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Estimating habitat characteristics associated with the abundance of free-roaming domestic cats across the annual cycle

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ABSTRACT

Context. Domestic cats (*Felis catus*) hold an important place in human society but can negatively impact ecosystems when roaming freely outdoors. **Aims.** Specific research goals included identifying factors associated with cat abundance over the year. **Methods.** We deployed trail cameras in Wellington County, Ontario, Canada to estimate what habitat characteristics were associated with cats in the spring/summer and the fall/winter. Within a subset of our study area, we also compared these findings to a previous study that used walking surveys. **Key results.** In the spring/summer, cat abundance was positively related to proximity to buildings and negatively related to distance to agriculture. In the fall/winter, cat abundance was negatively related to the presence of coyotes (*Canis latrans*) and positively related to proximity to major roads. Overall, cat abundance was higher in urban than rural locations, and higher in spring/summer compared to fall/winter. Both our results from trail cameras and walking surveys from a previous study identified that median income, woodlots, and major roads were important habitat characteristics associated with cats during the summer, and we discuss the costs and benefits associated with both approaches. **Conclusions.** Free-roaming cats are associated with different habitat characteristics in spring/summer versus fall/winter and vary in abundance across landscape type and season. **Implications.** The development of management strategies aimed at reducing free-roaming cats in temperate areas should incorporate seasonal and landscape patterns.

Keywords: companion animals, *Felis catus*, feral cats, free-ranging cat, habitat use, owned cats, seasonal effects, trail cameras, unmarked, urban.

Introduction

Free-roaming domestic cats (*Felis catus*), defined as owned or unowned cats allowed to roam outdoors unsupervised, can have adverse impacts on wildlife (Iverson 1978; Churcher and Lawton 1987; van Heezik *et al.* 2010; Blancher 2013; Loss *et al.* 2013; Woinarski *et al.* 2017), and spread disease that pose risks to human and cat health (Dubey and Jones 2008; Gerhold and Jessup 2013). Confronting these impacts involves recognising that cats also hold an important place in human society due to their role as companion animals and in pest control (Crowley *et al.* 2020). While the creation of socially acceptable management plans will involve input from multiple stakeholders, such as cat owners, veterinarians, and animal welfare organisations, rigorous studies on the ecology and distribution of free-roaming cats will play a key role in designing effective plans. An important initial step in designing management plans involves identifying where, and at what times of the year, cats are most abundant. One way to accomplish this step is to identify the habitat characteristics associated with cat abundance and how these relationships may change over the course of the year.

Several habitat characteristics have been shown to influence free-roaming cat abundance. Cat abundance may be high in high-density residential areas (Hall *et al.* 2000; Ferreira *et al.* 2011; Flockhart *et al.* 2016; Webster *et al.* 2019) not only because there is a high density of cat owners but because there are also fewer predators, such as coyotes, compared to nearby woodlots (Kays *et al.* 2015; Larson *et al.* 2015) or agricultural lands (Person and Hirth 1999). Unowned cats, in contrast, may be drawn to residential areas because of the abundance of food in the form of garbage, pet food left out by owners, or the presence of feeding stations run by cat-colony caretakers (Natoli 1985; Natoli *et al.* 1999; Liberg *et al.* 2000; Hatley 2003; Natoli *et al.* 2006; Tennent and Downs 2008). Residential areas can also provide shelter for unowned cats from inclement weather, either inside or alongside human structures (Calhoon and Haspelt 1989; Goszczyński *et al.* 2009). Within residential areas, higher densities of free-roaming cats have been recorded in low-income neighbourhoods (Flockhart *et al.* 2016), potentially because cat owners in these areas are less likely to undertake costly spaying or neutering (Chu *et al.* 2009). Although several studies have examined how cat abundance is related to specific habitat characteristics (Kays *et al.* 2015; Flockhart *et al.* 2016; Webster *et al.* 2019), drawing general conclusions from this body of work can be challenging, due to the lack of replication within and across geographic locations.

It is also challenging to draw general conclusions about habitat characteristics associated with cats because most work has occurred during the spring and summer (Van Aarde *et al.* 1996; Ferreira *et al.* 2011; Kays *et al.* 2015; Flockhart *et al.* 2016; Webster *et al.* 2019), and rarely during the fall and winter (Harper 2007; Goszczyński *et al.* 2009; Horn *et al.* 2011; Normand *et al.* 2019). Overcoming this seasonal bias is particularly crucial for areas of the world that show strong fluctuations in temperature over the course of the year and a corresponding shift in wildlife composition, both of which may influence the distribution of cats. Seasonal differences in cat abundance and habitat use could provide valuable information on when cats may be posing the biggest threat to native wildlife, which can help inform management actions where limited funds often pose the largest obstacle towards their successful implementation.

In this study, we used a network of trail cameras to examine factors explaining variation in local cat abundances in Wellington County, southwestern Ontario, Canada during two periods of the year (Fig. 1). The temperature in Wellington County can fluctuate by 69°C (−32 to +37°C) across the year (Government of Canada 2019), providing an opportunity to assess whether seasonality influences cat abundance and which habitat characteristics are associated with abundance. We tested predictions from several non-mutually exclusive hypotheses (summarised in Table 1) to explain whether variation in cat abundance in both the spring/summer and fall/winter could be explained, in part, by habitat characteristics. In addition to these hypotheses, we also compared our methodology of using point counts from trail camera photos with a recent study that used distance-based walking transect sampling (Flockhart *et al.* 2016) that overlapped in space (the same urban

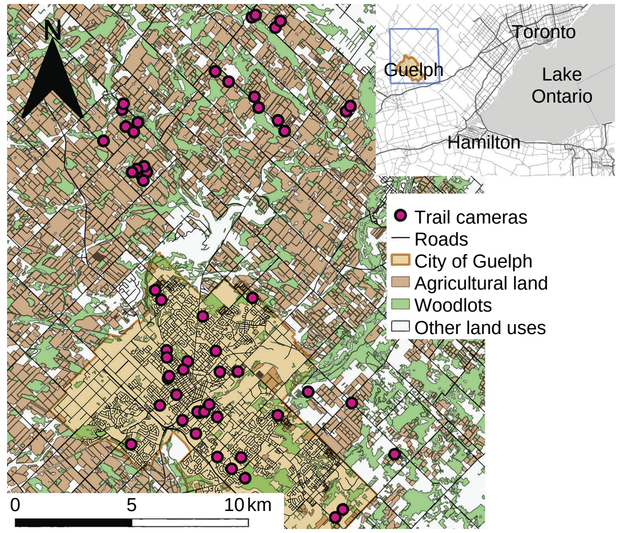

Fig. 1. Map of trail camera locations (pink circles, $n = 57$) in Wellington County, ON, Canada (outlined in blue on the inset map). Cameras were located on private property, and symbols appear large to conceal personal information related to private property. This map does not include other land characteristics that were not used in this study, such as waterways, commercial land, and recreational parks. Cameras were deployed approximately 8 times across 12 months (20 May 2018–6 April 2019) for 72-h periods, with 2–4 weeks between each deployment.

centre) and time of year (spring/summer) with this study. Comparing the similarities and differences in these two methods may help stakeholders, such as local cat organisations, environmental organisations, and researchers, decide on which methods may be most appropriate for their research goals given available time and resources.

Methods

Study site and trail cameras

Our study was conducted in Wellington County, Ontario, Canada (43.5448°N, 80.2482°W; Fig. 1), which includes the City of Guelph and the surrounding rural area and is on the traditional lands of the Mississaugas of the Credit First Nation of the Anishinaabe Peoples. The City of Guelph is an 8720-ha urban centre with a population of 131 500 people (Statistics Canada 2017) and is surrounded by agricultural land and small woodlots within Wellington County, as well as has some pockets of agricultural lands within the city limits. The city has a medium-sized university (28 700 students), a small downtown area (~ 15 ha), and >1000 ha of parks and open spaces. Like many North American cities, Guelph is mainly dominated by single-family, year-round (not seasonal) residential properties with private yards, and a few densely populated neighbourhoods consisting of multi-unit buildings, with small amounts of public space consisting of sidewalks, streets, and small parks. Guelph is

Table 1. Hypotheses and associated predictor variables used to explain local cat abundance in Wellington County, ON, Canada. Source indicates a study or studies that have provided evidence that supported the hypothesis.

Hypothesis	Hypothesised mechanism	Predictor variable	Source
Building Hypothesis 1	Cats are found close to buildings because their owners live there	Distance to nearest building (m)	Barratt (1997); Kays and DeWan (2004); Flockhart *et al.* (2016); Hanmer *et al.* (2017); Webster *et al.* (2019)
Building Hypothesis 2	Cats are found near buildings because there are easily accessible sources of food nearby (i.e. garbage/food supplied by their owners)	Distance to nearest building (m)	Natoli (1985); Calhoon and Haspelt (1989)
Building Hypothesis 3	Cats are found near buildings because buildings offer easily accessible shelter from weather	Distance to nearest building (m)	Natoli (1985); Calhoon and Haspelt (1989)
Busy Road Hypothesis	Cats avoid areas with busy roads because the roads act as movement barriers or physical hazards	Distance to nearest major road (m)	Klar *et al.* (2009)
Competitor Avoidance Hypothesis	Cats avoid woodlots because this reduces the number of their interactions with competitors (i.e. racoons, foxes)	Distance to nearest woodlot (m)	Atwood *et al.* (2004); Kays *et al.* (2015); Flockhart *et al.* (2016)
Agriculture Hypothesis	Cats avoid agricultural land because of predation risks and equipment that can lead to injuries	Distance to agricultural land (m)	Genovesi *et al.* (1995); Person and Hirth (1999)
Coyote Avoidance Hypothesis	Cats avoid areas where coyotes frequent because it reduces risk of predation	Presence of coyotes	Kays *et al.* (2015)
Income Hypothesis	Cats have a higher abundance in areas with low median household incomes because owned cats are less likely to be spayed/neutered, leading to an increase in the unowned cat population	Median household income (CAD)	Chu *et al.* (2009)
Seasonality Hypothesis 1	There will be more cats during the spring/summer because cats are more likely to produce young at this time of the year	Period of the year: spring/summer vs fall/winter	Nutter *et al.* (2004)
Seasonality Hypothesis 2	There will be more cats during the spring/summer because cat owners are more likely to let their cat outside during this time	Period of the year: spring/summer vs fall/winter	None
Landscape Hypothesis	There are more cats in urban than rural areas because there is a higher density of owners	Landscape type: urban/rural	Barratt (1997); Kays and DeWan (2004); Flockhart *et al.* (2016); Hanmer *et al.* (2017); Webster *et al.* (2019)
Landscape-time of the year Hypothesis	The period of the year will affect the abundance of cats in urban areas because owned cats are more likely to be let outside during the spring/summer compared with the fall/winter; however, the period of the year will not affect cat abundance in rural areas because rural cats are usually free to roam year round	Period of the year × landscape type	None

a rapidly expanding city but has room to grow and expand within its municipal boundaries, which means there is also some agricultural lands within the city boundaries.

From 2018 to 2019, we estimated cat abundance using photos taken from 57 sites, which consist of a single trail camera (O'Brien and Kinnaird 2008; Cunningham *et al.* 2020; Deith and Brodie 2020) set-up on private lands throughout the City of Guelph ($n = 30$), and a subsection of rural Wellington County ($n = 27$). Urban areas in Canada are typically defined by their municipal jurisdictional boundaries, but given that within Guelph's municipal boundary there are some agricultural areas, we refined our definition of urban versus rural. We considered camera sites *urban* if they had ≥10 residential units (single-detached homes, townhouse units, duplex units etc.) within a 100 m buffer around the site, these were typically located inside boundaries of the City of Guelph (28/29 *urban* sites were within the city). Sites were considered *rural* if they did not meet this criterion (but may have other non-residential buildings, i.e. barns) and were typically located outside Guelph's municipal boundary (26/28 *rural* sites were outside of the city). This resulted in a total of 29 urban and 28 rural sites (Fig. 1).

We opted to conduct our research only on privately owned property to avoid the risks of theft and vandalism and because the majority of land within our study site was privately owned. Each camera, was thus, set-up on private property after meeting with individual landowners and discussing their concerns and the location of the camera(s). Volunteer landowners within the City of Guelph were found through personal connections, giving presentations to local organisations, and through email broadcasts. We aimed to have cameras distributed across as many areas within the city as possible. In urban areas, cameras were typically placed in the backyards of single-family homes, which are usually close (within 25 m) to buildings. In areas outside the city limits, we selected two 10 km-by-10 km areas and knocked on doors to find volunteer landowners. While we attempted to evenly distribute cameras within these two areas, doing so was not always possible due to a lack of landowner permission, or simply being unable to contact the landowners. In rural areas, we used a more varied design with respect to proximity to buildings. We placed cameras close to buildings (homes and barns), and also at least 100 m from any structure (at the edges of farm fields where trees or fence posts to attach cameras were present), with several ($N = 12$) cameras placed > 100 m away from any structure. The specific location of cameras within a property (both urban and rural) was determined based on the characteristics of the property, with cameras being attached to trees or fence posts.

We took a number of steps to ensure our research was conducted cooperatively with landowners. We gave each landowner written information about the study and general protocols. Once they chose to participate, we notified landowners in writing (via email) when the cameras were going to be deployed and for how long and approximately when a researcher would be visiting the camera to refill the bait. The locations of all cameras have not been disclosed to maintain landowner privacy. All images of humans have been separated and stored on hard drives in locked rooms or cabinets and will be destroyed at the completion of this research and other research projects associated with this dataset.

We used Browning Strike Force HD Pro infrared trail cameras (model BTC-5HDP), with a 1/3 s picture trigger and an eight-photo burst at 1-min intervals, which generated enough photos to identify individuals and identify fast-moving animals (Rovero *et al.* 2013). Trail cameras were at least 100 m away from other cameras, if two were within 100 m or the same cat appeared at two sites ($N_{S/S} = 1$, $N_{F/W} = 2$) only a single camera was used in the analysis. We positioned cameras on poles or trees at cat level, 30–60 cm above the ground, and, when possible, pointed them towards animal corridors, such as pathways or along fence lines, to increase chances of detection.

We assessed if cat abundances (see statistical analysis) were associated with different habitat characteristics over the year, we divided the year into two seasonal periods based on climatic features of the study area: the spring/summer (1 April–22 September) and the fall/winter (23 September–31 March). In the spring/summer period, temperatures varied from an average of 10°C in April to 25°C in July and August, with rain precipitation ranging between an average of 60–75 mm/month. In the fall/winter period, temperatures typically range from an average of 13°C in October to -4°C in January and 3°C in March, with precipitation of rain or snow between 40 and 75 mm/month (Government of Canada 2019). We followed the general study design for assessing cat abundances outlined in Elizondo and Loss (2016). This involved 72-h deployment periods and baiting of the cameras. This method allowed us to deploy cameras across each time period, and also helped with landowner compliance and support, given many landowners were uncomfortable with having a camera deployed in their yard for an entire year or for multi-week periods. Cameras were deployed 5–9 times at each site for 72-h between 20 May 2018 and 6 April 2019, with 2–4 weeks between each 72-h sampling occasion. We deployed cameras by assigning a camera to one of four routes (two routes outside of the City of Guelph and two routes within the City of Guelph), with each route consisted of 11–17 cameras based on the length of time it took to complete the routes. Cameras within each route were deployed on the same day each round, and the routes cycled through in the same order to allow for even sampling across a given time period. We placed baits of ~20–28 g of sardines in front of each camera at the time they were first deployed at a site and re-filled the baits every 24-h. However, some days it was impossible to re-fill the bait due to the landowner not allowing land access or inclement weather (e.g. heavy snow to ice storms) that made it unsafe to access a camera. The use of bait meant that in most cases there were numerous images and bursts of a single cat, which helped us accurately identify individual cats. Given that the smell of sardines persists long after the bait is consumed and the frequency at which the bait was deployed at a given camera site (every 24 h), we do not suspect that how fast a bait was consumed affected our ability to detect cats. Cameras were typically deployed within 6 h of sunset between the hours of 1500–2100 h in the spring/summer and 1100–1700 h in the fall/winter with baits being refilled at approximately the same time as each camera's initial deployment. Cameras were taken down after at least 72-h had elapsed.

Cats were individually identified based on their colouration, coat pattern, and size. We could not differentiate between owned and unowned cats since many owned cats do not always wear collars when outside. Thus, we referred to all cats that were outside and unsupervised as 'free-roaming' cats. In a single case, multiple cats at a camera site looked almost identical ($n = 3$ cats at one camera site), we assumed that there were as many cats as the greatest number simultaneously seen in one photo (Elizondo and Loss 2016). While there could have been other cases of similar-looking cats that we counted as a single individual, cat identities were confirmed by a secondary observer, reducing the probability of this error. If an individual appeared at two sites within one season ($N_{S/S} = 1$, $N_{F/W} = 2$), we randomly removed one site using a coin toss, resulting in a total of 55 sites for the spring/summer ($n_{urban} = 28$, $n_{rural} = 27$) and 53 sites for the fall/winter ($n_{urban} = 26$, $n_{rural} = 27$). Of the 97 individually identified cats in the study, we removed two from the analysis because one was restrained by an owner using a leash and the other was confined within an e-fence. To view example images of cats, see Supplementary Figs S1–S4.

Statistical analysis

Abundance

To estimate cat abundance in the spring/summer and the fall/winter, we used two hierarchical N-mixture models (function *pcount*) from the *unmarked* package (Fiske and Chandler 2011) using R version 3.6.2 (R Core Team 2014) to model each period separately. This modelling approach was selected because hierarchical N-mixture models use the count of individuals/camera site during a sampling occasion to estimate local abundance while also accounting for over-dispersion and non-perfect detection, which ensures that the abundance estimates are not over- or under-estimated due to temporal variation between sampling occasions (Kéry and Royle 2015). There was an average of 3.2 72-h sampling occasions/camera site in the spring/summer ($n = 55$ sites) and 4.5 occasions in the fall/winter ($n = 53$ sites). Our hierarchical N-mixture model contained two sub-models; one for local abundance and one for detection probability. Abundance was estimated using a negative binomial distribution:

$$N_i \sim \text{negative binomial}\ (\lambda_i,\ \alpha)$$

where N_i is the abundance and λ_i is the mean local abundance of the study species at site i, and α is the dispersion parameter (Kéry and Royle 2015). However, abundance can also be affected by non-perfect detection, which can be modelled by detection probability, expressed as:

$$y_{ij} | N_i \sim \text{binomial}\ (N_i p_j)$$

where y_{ij} is the detection or non-detection of an individual at site i during the jth survey and p_j is the detection probability of an individual during the jth survey (Kéry and Royle 2015).

Detection covariates (p)

We accounted for the possibility that cats may not be detected even if they were present at a camera site, by modelling detection probability using variables that could influence cat behaviour during the sampling occasions (McClintock and White 2012): time of year (Julian date), average temperature (°C), average daily precipitation (mm), and baiting status of the camera site (baited or not-baited; Table 2). We included time of year (Julian date) in the detection probability models because owned cats may only be available for detection during certain periods of the year based on their owner's behaviour (i.e. an owner may decide to only allow their cats outside at certain times of the year). Temperature and rainfall were included because cats are less active during extreme temperatures, and cats normally take shelter from heavy rains (Churcher and Lawton 1987; Hall *et al.* 2000; Harper 2007; Goszczyński *et al.* 2009). We obtained temperature and precipitation data from the *weathercan* package in R (LaZerte and Albers 2018). Baiting status was included to account for the possibility of increased detection on baiting days (du Preez *et al.* 2014) because there were some days we were unable to bait due to logistical or weather constraints. All continuous variables were standardised before analysis. For additional information on detection covariates, see the Supplementary Material.

Site covariates (λ)

We included seven site covariates (Table 2) used to test predictions from hypotheses explaining variation in cat abundance (Table 1). The shapefiles for buildings were digitalised from aerial satellite photos from the 2020 Google Maps base map in QGIS (https://www.qgis.org/). The shapefiles for major roads, woodlots, and agricultural land were obtained from the Ontario Road Network (Ontario Ministry of Natural Resources and Forestry 2019), Ontario GeoHub (Smith 2018), and the Agricultural Resource Inventory (Ontario Ministry of Agriculture Food and Rural Affairs 2018), respectively. Distance (m) to the nearest building, major road, agricultural land, and woodlot was calculated to each camera site using the 'NNJoin' plugin in QGIS. The presence of coyotes at each camera site during each period of the year was determined using images from trail cameras. We obtained the total median household income of each census block that had a trail camera from the 2016 Canadian census (Statistics Canada 2016). Camera sites were considered to be in urban areas ($n_{s/s} = 28$, $n_{f/w} = 26$ cameras) if they had ≥10 residential buildings within a 100 m buffer area around the site, and rural areas if this was not the case ($n_{s/s} = 27$, $n_{f/w} = 27$ cameras). All continuous variables were standardised before analysis. See Supplementary Material for additional information on site covariates and derivation of shapefiles and Supplementary Figs S5 and S6 for the distribution of camera sites across variables.

Collinearity, model selection, and relative importance

Before model selection, we constructed the two global abundance models, one for the spring/summer and one for the fall/winter using all the detection and site covariates listed above. We then assessed the multicollinearity of these models using the variance inflation factor (VIF). VIF values indicates the change to a given variable's coefficient as a result of collinearity using a regression-based approach (Murray and Sandercock 2020), where 1 indicates no

Table 2. Descriptions of covariates used to estimate detection probability and local abundance of free-roaming cats in Wellington County, ON, Canada.

Variables	Description
Detection covariates	
temp	Average temperature (°C) over the 72-h sampling period
date	Julian day of the first day in the 72-h sampling period
precip	Average of the daily precipitation (mm) over the 72-h sampling period
bait	A binary variable indicating whether or not the camera site had been baited with sardines during the sampling period
Site covariates	
roads	Distance from the nearest major road to the trail camera (m)
woodlots	Distance from the nearest woodlot to the trail camera (m)
buildings	Distance from the nearest building to the trail camera (m)
agriculture	Distance from the nearest agricultural field to the trail camera (m)
landscape type	The landscape type of the trail camera site: urban or rural
coyotes	Whether or not a coyote had been recorded at the trail camera site during the period of the year: presence or absence
income	The median household income of the area that the trail camera is located (CAD)

multicollinearity and >1 indicates a greater likelihood of multicollinearity between covariates (Murray and Sandercock 2020). Variables that had a VIF >5 indicated that there was a substantial amount of multicollinearity between covariates, and that they should be removed from the global model (Murray and Sandercock 2020).

We ensured that the global models adequately fit the data prior to formal model selection by assessing their goodness of fit using Chi-squared Goodness-of-fit Tests for N-mixture models (function *Nmix.gof.test*) from the *AICcmodavg* package in R (Mazerolle 2019). We then started the model selection process and determined the top-ranking detection probability model, as determined through Akaike information criterion corrected for small sample size (AIC_c; Burnham and Anderson 2002; Burnham *et al.* 2011) with a fixed null abundance sub-model ($\lambda(.)$), by using the *dredge* function in the *MuMIn* package (Barton 2009; Mazerolle 2019). Once the top-ranking detection probability model was identified, we then determined the top-ranking abundance model using the *dredge* function (Kéry and Royle 2015). By fixing the variables from the top-ranked detection model in the global local abundance model, we were able to focus on the effect the site characteristics had on local abundance.

Relative importance of a variable was calculated as the summed Akaike weight of each model that contains the variable of interest but only when the model set is balanced (every variable appears in an equal number of models; Barton 2009). Relative importance varies from 0 to 1, with high values indicating a variable with greater relative importance compared to the other variables in the model set (MacKenzie *et al.* 2018). We used the *sw* function from the *MuMIn* package in R (Barton 2009) to calculate the relative importance of each variable.

Landscape type and period of the year

In addition to specific habitat characteristics, we were also interested in whether quantitative estimates of cat abundance varied by period of the year and landscape type. To do this, we used estimates of local cat abundance for each camera site from the two top models for each period of the year. We then used a linear mixed effects model with a Gaussian distribution and included fixed effects of landscape type (urban or rural camera sites), period of the year (fall/winter, spring/summer), and the interaction between the two. We also included a random effect of camera site ID.

Comparison of trail camera and distance-based walking transect sampling methods

We determined if point counts using photos from trail cameras (present study) and distance-based walking transect surveys (Flockhart *et al.* 2016) identified similar habitat characteristics associated with cats by qualitatively comparing the model selection results from these two analyses. We used only footage from urban camera sites within the city limits during spring/summer (n = 29 camera sites, 27 urban and 2 rural) because this footage corresponded with the time period of the walking transect survey. We then followed the same procedure detailed above to determine the top-ranked abundance model for the spring/summer local cat abundance at urban sites, as determined through AIC_c model selection, which included determining the variables from the top-ranked detection probability model and fixing them into the global abundance model. We then qualitatively compared the top-ranking models, as determined through AIC_c, from our results and the published results from Flockhart *et al.* (2016). In our study, we included the same variables as Flockhart *et al.* (2016): distance to major roads, distance to woodlots, and median household income. Although our study and Flockhart *et al.* (2016) both included an income variable, Flockhart *et al.* (2016) used 2006 Canadian census data, while we used 2016 Canadian census data. Flockhart *et al.* (2016) also included building density, whereas our study used distance to buildings. We used distance to buildings because our initial study site (where we examined the difference of rural versus urban landscapes) also encompassed rural areas, which are known to have lower building densities but, like urban areas, may have high numbers of cats associated with a single building if food is left out for cats (Barratt 1997). Finally, Flockhart *et al.* (2016) also included a land use variable but we did not because our trail camera network did not cover all of the major land uses in the City of Guelph.

Results

Local abundance

Over half of the camera sites recorded at least one cat in both spring/summer (60%, $n = 33/55$) and fall/winter (57% of camera sites, $n = 30/53$). The highest number of cats recorded at one camera site was 13, which occurred at a low-income urban residential site during the fall/winter. Thirty-seven percent ($n = 10/27$) of the rural camera sites recorded ≥ 1 cat in the spring/summer and 30% ($n = 8/27$) recorded ≥ 1 cat in the fall/winter, while the majority of urban camera sites (82%; $n = 23/28$ in the spring/summer and 85%; $n = 22/26$ in the fall/winter) recorded at least one cat during both periods of the year.

Spring/summer: detection probability

The global model for the detection probability of cats in the spring/summer included average temperature (°C), average daily precipitation (mm), presence of bait, and Julian date of camera deployment (Table 2). None of the covariates showed signs of multicollinearity (Supplementary Table S1). Detection probability was best explained by date, which had a positive effect on the detection probability of cats (Table 3, and the full table in Supplementary Table S2). Three other models ($p_2^{(\text{temp})}$, $p_3^{(.)}$, $p_4^{(\text{temp + date})}$) were also supported ($\Delta\text{AIC}_c < 2$), but these models had less weighting ($w_{2\text{–}4} < 0.16$) compared to the top model ($w_1 = 0.19$; Table 3). Thus, date was fixed in the global local abundance model to account for non-perfect detection.

Spring/summer: local abundance

Carrying forward the top-ranked detection probability model, the global model for cat abundance in the spring/summer included covariates of distance to the nearest building, distance to major roads, distance to agricultural land, distance to woodlots, median income, and presence of coyotes. No covariates showed signs of multicollinearity (Supplementary Table S1). The Goodness-of-fit Test suggested that this global model adequately fit the data ($X^2 = 175.8$, $P = 0.20$). We used this global model to generate a balanced set of models, from which the top-ranking local abundance model could be identified using AIC_c model selection.

The top ranked model for local cat abundance included distance to buildings ($\lambda_1^{(\text{buildings + agriculture})}$; Table 3, and the full table in Supplementary Table S3), suggesting that more cats were found closer to buildings, and farther from agriculture (Fig. 2). One other model had a $\Delta\text{AIC}_c < 2$, ($\lambda_1^{\text{buildings + agriculture + woodlots}}$), but this model's weight was considerably lower ($w = 0.08$) than the top model ($w = 0.22$; Table 3).

Table 3. Comparison of detection probability (p) and local abundance (λ) models ($\Delta\text{AIC}_c < 2$) based on the number of cats at a camera site during the spring/summer of 2018 in Wellington county, ON Canada. The global detection probability model was $p^{(\text{temp + date + precip + bait})}\ \lambda^{(.)}$, where $\lambda^{(.)}$ represents the null local abundance sub-model. The global local abundance model was $p^{(\text{date})}\ \lambda^{(\text{buildings + roads + agriculture + woodlots + income + coyotes})}$. See Table 1 for descriptions of covariates and Supplementary Table S2 for the full table.

Model	d.f.	logLik	AIC_c	ΔAIC_c	Weight
Detection probability					
$p^{(\text{date})}\ \lambda^{(.)}$	4	−164.71	338.2	0.00	0.19
$p^{(\text{temp})}\ \lambda^{(.)}$	4	−164.85	338.5	0.29	0.16
$p^{(.)}\ \lambda^{(.)}$	3	−166.10	338.7	0.46	0.15
$p^{(\text{temp + date})}\ \lambda^{(.)}$	5	−164.39	340.0	1.79	0.08
Local abundance					
$p^{(\text{date})}\ \lambda^{(\text{building + agriculture})}$	6	−150.92	315.58	0.00	0.22
$p^{(\text{date})}\ \lambda^{(\text{building + agriculture + woodlots})}$	7	−150.57	317.52	1.94	0.08

Fall/winter: detection probability

The global model for the detection probability of cats in the fall/winter included average temperature (°C), average precipitation (mm), presence of bait, and Julian date of camera deployment (Table 2). None of these covariates showed signs of multicollinearity (Supplementary Table S1). Detection probability was best explained by date, which was negatively associated with local cat abundance (Table 4, and the full table in Supplementary Table S4). While the second-ranked model ($p_2^{(\text{date + precip})}$) was also supported ($\Delta\text{AIC}_{c2} = 1.92$), it held less than half of the model weight ($w_2 = 0.16$) than the top-ranked model ($w_1 = 0.42$). Therefore, the covariate from the top-ranked detection model (date) was then fixed in the global local abundance model to account for non-perfect detection.

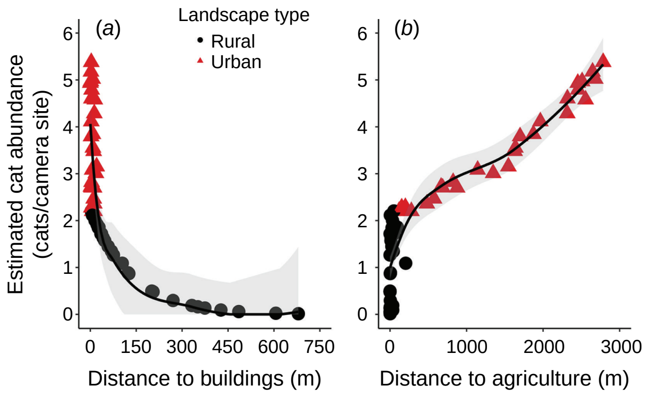

Fig. 2. Habitat characteristics associated with cats in Wellington County, ON during spring/summer 2018 include; (*a*) distance to the nearest building, (*b*) distance to the agriculture. These estimates were derived from the top local abundance model ($p^{date}\ \lambda^{buildings\ +\ agriculture}$) using AIC_c model selection. The landscape type of each camera site (rural: black circle, urban: red triangle) is also shown. Grey area represents 95% confidence intervals.

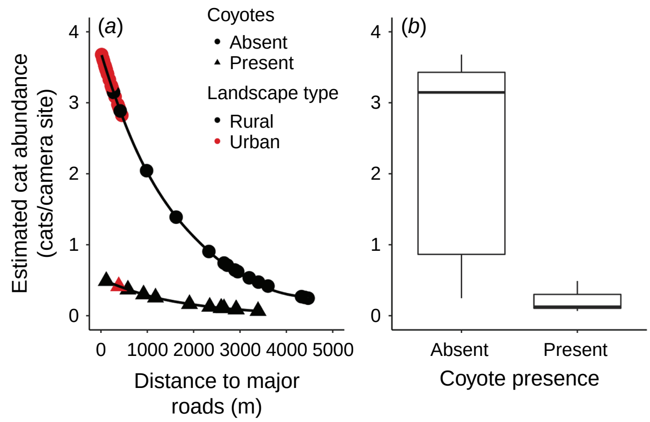

Fig. 3. Habitat characteristics associated with cats in Wellington County, ON during fall/winter 2018–2019 include; (*a*) distance to the nearest major road and (*b*) presence of coyotes. These estimates were derived from the top local abundance model ($p^{date}\ \lambda^{coyotes\ +\ roads}$) using AIC_c model selection. The presence (triangle) or absence (circle) of coyotes and landscape type (urban: red; rural: black) at each camera site are also shown. Grey area represents 95% confidence intervals.

Table 4. Comparison of detection probability (p) and local abundance (λ) models ($\Delta AIC_c < 2$) based on the number of cats at a camera site during the fall/winter of 2018–2019 in Wellington county, ON Canada. The global detection probability model was $p^{(temp\ +\ date\ +\ precip\ +\ bait)}\ \lambda^{(.)}$, where $\lambda^{(.)}$ represents the null local abundance sub-model. The global local abundance model was $p^{(date)}\ \lambda^{(buildings\ +\ agriculture\ +\ woodlots\ +\ income\ +\ coyotes)}$. See Table 1 for descriptions of covariates and Supplementary Table S4 for the full table.

Model	d.f.	logLik	AIC_c	ΔAIC_c	Weight
Detection probability					
$p^{(date)}\ \lambda^{(.)}$	4	−189.54	387.9	0.00	0.42
$p^{(date\ +\ precip)}\ \lambda^{(.)}$	5	−189.27	389.8	1.92	0.16
Local abundance					
$p^{(date)}\ \lambda^{(coyote\ +\ roads)}$	6	−176.20	366.22	0.00	0.21
$p^{(date)}\ \lambda^{(coyote\ +\ buildings\ +\ roads)}$	7	−175.71	367.91	1.69	0.09
$p^{(date)}\ \lambda^{(coyote\ +\ agriculture\ +\ roads)}$	7	−175.79	368.07	1.85	0.08

Fall/winter: local abundance

The global model for local cat abundance included distance to nearest building, distance to agricultural land, distance to woodlot, distance to major roads, median income, and presence of coyotes and the fixed detection probability model (p^{date}) to account for non-perfect detection. The Goodness-of-fit Test suggested that the global model adequately fit these data ($P = 0.06$, $X^2 = 374.5$). We used this global model to generate a set of models, from which the top-ranking local abundance model could be identified using AIC_c model selection.

The top-ranked abundance model included distance to major roads and presence of coyotes ($\lambda_1{}^{coyotes\ +\ roads}$; Table 4, and the full table in Supplementary Table S5), suggesting that cats were more likely to be found closer to roads and at camera sites where coyotes were absent (Fig. 3). Two other models, ($\lambda_2{}^{(buildings\ +\ coyotes\ +\ roads)}$ and $\lambda_3{}^{(coyotes\ +\ agriculture\ +\ roads)}$, were also supported by the data ($\Delta AIC_c < 2$), but these models had less weighting ($w_{2\text{–}4} < 0.09$) compared to the top model ($w_1 = 0.21$; Table 4).

Relative importance of variables and comparison across periods

The relative importance of a variable (summed Akaike weight) for estimating local cat abundance was compared between the spring/summer and fall/winter. For detection probability, date was the most important variable in both periods of the year (summed $w_{spring/summer} = 0.45$; summed $w_{fall/winter} = 0.99$). However, temperature was also a relatively important variable in the spring/summer (summed $w = 0.43$; Supplementary Table S6). For local abundance, the most important site characteristics for predicting abundance during the spring/summer were the distance to buildings (summed $w = 0.96$) and distance to agriculture (summed $w = 0.73$; Supplementary Table S7). During the fall/winter, the presence of coyotes (summed $w = 0.77$) and distance to major roads (summed $w = 0.85$) were important site characteristics.

Landscape type and period of the year

In the linear mixed effects model based on predicted cat abundance from the above spring/summer and fall/winter

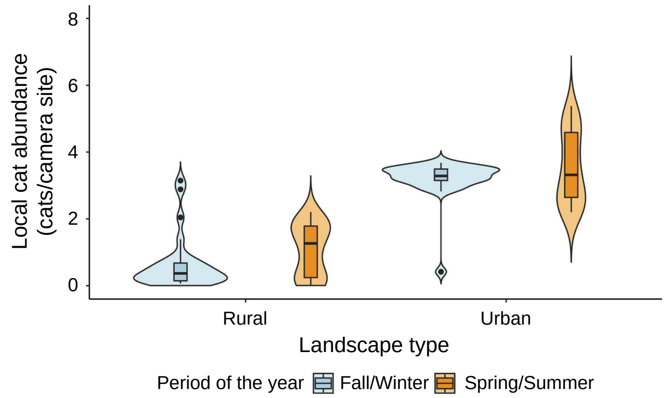

Fig. 4. Violin and box plots illustrating differences in estimated local cat abundances between rural and urban landscape types during the fall/winter (blue) and spring/summer (orange). The horizontal line within each box represents the median, and the upper and lower sides of the box represent the upper and lower quartile, respectively. Violin plots indicate the distribution of data over the range of values. Data were obtained from a linear mixed model to predict cat abundance that included landscape type, period of the year, and their interaction. Estimated local cat abundances were derived from the top ranking AIC_c models for each period of the year.

models, landscape type ($t = 11.06$, $P < 0.01$, 95% CI: 2.10–2.99), period of the year ($t = 2.25$, $P < 0.05$, 95% CI: 0.06–0.82) were predictors of local cat abundance, while their interaction was not ($t = -0.39$, $P = 0.69$, 95% CI: -0.65–0.43). Cat abundances were significantly lower in rural areas compared to the urban areas and higher during the spring/summer compared to the fall/winter (Fig. 4).

Comparison of trail camera and distance-based walking transect sampling methods

The only two models with a high degree of support ($\Delta AIC < 2$) from the Flockhart *et al.* (2016) study were $\lambda_1^{\text{building + woodlots + income + land use}}$ ($\Delta AIC_1 = 0$, $w_1 = 0.59$) and $\lambda_2^{\text{building + woodlots + income + land use + roads}}$ ($\Delta AIC_2 = 1.51$, $w_2 = 0.28$), while there were five models with a high degree of support from our spring/summer trail camera data ($\Delta AIC_c < 2$). These models included: $\lambda_1^{\text{(buildings + income)}}$, $\lambda_2^{\text{(buildings + woods)}}$, $\lambda_3^{\text{(buildings)}}$, $\lambda_4^{\text{(buildings + woods + income)}}$, and $\lambda_5^{\text{(buildings + roads + income)}}$. However, the first, second, and third ranked models held similar weights ($w_1 = 0.19$, $w_2 = 0.17$, $w_3 = 0.15$; Supplementary Tables S8, S9). Both methodologies indicated that there are estimated to be fewer cats near woodlots, in high median income areas, and far from buildings.

Discussion

Our study demonstrates that free-roaming domestic cats are associated with different habitat characteristics in spring/summer versus fall/winter and vary in abundance according to landscape type and season. Cats were estimated to be found in high numbers close to buildings and far from agriculture in the spring/summer, and in areas close to major roads and without coyotes in the fall/winter. Additionally, there were higher estimates of local cat abundance during the spring/summer compared to the fall/winter and in urban areas compared to rural areas in both periods of the year.

Our results showing that distance to buildings is an important habitat characteristic predicting cat abundance in the spring/summer is perhaps not surprising because areas near buildings equate with more cat owners and easy access to food and shelter. The relationship between cats and buildings is consistent with past studies conducted in the same city (Flockhart *et al.* 2016) and in other parts of the world (Calhoon and Haspelt 1989; Goszczyński *et al.* 2009; Ferreira *et al.* 2011; Webster *et al.* 2019). Previous studies directly tracking cats (Kays and DeWan 2004; Wood *et al.* 2016; Hanmer *et al.* 2017; Kays *et al.* 2020) have demonstrated that most owned cats do not roam far distances away from their owner's home. In our study, cats were most often recorded <100 m from buildings at all urban sites and most rural sites (14/27 rural sites were >100 m from a building and only two sites recorded at least one cat), although more urban than rural camera sites recorded at least one cat. Free-roaming cats likely still access natural habitats that are adjacent to buildings, regardless of whether they are in urban or rural landscapes. Direct tracking of both owned and unowned cats (including 'barn' cats) would be an effective approach for estimating the potential impact of cats whose homes are near naturalised or agricultural areas.

The presence of coyotes negatively influenced cat abundance in the fall/winter but had no effect on cats during the spring/summer. This difference may be linked to seasonal variation in coyote movements (Laundre and Keller 1981; Gosselink *et al.* 2003). In the spring and summer, coyotes typically have small home ranges centred around their den sites (Person and Hirth 1999; Way *et al.* 2001), which are usually not located close to residential buildings because of the lack of suitable habitat. However, when pups become more independent around mid-September, coyotes expand their home ranges (Way *et al.* 2001; Gosselink *et al.* 2003), an expansion that is more likely to encompass areas with residential buildings and, therefore, cats. This seasonal behavioural change may explain why more than double the number of camera sites recorded the presence of coyotes in the fall and winter ($n = 24$ camera sites) compared to the spring and summer ($n = 11$ camera sites; Supplementary Fig. S6). While two other studies provided evidence that cats avoided areas with coyotes (Gehrt *et al.* 2013; Kays *et al.* 2015), they did not specifically examine seasonal differences in coyote or cat occupancy because they treated the entire year as one sampling period.

The period of the year and landscape type may influence cat abundance because the overall abundance of cats was higher in urban than rural areas and during the spring/summer than the fall/winter. Whether such a difference in local cat abundances across seasons and landscape types translates to differences on impacts to wildlife is unknown, particularly given that our data suggest that there is still a lower overall abundance of cats roaming freely in rural areas compared to urban areas. However, it does support the notion that educational campaigns on the impacts of allowing cats to freely roam could be tailored to the intended audience based on whether the campaign is set in urban or rural landscapes (Lord 2008; McLeod *et al.* 2019).

Cat management recommendations

Given our finding that there were more cats found close to buildings in the spring/summer, predation pressure from cats may be greatest for native wildlife species that nest or roost close to or in buildings during this time (e.g. barn swallows; *Hirundo rustica*, little brown bats; *Myotis lucifugus*). Due to the disproportionate number of cats around buildings, these areas may act as sinks for ground nesting/foraging birds or small mammals (Blancher 2013; Webster *et al.* 2019). For example, cats may focus hunting efforts on point sources of food or shelter that are used by prey species, such as birds at feeders (Dunn and Tessaglia 1994; Lepczyk *et al.* 2004) or bat roosts inside barns (Ancillotto *et al.* 2013). One way to reduce the predation pressure on these prey species and decrease the number of free-roaming cats, may be to focus conservation or specific management efforts in the spring/summer on areas immediately surrounding buildings. This may be done for instance, by working with local cat welfare organisations (e.g. local Humane Societies or shelters) to create standardised protocols that require the evaluation of the risk to wildlife when homing 'working cats' (unadoptable cats that are often rehomed on farms for pest control) in barns, such as assessing the presence of federally or provincially species at risk nesting in or around farm structures, such as barn swallows (*Hirundo rustica*; threatened under the *Species at Risk Act*, SARA) and bobolinks (*Dolichonyx oryzivorus*; threatened under the SARA). Another method to reduce the number of free-roaming cats may be to conduct social science research to determine how to effectively frame messaging to work alongside landowners and cat owners, particularly those in urban residential areas, that changes how people view free-roaming cats (McLeod *et al.* 2019), and provide this messaging to stakeholders of influence, such as veterinarians or shelter workers, to promote, teach and encourage responsible cat ownership (i.e. keeping cats inside, providing indoor stimulation to cats, spay or neutering).

Comparison of trail camera and distance-based walking transect sampling methods

Our surveys using trail cameras identified similar habitat characteristics associated with cats as a previous study using distance-based walking transect surveys (Flockhart *et al.* 2016), with minor differences. Both studies found that cat abundances were influenced by buildings, income, and woodlots. The difference between the results from both methods may be attributed to the different coverage of the study site, the slight differences in covariates (i.e. building density versus distance to buildings), or the inclusion of a landscape variable in the Flockhart *et al.* (2016) study. For example, walking transect surveys (Flockhart *et al.* 2016) identified land use (i.e. industrial, commercial, parks, residential) as an important habitat factor, which was not included in our analysis due to the trail camera network coverage of the City of Guelph. The removal, addition, or slight change to a covariate may change the ranking order because AIC model selection only assesses and ranks the models included within the model set (Burnham and Anderson 2002). Thus, the addition of the landscape variable and the differences in how variables were measured in the Flockhart *et al.* (2016) study may partially explain the different order and weightings of the models between the two different methodologies.

While both methodologies identify buildings, income, and woodlots as important habitat characteristics associated with cat abundance, there are clear costs and benefits associated with each approach (Supplementary Table S10). Studies using trail cameras in urban areas present different challenges in comparison to those using walking transects. Urban trail camera studies involve extensive support and help from a variety of landowners which can create challenges in gaining full coverage of a study area or enough replicates of each habitat type or socioeconomic feature (Elizondo and Loss 2016). The main challenges that we experienced with setting up trail cameras in urban areas involved attracting and recruiting enough landowners, privacy concerns from landowners and local people, and the potential for theft or vandalism of equipment (none of our cameras, which were all on private lands, were vandalised or stolen). All of these factors led to difficulty in gaining full coverage of the City of Guelph. For example, we did not cover industrial, commercial, or high-density housing areas (i.e. areas dominated by apartment buildings) due to logistical challenges contacting landowners or gaining buy-in from stakeholders, as well as the concern of camera vandalism or theft in these more public areas. In contrast, walking transect surveys can be easily conducted in most land use types because these locations are accessible via public roads, pathways or trails. However, if a specific type of habitat only exists on private property, landowner consent would be required to access the area, similar to studies involving trail cameras. Future studies may benefit from longer periods of recruitment and advertising, which may involve, among other things, door-to-door inquires to find willing landowners, press releases, and community engagement.

In contrast to challenges associated with study design, a study using trail cameras is relatively easy to conduct because it requires minimal field work, ~30-h of field work (to manage 29 cameras with four 72-h camera deployments, with baiting every 24-h) compared to distance-based walking transect surveys, which require experienced surveyors and take ~105-h of field work (assuming 145 transects and two replicates of each 22 min long transect). However, it should be noted that setting up trail cameras involves extensive time recruiting, educating, and working with landowners. Data from trail cameras also require extensive processing (~232 h to process data from 29 cameras with four deployments each assuming it takes 1 h to sort through 1500 pictures and ~3000 pictures/3-day deployment, plus the additional time to input data after processing) compared to distance-based walking transect studies, which take ~20-h to input data. Advances in artificial intelligence could automate trail camera data processing, but current artificial intelligence capabilities are limited (Green *et al.* 2020). Despite these challenges, trail cameras have several benefits, especially for researchers interested in studying seasonal differences in species abundances, or interactions with multiple species, because cameras can be deployed throughout the year at different sites with little monetary or field personnel cost.

In conclusion, our main finding that free-roaming cats are associated with different habitat characteristics in spring/summer versus fall/winter and vary in abundance across landscape type and season, suggests that the development of management strategies aimed at reducing free-roaming cats in temperate areas should consider seasonal and landscape factors. Future studies on domestic cat abundances or spatial distribution, particularly in highly seasonal environments, should assess seasonal and landscape differences and such objectives are most effectively achieved using trail camera networks rather than walking transects. We also suggest that short camera deployment times with daily baiting may also allow for higher landowner buy-in, particularly for studies aiming to assess cat abundances across the year.

Animal ethics statement

The research was conducted under the Animal Utilisation Protocol from the University of Guelph (#4021), which outlines the compliance of animal ethics in the research.

Supplementary material

Supplementary material is available online.

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Data availability. The data that support this study will be shared upon reasonable request to the corresponding author.

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