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Authors: Coe, Seraiah T., Elmore, Jared A., Elizondo, Elisa C., and Loss, Scott R.

Source: *Wildlife Biology*, 2021(1)

Published By: Nordic Board for Wildlife Research

URL: <https://doi.org/10.2981/wlb.00799>

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# Free-ranging domestic cat abundance and sterilization percentage following five years of a trap–neuter–return program

Seraiah T. Coe, Jared A. Elmore, Elisa C. Elizondo and Scott R. Loss

S. T. Coe (<https://orcid.org/0000-0002-5880-180X>) ✉ ([secoe@okstate.edu](mailto:secoe@okstate.edu)), J. A. Elmore and S. R. Loss, Dept of Natural Resource Ecology and Management, Oklahoma State Univ., Stillwater, OK, USA. JAE also at: Dept of Wildlife, Fisheries and Aquaculture, Mississippi State Univ., Mississippi State, MS, USA. – E. C. Elizondo, Dept of Entomology and Wildlife Ecology, Univ. of Delaware, Newark, DE, USA.

Increasing free-ranging cat populations are a cause of concern for wildlife management and biodiversity conservation. Cats carry and transmit multiple diseases, annually deplete billions of birds and mammals in the mainland United States, and have caused extinctions and declines of wildlife populations worldwide. Trap–neuter–return (TNR) efforts, which entail trapping, sterilizing and releasing unowned free-ranging cats with the goal of reducing populations, have been implemented globally despite limited evidence of their ability to reduce cat numbers. To assess the effectiveness of a TNR program initiated in 2013 in Stillwater, Oklahoma, USA, we used trail cameras at 15 locations to estimate changes in cat abundance and the percentage of ear-tipped (i.e. sterilized) individuals between 2014 and 2018. We reviewed photographs to identify individual cats, and after accounting for detectability with mark–resight analyses, we estimated a non-significant decrease in abundance from 62 to 48 total cats across sampled locations. In 2018, approximately 27% of cats were ear-tipped compared to 0% in 2014, yet this percentage remains far below estimated sterilization levels needed for TNR to reduce unowned cat populations. Although additional long-term monitoring is needed, our results suggest that TNR conducted at its current intensity is unlikely to reduce Stillwater's cat population. Our research adds further evidence to the growing body of scientific literature indicating that TNR is ineffective in reducing cat populations.

Keywords: cat abundance, free-ranging cats, invasive species, mark–resight, Oklahoma, trap–neuter–return

Free-ranging domestic cats *Felis catus* (hereafter 'cats') present a global threat to small wildlife (Medina et al. 2011, Blancher 2013, Loss et al. 2013, Cove et al. 2018). They have contributed to at least 63 vertebrate extinctions worldwide (Doherty et al. 2016) and cause population declines in both island and mainland contexts (Van Heezik et al. 2010, Balogh et al. 2011, Loss and Marra 2017). In North America, cat predation is a top source of human–caused wildlife mortality (Calvert et al. 2013, Loss et al. 2015), annually killing 1.3–4 billion birds, 6.3–22.3 billion mammals, and hundreds of millions of reptiles and amphibians in the US alone (Loss et al. 2013). Abundant cat populations also create 'fear effects' that can alter prey behavior and suppress wildlife reproduction (Beckerman et al. 2007, Bonnington et al. 2013, Cove et al. 2019). Cats also carry pathogens and transmit diseases that affect wildlife and humans (e.g. rabies, toxoplasmosis, feline leukemia, plague

and covid-19) (Blanton et al. 2007, Gerhold and Jessup 2012, Lepczyk et al. 2015, Shi et al. 2020).

Free-ranging cats include those that are unowned and completely independent of humans (i.e. feral cats), those that live outdoors and are provided food and/or shelter by humans (i.e. semi-feral cats), and those that are owned but given outdoor access (i.e. free-ranging pet cats) (Baker et al. 2010). Managing environmental impacts of pet cats is relatively straightforward, as many animal welfare and conservation organizations agree pets should be kept indoors or only allowed outdoors with restraint (People for the Ethical Treatment of Animals 2015, The Humane Society of the United States 2020, The Wildlife Society 2020). Management of unowned cats is much more complex and controversial. An increasingly popular non-lethal approach to attempt to reduce unowned cat populations is trap–neuter–return (TNR). TNR involves trapping unowned cats, sterilizing and sometimes vaccinating them, marking processed individuals (e.g. by 'ear-tipping', removing the tip of an ear), and then releasing them into the environment.

The goal of TNR is to sterilize enough unowned cats so that reproduction is reduced and populations decline as cats eventually die. However, there is little rigorous evidence

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indicating TNR reduces cat populations (Longcore et al. 2009, Lepczyk et al. 2010, Hostetler et al. 2020). In fact, some studies indicate that TNR can result in increases in unowned cat populations due to food provisioning, illegal cat abandonment, and reproduction, immigration, and/or attraction of intact cats from surrounding areas (Castillo and Clarke 2003, Gunther et al. 2011). Many studies appearing to suggest TNR's effectiveness (Centonze and Levy 2002, Kreisler et al. 2019) are based on incomplete data reporting and anecdotal observations (e.g. by TNR colony caretakers), rather than robust scientific approaches to estimate changes in animal abundance. Proponents of TNR often claim its effectiveness using metrics that do not necessarily relate to free-ranging cat abundance (e.g. numbers of cats taken into or euthanized in shelters) (Spehar and Wolf 2018, Kreisler et al. 2019). Even when assuming cat populations are closed to immigration and abandonment, a situation that rarely occurs in mainland areas (Hostetler et al. 2020), demographic modeling studies suggest that reduction of populations requires a high percentage of unowned cats to be sterilized (e.g. 71–94%; Foley et al. 2005). Funding and logistical constraints prevent most TNR programs from achieving this sterilization level. Indeed, sterilization only appears to be effective if measures are also taken to prevent cat immigration and abandonment into the population and if large numbers of cats are permanently removed (e.g. by adoption and euthanasia) (Levy et al. 2003, Natoli et al. 2006, Spehar and Wolf 2017, 2018, Crawford et al. 2019).

Longitudinal studies that use rigorous scientific methods to estimate cat population abundance are needed to increase understanding of whether TNR can reduce unowned cat populations. To contribute to addressing this research gap, we used trail cameras to estimate changes in cat abundance and the percentage of sterilized cats between the first and fifth years of operation of a TNR program in Stillwater, OK, USA. Specifically, in 2018, we repeated methods of an earlier study conducted in 2014, one year after the TNR program was initiated (Elizondo and Loss 2016). This past study included a stratified random approach to sample cat abundance, estimated 62 total cats across 15 camera locations, and included zero observations of sterilized cats. Based on existing literature showing limited evidence of TNR's effectiveness, as well as Elizondo and Loss (2016) documenting no sterilized cats, we hypothesized that following five years of TNR there would be no significant decrease in cat abundance and only marginal increases in the percentage of sterilized cats.

## Material and methods

### Study area

We conducted trail camera surveys in Stillwater, Oklahoma, USA (Fig. 1), a small urban area of 76.5 km<sup>2</sup> with an estimated human population of 50 941 (World Population Review 2020). As in most US cities, Stillwater has an abundant free-ranging cat population. Although the total number of cats and percentages of owned free-ranging pets and unowned cats are unknown, local abundances can be exceptionally high (e.g. 15 individuals at one location in Eli-

zondo and Loss 2016). Organized cat feeding and sheltering stations/colonies are relatively rare in Stillwater, in part due to the nature of TNR activities in the study area. Specifically, unlike in many other cities, TNR program in Stillwater does not solely focus on trapping cats from such colonies, nor does it include establishment of feeding or sheltering colonies at release locations. Nonetheless, some residents feed cats at or near their homes, and cats are present across the entire city from its central downtown area to the outlying exurban edge. The coyote *Canis latrans*, a species that influences the distribution and abundance of cats (Kays et al. 2015), is also common around the city's periphery. Yet, out of 13 022 total photographs taken in this and the earlier study, we have captured only one image of a coyote, so the relationship between coyote and cat populations is unclear in the study area.

Since 2013, the College of Veterinary Medicine at Oklahoma State University (OSU) has run a TNR program known as 'Operation Catnip' that conducts sterilization clinics one Sunday each month during the academic year (mid-August to early-May). Clinics are run by volunteers, including pre-vet and vet students and community members; third- and fourth-year vet students typically perform sterilization surgeries. Members of the public are issued traps with which they capture cats in their neighborhood, and on the Saturday before each sterilization clinic, Operation Catnip volunteers also trap at locations where unowned cats have been reported by members of the public through an online form. Thus, unlike some TNR programs in other cities, trapping and release locations are broadly dispersed across the city (and even up to 30 miles away), and not focused on particular locations or cat colonies. A maximum of 200 cats are sterilized in each Sunday clinic. Before surgery, cats are checked for wounds, upper respiratory infections, pregnancy and microchips indicating ownership. Cats are then sterilized and given a rabies vaccine, and surgeons clip one ear (i.e. ear-tipping) (Fig. 2) to show they have been sterilized. All cats are then released at the location where they were captured (i.e. no new feeding or shelter stations are formed).

In 2014, Elizondo and Loss (2016) conducted a study that provided a basis for our study design, as well as baseline estimates of cat abundance and the percentage of sterilized individuals. In that study, 15 camera locations were selected based on two criteria. First, locations were selected to capture a gradient of urban development intensity; five cameras each were placed in high, medium and low urban density categories (USGS 2011). Second, these 15 locations were selected to avoid two known locations where, at the time, members of the public provided large quantities of food, resulting in high-density clusters/colonies of cats. Cameras were not placed in these areas because sampling at them would have greatly inflated abundance estimates and limited the ability to evaluate cat abundance patterns relative to urbanization. Other than the above criteria, camera locations were selected irrespective of other feeding efforts and other food sources (e.g. dumpsters); this resulted in sampling of broad variation in cat abundances. For this study, we sought to match sampling locations as closely as possible to those in the original study. Specifically, 12 of the 15 locations were exactly the same as in Elizondo and Loss (2016); for the remaining three locations, access or permission issues required us to move

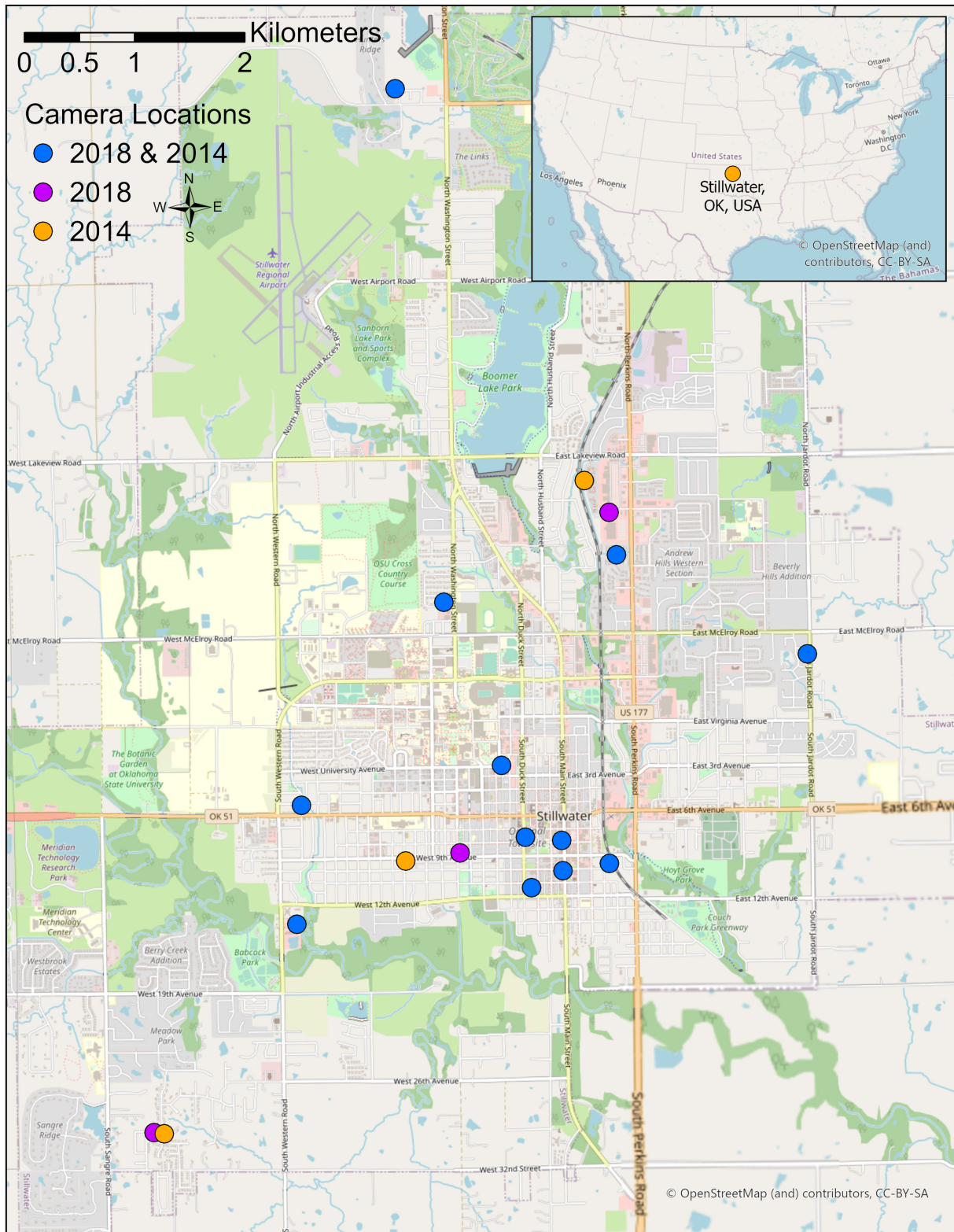


Figure 1. Map of 15 trail camera locations used in 2018 in Stillwater, OK, USA, to assess changes in cat abundance and sterilization percentages compared to an earlier study in 2014. Locations were selected in 2014 with a stratified random sampling approach capturing three levels of urban development intensity; in 2018, 12 camera locations were exactly the same as those used in 2014 and three were moved  $\leq 0.5$  km away (within the same urban development category) due to access/permission issues.

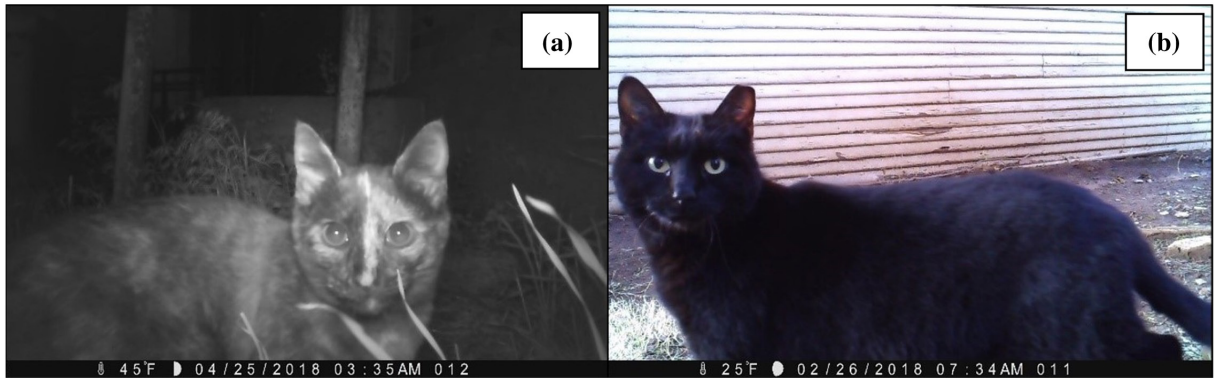


Figure 2. Examples of free-ranging domestic cats observed in Stillwater, OK, USA, showing: (a) an individual that has not been sterilized by a TNR program (note absence of ear-tip) and (b) a cat that has been sterilized (note presence of ear-tip on cat's left ear, or right ear as viewed in picture).

camera locations  $\leq 0.5$  km from original points and within the same category of urban development intensity (all sampling locations shown in Fig. 1).

### Field methods and statistical analyses

Full methodological details regarding trail camera protocols have been covered previously (Elizondo and Loss 2016). Briefly, at each of the 15 locations, we used a single trail camera (Browning Range Ops Series, model BTC-1) placed approximately 0–1 m above the ground, and when possible, angled towards buildings and corners between fences and buildings. We avoided tall vegetation that would cause visual obstruction and camera triggers. We programmed cameras to record three photographs for each trigger event, with a 3 s delay between photos and 30 s between trigger events. We baited each camera location using 1.5–2 ounces of canned tuna placed 1 m in front of the camera, which allowed for full-body photographs of cats to be taken while still being close enough to detect pelage characteristics. Between 25 February and 25 April 2018 (our primary sampling session for the below-described mark–resight analysis), we conducted three secondary sampling sessions, each spanning three consecutive nights and days and exactly one month apart from each other. We placed and baited trail cameras at least 1 h before sunset on the first night, rebaited each camera approximately 24 and 48 h later, and collected all cameras approximately 72 h after setup.

Following collection of trail cameras at the end of each secondary sampling period, we downloaded and sorted photos based on location. Individual cats were identified using pelage patterns, body shape, size (relative to surrounding permanent objects) and other defining features (e.g. presence of collars or ear-tipping) (Bengsen et al. 2011, Elizondo and Loss 2016). Similar to Elizondo and Loss (2016) and a previous study of melanistic leopards *Panthera pardus* (Hedges et al. 2015), the infrared images revealed striping patterns on cats with partly or entirely black pelages; however, these cryptic patterns were not distinct enough to contribute to identification. Therefore, for each camera location, we assumed there were as many black cats as the greatest number simultaneously seen in a single image. We created capture histories for all individuals across the three secondary sampling periods. We considered the first secondary session

to be the ‘marking’ (i.e. sighting) period and marked cats that were re-sighted in subsequent sessions to be recaptures.

We estimated cat abundance, accounting for detection probability, using program MARK (White and Burnham 1999). We used the Poisson log-normal mark–resight model because cats were individually identifiable, because we did not know the exact number of cats marked at the beginning of the first re-sighting period (i.e. some ‘marked’ cats could have died between the marking period and first re-sighting period), and because camera trapping is equivalent to sampling with replacement (i.e. secondary periods cannot be broken into discrete sampling events in which each individual has only a single chance to be captured) (McClintock et al. 2009, McClintock and White 2012, Elizondo and Loss 2016). We assumed the cat population was closed and that individual cat survival rates were constant during the primary sampling period. We also assumed trail cameras did not deter cats, as cats were likely acclimated to an urban setting with frequent human disturbances and abundant human-provided food. We conducted a paired samples t-test in R ver. 3.4.4 (<[www.r-project.org](http://www.r-project.org)>) to compare estimated cat abundances per camera from Elizondo and Loss (2016) to estimated cat abundances from the current study ( $n=15$  camera locations in both studies). For the three relocated sampling points, we paired data with each respective original point  $\leq 0.5$  km away.

### Results

We screened 9742 total photographs, including over 1254 capture events with at least one cat (range of cats per capture = 1–2). All cats that we observed could be identified as individuals based on pelage patterns, shape and relative size. We identified 35 individual cats, which resulted in a mean raw estimate of 2.3 cats per site (standard deviation [SD] = 1.4; range = 0–4), compared to 47 individuals and a mean of 3.1 cats per site (SD = 3.3; range = 0–14) from 3280 photographs in Elizondo and Loss (2016). As in Elizondo and Loss (2016), we observed no kittens (i.e. cats that are noticeably smaller), and unlike that study, which observed one cat at two different camera locations, all individuals only appeared at one location. Of cats we observed, 6 (17.1%) were ear-tipped, indicating sterilization (compared to zero ear-tipped in Elizondo

and Loss 2016), and 24 (68.6%) were not ear-tipped; for 5 cats (14.3%), images were not clear enough to determine if they had been ear-tipped. Additionally, eight cats had collars, indicating that at least 22.9% were owned pets.

After correcting for detectability with the mark–resight analysis, we estimated a total of 48 cats across the 15 camera locations (mean per location = 3.2 cats; median = 2.5; SD = 2.7; range = 0.0–9.9), compared to a detection-corrected estimate of 62 cats (mean = 4.1; median = 3.1; SD = 3.8; range = 0.0–14.9) in Elizondo and Loss (2016) (Fig. 3). There was no statistically significant difference between detection-corrected abundance estimates for the two studies ( $t = 0.83$ ;  $df = 14$ ;  $p = 0.42$ ). Compared to the observation of zero ear-tipped cats in Elizondo and Loss (2016), we estimate 27.3% sterilization based on raw counts of all ear-tipped cats (i.e. six ear-tipped out of 22 cats, excluding eight collared cats that were likely owned pets and unlikely to be targeted by TNR activities, and five cats for which images did not allow determination of ear-tipping status).

## Discussion

Using a standardized, replicated and randomized sampling approach that included trail cameras and mark–resight analyses to estimate cat abundance corrected for detection probability, we observed no significant change in free-ranging cat abundance between the first and fifth year after initiation of a TNR program in a small US urban area. We observed an increase in sterilized unowned cats from 0 to 27%, but this percentage remains well below estimated sterilization thresholds needed for TNR to reduce cat populations (Foley et al. 2005). These results suggest that, in cities of similar size with comparable cat populations and TNR efforts, five years of trapping and sterilization is insufficient to reduce unowned cat populations.

Even when assuming that unowned cat populations are closed to abandonment and immigration, a scenario never documented in past TNR studies in mainland areas (Hostetler et al. 2020), demographic models indicate

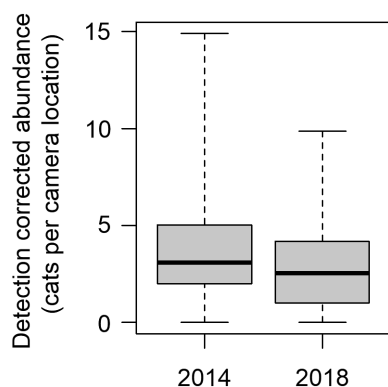


Figure 3. Comparison of free-ranging cat abundances estimated using trail cameras (with mark–resight analyses to correct for detectability) between 2014 and 2018 in Stillwater, OK, USA. Boldface horizontal lines indicate median abundance per camera location in each year; boxes indicate interquartile ranges, and whiskers indicate minimum and maximum values.

71–94% of unowned cats must be sterilized to reduce their populations (Foley et al. 2005). Further, many field studies indicate that TNR is only effective when combined with efforts to remove a large percentage of cats through adoption, euthanasia, and/or relocation. For example, in addition to sterilizing cats and releasing them back to the environment, 47% of cats were adopted out of the population in Levy et al. (2003), 18–80% were adopted in Crawford et al. (2019), 50% were euthanized in Andersen et al. (2004), 39% were adopted, euthanized or relocated in Spehar and Wolf (2017) and 43% were adopted or euthanized in Spehar and Wolf (2018). It is difficult to compare our estimated sterilization percentage to past studies because many studies evaluating TNR focus on other metrics like cat population size, cat intakes into shelters and numbers (but not percentages) of cats trapped and sterilized. Nonetheless, the sterilization percentage we estimate (27% over five years) is relatively low compared to studies reporting similar figures. For example, 70% of cats were sterilized over 18 months in Centonze and Levy (2002), 60% were sterilized over 10 years in Natoli et al. (2006) and 15% were sterilized each year in Lohr et al. (2012).

Assuming our random sample of camera locations is representative (i.e. that 27% of all cats in the study area are sterilized, equivalent to a linear increase in the cumulative sterilization percentage of 5.4% year<sup>-1</sup>), we estimate it would take at least 8–12 more years (or 13–17 years total from the program’s inception in 2013) to achieve the cumulative sterilization level of 71–94% from Foley et al. (2005). However, it is likely that even more time is required to reach this sterilization threshold or that it may never be achievable. This is because the above calculations assume no complicating factors that could further delay population eradication. These include: increased difficulty of trapping remaining cats if populations begin to decline; future reductions in TNR sterilization efforts (notably, this has already occurred in our study area, as the TNR program had paused their efforts between February and December of 2020 due to the SARS-CoV-2/COVID-19 pandemic); increased cat abandonment and colonization into the population and/or decreased adoption out of the population; density-dependent demographic responses to any achieved population declines (e.g. increased reproduction of unsterilized cats; decreased natural and human-caused mortality); and increases in populations of free-ranging pet cats (Lepczyk et al. 2010) with associated increases in interbreeding of unsterilized owned and unowned cats. Evidence that TNR requires even more time, or is unlikely to be successful at all, is provided by a modeling study of a volunteer-run TNR program (Lohr et al. 2012). Even when using a relatively high sterilization percentage of 15% year<sup>-1</sup> and assuming no immigration into the population, this study estimated that population extirpation would require 30 years of TNR; with immigration included, extirpation was modeled to be unachievable over any time frame assessed.

Factors specific to our study area should be considered when interpreting our results and their applicability to other TNR programs. Unlike many humane and animal welfare societies across the US, the Humane Society of Stillwater is not a ‘no-kill’ shelter (Humane Society of Stillwater 2020) and the city also has a separate organization that takes in

orphan kittens and does not release them back to the environment (D. Dutt, Tiny Paws Kitten Rescue, pers. comm.). The efforts of these two organizations may have contributed to the slight, but statistically non-significant, decline in cat abundance we observed, or they may have prevented an increase in abundance that can occur with TNR as a result of increased abandonment and colonization (Castillo and Clarke 2003). TNR programs in locations without such cat removal activities are likely to have a lower probability of success and require greater sterilization rates to reduce cat populations (Foley et al. 2005, Natoli et al. 2006, Crawford et al. 2019). Despite the existence of these other cat welfare programs, we believe our study design was capable of evaluating the effect of TNR by itself, since both the kitten rescue organization and humane society existed before the initiation of the TNR program in 2013 (i.e. these additional management efforts were essentially held constant over the period of our study).

Our study is relatively unique in having a broad spatial scope that involves estimation of cat population changes across an entire city. Most previous studies have evaluated TNR's effectiveness in discrete locations, such as one or more city parks, urban neighborhoods or TNR release locations where large numbers of cats are often provided food and shelter in colonies (Levy et al. 2003, Kilgour et al. 2017, Spehar and Wolf 2017, 2018, Crawford et al. 2019). This focus on discrete locations can overlook movements of and interactions between cats (such as territoriality) in the focal study area and surrounding areas – although our study still does not address such processes occurring at the interface between the city of Stillwater and its outlying areas. Although there are few large feeding and sheltering stations in our study area, it is unknown how our estimates of cat abundance and sterilization percentages are influenced by proximity to specific TNR trapping and release locations, including locations that may have been targeted on more than one occasion during the study period. However, our adherence to the original stratified random sampling approach (i.e. 12 of 15 cameras in the exact same locations; three cameras moved < 0.5 km away), makes it unlikely that our abundance estimates were systematically biased in relation to such locations. Furthermore, we argue that our approach is valid given that the stated goal of many TNR programs is not only to reduce local cat colonies, but also to contribute to large scale reductions in cat populations (e.g. across entire cities).

Our study has limitations that could be addressed in future research. We may have lacked sufficient replication of sampling locations, and thus statistical power, to detect changes in cat abundance. Future studies should seek to increase replication, and adding additional cameras that are more closely spaced would allow detailed tracking of individuals across multiple camera locations, and thus, the use of sophisticated analytical approaches like spatial capture–recapture methods (Cove et al. 2018). Another limitation is that during both 2014 and 2018, we only sampled cat populations over an approximately two month period during late-winter and early spring; this sampling window is shorter than other urban studies that used cameras to detect cats (Castillo and Clarke 2003, Kays et al. 2015). This approach generates a snapshot of cat abundance that allows rough

comparisons among years. However, future year-round research would provide a more comprehensive understanding of TNR's effectiveness throughout the entire year (e.g. in association with seasonal variation in TNR efforts and demographic processes in the free-ranging cat population). For the purposes of the mark–resight analysis, we assumed the cat population was closed; this assumption could have been violated as a result of processes such as those described above (e.g. adoption, intakes of orphaned kittens), as well as immigration and emigration of cats into and out of the population. We expect that cat reproduction and kitten removal would have relatively little influence on the degree to which this assumption is met in our study. Most cat reproduction in our study area appears to occur after the February to April period in which we sampled (peak kitten intakes by Tiny Paws Kitten Rescue are typically from May to August; D. Dutt, pers. comm.), and the short length of our sampling period also reduces the probability that this assumption would be violated. Moreover, because we used the same sampling and analysis methods as in Elizondo and Loss (2016), any bias introduced by violation of this assumption (e.g. due to factors like immigration/emigration) should not greatly affect conclusions about changes in cat abundance between 2014 and 2018.

## Conclusions and management recommendations

TNR is often portrayed to policymakers and the public as the only effective and publicly acceptable approach to reduce unowned cat populations. Yet, many studies used to support TNR and/or argue against lethal control methods include activities other than cat sterilization, such as adoption programs and even lethal control by euthanasia (Levy et al. 2003, Andersen et al. 2004, Spehar and Wolf 2017, 2018). This study adds to the growing body of literature indicating that TNR by itself is not an effective population control method for cats in the vast majority of cases (Andersen et al. 2004, Schmidt et al. 2009, Lohr et al. 2012, Hostetler et al. 2020). Even with many years of TNR efforts, sterilization percentages are likely to remain well below levels needed to result in significant, large-scale reductions in unowned cat populations. A thorough review of TNR alternatives is beyond the scope of this paper and has been provided elsewhere (Lepczyk et al. 2015, Loss and Marra 2017). However, given the ineffectiveness of TNR, as well as studies showing that other management approaches (including humane lethal methods) are both publicly acceptable (Lohr et al. 2014) and can contribute to cat population reductions, we argue there is a need to consider implementation of cat management approaches other than TNR. Furthermore, proponents of TNR also tend to ignore how returning cats to the outdoors continues to result in adverse effects on wildlife (through predation, fear effects and disease) and human health (through diseases like toxoplasmosis), issues which may be alleviated through alternative management efforts. Rigorous scientific monitoring of cat management approaches is also needed to evaluate, and if necessary, to adapt cat management efforts, such that cat populations and associated harmful effects to wildlife and humans are reduced.

**Acknowledgements** – We thank L. Chaffin and K. G. Elmore for fieldwork assistance, M. R. Elliston for providing information about Operation Catnip, D. Dutt of Tiny Paws Kitten Rescue in Stillwater for providing information about kitten intake, and Stillwater homeowners and business owners for allowing trail cameras on their property both in 2014 and 2018.

**Funding** – This study was funded by Oklahoma State University's Department of Natural Resource Ecology and Management and by the National Institute of Food and Agriculture (United States Department of Agriculture) Hatch Grant Funds through the Oklahoma Agricultural Experiment Station (OKL-02915). ECE also received funding to conduct the 2014 study from the Oklahoma Louis Stokes Alliance for Minority Participation and the Oklahoma Ornithological Society. JAE was supported by the Dr. Fritz L. Knopf Doctoral Fellowship.

## References

- Andersen, M. C. et al. 2004. Use of matrix population models to estimate the efficacy of euthanasia versus trap–neuter–return for management of free-roaming cats. – *J. Am. Vet. Med. Assoc.* 225: 1871–1876.
- Baker, P. et al. 2010. Domestic cat (*Felis catus*) and domestic dog (*Canis familiaris*). – In: Gehrt, S. D. et al. (eds), *Urban carnivores: ecology, conflict and conservation*. Johns Hopkins Univ. Press, pp. 157–172.
- Balogh, A. L. et al. 2011. Population demography of gray catbirds in the suburban matrix: sources, sinks and domestic cats. – *J. Ornithol.* 152: 717–726.
- Beckerman, A. P. et al. 2007. Urban bird declines and the fear of cats. – *Anim. Conserv.* 10: 320–325.
- Bengsen, A. et al. 2011. Estimating and indexing feral cat population abundances using camera traps. – *Wildl. Res.* 38: 732.
- Blancher, P. 2013. Estimated number of birds killed by house cats (*Felis catus*) in Canada. – *Avian Conserv. Ecol.* 8: 3.
- Blanton, J. D. et al. 2007. Rabies surveillance in the United States during 2006. – *J. Am. Vet. Med. Assoc.* 231: 540–556.
- Bonnington, C. et al. 2013. Fearing the feline: domestic cats reduce avian fecundity through trait-mediated indirect effects that increase nest predation by other species. – *J. Appl. Ecol.* 50: 15–24.
- Calvert, A. M. et al. 2013. A synthesis of human-related avian mortality in Canada. – *Avian Conserv. Ecol.* 8: 11.
- Castillo, D. and Clarke, A. L. 2003. Trap/neuter/release methods ineffective in controlling domestic cat 'colonies' on public lands. – *Nat. Areas J.* 23: 247–253.
- Centonze, L. A. and Levy, J. K. 2002. Characteristics of free-roaming cats and their caretakers. – *J. Am. Vet. Med. Assoc.* 220: 1627–1633.
- Cove, M. V. et al. 2018. Free-ranging domestic cats (*Felis catus*) on public lands: estimating density, activity and diet in the Florida Keys. – *Biol. Invas.* 20: 333–344.
- Cove, M. V. et al. 2019. Towards recovery of an endangered island endemic: distributional and behavioral responses of Key Largo woodrats associated with exotic predator removal. – *Biol. Conserv.* 237: 423–429.
- Crawford, H. M. et al. 2019. A case of letting the cat out of the bag – why trap–neuter–return is not an ethical solution for stray cat (*Felis catus*) management. – *Animals* 9: 171.
- Doherty, T. S. et al. 2016. Invasive predators and global biodiversity loss. – *Proc. Natl Acad. Sci. USA* 113: 11261–11265.
- Elizondo, E. C. and Loss, S. R. 2016. Using trail cameras to estimate free-ranging domestic cat abundance in urban areas. – *Wildl. Biol.* 22: 246–252.
- Foley, P. et al. 2005. Analysis of the impact of trap–neuter–return programs on populations of feral cats. – *J. Am. Vet. Med. Assoc.* 227: 1775–1781.
- Gerhold, R. W. and Jessup, D. A. 2012. Zoonotic diseases associated with free-roaming cats. – *Zoonoses Public Health* 60: 189–195.
- Gunther, I. et al. 2011. Demographic differences between urban feeding groups of neutered and sexually intact free-roaming cats following a trap–neuter–return procedure. – *J. Am. Vet. Med. Assoc.* 238: 1134–1140.
- Hedges, L. et al. 2015. Melanistic leopards reveal their spots: infrared camera traps provide a population density estimate of leopards in Malaysia. – *J. Wildl. Manage.* 79: 846–853.
- Hostetler, M. et al. 2020. How effective and humane is trap–neuter–release (TNR) for feral cats? – Univ. of Florida IFAS Extension, Publication #WEC423. <<https://edis.ifas.ufl.edu/uw468>>, accessed 8 Dec 2020.
- Humane Society of Stillwater. 2020. Mission statement. – <[www.hspets.org/page/home/about-us/mission-statement](http://www.hspets.org/page/home/about-us/mission-statement)>, accessed 8 Dec 2020.
- Kays, R. et al. 2015. Cats are rare where coyotes roam. – *J. Mammal.* 96: 981–987.
- Kilgour, R. J. et al. 2017. Estimating free-roaming cat populations and the effects of one year trap–neuter–return management effort in a highly urban area. – *Urban Ecosyst.* 20: 207–216.
- Kreisler, R. E. et al. 2019. Corrigendum: Decrease in population and increase in welfare of community cats in a twenty-three year trap–neuter–return program in Key Largo, FL: the ORCAT program. – *Front. Vet. Sci.* 6: 7.
- Lepczyk, C. A. et al. 2010. What conservation biologists can do to counter trap–neuter–return: response to Longcore et al. – *Conserv. Biol.* 24: 627–629.
- Lepczyk, C. A. et al. 2015. A review of cat behavior in relation to disease risk and management options. – *Appl. Anim. Behav. Sci.* 173: 29–39.
- Levy, J. K. et al. 2003. Evaluation of the effect of a long-term trap–neuter–return and adoption program on a free-roaming cat population. – *J. Am. Vet. Med. Assoc.* 222: 42–46.
- Lohr, C. A. et al. 2012. Costs and benefits of trap–neuter–release and euthanasia for removal of urban cats in Oahu, Hawaii. – *Conserv. Biol.* 27: 64–73.
- Lohr, C. A. et al. 2014. Identifying people's most preferred management technique for feral cats in Hawaii. – *Hum.-Wildl. Interact.* 8: 56–66.
- Longcore, T. et al. 2009. Critical assessment of claims regarding management of feral cats by trap–neuter–return. – *Conserv. Biol.* 23: 887–894.
- Loss, S. R. and Marra, P. P. 2017. Population impacts of free-ranging domestic cats on mainland vertebrates. – *Front. Ecol. Environ.* 15: 502–509.
- Loss, S. R. et al. 2013. The impact of free-ranging domestic cats on wildlife of the United States. – *Nat. Comm.* 4: 1396.
- Loss, S. R. et al. 2015. Direct mortality of birds from anthropogenic causes. – *Annu. Rev. Ecol. Evol. Syst.* 46: 99–120.
- McClintock, B. T. and White, G. C. 2012. From NOREMARK to MARK: software for estimating demographic parameters using mark–resight methodology. – *J. Ornithol.* 152: 641–650.
- McClintock, B. T. et al. 2009. A generalized mixed effects model of abundance for mark–resight data when sampling is without replacement. – In: Thomson, D. L. et al. (eds), *Modeling demographic processes in marked populations*. Springer Publishing, pp. 271–289.
- Medina, F. M. et al. 2011. A global review of the impacts of invasive cats on island endangered vertebrates. – *Global Change Biol.* 41: 3503–3510.
- Natoli, E. L. et al. 2006. Management of feral domestic cats in the urban environment of Rome (Italy). – *Prev. Vet. Med.* 77: 180–185.
- People for the Ethical Treatment of Animals [PETA] 2015. 14 billion reasons to keep cats inside. – <[www.peta.org/features/keep-cats-inside/](http://www.peta.org/features/keep-cats-inside/)>, accessed 8 Dec 2020.



- Schmidt, P. M. et al. 2009. Evaluation of euthanasia and trap–neuter–return (TNR) programs in managing free-roaming cat populations. – *Wildl. Res.* 36: 117.
- Shi, J. et al. 2020. Susceptibility of ferrets, cats, dogs and other domesticated animals to SARS–coronavirus 2. – *Science* 368: 1016–1020.
- Spehar, D. and Wolf, P. 2017. An examination of an iconic trap–neuter–return program: the Newburyport, Massachusetts case study. – *Animals* 7: 81.
- Spehar, D. and Wolf, P. 2018. A case study in citizen science: the effectiveness of a trap–neuter–return program in a Chicago neighborhood. – *Animals* 8: 14.
- The Humane Society of the United States 2020. Our position on cats. – <[www.humanesociety.org/resources/our-position-cats](http://www.humanesociety.org/resources/our-position-cats)>, accessed 8 Dec 2020.
- The Wildlife Society 2020. TWS issue statement: feral and free-ranging domestic cats. – <<https://wildlife.org/tws-issue-statement-feral-and-free-ranging-domestic-cats/>>, accessed 8 Dec 2020.
- United States Geological Survey [USGS] 2011. U.S. GAP/LANDFIRE national terrestrial ecosystems. – <<https://doi.org/10.5066/F7ZS2TM0>>, accessed 8 Dec 2020.
- Van Heezik, Y. et al. 2010. Do domestic cats impose an unsustainable harvest on urban bird populations? – *Biol. Conserv.* 143: 121–130.
- White, G. C. and Burnham, K. P. 1999. Program MARK: survival estimation from populations of marked animals. – *Bird Study* 46: 120–139.
- World Population Review 2020. Stillwater, Oklahoma population 2020. – <<https://worldpopulationreview.com/us-cities/stillwater-ok-population>>, accessed 8 Dec 2020.