


The small home ranges and large local ecological impacts of pet cats

R. Kays^{1,2} , R. R. Dunn³, A. W. Parsons^{1,2}, B. McDonald^{1,2}, T. Perkins⁴, S. A. Powers⁵, L. Shell⁶, J. L. McDonald⁷, H. Cole⁷, H. Kikillus⁸, L. Woods⁸, H. Tindle⁹ & P. Roetman⁹

1 North Carolina Museum of Natural Sciences, Raleigh, NC, USA

2 Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, NC, USA

3 Department of Applied Ecology, North Carolina State University, Raleigh, NC, USA

4 Geisel School of Medicine at Dartmouth, Hanover, NH, USA

5 Brody School of Medicine, East Carolina University, Greenville, NC, USA

6 SciStarter, Philadelphia, PA, USA

7 Centre for Ecology and Conservation, College of Life and Environmental Sciences, University of Exeter, Cornwall Campus, Penryn, UK

8 Victoria University of Wellington, Wellington, New Zealand

9 School of Natural and Built Environments, University of South Australia, Adelaide, Australia

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Correspondence

Roland Kays, NC Museum of Natural Sciences, 11 West Jones St, Raleigh, NC 27601, USA.

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Abstract

Domestic cats (*Felis catus*) are a conservation concern because they kill billions of native prey each year, but without spatial context the ecological importance of pets as predators remains uncertain. We worked with citizen scientists to track 925 pet cats from six countries, finding remarkably small home ranges (3.6 ± 5.6 ha). Only three cats ranged > 1 km² and we found no relationship between home range size and the presence of larger native predators (i.e. coyotes, *Canis latrans*). Most (75%) cats used primarily (90%) disturbed habitats. Owners reported that their pets killed an average of 3.5 prey items/month, leading to an estimated ecological impact per cat of 14.2–38.9 prey ha⁻¹ yr⁻¹. This is similar or higher than the per-animal ecological impact of wild carnivores but the effect is amplified by the high density of cats in neighborhoods. As a result, pet cats around the world have an ecological impact greater than native predators but concentrated within ~100 m of their homes.

Introduction

Domestic cats (*Felis catus*) are one of the most abundant carnivores on earth, with up to 600 million pet cats globally. The total number of domestic cats is almost certainly greater than the collective number of individuals of all other felid species combined. In their abundance, domestic cats represent a conservation conundrum that can pit animal-loving groups that support cats against other animal-loving groups concerned about native species conservation (Kikillus *et al.*, 2017; Marra and Santella, 2016). The conservation impact of free-ranging cats has been especially dire on small islands where naïve prey species are most vulnerable to novel predators, resulting in at least 33 extinctions (Medina *et al.*, 2011). The management of cats is complicated, in part, because the same species can be found living as a pet, as a free-ranging feral animal consuming only wild prey, or semi-wild in a colony with supplemental food and potentially very

high local cat densities (Kays & DeWan, 2004; Crowley *et al.*, 2019).

Loss & Marra (2017) recently summarized the scope of conservation problems caused by mainland cats as a result of their predation, disease and fear-related effects, and suggest that the field should move toward evidence-driven management of cats. However, much of the evidence they reviewed did not distinguish between pet, feral or colony cats, and management actions likely need to be customized to the type of domestic cat population. Knowing the relative risk posed by distinct types of cats could help prioritize different conservation actions. For example, should managers focus on encouraging owners to keep pets indoors, removing feral cats from protected areas, campaigning for ordinances against feeding cats in colonies, or all of the above?

A potential key difference in the behavior of pet and feral cats is with regard to how far they move (Kays & DeWan, 2004; Bengsen *et al.*, 2014; Hanmer *et al.*, 2017). Although

numerous studies have extrapolated the number of prey that cats kill, the spatial extent of cat predation has not been included in these analyses (Loss *et al.*, 2013; Kauhala *et al.*, 2015; Woinarski *et al.*, 2017). Wider ranging by cats could be worse for conservation as cats that move more may be more likely to traverse into natural habitats. However, reduced ranging could also be bad if it is associated with higher cat density or concentrates cat predation and thus intensifies their local ecological effects. In their meta-analysis of pet cat home-range size, Hall *et al.*, (2016) found young male cats in rural areas were the widest ranging, but they did not consider the consequences of these spatial result on the ecological impact of cats. Cat movements could also be affected by the local predator community. In the US, cats are rare in parks where coyotes roam (Kays *et al.*, 2015), but the response of individual cats to coyote predation risk has not been considered.

Here, we incorporate animal movement into an evaluation of the ecological impact of pet cats through a global citizen science cat-tracking study. We quantify the space use of 925 pet cats from six countries, evaluating regional differences, and testing hypotheses about what affects their movement. Specifically, we expect rural cats will range further, as will males and younger animals (Hall *et al.*, 2016). If cats reduce their range in the face of predation risk, we expect cats living with coyotes, which are well-documented cat predators, will have smaller ranges than those co-existing only with smaller predators, not known to kill cats (i.e. foxes). In addition, we combine movement data with predation estimates to provide the first spatially explicit consideration of the ecological impact of pet cats in comparison with feral cats and wild carnivores.

Materials and methods

We created Cat Tracker as four regional citizen science projects (USA, UK, Australia, New Zealand) to recruit volunteers to track their pet cats with small inexpensive 'I Got U' GPS loggers (Mobile Action Technology, Inc.) with a fix schedule of 1 fix per 3 min. for at least 5 days. These units performed well when outdoors, but collected some imprecise locations when indoors, resulting in a cloud of points within 30 m of the house when cats were inside. Volunteers returned the loggers and we processed the locations with the track optimization function in the @Trip PC software and then uploaded data to Movebank, where we used additional filters based on a maximum movement speed for cats of 47 km h⁻¹. We calculated home-range size as 95% aKDE using the CTTM package in program R v3.6.1 (R Development Team, 2018) to account for autocorrelation, and plotted correlograms for all individuals to evaluate if they had established a home range (Calabrese *et al.*, 2016).

We log transformed range size to normalize the distribution and used a simple linear regression to evaluate the determinants of cat home-range size. We used five covariates as fixed effects: a categorical indicator of country (Australia, New Zealand, UK or USA), cat age, sex, whether cats were neutered and local human population

size as a measure of urban development. We log transformed population density to make the distribution less skewed, and used it as a continuous variable in our model, but also used 369 people/km² as a threshold to categorize a site as rural or urban to compare with past categorical results (USDA, 2019). We ran a suite of 32 models in program R v3.6.1 using package MuMIn (Bartoń, 2014). We assessed relative model support using AICc and considered the top model to be separated from competing models by at least 4 AICc points (Burnham and Anderson, 2002). We used the GWPv3 dataset of human population density (CIESIN *et al.*, 2005) annotated for all cat locations using the EnvData tool of Movebank (Dodge *et al.*, 2013).

To characterize the habitat used by each cat, we intersected the cat GPS data with appropriate land-cover datasets: Australia (Willoughby *et al.*, 2018), New Zealand (Research, 2015), UK (Rowland *et al.*, 2017) and US (Homer *et al.*, 2015). To convert each of these into disturbed or natural habitats, we used the criteria reported in Table S1.

Cat tracking protocols and associated social surveys of cat owners were approved by the NC State Institutional Review Board (#3515), the NC Museum of Natural Sciences Animal Care and Use Committee (NCSM 2014-01), the University of South Australia's Animal Ethics Committee (project U33-14), the University of South Australia's Human Research Ethics Committee (project 33220), Victoria University of Wellington's Human Ethics Committee (#2014R11) and Victoria University of Wellington's Animal Ethics Committees (#20164), and the University of Exeter's College of Life and Environmental Sciences Ethics Committee (2017/1925). All tracking data are available through Movebank (DOI # pending).

Volunteers also filled out a questionnaire (Table S2) regarding their cat's behavior and hunting habits which we used to test predictions of home-range size and evaluate the ecological impacts of cats. Coyotes are well-documented predators of cats (Morey *et al.*, 2007; Grubbs & Krausman, 2009), and cats are rare where coyotes roam (Kays *et al.*, 2015), whereas there is no evidence that smaller predators such as foxes act as cat predators. As a local test for the effect of predators we used a t-test (JMP Pro v14, SAS) to compare the home range size of cats in suburban Connecticut, where coyotes occur, with those from nearby suburban Long Island, New York, where there are no coyotes.

We combined pet owner estimates of prey returned home, using an adjustment factor for animals killed but not eaten (multiplied by 1.2 or 3.3, Loss *et al.*, 2013), with home range size of each cat to estimate the number of prey each individual cat killed yr⁻¹ ha⁻¹. To put our estimate into ecological perspective, we also estimated this value for a typical wild 5 kg carnivore based on metabolic theory (Jetz *et al.*, 2004; Carbone *et al.*, 2007) and for a 5 kg wild congener from field data (*Felis chaus*, Katna *et al.*, 2019). To simplify the results, we describe the case of each predator in terms of how many 30 g mice they would kill yr⁻¹ ha⁻¹, using the estimate of 41.1 Cal per mouse (Golley, 1960).

Results

We tracked 925 pet cats from six countries with the largest samples coming from Australia (440), New Zealand (230), the US (154) and the UK (101, Figure 1, Table S3). Most cats were recruited as part of four local citizen science projects and borrowed project GPS units, but data from 19 cats came from volunteers from 12 US states, Canada and Denmark that purchased their own GPS unit (i.e. DIY volunteers). These DIY cats are included in global averages of range size but were not included in the model because they constituted relatively few cats from a smattering of diverse areas. We used data from eight cats that had ≥ 20 days of data to evaluate the change in home-range size with increased tracking duration, finding that the variance decreased sharply after 5 days, and the estimate became most precise after 10 days (Figure S1). Based on human population density, 325 of the tracked cats were living in rural areas, whereas 535 of the cats were in urban areas (Figure S4).

For our home-range estimates we excluded 46 animals that had fewer than 5 days of data (based on results from Figure S1) and four animals that had correlograms that did not level off, as would be expected if those cats had not established a home range or if we collected too few data on those cats to describe their home ranges. Only three animals had home ranges greater than 1 km²: a cat with a 2.2 km² range from the UK, and two cats from New Zealand with

2.1 and 8.6 km² ranges respectively. We considered these outliers and removed them from further analyses. Closer examination showed one NZ cat (Blue) roamed farm fields, and that the other (Penny) roamed natural areas. The UK cat (Max) walked 1.7 km along a road between two villages (St. Newlyn East and Trevilson) twice during the tracking period (Figure S2.).

The average home range for the remaining 875 cats was small, just 3.6 ± 5.6 ha (Figure 2a). If the three outlier cats with very large ranges are included, this value is $5.1 \text{ ha} \pm 31.2$. The top model of home range size included all five covariates was 4.12 AIC points lower than the next best model, but weakly explanatory ($r^2 = 0.15$) (Table S4). Residuals were symmetrical and clustered near the center of the plot, indicated adequate model fit. Significant covariates included weak negative relationships between cat range size and age (old cats roam less, Figure S4), population density (rural cats had ranges 1.6x larger than urban cats), and cats had smaller ranges in Australia (mean 2.5 ± 3.9 ha) than they did in other regions (NZ 4.3 ± 6.8 , UK 4.6 ± 7.3 , USA 4.7 ± 6.5). Animal sex (males move further) and neutered status (intact cats move more) were also significant factors in the model. Our t-test comparing North American cat home ranges living with (Connecticut) and without (Long Island, New York) coyotes found no significant difference in home-range size (d.f. = 33, $t = 0.38$, $P = 0.73$).

Our analysis of habitat use showed that most (75%) cats spent most (>90%) of their time in disturbed habitats

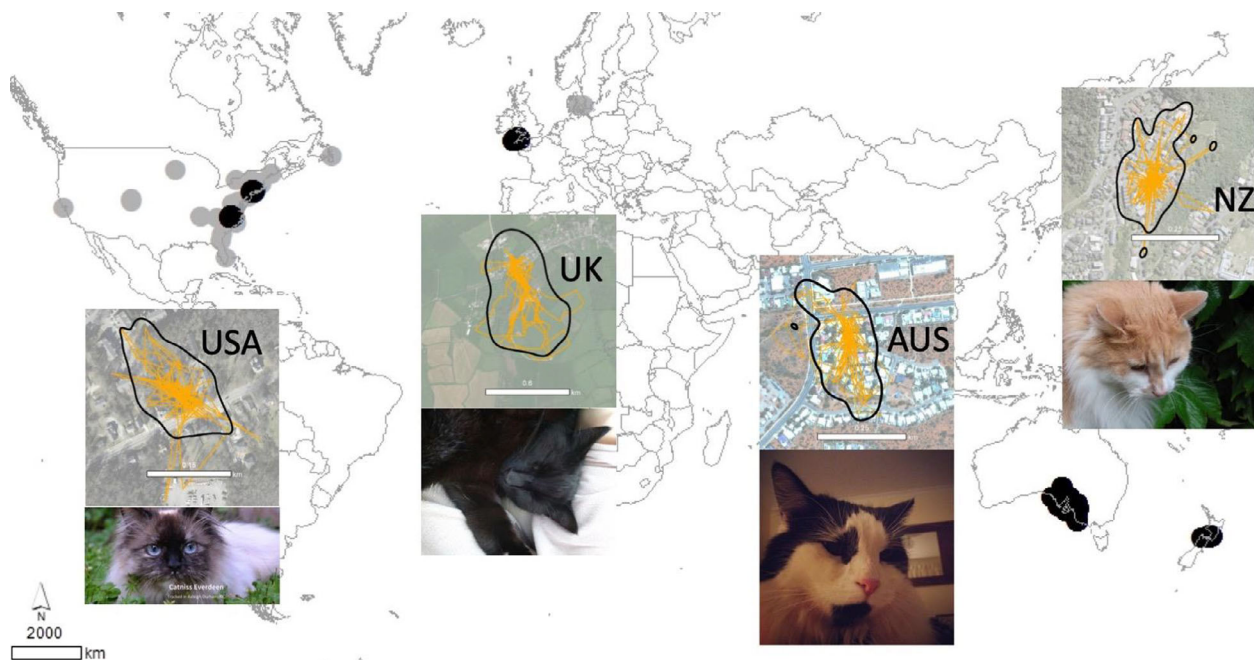


Figure 1 Map of cats tracked across our four primary study sites (black dots) and 19 additional DIY cats (grey dots). Inset maps show cat movement (orange lines) and 95% aKDE home-range boundaries (white lines). These four examples show one small range (Katniss Everdeen, USA, 1.6 ha), two typical ranges (Bugsy, AUS, 4.3 ha and Theo, NZ, 3.3 ha) and one larger than average home range (Worf, UK, 16.2 ha). Ortho imagery sources: Esri, DigitalGlobe, SecEys, Earthstar geographics, CNES/Airbus CS, USDA, USCS, AsrcGRID, IGN and the GIS User community.

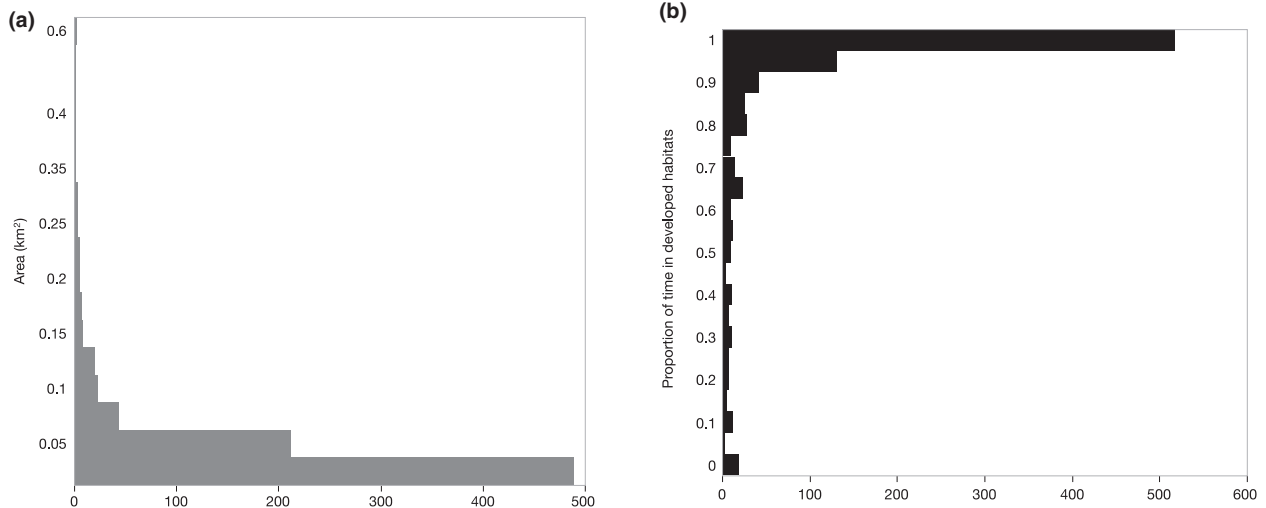


Figure 2 (a) Home range size for 875 pet cats from six countries (average 3.6 ± 5.6 ha) excluding three animals that ranged > 1 km². (b) Proportion of time each cat spent in disturbed habitats (average 88.0%), 75% of cats spent 90% or more of their time in disturbed habitats.

(average 88.0, Figure 2b). However, there were a minority (11%) of cats that spent most ($> 50\%$) of their time in natural habitats. While this is not necessarily an indication of habitat preference, without considering habitat availability, it is a good indication of where they spend their time, and thus where they are most likely to have an ecological impact.

Owners estimated the number of prey their cats returned per month to be 3.5, or 42 year⁻¹, on average (Figure S5). Other studies estimate that cats kill, but don't bring home, 1.2–3.3 prey for each prey they do bring home (Loss *et al.*, 2013), suggesting the pet cats in our study were killing 50.4–138.6 prey yr⁻¹. When considering the home range of these cats, we estimate they killed 12.2–38.9 prey yr⁻¹ ha⁻¹ (Table 1). To put this ecological impact in perspective, we estimated the prey/area consumed by a 5 kg carnivore based on metabolic theory (Jetz *et al.*, 2004; Carbone *et al.*, 2007) and a 4 kg jungle cat (*Felis chaus*) from field data (Mukherjee *et al.*, 2004). Pet cats are eating far less than expected based on their body size and metabolism, undoubtedly because they are being fed by their owners. However, the wild carnivores also roamed over areas 11–1250 times larger than did the domestic cats in our studies. As a result, the estimated total prey/ha/predator for wild carnivores is actually comparable to, or even lower than our estimate for pet cats. Pet cats that infrequently hunt kill about the same prey ha⁻¹ as wild carnivores, whereas pets that hunt more aggressively kill 2.3–4.8 times more prey ha⁻¹.

Discussion

Our citizen science cat-tracking study represents one of the largest studies of animal movement, with useful home ranges from 878 animals across six countries. The most striking result was the tiny areas used for most pet cats, averaging 0.036 km², with only 0.3% of animals moving more than 1 km². Given that similarly sized congeneric wild species, as

well as feral *F. catus*, typically have home ranges that are 10- to 20-fold larger (0.4–13 km² Sliwa, 2004; Bengsen *et al.*, 2014; Edwards *et al.*, 2001; Kitts-Morgan *et al.*, 2015; Monterroso *et al.*, 2009), it seems obvious that the reduction in movement by pet cats is the result of supplementary feeding by their owners. Pet cats don't need to cover large areas in search of food, and a few hectares seem to be a large enough area for them to meet any other inclinations. The consistency of this result in our large sample size suggests that this is a general trait for pet cats across a variety of urban, suburban and rural habitats around the globe. As predicted, cat movement declined with age and urbanization, males and intact cats moved further, matching previous studies (Hall *et al.*, 2016; Castañeda *et al.*, 2019). We also found no support for our hypothesis that cats would restrict their movement in response to the presence of local large predators (i.e. coyotes).

Our movement data allow us to add a spatial component to the evaluation of the ecological impact of cats for the first time. The tiny home range of these animals shows that pet cats are sticking close to home (e.g. ~100 m radius). In addition, our habitat use analysis shows this movement around homes is mostly (but not exclusively) in disturbed habitats, such as housing developments. As a result, the ecological impacts of pet cats are largest in the urban or suburban habitats around homes, and not out into the natural areas surrounding developments. This is good news for conservation, in as much as it means that most pet cats do not threaten species living in larger protected areas. However, it could be highly problematic for endangered species coexisting with people or living along the urban fringe. Even if a minority of pet cat activity is spent hunting in natural areas, the high density of cats could still threaten native species living there. For example, the ZEALANDIA native species sanctuary is near some of our tracked cats in New Zealand and includes species at risk from cat predation. In South Australia,

Table 1. Estimates of the per-animal ecological impact of pet cats in comparison with field data from wild cats and metabolic predictions for feral cats, and carnivores in general. Although predation rates of pet cats are lower than those of free-ranging predators, the ranges of pet cats are also smaller, making their individual ecological impact per area similar to wild predators

Predator	Cal/day	Mice d_{-1}^c	Energetic estimate mice year ⁻¹	Owner reported prey year ^{-1d}	Home range (ha)	Mice ha ⁻¹ year ⁻¹ cat ⁻¹
5 kg wild carnivore ^a	683	16.6	6066		359	16.9
4 kg Jungle Cat ^b	550	13.4	4884		605	8.1
Pet cat (this study)				51 (low)	3.6	14.2
				140 (high)	3.6	38.9

^aBased on macroevolutionary relationships (Jetz *et al.*, 2004; Carbone *et al.*, 2007).

^bEstimates of prey eaten in the wild from Mukherjee *et al.* (2004) and home-range size from Katna *et al.* (2019).

^cIf diet was only 30 g mice (41.1 Cal each, Golley, 1960), actually cats eat a variety of prey.

^dAverage 42.5 prey/year brought home from this study, multiplied by 1.2 or 3.3 correction factor for prey killed but not brought home from literature (Loss *et al.*, 2013).

numerous threatened species at risk from predation by domestic cats persist in and around urban areas, including Brushtail Possums (*Trichosurus Vulpecula*), Southern Brown Bandicoots (*Isoodon obesulus obesulus*) and Cunningham's Skinks (*Egernia cunninghami*). North America also has examples of endangered rodents (Kofron & Villablanca, 2016; Cove *et al.*, 2017) and rabbits (Cove *et al.*, 2018) that live close to housing developments, and are hence threatened by cat predation. It is difficult to ascertain what native species might have persisted or may yet recolonize urban areas if domestic cats were not present. Cats are opportunistic hunters of small vertebrates, so their prey are likely to be a reflection of the local fauna around their house, be they native or nonnative. While our study did not collect detailed data on exactly which species our study animals were killing, other studies have shown that pet cats kill alarming numbers of native species in some areas (Loss *et al.*, 2013).

Although pet cats kill fewer prey than do wild predators, their very small home ranges concentrate the impact of their hunting. Our estimates of prey killed per cat, per area are higher or similar to what we expect from wild carnivores that kill all their food (Table 1). Because they are fed by humans, domestic cats can live at high densities. Populations of 35.9 and 32 cats per km² have been reported in suburban New York (Kays & DeWan, 2004) and in a small Texas town (Schmidt *et al.*, 2007) respectively. These densities are about twice the theoretical maximum for a 5 kg wild carnivore (15.7 km²) based on mobility and energy supply (Stephens *et al.*, 2019). In the two examples above, the density of cats yields levels of predation 2–10 times that which would be expected due to wild carnivores. Although data on cat density are limited, our results add to a growing body of literature showing that pet cats play outsized ecological roles as predators near human residences and have the potential to locally reduce the populations of native prey (Loss *et al.*, 2018; Loss & Marra, 2017).

Given that other research has shown that cats are rare where coyotes roam (Kays *et al.*, 2015), we were surprised to find no difference in cat movement in our comparison of cats from suburban Connecticut (where coyotes live) with

those from nearby suburban Long Island New York, where coyotes have not yet colonized (Weckel *et al.*, 2015; Hody & Kays, 2018). This is a powerful comparison because the two study areas are very similar in terms of habitat and fauna, other than the absence of coyotes from one site. Either cats do not perceive coyotes as a risk or the average cat already moves so little that the presence of coyotes has an undetectable effect on total space use. Our results suggest that any increases in domestic cat numbers far from homes in natural areas without predators are more likely the result of feral cats rather than wide-ranging pets (Kays *et al.*, 2015).

Our results matched those of a previous meta-analysis (Hall *et al.*, 2016) in finding that older cats, male cats, and urban cats move less, but were different in that the effect of urbanization was relatively weak in our study. The effect of cat age was very similar across studies in that older cats did not move very far; we found no cats > 7 year had home ranges > 0.25 km². This could be due to the lethargy of older cats, or a higher mortality rate for cats that move farther, for example, from encountering predators or getting hit by cars. However, it is also noteworthy that most young cats in our study also had small ranges, and only a few individuals covered large areas (Figure S4). The difference between home-range size of urban and rural cats in our study (1.6×) was much smaller than found by Hall *et al.* (2016) (14.4×). However, it is difficult to discern the cause of this difference as the meta-analysis of Hall *et al.* (2016) used three different home-range measures and did not use a consistent criteria for classifying a site as rural or urban, instead relying on how the original study described their site.

Our sample only included 10 animals (3 females, 7 males, 1.1% of our total, Sup Table 1) that were not neutered, and so is not a very large sample for evaluating the movement of unaltered cats. The average range size was slightly larger for male cats that were intact (intact males 7.6 ± 4.4 ha, intact females 0.23 ± 0.11 ha, neutered males 3.6 ± 6.0 ha and neutered females 3.0 ± 4.4 ha) and was a significant predictor in our model (Table 1). Given the sex differences we observed in our small sample, and the

contrasting results on the effect of desexing in two other comparative movement studies (Hall *et al.*, 2016; Castañeda *et al.*, 2019), we suggest that this topic deserves more research.

The ecological impacts of pet cats are ultimately set by the attitudes and behavior of their owners. A recent survey in the UK showed that most pet owners who let their cats roam freely do so because they see it as important for cat health and welfare, and consider cat hunting part of nature's self-regulating ecological processes (Crowley *et al.*, 2019). Our study confirms that individual cats probably have similar ecological impacts to individual wild carnivores, but that these can often be greatly amplified to unnatural levels by the high densities that pet cats live at near human settlements. Conservation campaigns aiming to reduce cat predation of sensitive species should work with pet owners living in the immediate area (few 100 m). These programs could consider the population-level effects of cats, while also addressing concerns of individual cat health and welfare (McDonald *et al.*, 2015) by considering alternative behavioral enrichment options for indoor cats (Jongman, 2007) as well as the risk to outdoor cats from mortality factors like predation and vehicle collisions (Loyd *et al.*, 2013). As urbanization continues to spread across the globe, maintaining environments conducive to recolonization and persistence of sensitive species in urban and suburban areas will be key, and includes reducing the impacts of our domestic companion animals.

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References

- Bartoń, K. (2014). MuMin: Multi-model inference, version, 1.10.0.
- Bengsen, A.J., Algar, D., Ballard, G., Buckmaster, T., Comer, S., Fleming, P.J.S., Friend, J.A., Johnston, M., McGregor, H., Moseby, K. & Zewe, F. (2014). Feral cat home-range size varies predictably with landscape productivity and population density. *J. Zool* **298**, 112–120. <https://doi.org/10.1111/jzo.12290>.
- Burnham, K.P. & Anderson, R.D. (2002). *Model selection and multi-model inference*. New York: Springer.
- Calabrese, J.M., Fleming, C.H. & Gurarie, E. (2016). ctmm: an r package for analyzing animal relocation data as a continuous-time stochastic process. *Methods Ecol. Evol.* **7**, 1124–1132. <https://doi.org/10.1111/2041-210X.12559>.
- Carbone, C., Teacher, A. & Rowcliffe, J.M. (2007). The Costs of Carnivory. *PLoS Biol.* **5**, e22. <https://doi.org/10.1371/journal.pbio.0050022>.
- Castañeda, I., Bellard, C., Jarić, I., Pisanu, B., Chapuis, J.L. & Bonnaud, E. (2019). Trophic patterns and home-range size of two generalist urban carnivores: a review. *J. Zool.* **307**, 79–92. <https://doi.org/10.1111/jzo.12623>.
- Center for International Earth Science Information Network-CIESIN-Columbia University, FAO UNF and AP, CIAT CI de AT-. (2005). Gridded Population of the World Version 3 (GPWv3). Palisades, NY.
- Cove, M.V., Gardner, B., Simons, T.R., Kays, R. & O'Connell, A.F. (2017). Free-ranging domestic cats (*Felis catus*) on public lands: estimating density, activity, and diet in the Florida Keys. *Biol. Invasions* **20**, 333–344. <https://doi.org/10.1007/s10530-017-1534-x>.
- Cove, M.V., Gardner, B., Simons, T.R. & O'Connell, A.F. (2018). Co-occurrence dynamics of endangered Lower Keys marsh rabbits and free-ranging domestic cats: prey responses to an exotic predator removal program. *Ecol. Evol.* **8**, 4042–4052. <https://doi.org/10.1002/ece3.3954>.
- Crowley, S.L., Cecchetti, M. & McDonald, R.A. (2019). Hunting behaviour in domestic cats: an exploratory study of risk and responsibility among cat owners. *People Nat.* **1**, 18–30. <https://doi.org/10.1002/pan3.6>.
- Dodge, S., Bohrer, G., Weinzierl, R., Davidson, S.C., Kays, R., Douglas, D., Cruz, S.J.H., Brandes, D. & Wikelski, M. (2013). The environmental-data automated track annotation (Env-DATA) system: Linking animal tracks with environmental data. *Mov. Ecol.* **1**. <https://doi.org/10.1186/2051-3933-1-3>.
- Edwards, G.P., De Preu, N., Shakeshaft, B.J., Crealy, I.V. & Paltridge, R.M. (2001). Home range and movements of male feral cats (*Felis catus*) in a semiarid woodland environment in central Australia. *Austral. Ecol.* **26**, 93–101.
- Golley, F.B. (1960). Energy dynamics of a food chain of an old-field community. *Ecol. Monogr.* **30**, 187–206.
- Grubbs, S.E. & Krausman, P.R. (2009). Observations of coyote-cat interactions. *J. Wildl. Manage* **73**, 683–685.
- Hall, C.M., Bryant, K.A., Haskard, K., Major, T., Bruce, S. & Calver, M.C. (2016). Factors determining the home ranges of pet cats: a meta-analysis. *Biol. Conserv.* **203**, 313–320. <https://doi.org/10.1016/j.biocon.2016.09.029>.
- Hanmer, H.J., Thomas, R.L. & Fellowes, M.D.E. (2017). Urbanisation influences range size of the domestic cat (*Felis catus*): consequences for conservation. *J. Urban Ecol.* **3**, jux014.
- Hody, J.W. & Kays, R. (2018). Mapping the expansion of coyotes (*Canis latrans*) across America. *ZooKeys* **97**, 81–97. <https://doi.org/10.3897/zookeys.759.15149>.

- Homer, C., Dewitz, J., Yang, L., Jin, S., Danielson, P., Xian, G., Coulston, J., Herold, N., Wickham, J. & Megown, K. (2015). Completion of the 2011 National Land Cover Database for the conterminous United States—representing a decade of land cover change information. *Photogramm Eng Remote Sens.* **81**, 345–354.
- Jetz, W., Carbone, C., Fulford, J. & Brown, J.H. (2004). The scaling of animal space use. *Science (80-)* **306**, 266–268.
- Jongman, E.C. (2007). Adaptation of domestic cats to confinement. *J. Vet. Behav.* **2**, 193–196. <https://doi.org/10.1016/J.JVEB.2007.09.003>.
- Katna, A., Thaker, M., Kulkarni, A. & Vanak, A.T. (2019). *Habitat heterogeneity is essential for mesocarnivore conservation in human-dominated landscapes* International Congress for Conservation Biology. Kuala Lumpur, Malaysia: Society for Conservation Biology.
- 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. <https://doi.org/10.25225/fozo.v64.i1.a6.2015>.
- Kays, R.W. & DeWan, A.A. (2004). The ecological impact of inside/outside house cats around a suburban nature preserve. *Anim. Conserv.* **7**, 1–11.
- Kays, R., Costello, R., Forrester, T., Baker, M., Parsons, A., Kalies, L., Hess, G., Millsbaugh, J.J. & McShea, W. (2015). Cats are rare where coyotes roam. *J. Mammal.* **96**, 981–987. <https://doi.org/10.1093/jmammal/gyv100>.
- Kikillus, K.H., Chambers, G.K., Farnworth, M.J. & Hare, K.M. (2017). Research challenges and conservation implications for urban cat management in New Zealand. *Pacific Conserv. Biol.* **23**, 15–24.
- 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. <https://doi.org/10.1371/journal.pone.0120513>.
- Kofron, C.P. & Villablanca, F.X. (2016). Decline of the endangered morro bay kangaroo rat in California. *J. Fish Wildl. Manag.* **7**, 237–254. <https://doi.org/10.3996/102014-JFWM-078>.
- Loss, S.R. & Marra, P.P. (2017). Population impacts of free-ranging domestic cats on mainland vertebrates. *Front. Ecol. Environ.* **15**, 502–509. <https://doi.org/10.1002/fee.1633>.
- Loss, S.R., Will, T. & Marra, P.P. (2013). The impact of free-ranging domestic cats on wildlife of the United States. *Nat. Commun.* **4**, 1396. <https://doi.org/10.1038/ncomms2380>.
- Loss, S.R., Will, T., Longcore, T. & Marra, P.P. (2018). Responding to misinformation and criticisms regarding United States cat predation estimates. *Biol. Invasions.* **20**, 3385–3396. <https://doi.org/10.1007/s10530-018-1796-y>.
- 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.* **173**, 295. <https://doi.org/10.1136/vr.101222>.
- Marra, P.P. & Santella, C. (2016). *Cat wars: the devastating consequences of a cuddly killer*. Princeton, NJ: Princeton University Press.
- McDonald, J.L., Maclean, M., Evans, M.R. & Hodgson, D.J. (2015). Reconciling actual and perceived rates of predation by domestic cats. *Ecol. Evol.* **5**, 2745–2753. <https://doi.org/10.1002/ece3.1553>.
- Medina, F.M., Bonnaud, E., Vidal, E., Tershy, B.R., Zavaleta, E.S., Josh Donlan, C., Keitt, B.S., Corre, M., Horwath, S.V. & Nogales, M. (2011). A global review of the impacts of invasive cats on island endangered vertebrates. *Glob. Chang. Biol.* **17**, 3503–3510. <https://doi.org/10.1111/j.1365-2486.2011.02464.x>.
- Monterroso, P., Brito, J.C., Ferreras, P. & Alves, P.C. (2009). Spatial ecology of the European wildcat in a Mediterranean ecosystem: dealing with small radio-tracking datasets in species conservation. *J. Zool.* **279**, 27–35. <https://doi.org/10.1111/j.1469-7998.2009.00585.x>.
- Morey, P.S., Gese, E.M. & Gehrt, S. (2007). Spatial and temporal variation in the diet of coyotes in the Chicago metropolitan area. *Am. Midl. Nat.* **158**, 147–161.
- Mukherjee, S., Goyal, S.P., & Pitman, M.R.P.L. (2004). The importance of rodents in the diet of jungle cat (*Felis chaus*), caracal (*Caracal caracal*) and golden jackal (*Canis aureus*) in Sariska Tiger Reserve, Rajasthan, India. *J. Zool.* **262**, 405–411.
- Research L. (2015). LCDB v4. 1–Land Cover Database version 4.1, Mainland New Zealand online.
- Rowland, C., Morton, D., Carrasco Tornero, L., McShane, G., O’Neil, A. & Wood, C. (2017). Land Cover Map 2015 (25 m raster, GB).
- Schmidt, P.M., Pierce, B.L. & Lopez, R.R. (2007). Estimating free-roaming cat densities in urban areas: comparison of mark-resight and distance sampling. *Wildl. Biol. Pract.* **3**, 18–27. <https://doi.org/10.2461/wbp.2007.3.3>.
- Sliwa, A. (2004). Home range size and social organisation of black-footed cats (*Felis nigripes*). *Mammal. Biol.* **69**, 96–107. <https://doi.org/10.1078/1616-5047-00124>.
- Stephens, P.A., Vieira, M., Willis, S.G. & Carbone, C. (2019). The limits to population density in birds and mammals. *Ecol. Lett.* **22**, 654–663. <https://doi.org/10.1111/ele.13227>.
- Team, R.D.C. (2018). R, A Language and Environment for Statistical Computing. R Core Team Vienna, Austria. 3-900051-14-3.
- USDA. (2019). USDA Rural Classifications.
- Weckel, M., Bogan, D.A., Burke, R.L., Nagy, C. & Green, T. (2015). Coyotes go “bridge and tunnel”: A narrow opportunity to study the socio-ecological impacts of coyote range expansion on Long Island, NY pre- and post-arrival. *Cities Environ.* **8**, 1–28.
- Willoughby, N., Thompson, D., Royal, M. & Miles, M. (2018). South Australian Land Cover Layers: an Introduction and Summary Statistics.

Woinarski, J.C.Z., Murphy, B.P., Legge, S.M., Garnett, S.T., Lawes, M.J., Comer, S., Dickman, C.R., Doherty, T.S., Edwards, G., Nankivell, A., Paton, D., Palmer, R. & Woolley, L.A. (2017). How many birds are killed by cats in Australia? *Biol. Conserv.* **214**, 76–87. <https://doi.org/10.1016/j.biocon.2017.08.006>.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. The increase in home range (95% UD) size with longer durations of GPS tracking data for eight cats from the USA with at least 20 days of tracking data available.

Figure S2. Maps of movements of 3 outlier cats that had home ranges $> 1 \text{ km}^2$.

Figure S3. Human population density around our tracked cats, and their rural/urban classification based on a cutoff of 386 people/ km^2 .

Figure S4. The relationship between cat age and home range size showing a weak negative relationship and a tendency for some younger cats to move over much larger areas than average.

Figure S5. Prey killed by pet cats as reported by their owners.

Table S1. Reclassification scheme used to classify land-cover from four regions into disturbed or natural.

Table S2. Cat Tracker Owner Questionnaire.

Table S3. Home range estimates for 928 cats including.