the random effects model, with an estimated effect size of 14.5 (95% CI 9.5 to 22.0).

3.3. Linear mixed models

The final linear mixed model selected included the main effects terms: sex, 'agecat' and UR (in which all non-urban cats were combined in the rural category). This was the model considered to best fit the data. Desexed status was excluded because it was not significant (Table 2).

With each term tested after allowing for the other two terms, male cats had significantly larger home ranges than females, ($F_{(1, 283)} = 20.31$, $p < 0.001$), roaming up to twice as far (Table 2). Urban/rural housing density continued to be a significant predictor of log home range ($F_{(2, 283)} = 47.73$, $p < 0.001$),

with rural cats having home ranges over 10 times larger than urban cats (Table 2). Age was a significant predictor of log home range ($F_{(3, 283)} = 3.03$, $p = 0.030$). Adult cats had significantly larger home ranges than mature cats, but not young cats. Mature cats and young cats had similar home ranges (Table 2). The scatterplot of standardised residuals vs fitted values for the selected model showed no obvious outliers, and residuals did not vary systematically with fitted values. Therefore the selected model appears reasonable.

4. Discussion

Many previous studies found that the mean home ranges of male pet cats were larger than those for females, but this was not statistically significant (Kays and DeWan, 2004; Lilith *et al.*, 2008; Morgan, 2002; Thomas *et al.*, 2014). However, combining the evidence from all known studies showed that male cats do have statistically larger home ranges than females, using both meta-analysis and linear mixed models.

Liberg *et al.* (2000) suggested that in entire cats, male home ranges are determined by the availability of females and female home ranges are clustered around food sources. This led to the conclusion that desexing female cats is unlikely to have an effect on home range but that desexing male cats should decrease their home range, because they should become more interested in food than females (Barratt, 1997). We found no evidence to support this hypothesis from the meta-analysis or the mixed-effects model. Guttilla and Stapp (2010) also found that desexing had no impact on the movements of feral cats, so this conclusion is equally applicable to pet and farm cats. It also has implications for the management of cat colonies by trap-neuter-release (TNR) (Longcore *et al.*, 2009), because it is unlikely to reduce roaming by cats desexed and released. However, an unknown factor in the analyses is the age at which each cat was desexed. It is possible that if a cat is desexed as an adult once its home range has been established, desexing does not change its home range. This is suggested by Bradshaw (1992), citing data from Chipman (1990), who found that a male cat that had been desexed at age four had a similar home range to entire male cats. This was opposed to the other male cats (presumably desexed as kittens), which had similar home ranges to females, which were smaller

than those of entire male cats. It is possible that if a cat is desexed before it is sexually mature and its home range has not been fully established, desexing may reduce home range.

We found that categorical age had an impact on home range size, with adult cats (2–7 years) having significantly larger home ranges than mature (≥ 8 years) cats. There was no difference between adult cats and young cats (< 2 years) or young cats and mature cats. This is supported by data collected by Chipman (1990) cited in Bradshaw (1992), that showed that adult cats had larger home ranges than younger and older cats. Hervías et al. (2014) found that home range size increased with age while Morgan et al. (2009) found that younger cats had larger home ranges than older cats. It is possible that complex social interactions associated with age impact home range with young cats, with low status cats either confined to small home ranges or in some cases forced to roam widely in order to avoid more dominant cats. When cats are adults they can establish a more permanent home range, but as they age they are less able to defend their territory and it begins to decrease again.

We found no effect of husbandry on cat roaming behaviour. Using linear mixed models, there is no evidence that pet cats have different home ranges to farm cats. Only one study tested both farm and pet husbandry, and so we were unable to perform a meta-analysis for husbandry. Leyhausen (1979) showed that feeding is independent of hunting behaviour and it also appears that how often a cat is fed and whether it is kept for the purpose of hunting, whether it receives veterinary treatment and the quality of its relationship with humans (i.e. whether it is a pet and part of the family or considered just another farm animal) do not affect roaming behaviour.

We found strong evidence that housing density is a major predictor of home range. While the meta-analysis tested cats from rural areas against urban areas and the mixed model tested cats from either rural or farm areas against urban areas, results were consistent across both modelling approaches. Cats living in lower density areas, whether they were farm cats or rural pets, had much larger home ranges than cats from urban areas. This was expected based on evidence from other studies (Lilith *et al.*, 2008; Metsers *et al.*, 2010 ; van Heezik *et al.*, 2010).

At higher housing densities cats are more likely to encounter other cats, dogs or other deterrents to widespread roaming. Thus housing density can be considered a surrogate for cat density (Hall et al., 2016b), which may be the real factor underlying the effect of housing density on home range. In some environments, the presence of predators such as coyotes *Canis latrans* may be a confounding factor if they prey on cats roaming more widely from habitation (Crooks and Soulé, 1999), or cats may be cautious venturing into habitat that may support predators (Kays and DeWan, 2004). Thus housing density, cat density, predator activity and vegetation structure/remnant size may all interact to determine the observed home range of pet cats. While sample sizes and our wish to avoid overfitting in statistical models prevented assessments of many of these effects in meta-analysis or linear mixed models, we can make the robust generalisations that: male cats roam further than females, desexing is unlikely to change home range, and that roaming is most likely in cats aged 2–7 years.

In environmentally sensitive areas, some local governments are introducing buffer zones around nature reserves or remnant native vegetation to protect local wildlife from the potential impacts of pet cats (Baker, 2001; Buttriss, 2001; Lilith *et al.*, 2008; Moore, 2001). People living within these buffer zones are either prohibited from owning a pet cat or required to keep pet cats restricted to their property at all times. Lilith *et al.* (2008) and Metsers *et al.* (2010) quantified how wide these buffer zones should be, ranging from 360 m to 1.2–2.4 km respectively. The differences can be explained in terms of the great variability in individual cat roaming behaviour (Kays and DeWan, 2004; Metsers *et al.*, 2010; Morgan *et al.*, 2009). There is no one rule that applies to all cats in all locations, so area-specific data will be required to recommend suitable buffer zones. In areas of lower housing density the problem will be more acute.

Given that the individual roaming behaviour of cats is highly variable, changes over time and is also influenced by environmental factors, the best way to ensure that pet cats do not negatively impact the environment or themselves through roaming is to confine them to their owners' properties (Kauhala *et al.*, 2015). We have no evidence that popular husbandry techniques such as desexing or regular feeding reduce home ranges, nor did Hall *et al.* (2016b) find that effective anti-predator devices act by

reducing roaming behaviour. Our data show that mature cats roam less, so at best it is only younger animals that need to be confined.

However, confinement is unpopular for many owners (Lilith *et al.*, 2006; McHarg *et al.*, 1995; Perry, 1999; REARK, 1994a; REARK, 1994b; Rochlitz, 2005; Sims *et al.*, 2008). Therefore to encourage changes in cat husbandry, the attitudes towards cat confinement by cat owners and the general populace need to change (Granza *et al.*, 2016). In a study of the community attitudes and practices towards pet cats in six countries Hall *et al.* (2016a) found that respondents in four of these (China, Japan, the UK and the USA) were unlikely to believe that pet cats negatively impacted wildlife and therefore using the impact on wildlife as a motivation to encourage responsible cat husbandry would not cause a change in behaviour. This is supported by MacDonald *et al.* (2015), who found that the willingness of owners to bring their cats inside was prompted by the benefits to the cat or the positive impact on the owner, not wildlife protection. Therefore campaigns focusing on the benefits to cats and owners rather than the benefits to wildlife are more likely to elicit the desired change.

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References

- Anderson, D.R., 2008. Model Based Inference in the Life Sciences. Springer Science + Business Media LLC, New York.
- Baker, D., 2001. Cat curfew - Casey City Council. In: Murray, D. (Ed.), 10th Urban Animal Management Conference. Australian Veterinary Association, Melbourne.
- Baker, P.J., Bentley, A.J., Ansell, R.J., Harris, S., 2005. Impact of predation by domestic cats *Felis catus* in an urban area. *Mammal Rev.* 35, 302–312.

- Baker, P.J., Soulsbury, C.D., Iossa, G., Harris, S., 2010. Domestic cat (*Felis catus*) and domestic dog (*Canis familiaris*). In: Gehrt, S.D., Riley, S.P.D., Cypher, B.L. (Eds.), *Urban Carnivores: Ecology, Conflict and Conservation*. The Johns Hopkins University Press, Baltimore, pp. 157–172
- Barratt, D.G., 1997. Home range size, habitat utilisation and movement patterns of suburban and farm cats *Felis catus*. *Ecography* 20, 271–280.
- Beaumont, M., Barratt, E.M., Gottelli, D., Kitchener, A.C., Daniels, M.J., Pritchards, J.K., Bruford, M.W., 2001. Genetic diversity and introgression in the Scottish wildcat. *Mol. Ecol.* 10, 319–336.
- Beckerman, A.P., Boots, M., Gaston, K.J., 2007. Urban bird declines and the fear of cats. *Anim. Conserv.* 10, 320–325.
- Borenstein, M., Hedges, L.V., Higgins, J.P.T., Rothstein, H.R., 2009. *Introduction to Metaanalysis*. John Wiley and Sons, Ltd., West Sussex, United Kingdom.
- Bradshaw, J.W.S., 1992. *The Behaviour of the Domestic Cat*. CABI Publishing, UK.
- Buttriss, R., 2001. No cat zone - City of Kingston. In: Murray, D. (Ed.), *10th Urban Animal Management Conference*. Australian Veterinary Association, Melbourne
- Calver, M., Thomas, S., Bradley, S., McCutcheon, H., 2007. Reducing the rate of predation on wildlife by pet cats: the efficacy and practicability of collar-mounted pounce protectors. *Biol. Conserv.* 137, 341–348.
- Calver, M.C., Grayson, J., Lilith, M., Dickman, C.R., 2011. Applying the precautionary principle to the issue of impacts by pet cats on urban wildlife. *Biol. Conserv.* 144, 1895–1901.
- Carss, D.N., 1995. Prey brought home by two domestic cats (*Felis catus*) in northern Scotland. *J. Zool.* 237, 678–686.
- Chipman, P., 1990. Influence on the Home Range Size of Domestic Cats (*Felis catus*), in an Urban Environment Unpublished thesis Manchester Polytechnic, Manchester.
- Corbett, L.K., 1979. Feeding Ecology and Social Organization of Wildcats (*Felis silvestris*) and Domestic Cats (*Felis catus*) in Scotland Unpublished thesis University of Aberdeen, Aberdeen.
- Core Team, R., 2014. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Coughlin, C.E., van Heezik, Y., 2014. Weighed down by science: do collar-mounted tags affect cat behaviour? *Wildl. Res.* 41, 606–614.
- Crooks, K.R., Soulé, M.E., 1999. Mesopredator release and avifaunal extinctions in a fragmented ecosystem. *Nature* 400, 563–566
- Das, A., 1993. Nocturnal Carnivore (*Felis catus* and *Vulpes vulpes*) Activity in an Urban Native Park Unpublished thesis University of Melbourne, Australia.
- Dersimonian, R., Laird, N., 1986. Meta-analysis of clinical trials. *Control. Clin. Trials* 7, 177–188.
- Egenvall, A., Nødtvedt, A., Hågström, J., Ström Holst, B., Möller, L., Bonnett, B.N., 2009. Mortality of life-insured Swedish cats during 1999–2006: age, breed, sex and diagnosis. *J. Vet. Intern. Med.* 23, 1175–1183.
- George, W.G., 1974. Domestic cats as predators and factors in winter shortages of raptor prey. *Wilson Bull.* 86, 384–396.
- Granza, A., Teel, T., Vandewoude, S., Crooks, K., 2016. Understanding public perceptions of risk regarding outdoor per cats to inform conservation action. *Conserv. Biol.* 30, 276–286.

- Grayson, J., Calver, M.C., Styles, I., 2002. Attitudes of suburban Western Australians to proposed cat control legislation. *Aust. Vet. J.* 80, 536–543.
- Guttilla, D.A., Stapp, P., 2010. Effects of sterilization on movements of feral cats at a wildland-urban interface. *J. Mammal.* 91, 482–489.
- Hall, C.M., Fontaine, J.B., Bryant, K.A., Calver, M.C., 2015. Assessing the effectiveness of the Birdsbesafe® anti-predation collar cover in reducing predation by pet cats on wildlife in Western Australia. *Appl. Anim. Behav. Sci.* 173, 40–51.
- Hall, C.M., Adams, N.A., Bradley, J.S., Bryant, K.A., Davis, A.A., Dickman, C.R., Fujita, T., Kobayashi, S., Lepczyk, C.A., McBride, E.A., Pollock, K.H., Styles, I.M., Heezik, Y.v., Wang, F., Calver, M.C., 2016a. Community attitudes and practices of urban residents regarding predation by pet cats on wildlife: an international comparison. *PLoS One* 11, e0151962.
- Hall, C.M., Bryant, K.A., Fontaine, J.B., Calver, M.C., 2016b. Do collar-mounted predation deterrents restrict wandering in pet domestic cats? *Appl. Anim. Behav. Sci.* 176, 96–104.
- Hansen, C.M., 2010. Movements and Predation Activity of Feral and Domestic Cats (*Felis catus*) on Banks Peninsula Unpublished thesis Lincoln University, New Zealand.
- Hervías, S., Opiel, S., Medina, F.M., Pipa, T., Díez, A., Ramos, J.A., Ybáñez, R.R.D., Nogales, M., 2014. Assessing the impact of introduced cats on island biodiversity by combining dietary and movement analysis. *J. Zool.* 292, 39–47.
- Higgins, J.P.T., Thompson, S.G., Deeks, J.J., Altman, D.G., 2003. Measuring inconsistency in meta-analyses. *BMJ* 327, 557–560.
- Horn, J.A., Mateus-Pinilla, N., Warner, R.E., Heske, E.J., 2011. Home range, habitat use, and activity patterns of free-roaming domestic cats. *J. Wildl. Manag.* 75, 1177–1185.
- Jongman, E.C., 2007. Adaptation of domestic cats to confinement. *J. Vet. Behav.* 2, 193–196.
- Kauhala, K., Talvitie, K., Vuorisalo, T., 2015. Free-ranging house cats in urban and rural areas in the north: useful rodent killers or harmful bird predators? *Folia Zool.* 64, 45–55.
- Kays, R.W., DeWan, A.A., 2004. Ecological impact of inside/outside house cats around a suburban nature preserve. *Anim. Conserv.* 7, 273–283.
- Kenward, M.G., Roger, J.H., 1997. Small sample inference for fixed effects from restricted maximum likelihood. *Biometrics* 53, 983–997.
- Kitts-Morgan, S.E., Caires, K.C., Bohannon, L.A., Parsons, E.I., Hilburn, K.A., 2015. Free-ranging farm cats: home range size and predation on a livestock unit in Northwest Georgia. *PLoS One* 10, e0120513
- Lamari, L., 2015. Assess 2.0. Image Analysis Software for Plant Disease Quantification. APS Press <http://www.apsnet.org/apsstore/shopapspress/Pages/43696m5.aspx> Accessed August 26th, 2015.
- Lepczyk, C.A., Lohr, C.A., Duffy, D.C., 2015. A review of cat behavior in relation to disease risk and management options. *Appl. Anim. Behav. Sci.* 173, 29–39.
- Leyhausen, P., 1979. *Cat Behaviour: The Predatory and Social Behaviour of Domestic and Wild Cats*. Garland STPM Press, New York & London.
- Liberg, O., 1980. Spacing patterns in a population of rural free roaming domestic cats. *Oikos* 35, 336–349.
- Liberg, O., Sandell, M., Pontier, D., Natoli, E., 2000. Density, spatial organization and reproductive tactics in the domestic cat and other felids. In: Turner, D.C., Bateson, P. (Eds.), *The Domestic Cat: The Biology of Its Behaviour*. Cambridge University Press, Cambridge, United Kingdom, pp. 120–147.

- Lilith, M., Calver, M., Styles, I., Garkaklis, M., 2006. Protecting wildlife from predation by owned domestic cats: application of a precautionary approach to the acceptability of proposed cat regulations. *Austral Ecol.* 31, 176–189.
- Lilith, M., Calver, M., Garkaklis, M., 2008. Roaming habits of pet cats on the suburban fringe in Perth, Western Australia: what size buffer zone is needed to protect wildlife in reserves? In: Lunney, D., Munn, A., Meikle, W. (Eds.), *Too Close for Comfort: Contentious Issues in Human-Wildlife Encounters*. Royal Zoological Society of New South Wales, Sydney, Australia, pp. 65–72
- Longcore, T., Rich, C., Sullivan, L.M., 2009. Critical assessment of claims regarding management of feral cats by trap-neuter-return. *Conserv. Biol.* 23, 887–894.
- Loyd, K.A.T., Hernandez, S.M., Abernathy, K.J., Shock, B.C., Marshall, G.J., 2013. Risk behaviours exhibited by free-roaming cats in a suburban US town. *Vet. Rec.* 1-6
- Macdonald, D.W., Apps, P.J., 1978. The social behaviour of a group of semi-dependent farm cats, *Felis catus*: a progress report. *Carn. Gen. Newslet.* 3, 256–269.
- MacDonald, E., Milfont, T., Gavin, M., 2015. What drives cat-owner behaviour? First steps towards limiting domestic-cat impacts on native wildlife. *Wildl. Res.* 42, 257–265.
- McHarg, M., Baldock, C., Headey, B., Robinson, A., 1995. National People and Pets Survey. Urban Animal Management Coalition, Melbourne.
- Meek, P.D., 2003. Home range of house cats *Felis catus* living within a National Park. *Aust. Mammal.* 25, 51–60.
- Metsers, E.M., Seddon, P.J., Van Heezik, Y.M., 2010. Cat-exclusion zones in rural and urban-fringe landscapes: how large would they have to be? *Wildl. Res.* 37, 47–56.
- Moore, S., 2001. Cat confinement - does it work? In: Murray, D. (Ed.), 10th Urban Animal Management Conference. Australian Veterinary Association, Melbourne
- Morgan, S.A., 2002. Movements and Hunting Activity of House Cats (*Felis catus*) Living Around Travis Wetland, Christchurch, New Zealand Unpublished M.Sc. Thesis Lincoln University, New Zealand.
- Morgan, S.A., Hansen, C.M., Ross, J.G., Hickling, G.J., Ogilvie, S.C., Paterson, A.M., 2009. Urban cat (*Felis catus*) movement and predation activity associated with a wetland reserve in New Zealand. *Wildl. Res.* 36, 574–580.
- Nelson, S.H., Evans, A.D., Bradbury, R.B., 2005. The efficacy of collar-mounted devices in reducing the rate of predation of wildlife by domestic cats. *Appl. Anim. Behav. Sci.* 94, 273–285.
- Perry, G., 1999. Cats - perceptions and misconceptions: two recent studies about cats and how people see them. In: Murray, D. (Ed.), 8th Urban Animal Management Conference. Australian Veterinary Association, Melbourne.
- Pinheiro, J., Bates, D., Hardle, W., 2010. *Mixed-effects Models in S and S-PLUS*, e-Book. Springer, New York.
- Preisser, E.L., Bolnick, D.I., Bernard, M.F., 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology* 86, 501–509.
- REARK, 1994a. *The Cat in the Suburbs Survey in Sydney and Melbourne*. Petcare Information and Advisory Services, South Yarra, Victoria.
- REARK, 1994b. *The Metropolitan Domestic Cat. A Survey of the Population Characteristics and Hunting Behaviour of the Domestic Cat in Australia*. Petcare Information and Advisory Services, South Yarra, Victoria.

- Rochlitz, I., 2005. A review of the housing requirements of domestic cats (*Felis silvestris catus*) kept in the home. *Appl. Anim. Behav. Sci.* 93, 97–109.
- Schaalje, G.B., McBride, J.B., Fellingham, G.W., 2002. Adequacy of approximations to distributions of test statistics in complex mixed linear models. *Journal Agric. Biol. and Environ Stat.* 7, 512–524.
- Schär, R., Tschanz, B., 1982. Social behaviour and space utilization of farm cats using biotelemetry. *Proceedings of 7th International Symposium of Biotelemetry*. Stanford, pp. 1–4.
- Sims, V., Evans, K.L., Newson, S.E., Tratalos, J.A., Gaston, K.J., 2008. Avian assemblage structure and domestic cat densities in urban environments. *Divers. Disturb.* 14, 387–399.
- Sterne, J.A., Egger, M., Davey Smith, G., 2001. Investigating and dealing with publication and other biases in meta-analysis. *BMJ* 323, 101–105.
- Sterne, J.A.C., Sutton, A.J., Ioannidis, J.P.A., Terrin, N., Jones, D.R., Lau, J., Carpenter, J., Rücker, G., Harbord, R.M., Schmid, C.H., Tetzlaff, J., Deeks, J.J., Peters, J., Macaskill, P., Schwarzer, G., Duval, S., Altman, D.G., Moher, D., Higgins, J.P.T., 2011. Recommendations for examining and interpreting funnel plot asymmetry in meta-analyses of randomised controlled trials. *BMJ* 43, d4002.
- Sutton, A.J., Duval, S.J., Tweedie, R.L., Abrams, K.R., Jones, D.R., 2000. Empirical assessment of effect of publication bias on meta-analysis. *BMJ* 320, 1574–1577.
- Thomas, R.L., Fellowes, M.D.E., Baker, P.J., 2012. Spatio-temporal variation in predation by urban domestic cats (*Felis catus*) and the acceptability of possible management actions in the UK. *PLoS One* 7, e49369.
- Thomas, R.L., Baker, P.J., Fellowes, M.D.E., 2014. Ranging characteristics of the domestic cat (*Felis catus*) in an urban environment. *Urban Ecosyst.* 17, 911–921.
- Turner, D., Mertens, C., 1986. Homorange size, overlap and exploitation in domestic farm cats (*Felis catus*). *Behaviour* 99, 22–45.
- van Heezik, Y., Smyth, A., Adams, A., Gordon, J., 2010. Do domestic cats impose an unsustainable harvest on urban bird populations? *Biol. Conserv.* 143, 121–130.
- Warner, R.E., 1985. Demography and movements of free-ranging domestic cats in rural Illinois. *The J. Wildl. Manag.* 49, 340–346.
- Weber, J.-M., Dailly, L., 1998. Food habits and ranging behaviour of a group of farm cats (*Felis catus*) in a Swiss mountainous area. *J. Zool.* 245, 234–237.
- Willson, S.K., Okunlola, I.A., Novak, J.A., 2015. Birds be safe: Can a novel cat collar reduce avian mortality by domestic cats (*Felis catus*)? *Global Ecol. Conserv.* 3, 359–366.

Table 1. List of studies available for analysis, the number of cats included in the study and the factors that can be estimated from that study.

Study	No. cats	Radio tracking/GPS collar	Measurement used for analysis	Factor				
				Sex	Desexed status	Husbandry	Housing density	Age
(Barratt, 1997)	17	Radio	95% MCP	Yes	Yes	Yes		Yes
(Bradshaw, 1992)	2	Radio	95% MCP	Yes	Yes			Yes
(Carss, 1995)	1	Radio	100% MCP					Yes
(Chipman, 1990 in Bradshaw, 1992)	135	Radio	100% MCP	Yes				Yes ^a
(Corbett, 1979)	16	Radio	100% MCP	Yes				No
(Coughlin and van Heezik, 2014)	20	GPS	95 KDE	Yes				Yes
(Das, 1993 in Barratt, 1997)	13	Radio	100% MCP	Yes				Yes
(Hall et al., 2016b)	34	GPS	95 KDE	Yes			Yes	Yes
(Hansen, 2010)	8	GPS	95 KDE	Yes				Yes ^b
(Hervías et al., 2014)	9	GPS	95 KDE	Yes	Yes			Yes ^b
(Horn et al., 2011)	11	Radio	95 KDE	Yes				No
(Kays and DeWan, 2004)	11	Radio	95% MCP	Yes	Yes			Yes ^b
(Kitts-Morgan et al., 2015)	7	GPS	95 KDE	Yes	Yes			Yes
(Liberg, 1980)	10	Radio	100% MCP	Yes				Yes ^b
(Lilith et al., 2008)	16	Radio	95% MCP	Yes			Yes	Yes
(Macdonald and Apps, 1978)	4	Radio	100% MCP	Yes				Yes ^b
(Meek, 2003)	15	Radio	95% MCP	Yes	Yes			Yes
(Metsers et al., 2010)	38	GPS	95 KDE	Yes			Yes	Yes ^b
(Morgan, 2002)	21	Radio	100% MCP	Yes				Yes
(Schär and Tschanz, 1982)	5	Radio	100% MCP	Yes				Yes
(Thomas et al., 2014)	20	GPS	95% MCP	Yes				Yes
(Turner and Mertens, 1986)	11	Radio	95 KDE	Yes	Yes			Yes
(van Heezik et al., 2010)	31	GPS	100% MCP	Yes				Yes
(Warner, 1985)	11	Radio	100% MCP	Yes				Yes
(Weber and Dailly, 1998)	3	Radio	100% MCP	Yes				Yes
Total	469			24	7	1	3	23

^aStudy reported median rather than mean home range.

^bAge was not provided for all cats in the study.

Table 2. Summary of estimated effects from both the meta-analysis and mixed effects modelling approaches.

Factor	Meta-analysis		Mixed Effects Model	
	Estimated effect size (95% CI)	p-Value	Estimated effect size (95% CI)	p-Value
HR _{male} /HR _{female}	1.88 (1.46, 2.42)	< 0.001	1.83 (1.40, 2.37)	< 0.001
HR _{rural and farm} /HR _{urban}	Not tested		11.0 (6.66, 18.3)	< 0.001
HR _{rural} /HR _{urban}	14.4 (7.16, 28.8)	< 0.001	Not tested	
HR _{entire} /HR _{desexed}	1.13 (0.64, 2.00)	0.67	1.69 (0.90, 3.18) ^a	0.10
HR _{young} /HR _{adult}	Not tested		0.98 (0.65, 1.48)	0.91
HR _{young} /HR _{mature}	Not tested		1.56 (0.98, 2.51)	0.06
HR _{adult} /HR _{mature}	Not tested		1.60 (1.15, 2.22)	0.01

^aThe factor for desexed status was not included in the final mixed effects model because of a lack of significance. Its estimated effect size has been included in the table for comparison purposes only.

Fig. 1. Forest plot of the random effects meta-analysis of studies measuring the difference in male and female cat home ranges (on the log scale). There is evidence that male cats have a larger home range than female cats.

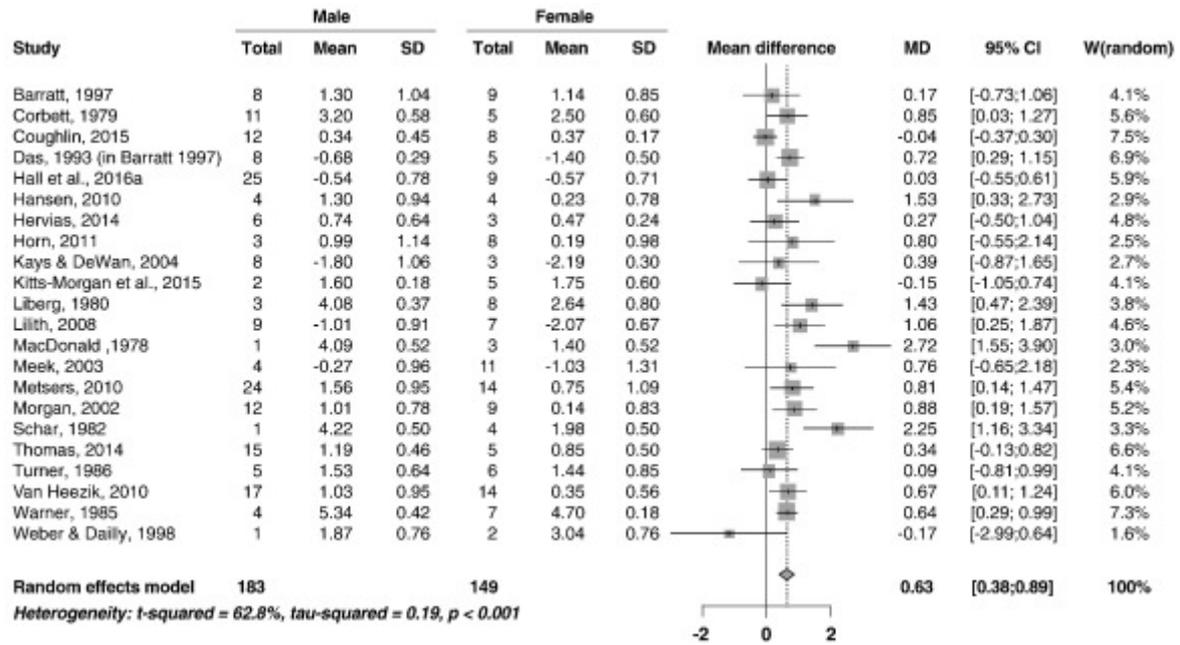


Fig. 2. Forest plot of the random effects meta-analysis of studies measuring the difference in entire and desexed cat home ranges (on the log scale). There is no evidence that entire cats have a different home range to desexed cats.

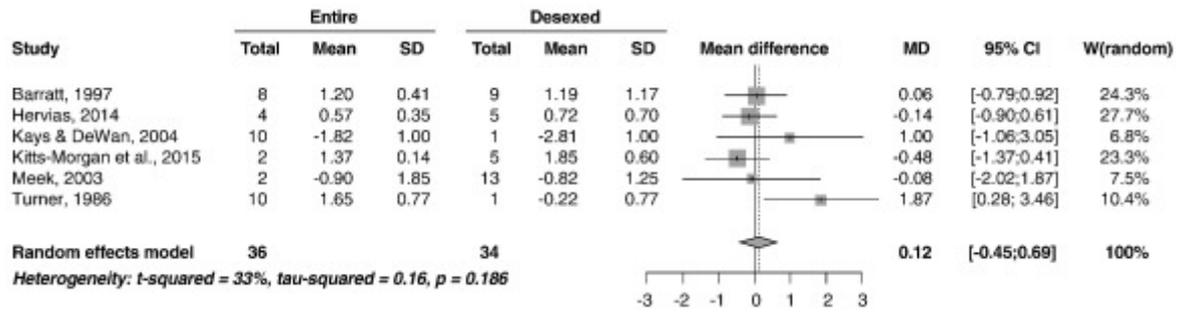


Fig. 3. Forest plot of the random effects meta-analysis of studies measuring the difference in home ranges between pet cats from rural areas and pet cats from urban areas (on the log scale). There is evidence that pet cats from rural areas have a larger home range than pet cats from urban areas.

