

Article

Weak Effects of Owned Outdoor Cat Density on Urban Bird Richness and Abundance

Genevieve C. Perkins ^{1,2}, Amanda E. Martin ^{1,3,*} , Adam C. Smith ^{1,3}  and Lenore Fahrig ¹

- ¹ Geomatics and Landscape Ecology Laboratory, Carleton University, 1125 Colonel By Drive, Ottawa, ON K1S 5B6, Canada; Genevieve.perkins@gov.bc.ca (G.C.P.); adam.smith2@canada.ca (A.C.S.); lenore.fahrig@carleton.ca (L.F.)
- ² Ministry of Forest, Lands, Natural Resource Operations and Rural Development, 3726 Alfred Avenue, Smithers, BC V0J 2N0, Canada
- ³ National Wildlife Research Centre, Environment and Climate Change Canada, 1125 Colonel By Drive, Ottawa, ON K1S 5B6, Canada
- * Correspondence: amanda.martin@canada.ca

Abstract: Domestic cats (*Felis catus*) are ubiquitous predators of birds in urban areas. In addition to the lethal effect of predation, there can also be sublethal, negative effects of domestic cats on individual birds. These effects have led to the inference that reducing outdoor cat densities would benefit urban bird communities. Here we estimate the likely result of policies/programs designed to reduce densities of owned outdoor cats in urban areas, estimating relationships between bird richness/abundance and cat densities across 58 landscapes in Ottawa, Ontario, Canada. We estimate that we would most likely observe one additional bird species, and 0.003 additional individuals per species, if policies/programs reduced owned outdoor cat densities to zero in an average landscape in Ottawa (with 130.2 cats/km²). However, these effects of cat density on birds were uncertain, with 95% confidence intervals crossing zero. Our findings—in combination with those of previous studies—suggest a need for research to resolve the apparent disconnect between the strong, negative effects of cats on individual urban birds and the weak, uncertain effects of cats on bird populations. Although measures that reduce owned outdoor cat densities are justified based on the precautionary principle, evidence to date does not support prioritizing these measures over those addressing threats that have consistently strong effects on bird populations.

Keywords: conservation; domestic cat; *Felis catus*; house cat; migration status; mortality; urban; cat predation; landscape of fear



Citation: Perkins, G.C.; Martin, A.E.; Smith, A.C.; Fahrig, L. Weak Effects of Owned Outdoor Cat Density on Urban Bird Richness and Abundance. *Land* **2021**, *10*, 507. <https://doi.org/10.3390/land10050507>

Academic Editor: Christine Fürst

Received: 1 April 2021

Accepted: 2 May 2021

Published: 10 May 2021

Publisher's Note: MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations.



Copyright: © 2021 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

1. Introduction

Free roaming domestic and feral cats (*Felis catus*) are ubiquitous predators of birds in urban areas. An individual cat may kill 10 s to 100 s of birds per year [1,2]. This, in turn, may lead to millions of birds killed per year in cities, where high cat densities are supported by an abundance of anthropogenic food sources and reduced predator densities. For example, Sims et al. [3] reported owned outdoor cat densities up to 1579 cats/km² in urban areas in the UK. Aguilar and Farnworth [4] estimated that unmanaged cat colonies could reach densities of 36 colonies/km² in Auckland City, New Zealand.

Cats can also affect urban bird populations indirectly. They can transmit diseases to birds, resulting in additional mortality [5–7]. Cats can reduce bird fitness by reducing access to high-quality foraging or nesting sites [8–10], and reduce fledgling success by increasing nest defense at the expense of provisioning young [11]. Additionally, the threat of predation can cause physiological changes in birds that reduce reproductive success [12].

These effects of cats on individual birds have led to the inference that reducing the density of free roaming cats in urban areas would increase the abundance and diversity of urban bird communities [13–15], although this view is not universal [16,17]. Nevertheless, this inference has, at least in part, led many urban municipalities to contemplate

or introduce legislation to keep owned cats indoors [18–20]. In direct response to the threat of domestic cats for birds and other animals, the Australian Capital Territory has designated “cat containment areas”, where residents are required to keep owned cats indoors or use purpose-built outdoor enclosures to keep them on the premises [21]. Conservation organizations have also implemented education programs designed to convince owners to keep their cats indoors (e.g., the “Cats Indoors” program of the American Bird Conservancy [15]).

However, this inference assumes a strong negative relationship between owned outdoor cat density and bird diversity and abundance. This assumption needs to be tested, as the effect of cat density could be small compared to other impacts on bird diversity and abundance in cities, and/or the effects of cat density on bird populations could be partly compensated by density-dependent effects. Several studies have evaluated the relationship between owned outdoor cat density and bird species richness/abundance across urban locations that vary in cat density. Some reported negative relationships [3,22,23], and some reported positive relationships [3,24]. Interpreting results of these studies can be difficult as the relationships between cat density and bird diversity/abundance are often evaluated without controlling for potentially confounding variables. For example, Sims et al. [3] found a strong correlation between urban densification (number of buildings per area) and cat density, but did not control for the potentially confounding effect of urban density on the relationship between cat density and bird richness in their analyses. This means that their estimated effect of cat density on bird richness may be instead due to other factors associated with urban densification, such as traffic volume and road density.

The overall effect of cat density on bird richness or abundance may also be weak or inconsistent if only some bird species are negatively affected by cats. Studies including only bird species with traits that make them susceptible to cat predation should estimate stronger negative effects of cats than studies including species that are resistant to cat effects. Traits that could place birds at higher risk are lower body mass [25], a tendency to nest and/or feed near the ground [26], or use of bird feeders [25]. In temperate regions migratory species might be more likely to be excluded from areas with cats than resident species. Migratory species generally select nesting sites later in the breeding season than resident species, when more owned cats are outdoors due to warmer weather [27–30]. A previous study has shown that migratory bird species can use information on the presence of predators (signs of urine and feces) to avoid high-risk breeding locations [31]. Thus, if migratory birds typically perceive higher cat densities at a given location than resident birds, and can use that information to avoid such sites, then this could result in stronger declines in bird richness and abundance with cat density for migratory species than resident species.

Here, we estimate the likely result of policies or programs designed to reduce densities of owned outdoor cats in urban areas. Specifically, we estimated relationships between owned outdoor cat density and urban bird richness and abundance in Ottawa, Ontario, Canada (Figure 1), while controlling for four potentially confounding predictors of bird richness and abundance: human population density, bird habitat availability, bird feeder density, and non-feline predation risk. We selected these variables based on *a priori* expectation that they could be correlated with cat densities across landscapes, and could have their own effects on bird species richness and abundance [32–35]. Thus, we included these variables in the analysis to make sure that the estimated relationships between cat density and bird richness/abundance reflected the effects of cat density on birds, rather than effects of these correlated variables. We also estimated the effects of bird traits on the relationship between cat density and bird richness and abundance. Specifically, we expected occurrence or abundance of bird species with low body mass, a tendency to nest or feed near the ground, and a tendency to use bird feeders to be most impacted by cats. We also expected stronger declines in bird richness and abundance with cat density for migratory species than resident species.

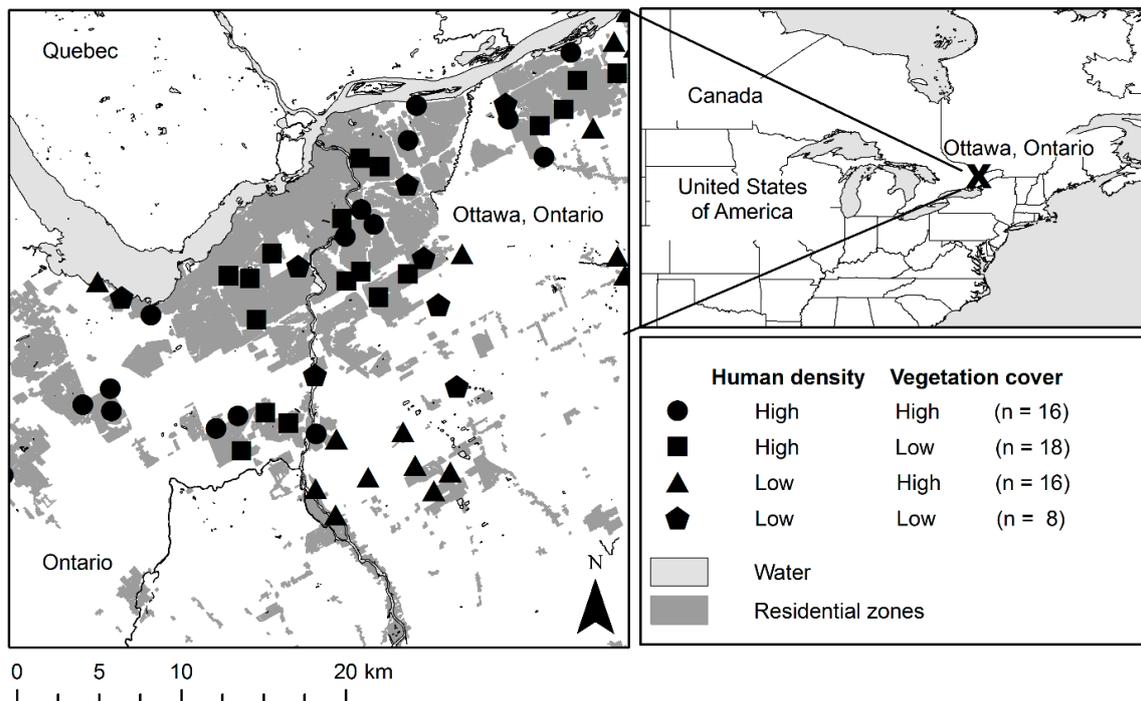


Figure 1. Locations of the 58 sample landscapes in Ottawa, Ontario, Canada. Each landscape is a 250 m × 250 m area centered on an Ottawa Bird Count survey location. Landscapes are classified by combinations of high or low human population density, and high or low vegetation cover. Human population density in each landscape is based on Statistics Canada 2011 Census data. Vegetation cover is the proportion of vegetation cover within each landscape, including all residential, commercial, and municipal areas covered by forest, individual trees, or mown grass.

2. Materials and Methods

2.1. Sample Landscape Selection

We selected 58 sample landscapes across Ottawa, Ontario, Canada centered on breeding bird sampling sites (point count locations) from the Ottawa Bird Count (OBC; Figure 1). Each landscape was 250 m in diameter, which was large enough to include most households that have cats whose home ranges overlap the 75-m radius bird point count circle at the center of the landscape (Figure 2). We based this on a 2400 m² mean owned outdoor cat home range in Albany, New York, USA, the urban area with published estimates of domestic cat home range sizes and a population size and climate as similar as possible to Ottawa's [36]. Assuming circular cat home ranges, the estimated radius of a cat home range is 27.6 m. Thus, a diameter of 205 m is the minimum circular area surrounding the bird point count location that would include the households of most cats overlapping the point count circle. We rounded this up to 250 m, to allow for variability in cat home range sizes. We then converted this to a square landscape to simplify surveying in the rectilinear street layout of Ottawa neighborhoods.

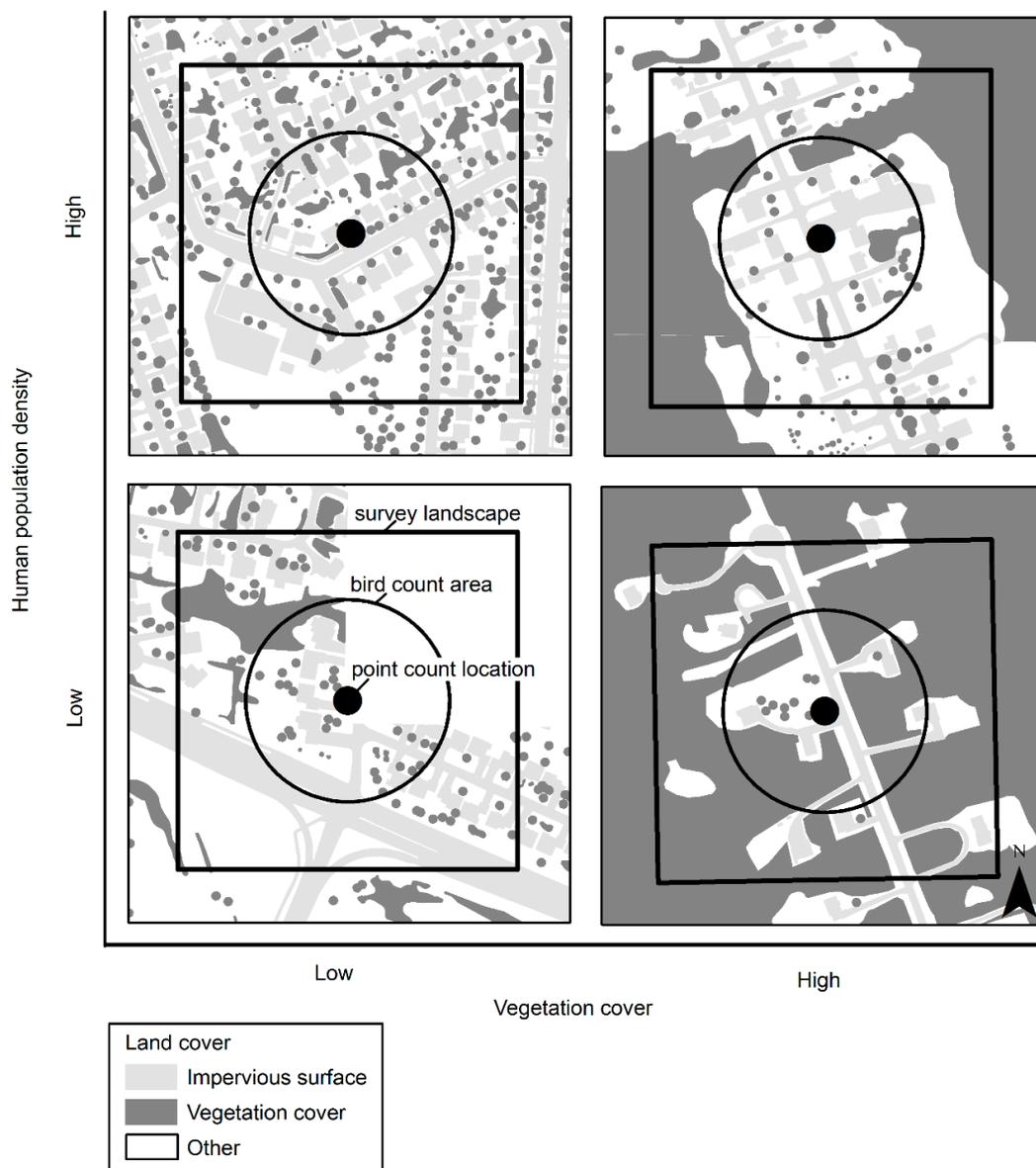


Figure 2. Four example landscapes (of 58) representing each of the four combinations of high and low human population density, and high and low vegetation cover. Each landscape was a 250 m × 250 m area centered on an Ottawa Bird Count point count location (central point). All birds within a 75 m radius of the point count location (central circle) were recorded and used to determine bird species richness and abundance. Door-to-door surveys were conducted within the 250 m × 250 m landscapes to estimate cat density, cat activity, bird feeder density, and the frequencies of squirrels and raccoons.

We primarily selected landscapes to limit collinearity between owned outdoor cat density and bird habitat availability, and to reduce the likelihood of confounding habitat effects with cat effects on birds. As we did not have cat density *a priori*, we initially indexed it with human population density, because they can be highly correlated [3]. We note that we only used human population density as an index of cat density for landscape selection; once landscapes were selected we collected data to directly estimate owned outdoor cat densities in each landscape (see Section 2.2 Data collection, below). To select our landscapes, we first used the “dissemination area” data from the Canadian census [37] to estimate human population densities within a 250 × 250 m area centered on each OBC location ($n = 166$). A dissemination area is defined as one or more neighboring city blocks with a population of 400–700 persons. If a landscape overlapped more than one

dissemination area, we used the area-weighted mean population density. We estimated bird habitat availability as the proportion of vegetation cover within each landscape, using 25-cm-resolution classified land cover data [38]. Vegetation cover included all residential, commercial, and municipal areas covered by forest, individual trees, or mown grass. To reduce collinearity between human population density and vegetation cover across our landscapes, we first specified a range of values for each variable within which the correlation between human population density and vegetation cover was low. We then further split each range into low versus high values. Finally, we selected, to the degree possible, an equal number of landscapes from each of the four combinations of low and high human population density and vegetation cover (Figures 1 and 2), under the following constraints. First, there had to be at least one residence within the landscape. Second, landscapes had to be >2.5 km inside the city boundary. This was to maximize the probability of sampling urban birds as this was the focus of our study. Third, landscapes had to be at least 1 km apart to reduce the likelihood of spatial autocorrelation. Fifty-eight OBC point count locations and their surrounding landscapes met the above criteria.

2.2. Data Collection

We estimated bird species richness and abundance from the 2014 data for the 58 selected OBC point count locations as, respectively, the observed number of species and the number of individuals for each species within 75 m of the point count location. The OBC is a volunteer, breeding-bird monitoring program that counts all birds seen or heard during 10-min point counts at randomly-selected, publicly-accessible locations within the city (e.g., sidewalks, roadsides) during the breeding season. OBC was developed by ornithologists and biostatisticians, and uses rigorous volunteer training and strictly standardized field methods to allow for consistent and comparable data across years and locations. The point counts were conducted in the morning (4:46–8:30) during the breeding season (June 5–30). We used bird observations from the 0–75 m distance class, because bird detectability is higher at shorter distances [39]. We used the data from 2014 because this was the year in which we sampled owned outdoor cat density, bird feeder density, and non-feline predation risk (see below).

We classified each bird species as belonging to either the high-risk or low-risk category separately for each of five species traits predicted to increase cat impacts on bird occurrence and abundance, as follows: the species (a) has a mean adult mass <150 g (as in [1]); (b) nests <2 m from the ground; (c) forages <2 m from the ground; (d) feeds at bird feeders; (e) is migratory. Otherwise, the species was classified as low-risk for the given trait. Classifications were primarily based on information obtained from Dunning [40] and Rodewald [41], and supplemented by additional literature, expert opinion, and other available bird survey data (see Table 1 for details).

Table 1. Classification of bird species as belonging to either the high-risk or low-risk category for each of five species traits predicted to affect species responses to cat density. Each trait was modeled as a binary variable, with each species assigned to either the high-risk (1) or low-risk (0) category. A species was classified as high-risk if it has a mean adult body size <150 g; nests <2 m from the ground; forages <2 m from the ground; feeds at bird feeders; and is migratory. Otherwise, the species was classified as low-risk, for the respective trait. Body mass measures were obtained from [40], bird feeder use from [1], and other life history information was obtained from [41], or as specified in the “Source” column.

Common Name (Scientific Name)	Body Size	Bird Feeder Use	Nesting Location	Feeding Location	Migration Status	Source
red-winged blackbird (<i>Agelaius phoeniceus</i>)	1	1	1	1	1	[42]
mallard (<i>Anas platyrhynchos</i>)	1	0	1	0	1	[42]
cedar waxwing (<i>Bombycilla cedrorum</i>)	1	1	1	0	0	
Canada goose (<i>Branta canadensis</i>)	0	0	1	1	0	[43]
northern cardinal (<i>Cardinalis cardinalis</i>)	1	1	1	1	0	[44]
purple finch (<i>Carpodacus purpureus</i>)	1	1	0	0	0	
brown creeper (<i>Certhia americana</i>)	1	1	0	0	0	[45]
chimney swift (<i>Chaetura pelagica</i>)	1	0	1	0	1	[46]
northern flicker (<i>Colaptes auratus</i>)	1	1	0	1	0	
rock pigeon (<i>Columba livia</i>)	0	1	1	1	0	[42]
eastern wood-pewee (<i>Contopus virens</i>)	1	0	0	0	1	
American crow (<i>Corvus brachyrhynchos</i>)	0	0	0	1	0	[44,47]
common raven (<i>Corvus corax</i>)	0	0	0	1	0	[48]
blue jay (<i>Cyanocitta cristata</i>)	1	1	0	1	0	[48]
gray catbird (<i>Dumetella carolinensis</i>)	1	0	1	1	1	[49]
common yellowthroat (<i>Geothlypis trichas</i>)	1	0	1	1	1	
house finch (<i>Haemorhous mexicanus</i>)	1	1	1	1	0	[42,47]
barn swallow (<i>Hirundo rustica</i>)	1	0	1	0	1	
wood thrush (<i>Hylocichla mustelina</i>)	1	0	0	1	1	
Baltimore oriole (<i>Icterus galbula</i>)	1	0	0	0	1	[50]
ring-billed gull (<i>Larus delawarensis</i>)	0	0	1	1	1	[47]
song sparrow (<i>Melospiza melodia</i>)	1	1	1	1	0	
brown-headed cowbird (<i>Molothrus ater</i>)	1	1	1	1	1	[42,48]
great crested flycatcher (<i>Myiarchus crinitus</i>)	1	0	0	0	1	
Nashville warbler (<i>Oreothlypis ruficapilla</i>)	1	0	1	0	1	
house sparrow (<i>Passer domesticus</i>)	1	1	1	1	0	[42,47,51]
rose-breasted grosbeak (<i>Pheucticus ludovicianus</i>)	1	0	0	0	1	
downy woodpecker (<i>Picoides pubescens</i>)	1	1	0	0	0	[45]
hairy woodpecker (<i>Picoides villosus</i>)	1	1	0	0	0	[45]
black-capped chickadee (<i>Poecile atricapillus</i>)	1	1	0	0	0	[47]
purple martin (<i>Progne subis</i>)	1	0	0	0	1	[48]
common grackle (<i>Quiscalus quiscula</i>)	1	0	0	1	1	
eastern phoebe (<i>Sayornis phoebe</i>)	1	0	0	0	1	

Table 1. Cont.

Common Name (Scientific Name)	Body Size	Bird Feeder Use	Nesting Location	Feeding Location	Migration Status	Source
yellow-rumped warbler (<i>Setophaga coronata</i>)	1	0	0	0	1	
yellow warbler (<i>Setophaga petechia</i>)	1	0	0	0	1	
pine warbler (<i>Setophaga pinus</i>)	1	0	0	0	1	
American redstart (<i>Setophaga ruticilla</i>)	1	0	0	1	1	
white-breasted nuthatch (<i>Sitta carolinensis</i>)	1	1	0	0	0	
American goldfinch (<i>Spinus tristis</i>)	1	1	1	1	1	[52]
chipping sparrow (<i>Spizella passerina</i>)	1	0	1	1	1	[48]
European starling (<i>Sturnus vulgaris</i>)	1	1	0	1	0	[42,44]
tree swallow (<i>Tachycineta bicolor</i>)	1	0	0	0	1	
house wren (<i>Troglodytes aedon</i>)	1	0	1	0	1	[44]
American robin (<i>Turdus migratorius</i>)	1	1	1	1	0	[47]
eastern kingbird (<i>Tyrannus tyrannus</i>)	1	0	0	0	1	[48]
warbling vireo (<i>Vireo gilvus</i>)	1	0	0	0	1	
red-eyed vireo (<i>Vireo olivaceus</i>)	1	0	0	0	1	
mourning dove (<i>Zenaida macroura</i>)	1	1	1	1	0	[42]
white-throated sparrow (<i>Zonotrichia albicollis</i>)	1	1	1	1	1	[53]

We estimated owned outdoor cat density, owned outdoor cat activity, bird feeder density, and non-feline predation risk using data collected during door-to-door surveys. We conducted these surveys in each of the 58 landscapes between April and August 2014. We visited landscapes in random order to avoid confounding effects of sampling date. We visited all houses in each landscape on weekdays between 3:00 pm and 8:00 pm. Participants could complete the survey in person or online. Participants were asked how many cats they owned and how much time (if any) each cat spent outdoors in the spring–summer. We focused on spring–summer because this corresponds to the timing of the OBC bird surveys. Participants were also asked questions relating to bird feeders and other predators in the neighborhood. The interviews were conducted in accordance with the Declaration of Helsinki, and all interview questions and methods were approved as a Minimal Risk Ethics Protocol by the Carleton University Research Ethics Board (Project 100857).

We measured cat density in each landscape using the method adapted from Baker et al. [54]:

$$D_i = \sum c_i + (r_i \times \sum c_i / n_i), \quad (1)$$

where $\sum c_i$ = number of cats that spent time outdoors summed for all interviews in landscape i , r_i = number of non-interviewed residences in landscape i , and n_i = number of interviews in landscape i . Thus $(r_i \times \sum c_i / n_i)$ estimates the number of cats at residences not interviewed, based on the sample of interviewed residences. The assumption here is that our sample of interviewees—and the frequency with which they own cats and let them spend time outdoors—is representative of the larger cat population within a study landscape. A similar assumption is made for the measures of cat activity and bird feeder density described below. We note that one could use other methods to estimate cat densities, for example, by using transect surveys [55] or trail cameras [56]. Such methods are appropriate for estimating densities of unowned (stray/feral) cats or all cats, provided that the sampling design and sampling effort can adequately account for low detection probabilities of domestic cats in urban environments [55]. However, we expect they would produce less accurate estimates of owned outdoor cat densities than using information provided directly from the people who own (or do not own) cats. This is primarily because errors would occur when classifying a detected cat as owned versus unowned.

The above measure of cat density excluded information on how much time cats spent outdoors. Therefore, we also created a measure of owned outdoor cat activity, using a modified version of the above equation where $\sum c_i$ was replaced by $\sum h_i$ = number of hours/day each owned cat spent outdoors, summed for all interviews in landscape i .

To estimate bird feeder density, participants in the door-to-door surveys were asked if they had bird feeders. We then calculated the density of bird feeders per site using the same equation as we used to estimate cat density, with the exception that $\sum c_i$ was replaced by $\sum f_i$ = number of residences with bird feeders summed for all interviews in landscape i .

Meta-analysis of predator removal experiments suggests that mammalian predators have a large negative impact on bird abundance [35]. Therefore, we used estimates of common mammalian predators in our study area to index non-feline predation risk: squirrels (*Tamiasciurus hudsonicus* and *Sciurus carolinensis*) and raccoons (*Procyon lotor*). Squirrels prey on bird eggs, nestlings, and adult birds [57]; indeed, Morris and Conner [58] found that ground nest depredation increased with the abundance of squirrels. Squirrels also compete with granivorous birds for food [59] and tree-nesting birds for nesting resources. Raccoons are also known to depredate bird nests [60]. To estimate squirrel and raccoon frequencies, participants in the door-to-door surveys were asked how often they saw squirrels/raccoons in their neighborhood during spring–summer. We used these answers to estimate the number of days per week squirrels/raccoons were observed, ranging from daily (seven times per week) to once per season (once every 12 weeks) to never (zero times per week). The squirrel/raccoon frequency for a landscape was the average frequency from all interviews in that landscape.

We note that we had also intended to include estimates of abundances of avian birds of prey from the OBC bird surveys as a third measure of non-feline predation risk for birds. However, this was not possible because a bird of prey was observed at only one of our 58 bird count locations in 2014.

We measured the remaining two predictor variables—human population density and bird habitat availability—using the same data sets used in landscape selection (described above). Human density was the area-weighted mean population density in the landscape. We did not know *a priori* the best measure of bird habitat availability, because different bird species may prefer different vegetation types. Therefore, we estimated five measures of bird habitat availability as the proportional cover of (1) individual trees, (2) forest, (3) mown grass, (4) tree canopy cover (individual trees + forest), and (5) urban greenspace (individual trees + forest + mown grass).

2.3. Data Analysis

We did not include bird detectability in our statistical models for four reasons. First, previous analyses using data from the OBC showed that its rigorous volunteer training and strictly standardized field methods result in very low variation in detectability among observers or traffic levels [33]. Second, models that attempt to correct for imperfect detectability can introduce bias and increase variance of the estimates when sample sizes are relatively small [61], producing less accurate estimates of abundance/occurrence than models that do not account for detectability. Third, applying a detection model, particularly within our multi-species abundance models, would have excluded all but the most common species. Finally, we confirmed that factors potentially influencing detectability (day of year, time of day, vehicle activity, and observer identity) were not strongly correlated with our predictor variables (see Figures S1–S6), indicating that variations in detectability are unlikely to influence our results. Thus, use of a fixed-radius point count was the most appropriate method of estimating bird species richness and abundance in our study [62].

We used a generalized linear model (GLM) with a Poisson distribution and log link to estimate the relationship between bird species richness and owned outdoor cat density, including human population density, bird habitat availability, bird feeder density, squirrel frequency, and raccoon frequency, to account for their possible effects. All predictors were standardized to a mean = 0 and SD = 1. To select the most appropriate measure of bird habitat availability, we repeated this analysis five times, each with a different measure of bird habitat availability (as described above). We retained the measure of habitat availability with the strongest positive relationship with bird species richness, based on the size of the standardized model coefficient. We used the standardized model coefficients to estimate effect sizes, and we used the modeled relationship between bird species richness and cat density to estimate the expected change in bird species richness if cat densities were reduced. The 95% confidence interval (CI) was used to capture the uncertainty in these estimates.

We modeled the relationship between bird abundance and cat density as described above, except that here we used a generalized linear mixed effects model (GLMM) with a negative binomial distribution and log link. We included a random effect of species, allowing for variability in the intercept, which accounts for differences in overall abundance among species. This approach allowed us to estimate the pooled cross-species effects of these predictors on bird abundance, while accounting for variation in overall abundance among species. We considered also allowing for among-species variability in the slope of the relationship between bird abundance and cat density. However, our conclusions were the same whether we accounted for among-species variability in the bird abundance-cat density relationship or not (Figure S7). Thus, we report the simpler model described above. We also estimated the relationships between bird richness/abundance and cat activity as described above for cat density.

Each of the five bird traits thought to affect the impact of cats on the occurrence and abundance of bird species was modeled as a binary variable, with each species assigned

to either the high-risk or low-risk category. To test for effects of bird traits on the effect of cat density on bird richness, we tested for standardized cat density \times bird trait interaction effects on bird richness. Since our sample size was limited ($n = 58$ landscapes) and a species' risk level for a given trait was generally independent of its risk level for the other four traits (see Table S1 and Figure S8), we modeled each cat density \times trait interaction in a separate GLM with a Poisson distribution and log link, for a total of five analyses, one for each bird trait. We did not combine the risk classifications for the five species traits into a single variable (e.g., by summing the risk levels for the five traits) because this would require us to set an *a priori* weighting of the relative importance of these traits for species' risk which, if wrong, could result in a failure to detect effects of traits on the relationship between bird richness and cat density. Human population density, bird habitat availability, bird feeder density, squirrel frequency, and raccoon frequency were also included in each model. Our prediction for a given trait would be supported if there was a significant cat density \times trait interaction (at $\alpha = 0.05$) indicating a steeper decline in bird richness with cat density for the high-risk than for the low-risk bird group. We also tested for the effects of bird traits on the bird abundance-cat density relationship as above, except that here we used GLMM with a negative binomial distribution and log link.

Analyses were conducted in R [63], using the 'glmmADMB' package [64,65] for GLMM.

3. Results

Overall, 49 bird species were recorded. Three to 18 species were recorded per point count location (mean = 8), with 4 to 71 individual birds per location (mean = 16). Cat density estimates were based on interviews of 663 households that responded to the survey, either in person or online (mean = 11 households per landscape, range = 1–50). Twenty-seven percent of interviewed households had at least one cat (179/663 interviewed households) and 55% (99/179) of households with a cat (or cats) let their cat(s) outside. In total, 146/276 owned cats in this survey spent time outdoors. The percent of interviewed households per landscape that had at least one cat that spent time outdoors ranged from 0 to 100% (mean = 16%) and owned outdoor cats were found in 67% of landscapes (39/58). Outdoor cat densities were 0.0–42.7 cats per landscape (mean = 8.1), or 0.0–683.4 cats/km² (mean = 130.2). Estimated cat activities were 0.0–480.0 outdoor cat hours/day per landscape (mean = 69.0 cat hours/day). Cat density and cat activity estimates were strongly correlated across landscapes, with a Spearman rank correlation (ρ) = 0.91. Human densities were 0.7–438.7 people/landscape (mean = 121.2) and vegetation covers were 0.05–1.00 (mean = 0.67). Cover of individual trees—which was selected as the most appropriate measure of bird habitat availability (Figure S9)—ranged from 0.00 to 0.17 (mean = 0.04). Squirrel frequency ranged from squirrels observed 0.3 days/week to 7.0 days/week (mean = 6.2) and raccoon frequency ranged from raccoons observed 0 days/week to 4.7 days/week (mean = 0.6). Bird feeder densities were 0.0–53.7 feeders/landscape (mean = 12.4). Relationships among our predictor variables were generally weak (Table S2). The strongest relationship was between cat and bird feeder densities ($\rho = 0.69$).

Interview response rates ranged from 33–100% of households per landscape (mean = 73%). There was no evidence that interview response rates were related to cat densities ($r = -0.08$, $p = 0.54$) or to cat activity ($r = -0.06$, $p = 0.65$), suggesting that response rates were not biased towards cat owners (or non-owners). Response rates were also unrelated to the other variables estimated from surveys: bird feeder density ($r = -0.12$, $p = 0.35$), squirrel frequency ($r = -0.21$, $p = 0.12$), and raccoon frequency ($r = -0.16$, $p = 0.23$).

We found a weak negative relationship between overall bird species richness and cat density, when controlling for potentially confounding variables (Figures 3a and 4a). However, high uncertainty in this estimate, based on the 95% CI, suggests that we cannot rule out the possibility of no change—or even a small decrease—in bird species richness if owned outdoor cat densities were reduced to zero. The effect of cat density on urban bird species richness was similar in magnitude to that of human population density, squirrel

frequency, and raccoon frequency; however, these other predictors had much stronger statistical support (95% CIs that did not cross zero; Figure 3a).

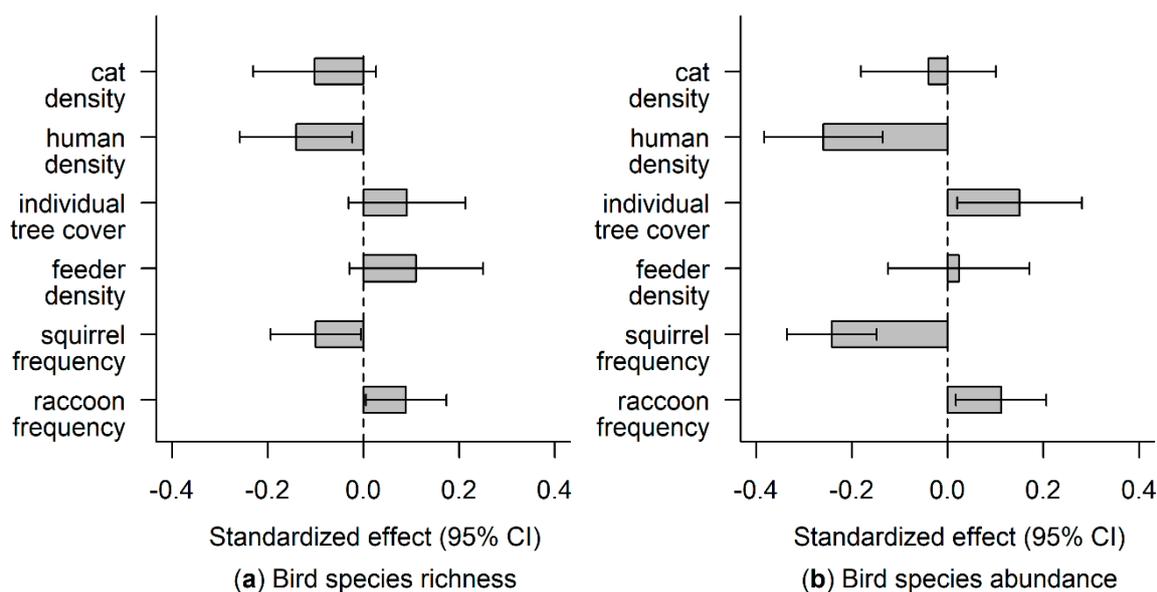


Figure 3. Standardized effects of owned outdoor cat density, human population density, individual tree cover, feeder density, squirrel frequency, and raccoon frequency on bird species (a) richness and (b) abundance. Bird richness and abundance decreased with human population density and squirrel frequency, and increased with raccoon frequency. Birds were more abundant in landscapes with more individual trees. Bird responses to cat density were weak. Relationships between bird species richness and the six standardized predictors were estimated from a generalized linear model with a Poisson distribution and a log link. Relationships between bird species abundance and the six standardized predictors were estimated from a generalized linear mixed effects model with a negative binomial distribution, log link, and random effect of species identity.

The relationship between the pooled abundance of birds and cat density was very weak (Figures 3b and 4b). And, as above, we cannot rule out the possibility of no change—or even a decrease—in abundance if owned outdoor cat densities were reduced to zero. The effect of cat density on bird abundance was small relative to other strongly-supported predictors in the model, i.e., human population density, individual tree cover, squirrel frequency, and raccoon frequency (Figure 3b). The effects of these other predictors on bird species abundance were 2.8–6.5 times the effect of cat density.

Comparison of models including cat activity to models including cat density suggest that cat activity—which included information on how much time owned cats spent outdoors—was a poorer predictor of bird species richness and abundance than cat density (Figure S10). The effects of cat density on bird species richness and abundance were, respectively, 2.7 times and 1.2 times the effect of cat activity.

There was evidence of stronger declines in bird richness and abundance with cat density for migratory species than resident species. We found a significant interaction effect between migration status and cat density on bird species richness ($z = -2.00$, $p = 0.05$) and abundance ($z = -2.07$, $p = 0.04$). The richness of migratory birds declined more strongly with increasing cat density than the richness of resident birds (Figure S11). Abundance declined with increasing cat density if the species was migratory (Figure S12a), but increased with cat density if the species was resident (Figure S12b).

We did not find strong statistical support for the expectation that bird species with low body mass, a tendency to nest or feed near the ground, or a tendency to use bird feeders would be most impacted by cats. The test for an interacting effect of cat density \times bird trait on bird species richness and abundance was non-significant for each of these traits (all $p > 0.26$; Figure S13).

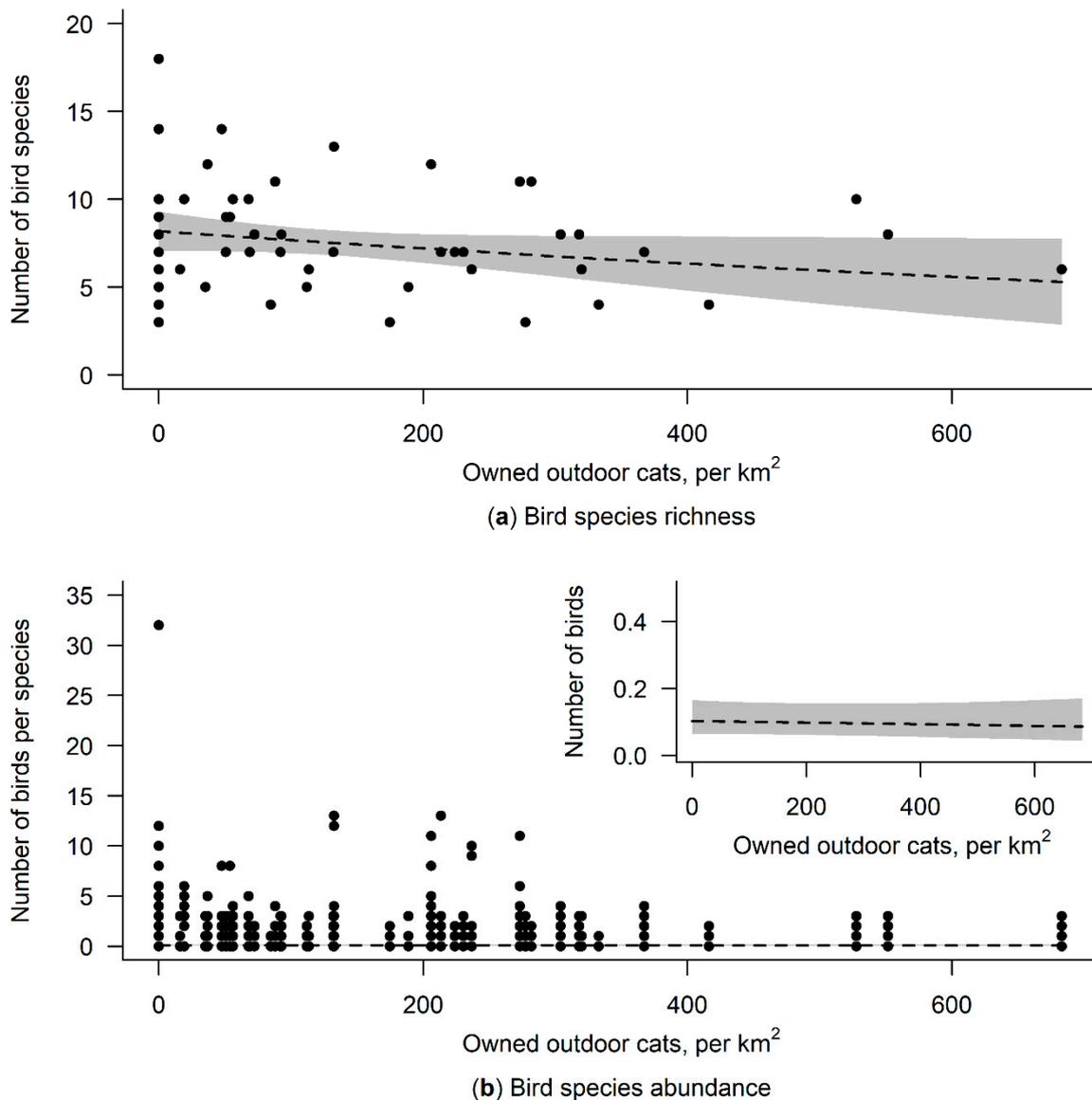


Figure 4. Relationships between owned outdoor cat density, measured as the number of cats/km², and bird species (a) richness and (b) abundance. The 95% confidence intervals (in grey) around the predicted curves include a slope of zero, indicating high uncertainty in the effects. The model predicts one additional bird species and 0.003 additional individuals per species if policies/programs reduced owned outdoor cat densities from 130.2 to zero cats/km² in the average landscape. Relationships between bird species richness and cat density were predicted from a generalized linear model with a Poisson distribution and a log link, holding human population density, individual tree cover, feeder density, squirrel frequency, and raccoon frequency at their mean values. Relationships between bird species abundance and cat density were predicted as described above, except that we used a generalized linear mixed effects model with a negative binomial distribution, log link, and random effect of species identity.

4. Discussion

We found that the richness and abundance of urban birds tended to be slightly lower in landscapes with high densities of owned outdoor cats than in landscapes with low densities of owned outdoor cats. We estimate that we would most likely observe one additional bird species in a point count, and 0.003 additional individuals per species, if policies/programs reduced owned outdoor cat densities to zero in an average landscape in our study city, i.e., a landscape with 130.2 cats/km². This translates into an expectation of 1.09× as many bird species and 1.03× as many individuals per species if all owned

cats were kept indoors in the average landscape. However, the effects of cat density on both bird species richness and abundance were uncertain, with 95% CIs crossing zero (Figure 3). This suggests that we cannot rule out the possibility of no change—or even a small decrease—in bird species richness or abundance if owned outdoor cat densities were reduced to zero.

Our findings are consistent with most previous studies of the relationship between owned outdoor cat densities and bird richness/abundance in cities [22,23,66–68]. A few studies have reported strong support for a negative effect of cat density on bird species richness [3,69]. However, it is not clear whether these strong effects reflect the effects of cat density on birds or effects of other potentially confounding factors such as urban densification. Cat density can correlate strongly with urban densification [3], and we found declines in bird species richness and abundance with increasing human population density (Figure 3). Previous studies have similarly found that there are more species and more individual birds in areas with medium-density human populations than high-density ones, i.e., over the range of values found within the city limits [70–72]. And Gagné and Fahrig [32] found that both the richness and abundance of birds declined with increasing housing densities in our city.

It is surprising that empirical studies, including ours, have found weak and uncertain effects of owned outdoor cats on bird populations in urban landscapes, given the large estimates of the numbers of birds killed by cats [1,2,50]. It is possible that owned outdoor cats have stronger negative effects on bird populations than we and others have found, but that such effects are difficult to detect for several reasons. First, in some studies collinearity between cat density and other predictors could obscure the effect of cats. Inclusion of collinear predictors in a regression-type model, as in our study, generally produces unbiased estimates of effect sizes [73]. However, even low to moderate collinearity can increase uncertainty in the estimated effects of collinear predictors [73,74]. We note, however, that this does not fully explain the uncertainty in estimated effects of cats in our study because other predictors in our models—human density, individual tree cover, squirrel frequency, and raccoon frequency—were also moderately collinear (Table S2) and we were able to detect their effects on bird richness and abundance. Confidence intervals for these other variables often excluded zero, unlike the CIs for cat density (Figure 3). Second, it is possible that owned outdoor cats have stronger negative effects on bird populations than we and others have found because an important confounding predictor was omitted from analysis, resulting in biased estimates of the effect of cats on birds [73]. We included five potentially confounding variables in our analysis to reduce this possibility. Additionally, we conducted supplementary analyses to determine whether gradients in weather conditions—or other variables that vary with latitude/longitude—could have affected our conclusions. This was not the case, as our conclusions about the effects of owned outdoor cats on birds were similar whether we included latitude and longitude in our models or not (Figure S14). Third, if owned outdoor cats have very strong, negative effects on birds then cats may drive bird populations to a minimal size—or even completely exclude some bird species—at even the lowest cat densities in a study. However, this cannot explain our results. If owned outdoor cats have a strong, negative effect on birds at even low cat densities, then we would expect to see fewer bird species and fewer individual birds at sites with owned outdoor cats than at sites without any cats. This was not the case (Figure S15). Fourth, if cats affect birds only at cat densities greater than those in our study, we would miss their effect. However, we note that Sims et al. [3] included study sites with owned outdoor cat densities more than twice that of the highest cat density in our study, and they found no evidence that cats had stronger effects on birds at densities greater than those in our study. Fifth, it is possible that areas with high cat densities act as sink habitats that are continuously replenished by birds from source areas with low cat densities, as suggested by Baker et al. [75] and Van Heezik et al. [76]. However, we suggest that such source-sink dynamics would be limited if birds can detect cats during breeding site selection and use this information to select sites with low perceived predation risk [31].

In this case we should observe a negative relationship between cats and birds. This is indirectly supported by our finding that migratory birds were less likely than resident birds to breed in areas with high cat densities, presumably because they select nesting sites later in the breeding season when more owned cats are outdoors [27–30].

Finally, we consider the possibility that measurement error may have caused the high levels of uncertainty around our estimated effects of owned outdoor cat density on bird species richness and abundance. With more precise measurements—or a larger sample size—perhaps we would have detected an effect of cat density on bird species richness/abundance. However, we suggest that measurement error in estimates of cat density and bird richness and abundance cannot explain why we did not find strong statistical support for a relationship between cats and birds. We were able to find strong statistical support for effects of human population density, individual tree cover, squirrel frequency, and raccoon frequency on birds (i.e., 95% CIs did not cross zero). This suggests that estimates of relative bird species richness and abundance were precise enough to allow detection of effects at our sample size (58 landscapes). Additionally, the fact that we found statistical support for effects of squirrel frequency and raccoon frequency on birds suggests that estimates of predator abundance from resident surveys can be precise enough to detect their effects on birds.

We note that, although we expected resident surveys to be the most appropriate method for estimating densities of owned cats (see Section 2.2 Data collection, above), other methods (e.g., camera trapping) may produce more precise estimates of squirrel and raccoon densities. Thus, if anything, we may have underestimated the support for effects of squirrels/raccoons on birds. These findings are consistent with the expectation that predator abundance can have a population-level impact on urban bird species; however, we actually observed more bird species and more birds per species in areas with more raccoons. Although raccoons can depredate bird nests [60], others have found that nest predation rates can actually be lower in areas with higher raccoon abundances [58], perhaps because they exclude other potential predators. Thus future studies are needed to understand the effects of other mammalian and avian predators of birds on urban bird populations.

Assuming the weak overall effect we—and others—have found is real, there is still the possibility that owned outdoor cats have strong effects on a subset of bird species that are not detected when effects on overall species richness and abundance are evaluated. We did find stronger negative effects for migratory than resident species. Based on these we can expect $1.20\times$ as many migratory bird species and $1.15\times$ as many individuals per species if all owned cats were kept indoors in the average landscape (with mean cat density 130.2 cats/km²). However, the effect of cats on the abundance of migratory birds was highly uncertain, suggesting that we cannot rule out the possibility of no change—or even a small decrease—in the number of migratory birds if owned outdoor cat densities were reduced to zero.

We suggest three potential reasons for the weak observed effect of owned outdoor cats on bird richness and abundance here and in previous studies. First, more abundant food resources for birds in areas with higher cat densities may offset negative effects of cat density on bird richness and abundance. For example, in our study there were more bird feeders in areas with high cat densities than in areas with low cat densities ($\rho = 0.69$; see Table S2). Access to high quality food resources can offset negative impacts of cat predation by increasing bird body condition. It may also increase breeding success, e.g., by increasing clutch sizes and chick growth rates [77]. Second, cats may replace natural predators of birds in areas with higher cat densities. For example, Malpass et al. [78] found no difference in rates of predation on northern cardinal (*Cardinalis cardinalis*) nests in forested parks and residential neighborhoods, despite finding that domestic cats were $5\times$ as likely to prey on nests in neighborhoods than in parks. Some natural predators of birds may be less abundant in areas with high cat densities because cats kill bird predators as well as birds. Dickman [69] suggested this explanation for the strong, negative correlation between nest predation rates and cat densities in their study. Cats might also replace other predators

if other predators switch to alternative prey in areas where cat densities are high. Third, cat predation on birds may not affect bird abundances if predation is compensated by density-dependent population regulation or if cats selectively remove unfit individuals from the bird population. For example, Baker et al. [54] found that birds killed by cats had significantly lower fat and muscle scores than individuals killed in building collisions, which could indicate that cats kill poorer quality birds. However, Holt et al. [35] found that bird abundance generally increases after predator removal or control, suggesting compensatory mortality is the least likely of our proposed explanations.

What Is Next for Urban Landscape Ecology?

The populations of many bird species are in decline. For example, there was an estimated 29% decline in the abundance of North American birds from 1970 to 2017, translating into a loss of ~3 billion birds [79]. Globally, 1486 bird species are at risk of extinction [80]. The widespread need for conservation action, combined with typically limited resources for action, means that conservation practitioners and policy-makers need to make sure their efforts are directed towards actions that will most effectively reverse bird population declines.

In this context, our findings—in combination with those of previous studies—suggest a pressing need for research to resolve the apparent disconnect between the strong negative effects of domestic cats on individual birds and the weak and uncertain effects of domestic cats on bird populations. This need is particularly pressing in urban landscapes, where outdoor cats can benefit from, for example, higher availability of anthropogenic food sources and lower predator densities. For such research the optimal design would be a BACI experiment comparing urban bird richness and abundance before and after the imposition of cat-control measures to control sites without such measures. Such studies must be designed to ensure that the scale of experimental units is large enough to represent effects of cats at the population level rather than the individual level, and that experimental treatments are designed to control for the effects of other factors. Importantly this means randomly assigning treatment and control sites. Also, it will be important to ensure that cat control measures do not also control other predators (e.g., [81]), making it impossible to disentangle the effects of cats on birds from the effects of other predators.

Although support for the expectation of a strong impact of domestic cats on urban bird richness and abundance has been mixed, cats do kill birds. Additionally, the welfare of cats can be improved by keeping them indoors (e.g., reducing risks of injury or mortality from roads, disease) [82]. Thus measures that reduce densities of owned outdoor cats are justified based on the precautionary principle [83], where conservation dollars are not limited. However, such conservation measures should not have priority over those addressing threats, such as habitat loss [33,84,85], that result in demonstrable declines in both migratory and resident bird populations.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/land10050507/s1>, Figure S1: Bivariate plots showing relationships between cat density (number of cats/landscape) and each of four variables that can influence bird detectability at the 58 landscapes, Figure S2: Bivariate plots showing relationships between human density (number of people/landscape) and each of four variables that can influence bird detectability at the 58 landscapes, Figure S3: Bivariate plots showing relationships between individual tree cover (proportional cover of individual trees within the landscape) and each of four variables that can influence bird detectability at the 58 landscapes, Figure S4: Bivariate plots showing relationships between bird feeder density (number of feeders/landscape) and each of four variables that can influence bird detectability at the 58 landscapes, Figure S5: Bivariate plots showing relationships between squirrel frequency (number of days squirrels were observed by homeowners per week, averaged for all surveys within the landscape) and each of four variables that can influence bird detectability at the 58 landscapes, Figure S6: Bivariate plots showing relationships between raccoon frequency (number of days raccoons were observed by homeowners per week, averaged for all surveys within the landscape) and each of four variables that can influence bird detectability at the 58 landscapes, Figure S7: Comparison of

the standardized effects of owned outdoor cat density, human population density, individual tree cover, feeder density, squirrel frequency, and raccoon frequency on bird species abundance from (a) a model that allowed for variation in overall abundance among bird species and (b) a model that allowed for among-species variation in overall abundance and relationships between abundance and cat density, Table S1: X^2 tests of association to determine whether a species' risk level for a given trait was independent of its risk level for each of the other four traits, Figure S8: Proportion of bird species classified as high-risk versus low-risk, for each pair of traits where a species' risk level for a given trait was not independent of its risk level for another trait, Figure S9: Standardized effects of five alternative measures of bird habitat availability on (a) bird species richness and (b) bird abundance, Table S2: Pairwise relationships among predictor variables, Figure S10: Estimated effects of owned outdoor cat activity, human population density, individual tree cover, feeder density, squirrel frequency, and raccoon frequency on bird species (a) richness and (b) abundance, Figure S11: Estimated relationships between owned outdoor cat density, measured as the number of cats/km², and the number of (a) migratory and (b) resident bird species, Figure S12: Estimated relationships between owned outdoor cat density, measured as the number of cats/km², and the number of (a) migratory and (b) resident birds per species, Figure S13: Marginal effects of owned cat density on birds with high-risk relative to low-risk species traits, Figure S14: Comparison of the standardized effects of owned outdoor cat density, human population density, individual tree cover, feeder density, squirrel frequency, and raccoon frequency on bird species (a) richness and (b) abundance between our main model (see main text and Figure 3) versus a model that also included UTM coordinates of the sampling locations, Figure S15: Effects of the presence-absence of owned outdoor cats, human population density, individual tree cover, feeder density, squirrel frequency, and raccoon frequency on bird species (a) richness and (b) abundance.

Author Contributions: Conceptualization, G.C.P., A.E.M., A.C.S. and L.F.; Formal analysis, G.C.P. and A.E.M.; Funding acquisition, L.F.; Investigation, G.C.P.; Methodology, G.C.P., A.C.S. and L.F.; Writing—original draft, G.C.P. and A.E.M.; Writing—review & editing, G.C.P., A.E.M., A.C.S. and L.F. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by a grant from the Natural Sciences and Engineering Research Council of Canada.

Institutional Review Board Statement: The study was conducted according to the guidelines of the Declaration of Helsinki, and approved by the Institutional Ethics Board of Carleton University (protocol code 100857, 30 November 2013).

Informed Consent Statement: Informed consent was obtained from all subjects involved in the study.

Data Availability Statement: The data collected for this study are available at <https://curve.carleton.ca/09f22c7f-2b38-4030-8eb3-73e85c94a292> (accessed on 7 May 2021).

Acknowledgments: We thank Oda Waldeland and Erik Pervin for assistance with fieldwork, the residents who completed our door-to-door cat surveys, and the skilled volunteer birders who conducted the Ottawa Bird Count surveys. We also thank the anonymous peer reviewers, whose comments helped us improve the quality of our manuscript.

Conflicts of Interest: The authors declare no conflict of interest.

References

- Blancher, P. Estimated Number of Birds Killed by House Cats (*Felis catus*) in Canada. *Avian Conserv. Ecol.* **2013**, *8*, 3. [CrossRef]
- Woinarski, J.C.Z.; Murphy, B.P.; Legge, S.M.; Garnett, S.T.; Lawes, M.J.; Comer, S.; Dickman, C.R.; Doherty, T.S.; Edwards, G.; Nankivell, A.; et al. How many birds are killed by cats in Australia? *Biol. Conserv.* **2017**, *214*, 76–87. [CrossRef]
- Sims, V.; Evans, K.L.; Newson, S.E.; Tratalos, J.A.; Gaston, K.J. Avian assemblage structure and domestic cat densities in urban environments. *Divers. Distrib.* **2007**, *14*, 387–399. [CrossRef]
- Aguilar, G.D.; Farnworth, M.J. Distribution characteristics of unmanaged cat colonies over a 20 year period in Auckland, New Zealand. *Appl. Geogr.* **2013**, *37*, 160–167. [CrossRef]
- Davis, A.A.; Lepczyk, C.A.; Haman, K.H.; Morden, C.W.; Crow, S.E.; Jensen, N.; Lohr, M.T. *Toxoplasma gondii* Detection in Fecal Samples from Domestic Cats (*Felis catus*) in Hawaii. *Pac. Sci.* **2018**, *72*, 501–511. [CrossRef]
- Hartley, W.J.; Dubey, J.P. Fatal Toxoplasmosis in Some Native Australian Birds. *J. Veter. Diagn. Investig.* **1991**, *3*, 167–169. [CrossRef]
- Dubey, J. A review of toxoplasmosis in wild birds. *Veter. Parasitol.* **2002**, *106*, 121–153. [CrossRef]

8. Forstmeier, W.; Weiss, I. Adaptive plasticity in nest-site selection in response to changing predation risk. *Oikos* **2004**, *104*, 487–499. [[CrossRef](#)]
9. Cresswell, W. Non-lethal effects of predation in birds. *Ibis* **2008**, *150*, 3–17. [[CrossRef](#)]
10. Sodhi, N.S.; Didiuk, A.; Oliphant, L.W. Differences in bird abundance in relation to proximity of Merlin nests. *Can. J. Zool.* **1990**, *68*, 852–854. [[CrossRef](#)]
11. Bonnington, C.; Gaston, K.J.; Evans, K.L. Fearing the feline: Domestic cats reduce avian fecundity through trait-mediated indirect effects that increase nest predation by other species. *J. Appl. Ecol.* **2013**, *50*, 15–24. [[CrossRef](#)]
12. Saino, N.; Romano, M.; Ferrari, R.P.; Martinelli, R.; Møller, A.P. Stressed mothers lay eggs with high corticosterone levels which produce low-quality offspring. *J. Exp. Zool. Part A Comp. Exp. Biol.* **2005**, *303A*, 998–1006. [[CrossRef](#)]
13. Dauphiné, N.; Cooper, R.J. Impacts of free-ranging domestic cats (*Felis catus*) on birds in the United States: A review of recent research with conservation and management recommendations. In *Proceedings of the Fourth International Partners in Flight Conference: Tundra to Tropics*; Rich, T.D., Arizmendi, C., Demarest, D.W., Thompson, C., Eds.; Partners in Flight: McAllen, TX, USA, 2009; pp. 205–219.
14. Kauhala, K.; Talvitie, K.; Vuorisalo, T. Free-ranging house cats in urban and rural areas in the north: Useful rodent killers or harmful bird predators? *Folia Zoöl.* **2015**, *64*, 45–55. [[CrossRef](#)]
15. American Bird Conservancy. “Cats Indoors” Program. Available online: <https://abcbirds.org/program/cats-indoors/> (accessed on 3 December 2020).
16. Lynn, W.S.; Santiago-Ávila, F.; Lindenmayer, J.; Hadidian, J.; Wallach, A.; King, B.J. A moral panic over cats. *Conserv. Biol.* **2019**, *33*, 769–776. [[CrossRef](#)]
17. Royal Society for the Protection of Birds. Are Cats Causing Bird Declines? Available online: <https://www.rspb.org.uk/birds-and-wildlife/advice/gardening-for-wildlife/animal-deterrents/cats-and-garden-birds/are-cats-causing-bird-declines/> (accessed on 28 March 2021).
18. City of Barrie. *A by-Law of The Corporation of the City of Barrie to Regulate and Govern Animals Including Exotic Animals within City and to Repeal by-Law 88-260*; Part 4, Section 4.14.0.0.0 to 4.14.15.0.0 Regarding Animals Including Exotic Animals and by-Law 2006-257 Reg; City of Barrie: Barrie, ON, Canada, 2015.
19. City of Peterborough. *By-Law Number 17-096 Being a by-Law to Enact City of Peterborough Animal by-Law 17-096, a by-Law to Regulate the Keeping of Animals and to Repeal Associated Animal by-Laws 1984-138, and 16-079*; City of Peterborough: Peterborough, ON, Canada, 2017.
20. Government of Western Australia. *Statutory Review of the Cat Act 2011 and Dog Amendment Act 2013 Report*; G.O.W.A.: Leederville, Australia, 2019.
21. ACT Government. ACT Government City Services, Cat Containment. Available online: <https://www.cityservices.act.gov.au/pets-and-wildlife/domestic-animals/cats/cat-containment> (accessed on 28 April 2021).
22. Marzluff, J.M.; Clucas, B.; Oleyar, M.D.; DeLap, J. The causal response of avian communities to suburban development: A quasi-experimental, longitudinal study. *Urban. Ecosyst.* **2016**, *19*, 1597–1621. [[CrossRef](#)]
23. Belaire, J.A.; Whelan, C.J.; Minor, E.S. Having our yards and sharing them too: The collective effects of yards on native bird species in an urban landscape. *Ecol. Appl.* **2014**, *24*, 2132–2143. [[CrossRef](#)]
24. Thomas, J.W.; DeGraaf, R.M.; Mawson, J.C. *Determination of Habitat Requirements of Birds in Suburban Areas*; USDA Forest Service: Upper Darby, PA, USA, 1977.
25. Dunn, E.H.; Tessaglia, D.L. Predation of birds at feeders in winter. *J. Field Ornithol.* **1994**, *65*, 8–16.
26. Cooper, C.B.; Loyd, K.A.T.; Murante, T.; Savoca, M.; Dickinson, J. Natural History Traits Associated with Detecting Mortality Within Residential Bird Communities: Can Citizen Science Provide Insights? *Environ. Manag.* **2012**, *50*, 11–20. [[CrossRef](#)]
27. Morrissey, C.A. Effect of altitudinal migration within a watershed on the reproductive success of American dipper. *Can. J. Zool.* **2004**, *82*, 800–807. [[CrossRef](#)]
28. Sullivan, B.L.; Wood, C.L.; Iliff, M.J.; Bonney, R.E.; Fink, D.; Kelling, S. eBird: A citizen-based bird observation network in the biological sciences. *Biol. Conserv.* **2009**, *142*, 2282–2292. [[CrossRef](#)]
29. Horn, J.A.; Mateus-Pinilla, N.; Warner, R.E.; Heske, E.J. Home range, habitat use, and activity patterns of free-roaming domestic cats. *J. Wildl. Manag.* **2011**, *75*, 1177–1185. [[CrossRef](#)]
30. Krauze-Gryz, D.; Gryz, J.B.; Goszczyński, J.; Chylarecki, P.; Zmihorski, M. The good, the bad, and the ugly: Space use and intraguild interactions among three opportunistic predators—cat (*Felis catus*), dog (*Canis lupus familiaris*), and red fox (*Vulpes vulpes*)—under human pressure. *Can. J. Zool.* **2012**, *90*, 1402–1413. [[CrossRef](#)]
31. Forsman, J.T.; Mönkkönen, M.; Korpimäki, E.; Thomson, R.L. Mammalian nest predator feces as a cue in avian habitat selection decisions. *Behav. Ecol.* **2013**, *24*, 262–266. [[CrossRef](#)]
32. Gagné, S.A.; Fahrig, L. Do birds and beetles show similar responses to urbanization? *Ecol. Appl.* **2011**, *21*, 2297–2312. [[CrossRef](#)]
33. Smith, A.C.; Francis, C.M.; Fahrig, L. Similar effects of residential and non-residential vegetation on bird diversity in suburban neighbourhoods. *Urban. Ecosyst.* **2014**, *17*, 27–44. [[CrossRef](#)]
34. Fuller, R.A.; Warren, P.H.; Armsworth, P.R.; Barbosa, O.; Gaston, K.J. Garden bird feeding predicts the structure of urban avian assemblages. *Divers. Distrib.* **2008**, *14*, 131–137. [[CrossRef](#)]
35. Holt, A.R.; Davies, Z.G.; Tyler, C.; Staddon, S. Meta-Analysis of the Effects of Predation on Animal Prey Abundance: Evidence from UK Vertebrates. *PLoS ONE* **2008**, *3*, e2400. [[CrossRef](#)] [[PubMed](#)]

36. Kays, R.W.; Dewan, A.A. Ecological impact of inside/outside house cats around a suburban nature preserve. *Anim. Conserv.* **2004**, *7*, 273–283. [[CrossRef](#)]
37. Statistics Canada. *Population and Dwelling Counts, for Canada, Provinces and Territories, 2011 Census*; Statistics Canada: Ottawa, ON, Canada, 2011.
38. City of Ottawa. *National Capital Commission 1:2,000 City of Ottawa Topographic Map*; City of Ottawa: Ottawa, ON, Canada, 2013.
39. Diefenbach, D.R.; Brauning, D.W.; Mattice, J.A. Variability in Grassland Bird Counts Related to Observer Differences and Species Detection Rates. *Auk* **2003**, *120*, 1168–1179. [[CrossRef](#)]
40. Dunning, J. *CRC Handbook of Avian Body Masses*, 2nd ed.; Taylor & Francis Ltd.: Boca Raton, FL, USA, 2007.
41. Rodewald, P. The Birds of North America Online. 2015. Available online: <https://birdsoftheworld.org/bow/home> (accessed on 1 November 2013).
42. Blair, R.B. Land Use and Avian Species Diversity Along an Urban Gradient. *Ecol. Appl.* **1996**, *6*, 506–519. [[CrossRef](#)]
43. Leblanc, Y. Egg mass, position in the laying sequence, and brood size in relation to Canada Goose reproductive success. *Wilson Bull.* **1987**, *99*, 663–672.
44. Chamberlain, D.E.; Cannon, A.R.; Toms, M.P.; Leech, D.I.; Hatchwell, B.J.; Gaston, K.J. Avian productivity in urban landscapes: A review and meta-analysis. *Ibis* **2009**, *151*, 1–18. [[CrossRef](#)]
45. Blewett, C.M.; Marzluff, J.M. Effects of Urban Sprawl on Snags and the Abundance and Productivity of Cavity-Nesting Birds. *Condor* **2005**, *107*, 678–693. [[CrossRef](#)]
46. Fitzgerald, T.M.; van Stam, E.; Nocera, J.J.; Badzinski, D.S. Loss of nesting sites is not a primary factor limiting northern Chimney Swift populations. *Popul. Ecol.* **2014**, *56*, 507–512. [[CrossRef](#)]
47. North American Bird Conservation Initiative U.S. Committee. *The State of The Birds, United States of America, 2009*; North American Bird Conservation Initiative U.S. Committee: Washington, DC, USA, 2009.
48. Marzluff, J.M. Effects of urbanization and recreation on songbirds. USDA Forest Service General Technical Report RM-GTR-292. In *Songbird Ecology in Southwestern Ponderosa Pine Forests: A Literature Review*; Block, W.M., Finch, D.M., Eds.; U.S. Dept. of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: Fort Collins, CO, USA, 1997; pp. 89–102.
49. Balogh, A.L.; Ryder, T.B.; Marra, P.P. Population demography of Gray Catbirds in the suburban matrix: Sources, sinks and domestic cats. *J. Ornithol.* **2011**, *152*, 717–726. [[CrossRef](#)]
50. Loss, S.R.; Will, T.; Marra, P.P. The impact of free-ranging domestic cats on wildlife of the United States. *Nat. Commun.* **2013**, *4*, 1396. [[CrossRef](#)]
51. Shaw, L.M.; Chamberlain, D.; Evans, M. The House Sparrow *Passer domesticus* in urban areas: Reviewing a possible link between post-decline distribution and human socioeconomic status. *J. Ornithol.* **2008**, *149*, 293–299. [[CrossRef](#)]
52. Peak, R.G. An Experimental Test of the Concealment Hypothesis using American Goldfinch Nests. *Wilson Bull.* **2003**, *115*, 403–408. [[CrossRef](#)]
53. Glennon, M.J.; Kretser, H.E. Size of the ecological effect zone associated with exurban development in the Adirondack Park, NY. *Landsc. Urban. Plan.* **2013**, *112*, 10–17. [[CrossRef](#)]
54. Baker, P.J.; Molony, S.E.; Stone, E.; Cuthill, I.C.; Harris, S. Cats about town: Is predation by free-ranging pet cats *Felis catus* likely to affect urban bird populations? *Ibis* **2008**, *150*, 86–99. [[CrossRef](#)]
55. Flockhart, D.T.T.; Norris, D.R.; Coe, J.B. Predicting free-roaming cat population densities in urban areas. *Anim. Conserv.* **2016**, *19*, 472–483. [[CrossRef](#)]
56. Elizondo, E.C.; Loss, S.R. Using trail cameras to estimate free-ranging domestic cat abundance in urban areas. *Wildl. Biol.* **2016**, *22*, 246–252. [[CrossRef](#)]
57. Callahan, J.R. Squirrels as predators. *Gt. Basin Nat.* **1993**, *53*, 137–144.
58. Morris, G.; Conner, L.M. Effects of forest management practices, weather, and indices of nest predator abundance on nest predation: A 12-year artificial nest study. *For. Ecol. Manag.* **2016**, *366*, 23–31. [[CrossRef](#)]
59. Bonnington, C.; Gaston, K.J.; Evans, K.L. Relative Roles of Grey Squirrels, Supplementary Feeding, and Habitat in Shaping Urban Bird Assemblages. *PLoS ONE* **2014**, *9*, e109397. [[CrossRef](#)]
60. Staller, E.L.; Palmer, W.E.; Carroll, J.P.; Thornton, R.P.; Sisson, D.C. Identifying predators at northern bobwhite nests. *J. Wildl. Manag.* **2005**, *69*, 124–132. [[CrossRef](#)]
61. Welsh, A.H.; Lindenmayer, D.B.; Donnelly, C.F. Adjusting for one issue while ignoring others can make things worse. *PLoS ONE* **2015**, *10*, e0120817. [[CrossRef](#)] [[PubMed](#)]
62. Hutto, R.L. Should scientists be required to use a model-based solution to adjust for possible distance-based detectability bias? *Ecol. Appl.* **2016**, *26*, 1287–1294. [[CrossRef](#)] [[PubMed](#)]
63. R Core Team. *R: A Language and Environment for Statistical Computing*; Version 3.5.1; R Foundation for Statistical Computing: Vienna, Austria, 2015.
64. Fournier, D.A.; Skaug, H.J.; Ancheta, J.; Ianello, J.; Magnusson, A.; Maunder, M.N.; Nielsen, A.; Sibert, J. AD Model Builder: Using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optim. Methods Softw.* **2012**, *27*, 233–249. [[CrossRef](#)]
65. Skaug, H.; Fournier, D.; Bolker, B.; Magnusson, A.; Nielsen, A. Generalized Linear Mixed Models Using “AD Model Builder”. 2015. Available online: <http://glmmadmb.r-forge.r-project.org/> (accessed on 26 April 2021).

66. Grayson, J.; Calver, M.; Lymbery, A. Species richness and community composition of passerine birds in suburban Perth: Is predation by pet cats the most important factor? In *Pest or Guest: The Zoology of Overabundance*; Lunney, D., Eby, P., Hutchings, P., Burgin, S., Eds.; Royal Zoological Society of New South Wales: Mosman, Australia, 2007; pp. 195–207.
67. Parsons, H.; Major, R.E.; French, K. Species interactions and habitat associations of birds inhabiting urban areas of Sydney, Australia. *Austral. Ecol.* **2006**, *31*, 217–227. [[CrossRef](#)]
68. Paker, Y.; Yom-Tov, Y.; Alon-Mozes, T.; Barnea, A. The effect of plant richness and urban garden structure on bird species richness, diversity and community structure. *Landsc. Urban. Plan.* **2014**, *122*, 186–195. [[CrossRef](#)]
69. Dickman, C.R. House cats as predators in the Australian environment: Impacts and management. *Hum.-Wildl. Confl.* **2009**, *3*, 41–48.
70. Koh, C.-N.; Lee, P.-F.; Lin, R.-S. Bird species richness patterns of northern Taiwan: Primary productivity, human population density, and habitat heterogeneity. *Divers. Distrib.* **2006**, *12*, 546–554. [[CrossRef](#)]
71. Tratalos, J.; Fuller, R.A.; Evans, K.L.; Davies, R.G.; Newson, S.E.; Greenwood, J.J.D.; Gaston, K.J. Bird densities are associated with household densities. *Glob. Chang. Biol.* **2007**, *13*, 1685–1695. [[CrossRef](#)]
72. Evans, K.L.; Greenwood, J.J.; Gaston, K.J. The positive correlation between avian species richness and human population density in Britain is not attributable to sampling bias. *Glob. Ecol. Biogeogr.* **2007**, *16*, 300–304. [[CrossRef](#)]
73. Smith, A.C.; Koper, N.; Francis, C.M.; Fahrig, L. Confronting collinearity: Comparing methods for disentangling the effects of habitat loss and fragmentation. *Landsc. Ecol.* **2009**, *24*, 1271–1285. [[CrossRef](#)]
74. Graham, M.H. Confronting Multicollinearity in Ecological Multiple Regression. *Ecology* **2003**, *84*, 2809–2815. [[CrossRef](#)]
75. Baker, P.J.; Bentley, A.J.; Ansell, R.J.; Harris, S. Impact of predation by domestic cats *Felis catus* in an urban area. *Mammal. Rev.* **2005**, *35*, 302–312. [[CrossRef](#)]
76. Van Heezik, Y.; Smyth, A.; Adams, A.; Gordon, J. Do domestic cats impose an unsustainable harvest on urban bird populations? *Biol. Conserv.* **2010**, *143*, 121–130. [[CrossRef](#)]
77. Robb, G.N.; McDonald, R.A.; Chamberlain, D.E.; Bearhop, S. Food for thought: Supplementary feeding as a driver of ecological change in avian populations. *Front. Ecol. Environ.* **2008**, *6*, 476–484. [[CrossRef](#)]
78. Malpass, J.S.; Rodewald, A.D.; Matthews, S.N.; Kearns, L.J. Nest predators, but not nest survival, differ between adjacent urban habitats. *Urban. Ecosyst.* **2018**, *21*, 551–564. [[CrossRef](#)]
79. Rosenberg, K.V.; Dokter, A.M.; Blancher, P.J.; Sauer, J.R.; Smith, A.C.; Smith, P.A.; Stanton, J.C.; Panjabi, A.; Helft, L.; Parr, M.; et al. Decline of the North American avifauna. *Science* **2019**, *366*, 120–124. [[CrossRef](#)] [[PubMed](#)]
80. IUCN. IUCN Red List Version 2020-2 Table 1b: Numbers of Threatened Species by Major Groups of Organisms (1996–2020). Available online: <https://www.iucnredlist.org/resources/summary-statistics#SummaryTables> (accessed on 7 October 2020).
81. Stokeld, D.; Fisher, A.; Gentles, T.; Hill, B.M.; Woinarski, J.C.Z.; Young, S.; Gillespie, G.R. Rapid increase of Australian tropical savanna reptile abundance following exclusion of feral cats. *Biol. Conserv.* **2018**, *225*, 213–221. [[CrossRef](#)]
82. Tan, S.M.; Stellato, A.C.; Niel, L. Uncontrolled Outdoor Access for Cats: An Assessment of Risks and Benefits. *Animals* **2020**, *10*, 258. [[CrossRef](#)] [[PubMed](#)]
83. Calver, M.C.; Grayson, J.; Lillith, M.; Dickman, C.R. Applying the precautionary principle to the issue of impacts by pet cats on urban wildlife. *Biol. Conserv.* **2011**, *144*, 1895–1901. [[CrossRef](#)]
84. Barth, B.J.; FitzGibbon, S.I.; Wilson, R.S. New urban developments that retain more remnant trees have greater bird diversity. *Landsc. Urban. Plan.* **2015**, *136*, 122–129. [[CrossRef](#)]
85. Hedblom, M.; Söderström, B. Landscape effects on birds in urban woodlands: An analysis of 34 Swedish cities. *J. Biogeogr.* **2010**, *37*, 1302–1316. [[CrossRef](#)]