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Predicting free-roaming cat population densities in urban areas

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Abstract

Although free-roaming cats can have a significant impact on the environment, and substantial resources have been invested to find humane alternatives for managing free-roaming cat populations, there are no empirical estimates of free-roaming cat population size in medium to large cities. In addition, little is known about factors limiting free-roaming cat population size and distribution. Using Guelph, ON, Canada (pop: 120 000; 86.7 km^2) as a case-study, we apply replicated distance transect sampling and likelihood-based hierarchical modelling to compare human-mediated landscape patterns of land use, distance to roads, distance to wooded areas, building density and socio-economic status to explain the abundance of free-roaming cats. We then derive an empirical estimate of total population size and present a spatially explicit prediction of free-roaming cat density across an entire city. Cat abundance was highest in residential areas and lowest in commercial and institutional areas, negatively related to median household income, and positively related to distance from woods and building density. Total population size was estimated to be 7662 (95% bootstrap CI: 6145–9966) for Guelph; free-roaming cat density varied from 0 to 49.4 cats per ha. Our estimate overlapped with an independent estimate of indoor-outdoor cats (11 927; 95% CI: 6361–20 989) derived from random surveys of city residents, which implies our distance transect methodology was relatively robust and unbiased. Our approach used simple geographical information that is readily available for most urban areas in North America and can be applied broadly to inform cat management in urban areas. Finally, our results suggest that free-roaming cat density in cities could be determined by bottom-up processes (e.g. enhanced food availability in residential areas) as well as top-down processes (e.g. enhanced susceptibility to coyote predation near wooded areas) which are typically reserved to explain wildlife populations in natural environments.

Introduction

Free-roaming domestic cats *Felis catus* are abundant in urban environments (Schmidt, Lopez & Collier, 2007*a*; Sims *et al.*, 2008), can have adverse environmental impacts (van Heezik *et al.*, 2010; Blancher, 2013; Loss, Will & Marra, 2013) and pose risks to public health (Gerhold & Jessup, 2013). Addressing these impacts, coupled with objections to euthanizing individuals, underscore the challenge of identifying socially acceptable approaches to manage free-roaming cat populations (Levy & Crawford, 2004; Stoskopf & Nutter, 2004). Achieving an acceptable approach first requires robust estimates of cat population size. Cat abundance is likely to vary based on human-ownership patterns (Sims *et al.*, 2008), access to food (Calhoon & Haspel, 1989; Mirmovitch, 1995) and veterinary care (Finkler, Hatna & Terkel, 2011*a*), avoidance of predators (Crooks & Soulé, 1999) and breeding opportunities (Finkler *et al.*, 2011*a*). Identifying human- or environment-mediated limiting factors is important because decision-makers must choose among several, often competing and emotionally charged, interventions that target different demographic vital rates that influence population abundance (Andersen, Martin & Roemer, 2004; Budke & Slater, 2009; Schmidt *et al.*, 2009; McCarthy, Levine & Reed, 2013; Miller *et al.*, 2014). For example, recent cost-benefit analyses to address free-roaming cat populations have focused on how resources should be allocated towards trap-neuter-return programmes of feral cats, trap-euthanasia programmes, adoption programmes for socialized stray cats or subsidization of spay/neuter programmes for indoor-outdoor cats (Frank & Carlisle-Frank, 2007; Lohr, Cox & Lepczyk, 2013). These decisions hinge on accurate and robust estimates of population size, with associated confidence intervals. In addition, predictive surfaces of population density across entire cities are critical for spatial allocation of scarce resources to guide optimal interventions (Stoskopf & Nutter, 2004; Loyd & DeVore, 2010).

Quantifying population size of cats is challenging for a number of reasons. In urban areas, free-roaming cats are comprised of stray, feral and owned (indoor-outdoor) individuals (Levy & Crawford, 2004). Cats from these groups have different outdoor activity patterns (Clancy, Moore & Bertone, 2003) and home ranges (Schmidt *et al.*, 2007*a*; Horn *et al.*, 2011) that presumably would influence rates of temporary emigration from the sampling location (Chandler, Royle & King, 2011). Furthermore, akin to most wildlife, cats are not detected perfectly by observers (Schmidt, Pierce & Lopez, 2007*b*; Cruz, Glen & Pech, 2013) but, contrary to most wildlife, some cats may have intermittent outdoor access based on the behaviour of their owners and not be continuously available for detection (Clancy *et al.*, 2003). These factors highlight the need for estimates of population size to account for the observation process (Buckland *et al.*, 2001; Royle, Dawson & Bates, 2004). Robust estimates of free-roaming cats in large urban areas also require replicated samples across a range of land uses, comparison of models to explain population abundance, and the ability to extrapolate estimates to areas that were not sampled to infer cat population abundance across an entire urban landscape. Distance sampling is a robust method to account for these sampling challenges and is amendable to testing biological hypotheses regarding cat abundance via model selection (Buckland *et al.*, 2001).

In this paper, we use five variables to explain spatial variation in free-roaming cat population density in urban areas. The first is land use patterns where we predicted highest cat ownership in residential areas dominated by indoor-outdoor cats and where, presumably, unowned cats have access to intentionally provided food (Sims *et al.*, 2008) or trash (Calhoon & Haspel, 1989) and higher abundance of wild prey (e.g. non-native rodents and urban-adapted birds attracted to bird feeders; Fuller *et al.*, 2008). The second is socio-economic status where we predict a higher abundance of cats in low socio-economic neighbourhoods where the probability of cats being sterilized by their owners is lower (Finkler, Hatna & Terkel, 2011*b*). The third is building density where we predict a higher abundance of indoor-outdoor cats in areas of higher building density (Sims *et al.*, 2008). In large urban areas, a heterogeneous mixture of land uses, building density and socio-economic levels need to be considered as they could result in complex spatial population densities of cats (Finkler *et al.*, 2011*b*).

The other two variables were distance to environmental landscape features such as wooded areas and major roads. Fewer cats would be expected near wooded areas may reflect exposure to predators (i.e. coyotes; Atwood, Weeks & Gehring, 2004; Gese, Morey & Gehrt, 2012) that use these habitats (Crooks & Soulé, 1999; Gehrt *et al.*, 2013; Kays *et al.*, 2015). However, cats may be attracted or repelled from wooded areas if birds occupying wooded areas were more or less abundant than adjacent built-up areas. Similarly, cat densities may be higher or lower near major roads. We would predict fewer cats near major roads either if cats avoided roads or cats near roads had higher mortality rates (Caro, Shargel & Stoner, 2000; Taylor *et al.*, 2002; Klar, Herrmann & Kramer-Schadt, 2009). Alternatively, cats may be more abundant if food availability was higher or if exposure to competitors and predators was lower near major roads. Of course, all of the variables we considered are not mutually exclusive, as the abundance and distribution of cats could be influenced by human-mediated and environmental factors simultaneously (Odell, Theobald & Knight, 2003).

Here, we first use replicated distance-based transect sampling and likelihood-based hierarchical modelling to examine five variables to explain free-roaming cat population density. We then use published data to estimate the proportion of cats that are available for detection to derive an empirical estimate of total free-roaming cat population size and a spatially explicit estimate of free-roaming cat density across a large city. Finally, we compare our population estimate to an independent estimate of the number of indoor-outdoor cats derived from random surveys of city residents to examine if the distance transect sampling methods employed are adequate for estimating free-roaming cats in urban areas.

Materials and methods

Study area and geographical data

We conducted our study in the city of Guelph, ON (43.55°N, 80.25°W), a 8671 ha urban centre in an eastern-forested eco-region with a population of 120 000 people. The city is characterized by single-family residences, a university institution with enrolment of *c.* 25 000 students, and a small downtown (*c.* 15 ha). Spatial datasets for land use, median income, wooded areas, buildings and major roads (Fig. 1) were entered into a geographical information system (Supporting Information Table S1), overlaid with the transect routes (see below) to obtain route-level covariate values, and used to develop city-wide predictive estimates of free-roaming cat population density. Original vector datasets (Fig. 1) were converted into raster layers using the *Feature to raster* tool in ArcMap 10.1 (ESRI 2012) with a resolution of 1 ha. For each cat transect route, we extracted the mean covariate value using the *isectliners* tool (Beyer, 2011).

We obtained land use data from 2011 but omitted agricultural and other land uses (e.g. landfills, aggregate resource extraction) within city limits due to safety concerns or private-property access that prevented sampling these areas for free-roaming cats; these land uses (combined 518 ha) were assumed to have no cats (Supporting Information Table S1). Our reduced land use dataset covered 8153 ha and had five categories: commercial, industrial, institutional, parks and residential (Fig. 1). Median income data for dissemination areas were obtained from 2006 Canada Census data (Supporting Information Table S1) and linked to spatial coordinates using cartographic boundary files (Fig. 1). Road data were line features of highway and major road casements

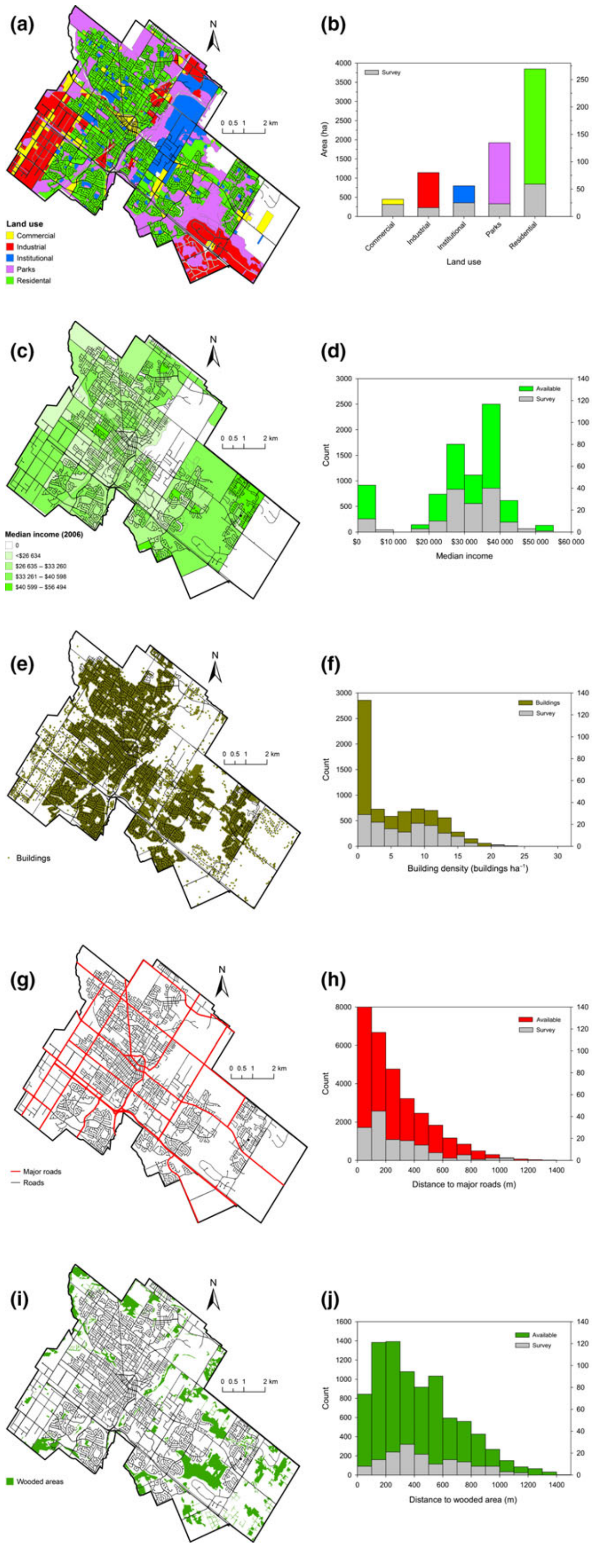

Figure 1 Explanatory variables to explain free-roaming cat density in the city of Guelph, ON. The location of five land uses (a) and the histogram (b) of land uses area (multiple colours, left axis) and the number of transect routes (grey, right axis). White areas were either agricultural or other (e.g. landfills) and were omitted because they could not be sampled. Statistical models supported pooling commercial and institutional land use areas to explain free-roaming cat density. Median income for areas in Guelph (c) and the histogram (d) of the median income values for 1 ha raster cells across the entire city (green, left axis) and the number of transect routes (grey, right axis). The location of buildings (e) and the histogram (f) of building density (brown, left axis) and the number of transect routes (grey, right axis). The location of major roads in the city of Guelph (g) and histogram (h) of the distance to major roads for 1 ha raster cells across the entire city (red, left axis) and the number of transect routes (grey, right axis). The location of wooded areas in Guelph (i) and histogram (j) of the distance to wooded area for 1 ha raster cells across the entire city (green, left axis) and the number of transect routes (grey, right axis).

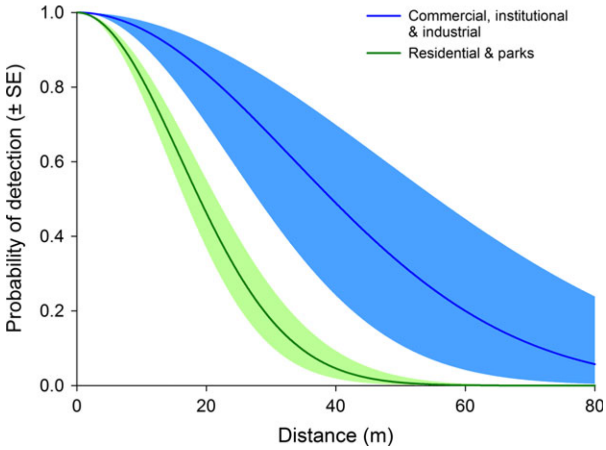

Figure 2 The mean (line) ± SE (shaded) half normal function showing the probability of detection (*P*) of a free-roaming cat by distance for land use patterns classified into two categories: commercial, institutional and industrial land uses (blue) and parks and residential land uses (green).

(Supporting Information Table S1) and for each raster cell we calculated the distance in metres to the nearest major road feature using the *Euclidean distance* tool in ArcMap (Fig. 1). Wooded areas were polygons of forest at least 2 m in height (Supporting Information Table S1) and for each raster cell we calculated the distance to the nearest wooded area using the *Euclidean distance* tool (Fig. 1). Points of buildings (Supporting Information Table S1) were summed for each raster cell to provide a measure of building density (Fig. 1).

Distance transect sampling

Between July 7, 2014 and August 28, 2014, we counted cats along routes using distance sampling and assumed cats were detected independently (Buckland *et al.*, 2001; Schmidt *et al.*, 2007*b*). To derive sampling routes (transects) we used the *genstratrandompnts* function (Beyer, 2011) to generate stratified-random points across land uses and snapped points to the nearest road or trail (parks only). We then demarcated routes of *c.* 2 km to encompass the designated land use (Table 1). Routes were not straight lines but, rather, were loops that allowed us to walk two consecutive replicates. Each replicate took on average 22 min (SD = 11) to complete, at a speed of *c.* 5 km h^{-1} in the morning (start time 06:16–09:28) or evening (start time 17:25–20:38). Mornings and evenings were chosen to maximize the chance of observing cats which, we reasoned, was a balance between matching maximum cat activity levels (crepuscular and nocturnal periods; Horn *et al.*, 2011; Kays *et al.*, 2015) and having enough daylight for observers to see the cats. For each cat observed, we recorded the replicate (1 or 2) and the perpendicular distance off the transect line using a handheld rangefinder (Buckland *et al.*, 2001). An empirical sightings histogram (Supporting Information Fig. S1) indicates that most cats are up to 5 m off the line so we accounted for this possibility using a 5 m left-truncation point and rescaled the distance data (Alldredge & Gates, 1985). An explanation of how we met the assumptions of distance sampling is provided in the Supporting Information.

Repeated distance sampling is often done between seasons or years because counts are expected to vary based on temporary random emigration of individuals (Chandler *et al.*, 2011). For our purposes, 'temporary emigration' could result both from emigration per se but also from indoor-outdoor cats being taken inside by their owners (Clancy *et al.*, 2003). Since transects were conducted back to back over <1 h, we assumed they were simply replicated counts that would reduce variation in estimating site-level population size. To this end, we stacked our replicated data after testing for homogeneity in the replicated counts using the difference in Akaike information criterion (ΔAIC = 0.6; Burnham & Anderson 2002), which has been justified in situations with sparse count data (Yamaura *et al.*, 2011; Linden & Roloff, 2013).

One unique characteristic of sampling cat populations in urban areas is that their 'availability' could be strongly dependent upon humans. For instance, owned cats given outdoor access have a certain probability of being sampled dependent upon the length of time they are left outside and the duration of sampling; we assumed that most of the cats we observed were indoor-outdoor cats. In cases where objects are not continuously available for detection, Buckland *et al.* (2001) suggested that abundance estimates from line transect surveys could be adjusted based on a known abundance. This would provide the ability to calculate the proportion of known individuals available for detection, which can serve as a multiplier on abundance.

To estimate the proportion available for detection, we used two approaches. First, we used data from Schmidt *et al.* (2007*b*) who compared observed counts of radio-collared cats from 20 distance transect surveys in Caldwell, Texas, U.S.A with the actual number radio-collared cats known to be in the study area, as determined through radio telemetry. From this, we fit an intercept-only logistic regression to model the proportion of cats available to be detected, termed *c*. The estimate of the proportion of cats available to be detected during transects was $c = 0.051$ (95% CI: 0.034–0.075). Dividing our distributional population abundance estimates derived from the transect data by mean estimate of *c* represents a corrected free-roaming cat population abundance. This approach assumes similar behaviour of free-roaming cats in Texas compared to Ontario, which could be violated if differences in weather, habitat, or cat owner behaviour (e.g. Clancy *et al.*, 2003) between these sites influences estimates of availability. However, we are not aware of any evidence of how these factors may specifically play a role in availability estimates and is therefore justified based on consistent season, daily timing of surveys and not sampling during inclement weather between our study and that of Schmidt *et al.* (2007*b*). Second, we validated the proportion of cats available for detection by dividing our city-wide free-roaming cat population estimate derived from

Table 1 Summary statistics of the transects done in different land uses including the number of routes, mean and standard deviation route length and the total number of cats observed and the mean (range) of the number of cats seen on each replicate in Guelph, ON

			Replicate 1		Replicate 2	
Land use	N	Transect length (km) mean ± SD	Total cats	Mean cats (range)	Total cats	Mean cats (range)
Commercial	22	1.1 ± 0.64	1	0.05 (0–1)	0	0 (0)
Industrial	16	2.0 ± 0.80	16	1.00 (0–5)	11	0.69 (0–5)
Institutional	25	1.1 ± 0.69	2	0.08 (0–1)	2	0.08 (0–1)
Parks	23	1.4 ± 0.96	3	0.13 (0–2)	2	0.09 (0–1)
Residential	59	2.1 ± 0.45	78	1.32 (0–12)	64	1.08 (0–6)

the distance sampling data by an independent estimate of indoor-outdoor population size in Guelph (see below). Overlap in the proportion of cats observed to that derived from data in Schmidt *et al.* (2007*b*) would provide support for our estimate of the proportion of cats available for detection.

Statistical analysis

We used count distance sampling (function *gdistsamp*) in the *unmarked* package (Fiske & Chandler, 2011) in Program R (R Core Team 2014) to fit hierarchical models using maximum likelihood. The hierarchical model uses counts of individuals at $i = 1, 2, \ldots, R$ routes to separate the state processes of population abundance while accounting for the observation process of the counts made during sampling (Royle *et al.*, 2004). The two-level hierarchical model contains sub-models for the probability of detection (P) and abundance (λ; Royle *et al.*, 2004; Chandler *et al.*, 2011)

$$N_i \sim \text{Negative Binomial}(\lambda, \alpha)$$

$$\mathbf{y}_i \sim \text{Multinomial}(N_i, \pi_i)$$

where N_i is the population at site i with mean λ and dispersion parameter α and $\mathbf{y}_i$ is a vector of counts at route i that arise conditional on N_i, and π_i is the vector of multinomial cell probabilities of the detection probability (P_{ij}). The detection probability was modelled using the half-normal detection function $g(r) = \exp(-r^2/2\sigma_i^2)$, where r is the perpendicular distance and σ_i is the scale parameter at site i, and the multinomial cell probabilities were derived by integrating $g(r, \sigma_i)$ over the area (A_j) of distance class j defined by the distance break-points. Population density (D) was estimated across the actual transect area (A) as $\widehat{D} = \hat{\lambda}/A$ (Chandler *et al.*, 2011).

As an initial step to assess the distribution of the count data, we compared a null model ($\lambda^{\cdot}$ $p^{\cdot}$) under a Poisson and negative-binomial mixture distribution and retained this form throughout the analysis. Our data were zero-inflated and were, therefore, best fit using the negative-binomial compared to the Poisson model (ΔAIC = 77), which requires the dispersion parameter (α) to be estimated.

The probability of detection during counts (P) is the monotonically decreasing probability of detecting an animal that is present given an increasing distance to the observer denoted by the scale parameter [ln (σ); Buckland *et al.*, 2001]. Given that our sampling was stratified by land use, we considered two simple models to explain variation in p with land use pooled into two categories. The first model ($p^{\text{Resid-Park,Other}}$) reflected the short sight-lines in parks and residential areas caused by trees/vegetation in parks or fences of residences that restricted observations. In contrast, longer sight-lines occurred in commercial, industrial and institutional areas because building density is low and open spaces between and around buildings are large. The second model ($p^{\text{Resid,Other}}$) considered differences between residential areas compared to all others (commercial, industrial, institutional and parks). Residential areas were quite cluttered and complex (e.g. cars, trees, fences) compared to the simple, rather homogenous structure of the observation area in all other land use types (e.g. unobstructed building fronts and alley ways, open fields, parking lots).

Once we had formulated the best model to explain detection probability, our goal was to test five variables to explain free-roaming cat density in urban areas. The null model considered density as a constant value across the city ($\lambda^{\cdot}$; Schmidt *et al.*, 2007*b*). We then tested all combinations of our five variables using additive models including the global model ($\lambda^{\text{wood + road + income + building + land use}}$). There were few observations of cats in commercial and institutional areas so we pooled these two categories to increase statistical power (Table 1). We used AIC to determine which hypothesis held the most support given the data under the principle of parsimony to explain the density of free-roaming cats in a large urban areas (Burnham & Anderson 2002).

We used parametric bootstrapping to evaluate the goodness-of-fit of the best model by simulating 200 data sets from our model and refit the model to compute a fit statistic (Sillett *et al.*, 2012). We compared the fit of the observed data set to the distribution obtained from the simulations using the Freeman–Tukey statistic available in *unmarked* (Fiske & Chandler, 2011). Following convention, we assumed the top model to fit the data if the observed value was not beyond the 0.05 percentile of the reference distribution.

We then used the best model to predict free-roaming cat abundance at each of the 8153 cells in the city, given the parameter estimates from our model and the spatial covariates, to produce a spatially explicit observed free-roaming cat density map. We then adjusted the observed estimate to account for the proportion of cats available during sampling by dividing each grid cell by c, as explained above. We used the sum of the expected abundances across the city as the estimate of total population size and calculated uncertainty in our estimate using a parametric bootstrap with 200 simulations (Sillett *et al.*, 2012).

Independent estimate of indoor-outdoor cat population size

A common approach to estimate population size of owned cats is to survey a sample of households about the number of cats they own and then extrapolate these data across large geographical areas with a known number of households (Sims *et al.*, 2008; Murray *et al.*, 2010; Canadian Federation of Humane Societies 2012; Downes *et al.*, 2013). The number of indoor-outdoor cats was considered the product of the number of households, the estimated number of owned cats per household and the probability of owned cats having access to the outdoors in Guelph. In collaboration with the Guelph Cat Population Taskforce, 115 random surveys of citizen living in Guelph were conducted between December 5, 2014 and May 20, 2015 and asked how many cats they owned and if these cats have access to the outdoors. We approached citizens at the public library, farmers market, and at a bowling alley/retail store complex (Supporting Information Table S2). We fit two intercept-only models using these data. The first was a quasipoisson generalized linear model to estimate the number of cats per household and the second was a binomial generalized linear model to estimate the probability of owned cats having access to the outdoors. The total number of households in Guelph (54 725) was derived from 2011 census data (Statistics Canada 2011). Finally, we multiplied the average number of cats per home and proportion of outdoor cats with associated confidence interval by the number of households to derive the number of outdoor cats in Guelph. We assumed that no respondents were members of the same household. The citizen questionnaire survey received Research Ethics Board Approval from the University of Guelph (REB#14JN012).

Results

Free-roaming cat transects

We conducted 145 transects and observed 100 cats on the first replicate and 79 cats on the second replicate among the different land uses (Table 1). Most cats were observed in residential areas or industrial areas with few cats observed in commercial areas, institutional areas and parks (Table 1). Residential areas were the most common land use (47%) followed by parks (24%), industrial (14%), institutional (10%) and commercial areas (5%) (Fig. 1). Left-truncation removed six observations from the final data set used in the analysis (Supporting Information Fig. S1).

Model selection and goodness of fit

Detection probability was best explained by variation between residential and parks compared to commercial, industrial and institutional land use categories (Supporting Information Table S3). At a given distance, the probability of detection was lower for residential areas and parks compared to commercial, institutional and industrial areas (Fig. 2). In fact, the perpendicular distance corresponding with the 50% detection probability was more than two times further for commercial, industrial and institutional areas (39.4 m) compared to residential/parks areas (19.0 m) and did not overlap over the entire viewing distance (Fig. 2).

Free-roaming cat population abundance was best explained by land use, median income, building density and distance to wooded areas (Table 2). The most parsimonious model accounted for 59% of the AIC weight while the global model, which included distance to roads, held an additional 28% of the AIC weight indicating a large number of variables explain free-roaming cat abundance (Table 2). Cat abundance was highest in residential areas, moderate in industrial areas and parks, and lowest in commercial and institutional areas, negatively related to median income, positively related to distance from woods, and positively related to building density (Table 3). The bootstrap *P*-value from the goodness-of-fit simulations for the best-fitting model (Table 2) was $P = 0.46$ suggesting that the negative-binomial model, and the associated dispersion parameter (Table 3), adequately fit the data.

Free-roaming cat population size and density

Estimated abundance from the transect data was 389 (95% bootstrap CI: 312–506). After adjusting for the proportion of cats that could have been observed, the total free-roaming cat population size for the city of Guelph was estimated to be 7662 (95% CI: 6145–9966). Cat population density was the highest in high-density low-income residential neighbourhoods that were further from wooded areas (Fig. 3). The lowest population densities were in low-density high-income commercial/institutional lands near wooded areas (Fig. 3). Spatial heterogeneity of predicted free-roaming cat population density across the city was dramatic and showed several hotspots of maximum density (49.4 cats per ha; Fig. 4).

Table 2 Comparison of models (ΔAIC < 10) to explain free-roaming cat density (λ) in Guelph, ON

Model	AIC	ΔAIC	w_i	K
Wood + income + building + land use	524.1	0	0.59	10
Wood + road + income + building + land use	525.7	1.51	0.28	11
Wood + building + land use	527.8	3.69	0.09	9
Wood + road + building + land use	529.8	5.61	0.04	10

Specific variables are indicated in Table 3. The information for each hypothesis includes the Akaike information criterion value (AIC), difference in AIC compared to the top model (ΔAIC), Akaike weight (w_i) and number of model parameters (K). The full candidate model list is presented in Supporting Information (Table S3).

Table 3 Parameter estimates from the model $\lambda^{\text{wood + income + building + land use}}\ p^{\text{Resid-Park,Other}}$ to explain observed free-roaming cat population abundance in Guelph, ON

Submodel	Coefficient	Est. (SE)
Abundance, ln (λ)	Wood	0.418 (0.0953)
	Income	−0.409 (0.163)
	Building	0.664 (0.163)
	Commercial/institutional	−5.482 (0.509)
	Industrial	−3.107 (0.300)
	Parks	−3.900 (0.515)
	Residential	−2.938 (0.233)
Detection, ln(σ)	Commercial/institutional/ industrial	3.51 (0.176)
	Residential/parks	2.78 (0.066)
Dispersion, α		1.51 (0.681)

Note that slopes of the linear covariates are for the standardized values of income, wood and building.

Independent indoor-outdoor cat population size

The number of cats owned per household in Guelph was 0.52 (95% CI: 0.39–0.70) and the probability of an owned cat having outdoor access was 0.42 (95% CI: 0.30–0.54). When taken together, this resulted in an estimate of 11 927 (CI: 6361–20 989) owned indoor-outdoor cats in Guelph in 2014, which overlaps with our free-roaming cat population estimate of 7662 from the distance-based sampling.

Finally, we validated the proportion of cats available for detection by dividing our city-wide free-roaming cat population estimate derived from distance sampling (389 cats) by our independent estimates of indoor-outdoor population size in Guelph. The mean detection was 0.033 (95% CI: 0.019–0.061) which overlapped the lower end of the estimate from Schmidt *et al.* (2007*b*; $c = 0.051$; 95% CI: 0.034–0.075). Our data suggest, if these findings are representative, a rule of thumb is for each free-roaming cat seen in Guelph, a further 16–54 cats are not seen.

Discussion

Using distance-based sampling that accounted for imperfect detection, we found cat abundance differed between land uses, declined with increasing median income levels and increased with distance to both wooded areas and building density. Our population estimate of 6145–9966 cats is the first empirical estimate of free-roaming cat population size across a large urban area that provides an ecological context to assess the magnitude of risks posed by cats to urban wildlife and public health as well as provides a baseline for assessing the impact of various approaches to cat population management. Importantly, our distance-based approach overlaps an independent estimate based on a randomized survey of citizens and aligns with previously published parameters. Our map of predicted population density avoids spatial-biases that may arise in non-randomized data collection schemes (Aguilar & Farnworth, 2012, 2013; Reading, Scar-

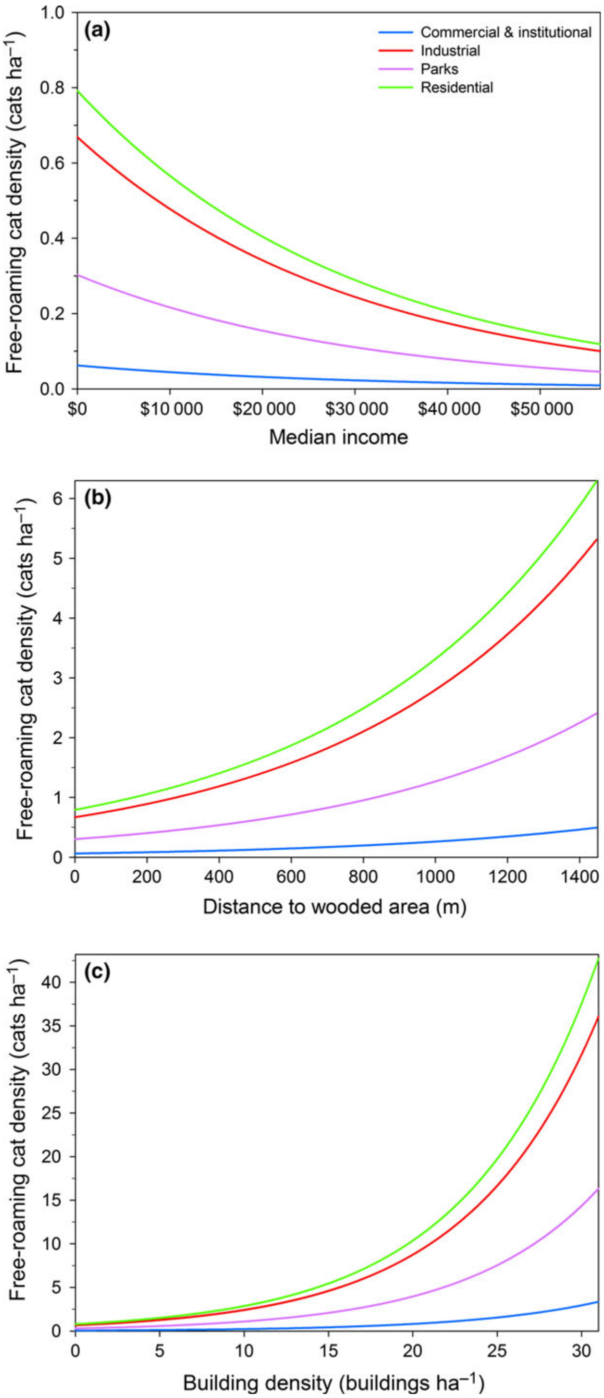

Figure 3 Expected free-roaming cat population density after adjusting for availability for each land use as a function of covariates from the top model. (a) Negative relationship between income and free-roaming cat population density when distance to wooded areas and building density is constant at 0. (b) Positive relationship between distance to wooded areas and free-roaming cat density when income and building density is constant at 0. (c) Positive relationship between building density and free-roaming cat density when income and distance to wooded areas is constant at 0.

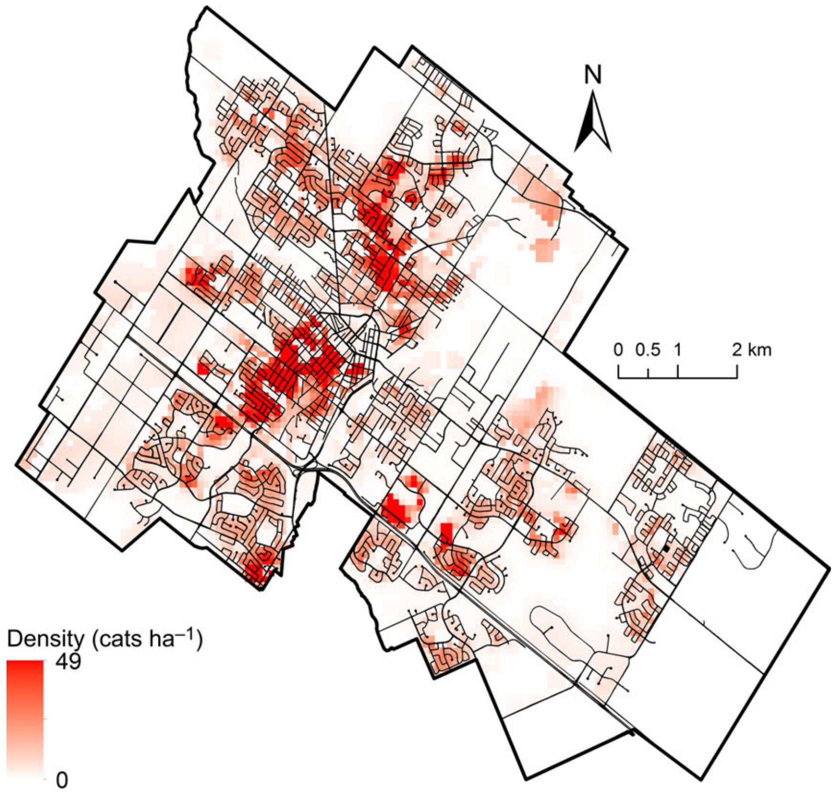

Figure 4 Predicted free-roaming cat density (cats per ha), after adjusting for the availability of cats to be observed during sampling, for Guelph, ON, as a function of income, land use and distance to wooded areas and building density from the top model used to explain the abundance of free-roaming cats.

lett & Berliner, 2014) or homeowner-based surveys that are restricted to residential areas (Sims *et al.*, 2008; Murray *et al.*, 2010) and, therefore, provides managers with unbiased information for targeting interventions to address abundant cats in urban areas.

Land use is predicted to be an important attribute to understanding free-roaming cat population dynamics (Crooks & Soulé, 1999; Odell *et al.*, 2003). We found residential areas to have the highest densities of cats and commercial and institutional lands to have the lowest. Intuitively, this makes sense if many of the cats we observed during transects were indoor-outdoor cats (Sims *et al.*, 2008) as we assumed in our study. The negative relationship with income implies that socio-economic level influences the number of owned cats, the probability that cats will be let outdoors, or the rate of sterilization that define fecundity. Previous research has found no relationship between household income and cat ownership (Murray *et al.*, 2010) or employment level, a proxy for socio-economic level, and the probability owned cats will have access to outdoors (Clancy *et al.*, 2003). In contrast, the probability of an owned cat being sterilized increases with socio-economic level (Chu, Anderson & Rieser, 2009; Finkler *et al.*, 2011*a*). Taken together, our results suggest higher free-roaming cat abundance may result from increasing breeding opportunities (Finkler *et al.*, 2011*b*) in addition to access to human-derived food resources (Calhoon & Haspel, 1989). These relationships, akin to those often posed for wildlife, suggest that free-roaming cat abundance may be partially driven by bottom-up processes. If so, then it is important to consider that limiting food availability may be an effective intervention to reduce the resources available to free-roaming cats.

In contrast, the distribution of predators, such as coyotes, may impose top-down limitation on free-roaming cat populations in urban areas (Crooks & Soulé, 1999; Taylor *et al.*, 2002; Kays *et al.*, 2015). We found a positive correlation between the abundance of cats and distance from wooded areas. The assumption that wooded areas present suitable habitat for coyotes in cities is based on data that show coyotes select wooded habitats (Atwood *et al.*, 2004; Gese *et al.*, 2012), avoid urban development (Gehrt, Anchor & White, 2009) and influence prey community structure within patches (Crooks & Soulé, 1999). Collectively, these data imply that predation risk is lower with increased distance to wooded areas. These top-down processes, however, remain unlikely to result in strong predator-prey regulation given disparity of the negative correlation between coyote-human space use (Gehrt *et al.*, 2009; Kays *et al.*, 2015) and the positive correlation between cat-human space use from our analysis (Crooks & Soulé, 1999). Thus, if land use reflects bottom-up processes that control cat abundance via food availability, it implies that the susceptibility to predation depends on cat behaviour and level of dependence of human-provided food.

Admittedly, the results we present linking free-roaming cat abundance to environmental covariates is correlational and assumes *a priori* causal relationships based on previous research. While our results, and the direction of the proposed relationships, were consistent with the predictions of bottom-up and top-down control of population abundance, experimentally testing the proposed underlying mechanisms and potential confounding variables that limit cat populations presents a significant challenge. A feasible test of the assumptions of the hypotheses explaining free-roaming cat abundance might include collecting data on top-down factors such as coyote abundance (Crooks & Soulé, 1999; Gehrt *et al.*, 2009; Lukasik & Alexander, 2011; Kays *et al.*, 2015), and bottom-up factors such as wild prey abundance (Crooks & Soulé, 1999; Fuller *et al.*, 2008; Hepinstall, Marzluff & Alberti, 2009) and the distribution of sterilized cats. Meta-analyses sampling a large number of cities would be one effective way to test the generality of top-down or bottom-up processes. This approach should be paired with small-scale studies focused on variables that confound diagnosis of top-down or bottom-up processes. For instance wild prey composition and abundance may differ by forest patch size, location, or proximity to residential areas (Hepinstall *et al.*, 2009), which would imply bottom-up rather than top-down processes determine free-roaming cat abundance.

Free-roaming cats are comprised of stray, feral and owned (indoor-outdoor) individuals, which behave differently. These categories are loose definitions that usually relate to the dependence on humans for food resources, level of socialization and daily activity patterns (Levy & Crawford, 2004). The result is that each group may have different probability of detection or temporary emigration based on activity patterns (Clancy *et al.*, 2003; van Heezik *et al.*, 2010) and movement rates (Schmidt *et al.*, 2007*a*; Horn *et al.*, 2011). In this paper, we suggest the concept of temporary emigration can have two meanings for owned, free-roaming cats. As per the usual definition, cats could move away from the sampling area and be unavailable to be counted (Chandler *et al.*, 2011). In addition, they could be 'removed' or 'added' from the sampling area by owners taking cats inside or letting them out at prescribed times of the day (Clancy *et al.*, 2003). Few data exist to estimate these parameter values *a priori*, although they likely warrant further investigation given both addition-removal and temporary emigration will influence estimates of abundance (Chandler *et al.*, 2011). While we ignored categorizing cats in our analysis, we nevertheless corrected for the effects of addition-removal of indoor-outdoor cats given that many of the cats that we observed were well socialized to people. However, to fully quantify population dynamics amongst all components of the free-roaming cat population, it would be wise to consider these group-level effects using several individual-based capture-recapture studies to derive probabilistic assignment of individuals to categories (Kendall, Hines & Nichols, 2003; Choquet, Lauriane & Pradel, 2009).

Our approach used simple geographical information that is readily available for most urban areas in North America to predict free-roaming cat population size. For example land use categories from municipalities and socio-economic metrics from census data are available for most large cities in North America and our analysis suggest that multiple factors better explain free-roaming cat abundance compared to considering cat abundance to be constant (Schmidt *et al.*, 2007*b*). The benefit of using this approach is that quickly and easily obtainable data can be applied to understand and estimate the abundance of free-roaming cats across time and space for almost any city in North America with a minimal amount of field data. These efforts would contribute to understanding the spatio-temporal impact of free-roaming cats on wildlife viability (Sims *et al.*, 2008; van Heezik *et al.*, 2010) because they are independent of cat abundance estimates based strictly on homeowner surveys that are restricted to only a portion of the urban landscape (residential lands occupy <50% of the land area of Guelph) and can be overlapped with spatial occupancy and abundance patterns of different wildlife species (e.g. Hepinstall *et al.*, 2009) to assess risk. Unfortunately, few data are available for comparisons with our study, so it is possible that different factors explain cat populations in different areas or how variation in methodology may yield different results.

Understanding the factors that explain cat population dynamics informs where and how management might proceed most efficiently to reach multiple societal objectives (Loyd & DeVore, 2010; Martin *et al.*, 2010). Achieving collective support amongst citizens, animal welfare advocates, environmental activists and policy makers demand that we acquire, and make use of, this information to implement several interventions across space and time, to account for how population density is regulated (Yokomizo *et al.*, 2009) and to address often conflicting objectives (e.g. Chadès, Curtis & Martin, 2012). This is especially true when interventions to manage overabundant cats, both to reduce environmental impacts coupled with a concern for humane alternatives, are considered in isolation. For example attempts to reduce population size through attrition by sterilizing feral cats could be ineffective where individuals disperse (Schmidt *et al.*, 2009; Miller *et al.*, 2014) or if colonies of sterilized cats are more prone to immigration by unsterilized cats (Gunther, Finkler & Terkel, 2011). If dispersal is density-dependent (Matthysen, 2005), local density is mediated through predator distribution (Crooks & Soulé, 1999; Kays *et al.*, 2015) and, as our study suggests, food availability and breeding opportunities, then single strategies to address abundant cats in urban areas are unlikely to result in the optimal allocation of resources.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Histogram of the empirical sightings distances of free-roaming cats from Guelph, ON.
Table S1. Vector data files.
Table S2. Results of the survey of citizens at three locations in Guelph, ON to estimate the number of owned cats and the probability of cats having outdoor access.
Table S3. Comparison of models to describe free-roaming cat population density (λ) and probability of detection (*P*) in Guelph, ON.