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Using trail cameras to estimate free-ranging domestic cat abundance in urban areas

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The domestic cat *Felis catus* is one of the most ecologically harmful invasive species on earth. Predation by free-ranging cats poses a serious global threat to small vertebrates and is a leading source of anthropogenic mortality for birds and small mammals in North America. However, little is known about the size of cat populations, especially in urban areas where both cats and wildlife are abundant. Methods to quantify free-ranging cat populations are needed to understand the magnitude of threats facing wildlife populations and to inform decisions about prioritizing conservation and cat population management. We assessed the utility of trail cameras and sight–resight analysis for estimating free-ranging cat abundance in a small urban area (Stillwater, OK, USA). We also evaluated whether relationships exist between cat abundance and both urban development intensity and human population density. Even with relatively large cat populations, we identified the vast majority (~96.5%) of individual cats in both day-time and night-time photos. We found no relationship between cat abundance and either urban development intensity or human population density. This finding combined with the large numbers of cats observed suggests that cats may be abundant in our study area regardless of urban context. Sampling free-ranging cat populations across a broad range of urbanization intensities that capture a variety of human behaviors and/or cat management policies is needed to shed light on the drivers of cat population abundance. Trail cameras show promise as a highly useful tool for achieving this objective in the context of wildlife conservation management.

Free-ranging domestic cats *Felis catus* present a global threat to small vertebrates (Medina et al. 2011, Blancher 2013, Loss et al. 2013). Free-ranging cats include those that are unowned and completely independent of humans (i.e. feral cats), those that live outdoors but are partially subsidized by humans that provide food and/or shelter (i.e. semi-feral cats), and those that are owned but given outdoor access (i.e. free-ranging pet cats) (Baker et al. 2010). Free-ranging cats cause direct wildlife mortality by predation (Baker et al. 2005, Van Heezik et al. 2010, Balogh et al. 2011) and indirect "fear effects" that alter animal behavior and can decrease fecundity of small wildlife species (Beckerman et al. 2007, Bonnington et al. 2013). In the US alone, free-ranging cats are estimated to kill 1.3–4 billion birds and 6.3–22.3 billion mammals each year, and are likely the single greatest source of direct anthropogenic mortality for these taxa (Loss et al. 2013). Reptiles and amphibians can also comprise a large portion of domestic cat kills (Mitchell and Beck 1992, Read and Bowen 2001, Loyd et al. 2013), and preliminary US estimates of annual mortality are in the hundreds of millions for both taxa (Loss et al. 2013).

The broad range of uncertainty in national cat predation estimates is primarily due to a lack of information about the abundance of feral cat populations (Blancher 2013, Loss et al. 2013). Populations of free-ranging pet cats can be estimated from a combination of: 1) national surveys of the number of pet cats (American Pet Products Association 2011, American Veterinary Medical Association 2012), and 2) empirical studies that estimate the proportion of pet cats allowed outdoors (American Pet Products Manufacturers 1997, Marketing and Research Services 1997, Levy et al. 2003, Lepczyk et al. 2004, American Bird Conservancy 2012). For example, the US pet cat population has been placed at roughly 90 million, of which 40–80% (36–72 million cats) are allowed outdoors (Lepczyk et al. 2010, Loss et al. 2013). Unlike free-ranging pets, estimates of the abundance of feral and semi-feral cat populations – which range from 30 to 120 million (reviewed by Loss et al. 2013) – are entirely speculative.

Estimating abundance of cat populations, along with drivers of spatio-temporal variation in abundance, has important implications for wildlife and cat management, including in urban areas. Urban areas provide significant habitat for wildlife (Lepczyk and Warren 2012, Belaire et al. 2014) and harbor large numbers of cats (Levy et al. 2003, Lepczyk et al. 2004, Baker et al. 2005, Natoli et al. 2006). Information about free-ranging cat numbers facilitates quantification of predation mortality (Loss et al. 2013) and should provide an approximation of the threat cats pose to wildlife populations. Rigorously quantified cat abundance estimates could also be used to support decisions about where and when to enact cat population management and to determine whether various management measures can successfully reduce populations. These often controversial decisions and determinations of success are typically based on anecdotal observations of cat abundance, not carefully collected and objective data (Longcore et al. 2009).

Other components of free-ranging cat biology have been investigated in urban areas. Studies have assessed habitat use and movements of cats and documented, for example, that they spend relatively little time within forested areas and instead select for gardens and edges of undeveloped areas (Kays and DeWan 2004, Van Heezik et al. 2010, Gehrt et al. 2013). Furthermore, cat population abundance in urban areas has been shown to increase with housing density (Sims et al. 2008, Thomas et al. 2012) and to be related to socioeconomic traits of urban residents (Murray et al. 2010). Despite these valuable studies, further elucidation of the drivers of cat population abundance in urban areas is needed, and this effort relies on effective and efficient methods for estimating cat abundance.

A promising approach for estimating free-ranging cat abundance is the use of trail cameras to conduct sight–resight analysis (Glen et al. 2014, McGregor et al. 2015). Trail cameras have been used to estimate free-ranging cat numbers in rural settings (Bengsen et al. 2011, 2012, Jones and Downs 2011, Glen et al. 2014, McGregor et al. 2015), but the relatively high abundance of free-ranging cats in urban areas could complicate the identification of individual cats, a crucial step for sight–resight analyses. Furthermore, although trail cameras have been used to study free-ranging cats, no explicit treatment of the advantages and disadvantages of this technology – along with trouble-shooting approaches – has been presented in the context of potential broad application to urban wildlife research and management. Thus, our primary objective was to assess whether trail cameras and sight–resight techniques can be used to estimate abundance of free-ranging cats in an urban setting. Secondarily, we analyzed whether cat abundance varies predictably with urbanization intensity and human population density in a small US city. Our results provide an illustration of the potential uses, limitations, and data needs for efficient and effective use of this technology.

Methods

Study area

The study area for this research was the city of Stillwater, Oklahoma, USA. Stillwater is approximately 75 km^2, has a population of approximately 46 000 people, and is in central Oklahoma near the intersection of the Central Great Plains, Flint Hills and Cross Timbers Level III Ecoregions (United States Environmental Protection Agency 2015). According to US Geological Survey GAP Analysis data (United States Geological Survey 2012), urban land cover categories in the study area include "developed, high intensity" (hereafter, high intensity), "developed, medium intensity" (hereafter, medium intensity) and "developed, low intensity" and "developed, open space" (hereafter, both considered low intensity).

Stillwater hosts an active trap–neuter–return (TNR) program for cats ('Operation Catnip') which captures feral and semi-feral cats and spays/neuters, vaccinates and marks them by removing the tip of their ear (i.e. 'ear tipping') before releasing them at points of capture. Additionally, there are several locations in Stillwater at which citizens supplement free-ranging cats with food, thus creating high density cat colonies in localized areas. We used information provided by Operation Catnip about known locations of release points and cat colonies to avoid placing cameras near large concentrations of cats (i.e. ≥ 10 known cats in one colony or released at one point). Because we avoided these clusters of cats, our estimates are likely to be low-end figures for the study area. Within remaining acceptable areas, we asked homeowners and business-owners in each of the above urbanization intensity categories for permission to use their property as a study site. From among the properties we were allowed to access, we selected five sites in each of the three urbanization intensity categories while still meeting constraints related to colony locations. Within each urbanization intensity category, and to minimize spatial autocorrelation between sampling points, we also chose sites to be as far apart as possible within these constraints. Because Stillwater has a relatively small core area of high density development, our high intensity sites were all located within a 1.13 km^2 area.

Field methods

We placed a single infrared-equipped trail camera (Browning Range Ops Series, model BTC-1) at each site. We placed trail cameras 0–1 m above the ground and angled toward buildings and corners when possible to control the angle from which cats entered the camera's frame (Fig. 1) and to capture a horizontal detection width of 1.5–3.0 m. We avoided tall vegetation to prevent visual obstruction of the trail camera and false triggers from vegetation movement. We programmed cameras to record four photographs for each trigger event, with a 3 s delay between photos and 30 s between trigger events.

We baited each trail camera location using canned tuna placed 1 m from the camera. We selected tuna as bait because preliminary sampling showed that its scent attracts cats even after the bait has been consumed. The distance between the camera and bait allowed for full-body photographs of cats to be taken while still being close enough to detect pelage characteristics. Visual lures have previously been used to attract free-ranging cats to trail cameras in open landscapes (Bengsen et al. 2011). However, because our study was conducted in an urban area with many visual obstructions (e.g. fences and buildings), a visual lure was not useful.

Our primary sampling session consisted of a two month period between 23 February and 21 April 2014. Within the

Figure 1. A night-time trail camera image illustrating the typical side view of cats captured based on the camera set up approach used in the Stillwater, OK study area; the image is of an orange tabby patterned cat, which we were able to determine because a single collared individual appeared in both day-time and night-time photos at one site.

primary sampling session, there were three secondary sampling sessions, each roughly one month apart and spanning three consecutive nights and days. We placed trail cameras at approximately 1 h before sunset on the first night and collected them 72 h later. We baited each site on the first night with 1.5–2 ounces of tuna and re-baited in a similar manner 1–2 h before sunset on each subsequent night of the sampling session.

Data analysis

We examined photographs from each site and identified individual cats using pelage patterns, body shape, size (relative to surrounding permanent objects), and other defining features, such as collars (Bengsen et al. 2011). In some cases, we were unable to identify entirely black cats as individuals using these criteria; however, overall body size and presence/absence of collars were both useful characteristics for confirming the identification of several black cats. Similar to a previous study of melanistic leopards *Panthera pardus* (Hedges et al. 2015), the infrared images revealed striping patterns on cats with partially black or entirely black pelages (Supplementary material Appendix 1 Fig. A1–A2); however these cryptic patterns were not distinct enough to contribute to identification. We therefore assumed that sites with black cats were visited by only one cat of that pelage type unless distinguishing features were present or multiple black cats were captured in the same photograph. In the latter case, we assumed there were as many black cats as the greatest number simultaneously seen in one photo. Under this assumption, all but two cats were identifiable as individuals. For all cats identified to individual, we created capture histories across the three secondary sampling periods. We considered the first secondary session the ‘marking’ (i.e. sighting) period, and we considered marked cats that were re-sighted in subsequent sessions to be recaptures.

To generate cat abundance estimates, we used the Poisson log-normal mark–resight model in MARK (program MARK, <http://warnercnr.colostate.edu/~gwhite/mark/mark.htm>, accessed 9 March 2016). We chose this model because: 1) cats were individually identifiable (see Results), 2) 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 the first re-sighting period), and 3) camera trapping approaches are equivalent to sampling with replacement (i.e. secondary periods cannot be broken into discrete sampling events during which each individual has only a single chance to be captured) (McClintock et al. 2009, McClintock and White 2012). This model allowed us to account for detectability of cats as well as for seen, unidentifiable individuals. Only one cat was seen at more than one site, and we treated this cat as a new individual at both sites. As required by the Poisson log-normal mark–resight model, we assumed a closed population of cats throughout the primary sampling period and that survival rates did not differ between individuals. We also assumed that trail cameras did not repel cats from the sites, as cats were likely acclimated to an urban setting characterized by frequent anthropogenic disturbances and abundant human-provided food sources. Additionally, we assumed that each individual cat was equally likely to be captured, an assumption which we further describe in the Discussion. We used point estimates of cat abundance from each site for subsequent statistical analyses.

All statistical analyses were conducted using R ver. 3.0.1 (<www.r-project.org>). We compared cat abundance among the three urbanization intensity categories using a one-way ANOVA test. Cat abundance was ($\ln + 1$) transformed to meet normality assumptions. Because there was a high statistical outlier of cat abundance (Results), we repeated statistical analysis with and without the outlier. Because previous research has indicated a strong correlation between cat abundance and human population density in urban areas (Sims et al. 2008), we also used linear regression analyses to test whether cat abundance was related to human population density, both within the census block containing the camera and averaged across all census blocks within 500 m of the camera location. To characterize human population density at the above spatial extents, we used ArcGIS 10.1 (Environmental Systems Research Institute [ESRI], Redlands, California) and a previously developed spatial data layer that summarized 2010 US census data (Radeloff et al.

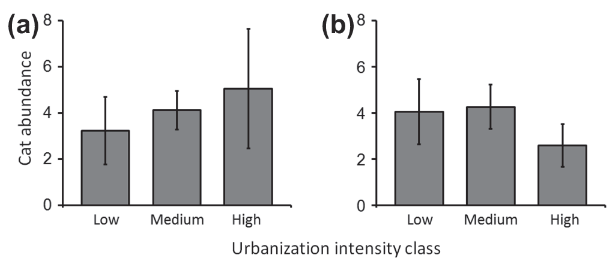

Figure 2. Comparison of domestic cat abundance (mean $\pm$ SE) among low, medium, and high intensity urban classes in Stillwater, OK (categories based on classifications of USGS Gap Analysis Program); analysis was repeated with a statistical outlier included (a) and excluded (b). The overall ANOVA model was significant in each case, but no pairwise comparisons were significant (all $p \geq 0.31$).

2010). Statistical significance for all analyses was judged at $\alpha = 0.05$.

Results

Across all 15 trail cameras and 135 total trap-days/nights, we identified a total of 47 cats as individuals (mean count = 3.1 cats per site, SD = 3.3, range = 0–14) from 820 camera trigger events (3280 total photos). Approximately 84% of images were night-time captures, but we still confidently identified an estimated 95.65% of all cats. Identification problems occurred primarily with black cats. We detected a minimum of nine black cats across sites, and given the assumptions discussed in the methods, we identified seven as individuals. On several occasions, two unidentified black cats appeared in the same photograph but were not distinguishable from one another when captured separately. All cats that appeared black or partially black during the day showed a melanistic tabby pattern in infrared images (i.e. faint striping was visible on black portions of the pelage). We confirmed this by viewing both day-time and night-time photos of partially-black cats with unique pelage patterns. Cats with an orange tabby pattern (Fig. 1) appeared completely white when captured at night, as determined by matching night-time and day-time photos of one collared individual. Other cat pelage types that we observed included gray, marbled, gray tabby, white and black, tortoiseshell, Siamese, and combinations of various pelage types (examples of pelage types in Supplementary material Appendix 1 Fig. A1–A10). Of the 47 identifiable cats, 44 were short-haired and 3 were long-haired. We detected 5 (10.9%) individuals that were collared, and although an active TNR program operates in Stillwater, we detected no ear-tipped cats. All cats appeared to be adults based on their large body size.

After accounting for detectability using sight–resight analysis, our abundance estimates averaged 4.14 cats per site (SD = 3.77, range = 0–14.89). The relatively small difference between raw counts and detectability-corrected abundances was likely a result of high recapture rates at each site (average recapture rate = 52.2%). We documented very little site-to-site movement of individuals, with only one individual recorded at two sites that were 0.2 km apart.

The overall ANOVA model indicated significant differences in cat abundance among urbanization intensity classes, both for the analysis that included all 15 sites ($F = 16.45$; $DF = 3,12$; $p < 0.01$) and the analysis without the high outlier ($F = 17.85$; $DF = 3,11$; $p < 0.01$). However, in both analyses, no pairwise comparisons among group means were statistically significant ($p \geq 0.45$ for all comparisons in full analysis; $p \geq 0.31$ for all comparisons with outlier removed). There was no significant relationship between cat abundance and human population density, either within the census block containing the camera (coefficient estimate = 0.0001 ± 0.0002 (SE); $t = 0.54$, $DF = 15$, $p = 0.61$) or averaged across census blocks within 500 m of the camera location (coefficient estimate = 0.0001 ± 0.0002 (SE); $t = 0.717$, $DF = 15$, $p = 0.49$).

Discussion

The vast majority of cats in our study area were individually identifiable using trail cameras. We encountered more pelage variation (at least nine pelage types) and higher abundances of cats than a similar rural study that documented 88.5% grey tabbies with only three other pelage patterns noted and a maximum of three cats per site (Bengsen et al. 2011). Thus, the use of trail cameras and sight–resight analysis appears to be highly useful for estimating the abundance of free-ranging cats in urban areas, even when cat populations are abundant. We found no relationship between cat abundance and either urban development intensity or human population density. However, our limited sample size of camera trapping sites likely influenced our statistical power to examine drivers of variation in cat abundance. Nonetheless, this result does not change our conclusion about the likely utility of trail cameras for estimating free-ranging cat abundance.

Using trail cameras to estimate cat abundance

The use of trail cameras appears to be an efficient and effective way to estimate cat abundance in urban areas. We found no clear indication that capture probability varied among individual cats, although more extensive observation of cat behavior near trail cameras may be needed to determine if and when this assumption is violated. We determined this through observations of the normal range of cat behaviors on cameras, which suggests that cameras were integrated into cats' home ranges and normal activities. For example, some cats rubbed their faces against cameras to scent mark them. We did observe one example of a large cat causing a smaller cat to leave the camera frame. However, the smaller cat returned in subsequent captures within the sampling period, and there was no evidence of a single cat remaining in an area once bait had been consumed. In many cases, multiple cats fed simultaneously at the same bait station without any agonistic interactions (e.g. hissing, fighting) observed. Furthermore, our use of relatively small amounts of tuna attracted cats without appearing to cause individuals to feed long enough to preclude other cats from entering the camera frame.

We were able to identify the vast majority of cats in our study, but our experience with black cats suggests that researchers in areas with high proportions of black cats, or of other types of uniformly colored cats, could have difficulty identifying individuals. This identification difficulty could translate into greater uncertainty in abundance estimates. Infrared images revealed subtle striping patterns on black portions of cat pelages; however, these patterns were not distinct enough to allow identification of individual cats. Further research is needed to determine whether the use of infrared images can help identify a greater proportion of black cats in some populations, as has been shown for melanistic leopards in Peninsular Malaysia (Hedges et al. 2015). Similarly, because we observed that cats with orange tabby patterns had no distinguishing characteristics at night, infrared captures of cats with this pelage type may also prove problematic when a larger number of such cats exist in a population.

Support for the assumption that the cat populations at our sites were closed at the time of the trail camera surveys was provided by: 1) the relatively high recapture rates we observed, which is indicative of relatively high survival rates, 2) the complete absence of kittens in camera images, suggesting limited recruitment during the study, and 3) the minimal site-to-site movement that we detected. Detectability-corrected abundance estimates were only slightly higher than – and in some cases, exactly the same as – the raw counts based on visual assessment of photographs. We attribute this similarity to the high rate of recaptures during the study period. We originally had concerns about double-counting of cats from adjacent camera locations within Stillwater's small high intensity urban area. However, we concluded that sites in this urbanization intensity class can still be considered as independent replicates because we observed only one occurrence in our entire study of an individual cat being recorded at two camera locations.

Cat abundance in relation to urbanization

We found no evidence of differences in free-ranging cat abundance among three categories of urban development intensity or in relation to human population density, both within the census block containing cameras and averaged across all census blocks within 500 m of cameras. This finding has four (potentially non-mutually exclusive) explanations. First, cats could be abundant regardless of characteristics of the urban landscape. This explanation is supported by our formal observation that the majority of our trail cameras captured numerous cats and by previous studies that have documented large cat populations across urban areas (Levy et al. 2003, Lepczyk et al. 2004, Baker et al. 2005, Natoli et al. 2006).

Second, cat abundance could be more closely tied to TNR release points and feeding colonies than to characteristics of the urban landscape. We selected sampling points to avoid major TNR release points and major cat feeding colonies established independent of the TNR program. Although we still expected to observe ear-tipped TNR cats, none were detected at any of our camera locations. This could indicate that we were sampling a high proportion of free-ranging pet cats and/or that the TNR program is sterilizing a very small fraction of the entire cat population. Very little scientific evidence exists to suggest that TNR efforts can reduce cat populations, and future analyses that assess the proportion of neutered cats at varying distances from TNR release points and colonies would provide insight into whether these activities result in enough cats being captured and sterilized to stabilize, reduce and eradicate cat populations.

Third, cat population abundance in Stillwater could be more closely tied to other anthropogenic variables. Other studies in urban areas have shown that cat abundance can be positively related to housing/building density and distance to woodland and inversely related to median household income (Sims et al. 2008, Thomas et al. 2012, Flockhart et al. 2016). Other factors that could influence abundance include rates of cat abandonment, amount and type of human subsidization (including food and shelter provided both purposefully and incidentally), and the proportion of the cat population consisting of free-ranging pets (among other potential factors described under 'Conclusions and recommendations'). We are uncertain why our data indicated no relationship between cat abundance and human population density, but it is worth noting that our study was conducted in a much smaller city and at a much smaller scale than previous studies illustrating this relationship (46 000 residents compared to 230 000 residents in Thomas et al. 2012; across a 75 km^2 city versus across multiple urban areas in Sims et al. 2008).

Fourth, our replication of study sites could have been insufficient. This possibility is supported by our finding of non-significant pairwise comparisons in the urbanization intensity analyses despite significant overall ANOVA models. A study with greater replication and/or covering a larger and more diverse urban area could potentially reveal relationships between free-ranging cat numbers and ecological and sociological characteristics of the urban landscape.

Conclusions and recommendations

The ability to better quantify numbers of free-ranging cats will allow for a clearer understanding of the anthropogenic threats facing wildlife species of management concern. This information can be used to inform future management decisions for both wildlife and cat populations. Our study suggests that free-ranging cats are abundant throughout a small US city and are therefore likely to constitute a threat to a variety of wildlife species ranging from the urban center to the outer urban fringe. Studies that seek to identify drivers of spatio-temporal variation in cat abundance may need to sample in a broad variety of urbanization intensities and capture large variation in ecological or human related factors (e.g. average number of pet cats per household; percentage of cat owners that allow pet cats outside; total cat-hours outside for pet cats; numbers of semi-feral and feral cats released by TNR programs; numbers of informal human-provided shelters and feeding stations for semi-feral cats).

The use of camera traps for wildlife research, including the recommended camera technology, study designs, and data collection approaches for different applications, has been thoroughly covered elsewhere (Bengsen et al. 2011, Kays et al. 2009, Fleming et al. 2014). Here we focus on specific recommendations for studies of domestic cats in urban areas. To successfully utilize trail cameras to identify individual cats, we recommend the use of a multi-shot mode (i.e. multiple photos taken per camera trigger) to generate a series of photographs that portray multiple views and angles of each cat and therefore increase ease of individual identification. Our study design did not specifically allow testing of different delays between trigger events and individual photos. Because we occasionally observed cats that were moving too fast to be captured on more than one photo, camera users can consider shortening trigger intervals to < 30 s and photo intervals to < 3 s when camera memory and battery space are sufficient. Nonetheless, because we frequently captured the same cat on multiple photos within a trigger event, the 3 s photo interval appears to be effective in most cases. We also recommend the use of a small amount (e.g. 1–2 oz.) of canned tuna as an attractant because: 1) the scent attracts cats to trail camera locations even after it has been consumed, and 2) the relatively small amount of tuna provides only a temporary food source and therefore prevents a few cats from monopolizing the camera site. During trail camera set-up, the angle of approach by cats should be controlled (i.e. by pointing cameras toward corners, walls or other restricting structures) to provide lateral views and therefore the maximum area of pelage visible for analysis. If possible, an object of known dimension should be placed as a size reference to aid in the differentiation of uniformly colored cats. We also recommend the use of infrared cameras in urban studies because: 1) most cat captures occured at night, 2) infrared light does not appear to alter the behavior of cats, and 3) infrared captures provide clear images of nearly all types of pelage characteristics.

A spacing distance of at least two cameras per average animal home range has previously been recommended for maximizing capture probability in sight–resight studies (Dillon and Kelly 2007). Previous research indicates substantial variation in cat home range size in urban areas, with unowned feral cats tending to have the largest home ranges and owned free-ranging pets tending to have the smallest home ranges (Schmidt et al. 2007, Tennent and Downs 2008, Horn et al. 2011). Trail camera spacing should ideally be based on the home ranges of the cat populations of interest. Although studies in urban areas are likely to be limited by logistic constraints (e.g. access to private property, potential theft of camera equipment), we recommend that, whenever possible, researchers seek to achieve the above-suggested spacing interval.

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Supplementary material (available online as Appendix wlb-00237 at <www.wildlifebiology.org/appendix/wlb-00237>). Appendix 1.