



Original Research Article

The truth about cats and dogs: Landscape composition and human occupation mediate the distribution and potential impact of non-native carnivores

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ABSTRACT

Humans alter landscapes and native species distributions in many ways, including alterations mediated via domestic pets. While the negative impacts of domestic cats are well documented worldwide, the ecological effects of domestic dogs have received less scientific attention, particularly in the United States. Prevalence of free-ranging dogs may be especially problematic in areas with low density, but relatively ubiquitous human populations. We used camera-trap data collected during a 2008–2010 landscape-scale study consisting of 1181 camera stations (357 camera clusters) stratified over 16 counties in southern Illinois, USA, to estimate occupancy for domestic cats and dogs. We compared models of occupancy for three land cover types (forest, grassland, and wetland) in relation to anthropogenic features and estimated and compared the proportion of the region occupied by each species. Cats occurred across a moderate proportion of the landscape ($\bar{\psi} = 0.44 \pm 0.13$ SE) and were associated with anthropogenic features. Moreover, we found domestic dog occupancy was greater across the landscape ($\bar{\psi} = 0.59 \pm 0.09$), influenced more generally by land cover type, and was highest on grasslands and privately owned land. Domestic cat occupancy was more localized than that of dogs and less influenced by land cover type compared to anthropogenic features. Model averaged probability of dog occupancy was >0.50 across 19,049.39 km² of the region ($>99\%$), but only 2270.53 km² (11.8%) for cats. Thus, while domestic cats may pose a more intensive threat to wildlife within the area they occupy, the impact of domestic dogs is likely to be more geographically extensive. Predicting the potential effects of these non-native species is complicated by a nuanced interaction between landscape composition, human density, and human behavior, and upends simplistic perceptions of the relative threats posed by the two species.

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1. Introduction

The current Anthropocene epoch is characterized by profound human influences resulting in global environmental degradation, defaunation, and loss of biodiversity (Dirzo et al., 2014; Lewis and Maslin, 2015; Tucker et al., 2018). The world-wide introduction and support of free-ranging domestic pets are a primary mechanism of human disturbance to native animal populations (Bellard et al., 2016; Clavero and García-Berthou, 2005; Doherty et al., 2016). Domestic cats (*Felis catus*) and dogs (*Canis familiaris*) can cause devastating damage to native wildlife populations, directly through predation (Doherty et al., 2017; Loss et al., 2013), or indirectly through disease transmission (Brown et al., 2008; Furtado et al., 2016) and fear-mediated behavioral or demographic responses (Banks and Bryant, 2007; Bonnington et al., 2013; Farris et al., 2017; Zapata-Ríos and Branch, 2016). The threat is of increasing concern as domestic dog and cat populations are associated with almost all human populations, and as the human population has increased in density and expanded in range, so have the populations of domestic cats and dogs (Gompper, 2014a; Loss and Marra, 2017).

Variation in human attitudes towards domestic pets can modify the intensity and spatial scale of disturbance (Gompper, 2014a; Gramza et al., 2016; Parsons et al., 2016). Domestic pets are often entirely dependent on anthropogenic resources (Gompper and Vanak, 2008; Vanak and Gompper, 2009a, 2009b). As such, local distribution and demographics of human populations, commonly described along an urban-rural gradient, will determine where domestic pet-wildlife interactions are most likely to occur (Gompper, 2014a). Depending on local regulations and customs, domestic dogs and cats may be mostly constrained to human dwellings, or they may be free-ranging with varying degrees of dependence on humans. This dependence can range from owned companion or work animals to human-supplemented feral populations (Doherty et al., 2017; Loss and Marra, 2017). Thus, the extent of potential impacts to local environments can differ by region, human attitudes, and the distribution of human populations relative to wildlife habitat.

Numerous studies have attempted to quantify damage from domestic cats (Loss et al., 2013). However, impacts of domestic dogs have only recently received attention (Doherty et al., 2017; Gompper, 2014b; Hughes and Macdonald, 2013; Young et al., 2011). Domestic cats are intensive hunters presenting an immediate threat to native species (Dickman and Newsome, 2015) resulting in 7 times more local extirpations and extinctions compared to dogs (Doherty et al., 2016). Although they kill native wildlife more frequently, domestic cats are typically smaller than most domestic dogs, and thus can have smaller exploratory forays (Kays and DeWan, 2004) and be restricted in range by predation from larger native species (Crooks and Soule, 1999). In contrast, domestic dogs may range farther from human associated habitats (Young et al., 2011), are less susceptible to smaller-bodied predators (Ritchie et al., 2014), and commonly are brought by humans into remote areas for sport and other types of recreation (Wierzbowska et al., 2016). As a result, impacts from domestic cats may be intense but restricted to areas in close proximity to human dwellings, while impacts of dogs may be more pervasive across the landscape (Gompper, 2014a).

Studies in developing countries have found high rates of free-ranging dog occupancy and negative effects on native species (Farris et al., 2016; Silva-Rodríguez and Sieving, 2012; Zapata-Ríos and Branch, 2018). However, few studies within the contiguous United States have identified free-ranging dogs as a potential widespread conservation issue (Doherty et al., 2016; Young et al., 2011), but some do note high dog use congruent with human land use (Parsons et al., 2016). This may be because most studies in the US have occurred in centers of human density or protected areas with restrictions on dog activity where it is difficult to parse effects of dogs from general anthropogenic effects (Forrest and St. Clair, 2006; George and Crooks, 2006; Reed and Merenlender, 2011; Weston et al., 2014). In these areas, public perception and leash regulations can reduce the presence of free-ranging dogs as owners may restrain dogs (Parsons et al., 2016) and efforts to reduce the stray or feral population may receive greater attention and resources (Lord et al., 1998). However, there are many areas of the US where human density is lower and social norms concerning dog ownership are relaxed, including rural agricultural areas, areas with a tradition of hunting with dogs, and areas where dogs are used as guard animals for pastured livestock. As a result, domestic dogs may have considerable impacts on native wildlife populations (Home et al., 2017) including direct and non-consumptive effects on prey populations (Banks and Bryant, 2007; Lord et al., 2001; Silva-Rodríguez and Sieving, 2012), but also on mesopredator populations as a perceived or real predator (Gompper and Vanak, 2008; Vanak and Gompper, 2010, 2009a), and closely associate wild populations as disease reservoirs and vectors (Acosta-Jamett et al., 2011; Kat et al., 1995; Knobel et al., 2014).

We assessed domestic dog and cat occupancy in relation to anthropogenic features across three land cover types in the midwestern United States. We expected that occupancy of dogs and cats would decrease with distance from anthropogenic features, increase with density of human features, and be greater on privately owned parcels compared to publicly owned and managed lands. We predicted domestic dog occupancy would be higher compared to domestic cats and affect a larger proportion of the overall landscape. We also evaluated how the relationship between domestic pet occupancy to anthropogenic features changed by land cover type and used this information to assess potential impacts to native species and identified areas where conservation actions would be most effective to reduce potential impacts of domestic dogs and cats.

2. Material and methods

2.1. Study area and data collection

We established a landscape-scale camera-trap study across 16 counties in southern Illinois, USA (Fig. 1), comprising 16,058 km² of the Southern Till Plain, Wabash Border, Shawnee Hills, Ozarks, Lower Mississippi River bottomlands, and Coastal Plain natural divisions of Illinois (Lesmeister et al., 2015; Neely and Heister, 1987; Schwegman, 1973). The study area consisted primarily of agricultural croplands (44%), open water (5%), and forest (20%), grasslands including pastures (19%), and wetlands (9%), permeated by anthropogenic features and urban land uses (4%; Illinois Department of Natural Resources, 1996, Fig. 1). Mean slope in the study area was 6.6 across a 92 m–316 m elevational gradient. Mean temperature was 5.4 ± 0.4 °C ($\pm$ SE throughout) and mean precipitation was 2.6 ± 0.2 cm per week during the study period (January–April; National Oceanic and Atmospheric Administration, 2010).

We conducted the camera-trap study from January 2008–April 2010. We divided the study area into 2.6-km² sections and employed a stratified random sampling approach to select 357 sections ranging from 11% to 100% forest cover (see Lesmeister et al., 2015 for details). We established a cluster of camera traps (3–4 camera stations with ≥ 250 m spacing) within each 2.6-km² section, resulting in 1188 camera stations within the 357 camera clusters. Each camera station was equipped with 1 digital remote camera (Cuddeback Excite [2.0 megapixel] or Capture [3.0 megapixel], Non Typical, Inc., Park Falls, WI) with passive infrared sensors and incandescent flash illumination. We secured cameras to trees at a height of approximately 0.5 m and pointed cameras towards game trails when present. To increase detection rates, we placed a can of sardines and fatty acid scent disk bait (U.S. Department of Agriculture Pocatello Supply Depot, Pocatello, ID) approximately 2 m in front of each camera. We set cameras to be active 24 h each day with a 1-minute delay between photographs.

To achieve a landscape-scale study design, we stratified sampling across years and months within a single season (January–April). Each camera cluster was surveyed within one of three years (2008–2010) for three weeks during the survey period. We visited camera clusters weekly to collect data and rebait and removed cameras after 3 weeks to redeploy at other clusters.

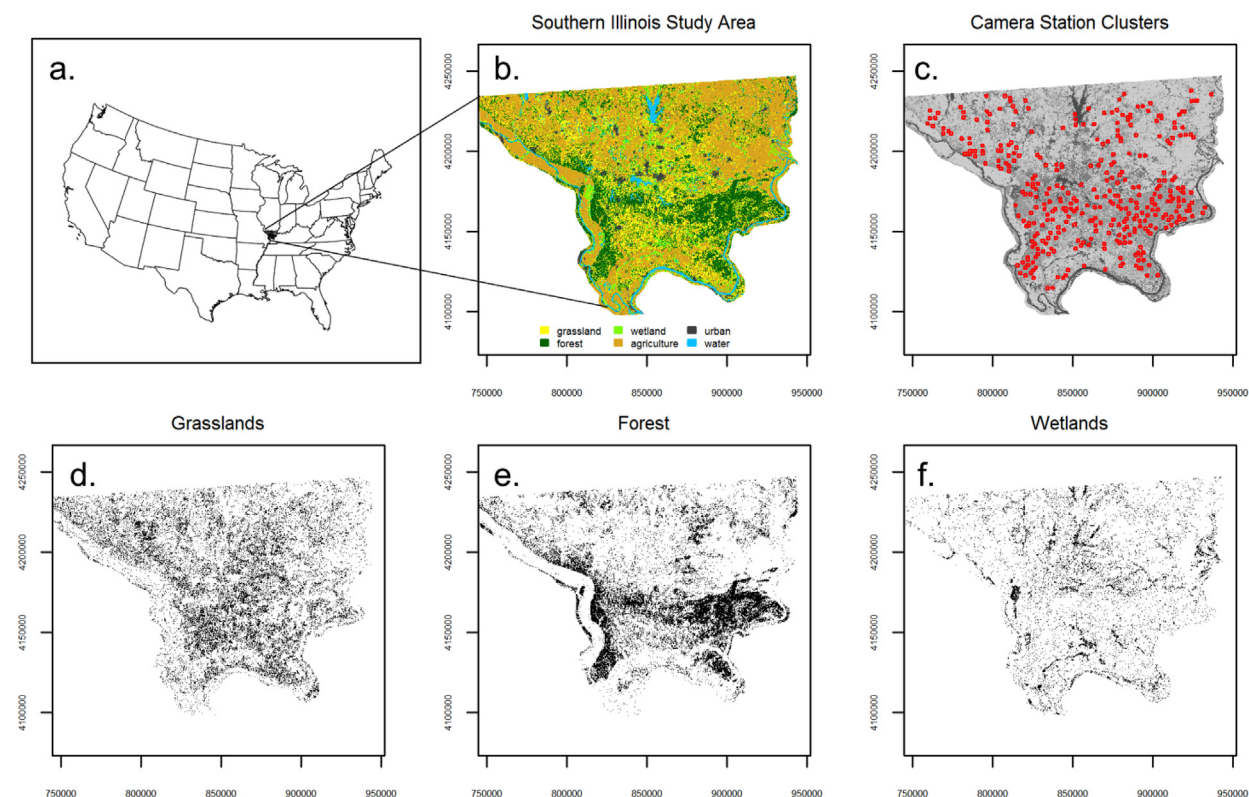


Fig. 1. The study area in southern Illinois, USA shown in black (a) is comprised of 6 land cover types based on National Land Cover Data at 30 m $\times$ 30 m resolution (b) across the 16,058 km² region. The 1188 camera stations were arranged in 357 clusters shown in red (c). Occupancy models for domestic dogs and cats were compared across candidate sets including covariates representing the proportion of grassland (d), forest (e), and wetlands cover types for 50 ha and 250 ha areas surrounding each camera cluster. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

We compiled covariates representing proximity to and density of human populations, and land ownership for each cluster. For each camera station, we measured distance to the boundary of the nearest municipality for coarse-scale anthropogenic influence, distance to nearest human structure for fine-scale anthropogenic influence (Illinois State Geological Survey, 2005), number of structures/hectare to represent an index of extent of human influence, and we recorded whether a camera station was on public or private land (see Lesmeister et al., 2015 for details). We also calculated the number of structures/ha and the % cover for each land cover type of interest (forest, grassland, and wetland) within two buffer distances from each camera station representing 50 ha and 250 ha sites and averaged these metrics over camera stations within a cluster. We compared these two buffer sizes because home range sizes are poorly understood for domestic dogs and cats and their foray distances can be highly variable and unpredictable (Lilith et al., 2008; Meek, 1999; Sepúlveda et al., 2015).

2.2. Data analyses

We implemented single-species single-season occupancy models (MacKenzie et al., 2002) in R (R Core Team, 2016) using the RPresence package (MacKenzie and Hines, 2017) to investigate how domestic dog and cat occupancy changed with anthropogenic features and local land cover composition. We used a sequential process to compare models and estimate detection probability (p) and then occupancy (ψ). We first fit models of detection for each domestic species using environmental and time-dependent covariates (survey week, mean temperature and mean precipitation for each survey week, month, and year), and an indicator variable (previous detection) to account for potential behavioral response to encountering the camera & bait. For this detection modeling step, we constrained occupancy to a single value ($\psi(\cdot)$) and assessed relative support for each detection model by AICc (Burnham and Anderson, 2003).

After identifying the detection models with the greatest support, we compared support for a set of candidate occupancy models for each species and land cover type. Specifically, we aimed to evaluate whether domestic species occupancy was more strongly associated with anthropogenic covariates or land cover (main effects), and also whether the effect of anthropogenic factors differed across a gradient of land cover dominance (interactive effects). We constructed 3 subsets of candidate models for each species using the proportion of 3 land cover types as covariates: forest, grassland, and wetland. These 3 land cover types represent different suites of wildlife species that could potentially be impacted by domestic dogs and cats. Each candidate model set involved the land cover covariates (e.g., % forest cover at 50 ha scale, % wetland cover at 250 ha scale) and anthropogenic covariates (distance to structure, distance to nearest municipality border, structures/ha at 50 ha scale, structures/ha at 250 ha scale, and public or private land ownership), and included all single-variable models and additive combinations of anthropogenic covariates and the land cover type (e.g., ψ (distance to municipality + land ownership + % forest cover at the 50 ha scale)). We matched spatial scales to the land cover covariate when structure density was included as a variable in the candidate model (e.g., ψ (structures/ha at 50 ha scale + % forest cover at 50 ha spatial scale)). After comparing all single-variable and additive combinations in each candidate set for each land cover type, we tested if there was an interaction between anthropogenic covariates and the % land cover variable for candidate models within 5 Δ AICc of the top ranked model, as land cover was the variable for which we were interested in estimating changes in occupancy. We kept models with interaction terms in the final model set if they were ranked higher than respective candidate models with additive terms.

We compared models within and across land cover types using AICc and evidence ratios for variables derived by summed model weights (w_i) for each species. We used model-averaged estimates from the full set of candidate models (all land cover sets) for each species to predict occupancy across the study area at a 2.15×2.15 km raster pixel resolution. We used predicted surfaces to compare the overall potential impacts of domestic dogs compared to cats by summing the total area of the overall landscape with a predicted probability of occupancy >50% for each species. Finally, we calculated several class statistics including aggregation index, patch cohesion index (McGarigal et al., 2012) for the study area ($30 \text{ m} \times 30 \text{ m}$ resolution raster) using the SDMTools package in R (VanDerWal et al., 2014), to aid in interpretation of results. Class statistics quantified the high degree of fragmentation in the study area. Aggregation index ranges from 0–100 with values of 0 representing maximum disaggregation among patches of a land cover type. Patch cohesion index ranges from 0–100 and describes the physical connectedness of cover types with values close to 0 representing low connectedness.

3. Results

The camera-trap effort resulted in 102,711 photographic detections of endothermic animals over 29,988 camera days at the 1188 camera locations (357 camera clusters) surveyed (detailed in Lesmeister et al., 2015). We recorded 2203 photographs of domestic dogs and 685 of domestic cats at the 357 camera clusters, which resulted in 188 dog and 92 cat detections over the 1071 camera cluster survey weeks (sum of number of camera clusters operational during the survey week occasions). Of the domestic dog detections, 11 events were associated with humans, and in only one event was a dog on leash. However, nearly all dogs detected appeared in good health and were wearing collars, suggesting most individuals were owned pets. Domestic dogs were detected at 52% of the camera clusters while domestic cats were only detected at 26% (naïve occupancy). The mean model-averaged estimate of occupancy across all species-specific model sets was 0.59 (± 0.09 SE) for dogs and 0.44 (± 0.13) for cats.

There was substantial support for a single model of detection for dogs ($p(\text{year} + \text{survey})$, $w_i = 0.79$). All competitive models for domestic dog occupancy included both anthropogenic covariates and land cover composition, with site covariates

measured at the 250 ha scale (Table 1). Additive models including % grassland as the land cover covariate had greatest support in general, including the overall top-ranked model (Table 1, Fig. 2). Predicted dog occupancy increased with % grassland, structures/ha, and private land ownership and decreased with distance to structure or municipality. For instance, 75% of detections occurred <500 m from human-made structures (maximum = 1.75 km, also the maximum distance of any camera from a structure). The top-ranked model with % forest included an interaction with land ownership (Table 1), suggesting that forest cover is more likely to be positively associated with domestic dog occupancy on private than public land (Fig. 3). Among land cover types, we found the least support for domestic dog association with % wetland (Table 1) with some evidence that occupancy was negatively related to % wetland (Fig. 3).

For domestic cats, our data lent strong support ($w_i > 0.99$) to a single detection model including an interaction between study year and previous detection, suggesting that the behavioral response of cats to exposure to cameras and bait varied over time. Occupancy modeling results were less consistent for domestic cats than dogs, although cat occupancy also showed greater support for models with site covariates measured at the 250 ha scale than the 50 ha scale. All highly supported ($\Delta AICc < 2$) models included anthropogenic covariates, but not all included land cover. We found support for domestic cat occupancy being associated with both % wetland and % forest but not % grassland; some models without any land cover variable had $\Delta AICc < 2$ (Table 2), indicating relatively weak evidence for the importance of land cover. Generally, domestic cat occupancy increased with structures/ha and private land ownership, but decreased with % wetland, % forest, and distance to structure or municipality (Table 2, Fig. 3). Similar to dogs, 75% of cat detections occurred <508 m from human-made structures, although occupancy rates were lower and the maximum distance from structures for cat detections was less (1.34 km). The overall top model included distance to structure, structures/ha, and an interaction between land ownership and % wetland within 250 ha (Table 2), suggesting that wetland dominance had a stronger negative effect on domestic cat occupancy on private than public lands (Fig. 3).

When model averaged estimates were predicted across the landscape, estimated probability of dog occupancy was >0.50 at >99% of raster pixels (representing 19,049.39 km²), whereas cat occupancy was likely in only 11.8% of raster pixels (2270.53 km²). We found little correlation (Pearson's $r = 0.13$) of model-averaged predicted occupancy (at the raster pixel level) between domestic dogs and cats. Patch cohesion indices for all cover types <10 (9.75–9.99) demonstrating high levels of fragmentation and aggregation indices were highest for agriculture (91.16), less for forest (82.98), and lowest for grasslands (74.40), wetlands (72.72), and urban (72.65) land cover types.

4. Discussion

Overall, probability of domestic dog occupancy was greater than domestic cat occupancy and presented potential for interaction with wildlife over a larger proportion of the landscape in southern Illinois. Domestic dog occupancy was more strongly influenced by land cover type, compared to domestic cat occupancy, which was influenced to a greater degree by anthropogenic features (Fig. 2). However, domestic dog occupancy was also strongly related to land ownership, after

Table 1

AICc table for top-ranked ($\Delta AICc < 5$) domestic dog single-season occupancy models over three land cover types (forest, grasslands, or wetlands) in relation to anthropogenic features at two different scales (50 ha and 250 ha) in southern Illinois, USA. The detection model structure was $p(\text{survey week} + \text{year})$ for all models. Camera-trap data was collected from 357 camera-station clusters across 16 counties, rotating sites from 2008–2010. Top ranked models ($\Delta AICc < 2$) for full candidate set including all land cover types and anthropogenic covariates are in bold. Negative effects are in italics with land ownership private = 1.

Land cover type	Model ^a	$\Delta AICc$	w_i^b	K^c	-logLik2	AICc
Forest	$\psi(\text{distance to structure} + \text{structures/ha} + \text{land ownership} \times \% \text{ forest cover})_{250\text{ha}}$	0	0.38	11	1159.31	1182.08
	$\psi(\text{distance to municipality} + \text{structures/ha} + \text{land ownership} \times \% \text{ forest cover})_{250\text{ha}}$	1.52	0.18	11	1160.83	1183.60
	$\psi(\text{distance to structure} + \text{structures/ha} + \text{land ownership} + \% \text{ forest cover})_{250\text{ha}}$	2.69	0.10	10	1164.13	1184.76
	$\psi(\text{distance to structure} + \text{land ownership} \times \% \text{ forest cover})_{250\text{ha}}$	3.35	0.07	10	1164.79	1185.42
	$\psi(\text{distance to municipality} + \text{structures/ha} + \text{land ownership} + \% \text{ forest cover})_{250\text{ha}}$	4.22	0.05	10	1165.66	1186.29
	$\psi(\text{land ownership} + \text{distance to structure} + \text{structures/ha} \times \% \text{ forest cover})_{250\text{ha}}$	4.62	0.04	11	1163.93	1186.70
	$\psi(\text{structures/ha} + \text{land ownership} + \text{distance to structure} \times \% \text{ forest cover})_{250\text{ha}}$	4.76	0.04	11	1164.07	1186.83
	$\psi(\text{distance to structure} + \text{structures/ha} + \text{land ownership} + \% \text{ grassland cover})_{250\text{ha}}$	0	0.22	10	1158.73	1179.37
	$\psi(\text{distance to structure} + \text{structures/ha} + \% \text{ grassland cover})_{250\text{ha}}$	0.26	0.19	9	1161.11	1179.63
	$\psi(\text{distance to municipality} + \text{structures/ha} + \text{land ownership} + \% \text{ grassland cover})_{250\text{ha}}$	0.98	0.14	10	1159.71	1180.35
Grassland	$\psi(\text{distance to municipality} + \text{structures/ha} + \% \text{ grassland cover})_{250\text{ha}}$	1.01	0.13	9	1161.86	1180.38
	$\psi(\text{distance to structure} + \text{land ownership} + \% \text{ grassland cover})_{250\text{ha}}$	1.37	0.11	9	1162.22	1180.74
	$\psi(\text{distance to structure} + \% \text{ grassland cover})_{250\text{ha}}$	2.37	0.07	8	1165.33	1181.74
	$\psi(\text{structures/ha} + \text{land ownership} + \% \text{ grassland cover})_{250\text{ha}}$	2.48	0.06	8	1165.44	1181.85
	$\psi(\text{distance to municipality} + \text{Land ownership} + \% \text{ grassland cover})_{250\text{ha}}$	4.34	0.03	9	1165.19	1183.71
	$\psi(\text{distance to structure} + \text{structures/ha} + \text{land ownership} + \% \text{ wetland cover})_{250\text{ha}}$	0	0.43	10	1164.03	1184.67
	$\psi(\text{distance to municipality} + \text{structures/ha} + \text{land ownership} + \% \text{ wetland cover})_{250\text{ha}}$	0.69	0.30	10	1164.72	1185.35
	$\psi(\text{distance to structure} + \text{land ownership} + \% \text{ wetland cover})_{250\text{ha}}$	3.34	0.07	9	1169.48	1188.00
	$\psi(\text{distance to municipality} + \text{structures/ha} + \% \text{ wetland cover})_{250\text{ha}}$	3.73	0.06	9	1169.88	1188.40
	$\psi(\text{distance to structure} + \text{structures/ha} + \% \text{ wetland cover})_{250\text{ha}}$	4.05	0.03	9	1170.19	1188.71
Wetlands						

^a Detection model: $p(\text{survey week} + \text{year})$.

^b Model weight calculated for models within a single land cover type candidate set.

^c Number of parameters.

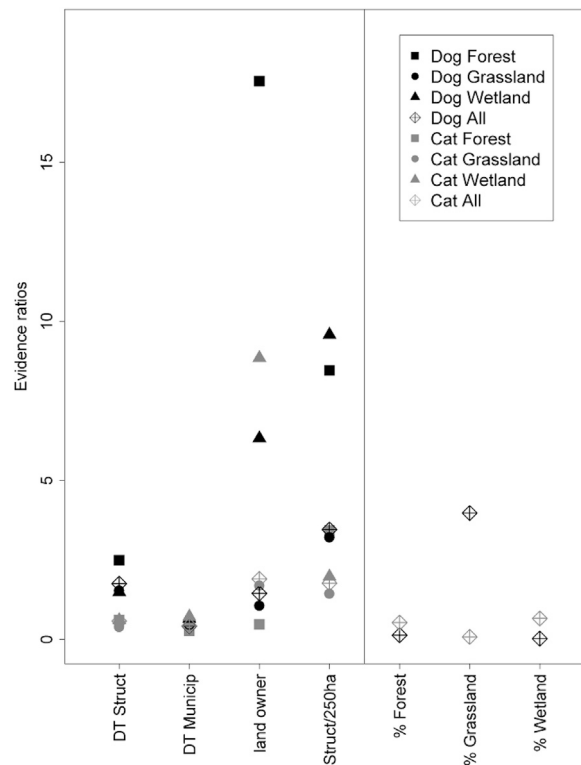


Fig. 2. Evidence ratios for summed model weights measuring support for anthropogenic features (left panel) and natural land cover types (left panel) calculated for domestic dog (black symbols) and cat (gray symbols) single-season occupancy candidate model sets.

accounting for forest dominance, whereas structure density affected dog occupancy in models including grassland and wetland land cover types. Thus, while domestic cats may pose a more intensive threat to wildlife within the area they occupy, the potential impact of domestic dogs is likely to be more geographically extensive. Predicting the potential effects of these non-native species is complicated by a nuanced interaction between landscape composition, human density, and human behavior.

Our finding that domestic cat occupancy was more localized than that of dogs can upend simplistic perceptions of the relative threats posed by the two species. In the context of their ecological impact, domestic cats typically receive more attention than dogs in North America (Doherty et al., 2017) due to their intensive hunting behaviors. However, the net impact of one species on others (e.g., via predation) can depend on its spatial distribution as much as (or more than) it depends on the mean abundance. In the case of predation, substantial spatial heterogeneity in predator abundance or predation risk can stabilize otherwise unstable dynamics between specialists and their prey (Hassell et al., 1991) and promote persistence of sparse prey threatened by persistently abundant generalists (Goodwin et al., 2005; Schmidt and Schaubert, 2008). Factors that concentrate risk in some areas while others serve as refugia reduce overall predator impact because hunting effort is wasted in areas where prey have already been depleted, and because prey can become numerically concentrated in refugia by actively selecting those sites as well as by passive selection mechanisms (Schauber et al., 2007). By similar processes, spatial heterogeneity can reduce efficiency of disease transmission and ecological impacts of nutrient deposition. Based on their greater overall probability occupancy and weaker spatial association with human dwellings in the region, we suggest that domestic dogs pose greater potential for ecological impacts than commonly appreciated.

The observed pattern of domestic cat occupancy associated with anthropogenic features and human densities, is congruent with previous studies (Pearre and Maass, 1998; Sims et al., 2008). Cats can be a significant source of mortality for a wide range of taxa including birds, small mammals, and reptiles (Loss et al., 2013). The close association of the cats detected in our study to human population density suggests many outdoor cats were owned or subsidized and protected by humans and most cats detected appeared to be in good physical conditions. Food supplementation decouples cat populations from the abundance of prey (Newton, 1998; Sims et al., 2008) and outdoor cats can also have direct and indirect sublethal effects on birds (Bonnington et al., 2013), such as reducing parental care and increasing vulnerability to other predators. Supplemented populations of cats can also serve as reservoirs for parasites and pathogens and increase disease transmission among native felids (Bevins et al., 2012; Brown et al., 2008; Gerhold and Jessup, 2013). While domestic cat occupancy was lower than dogs, cats still occupied a greater proportion of the study area than similar-sized native mesopredators including red fox (*Vulpes*

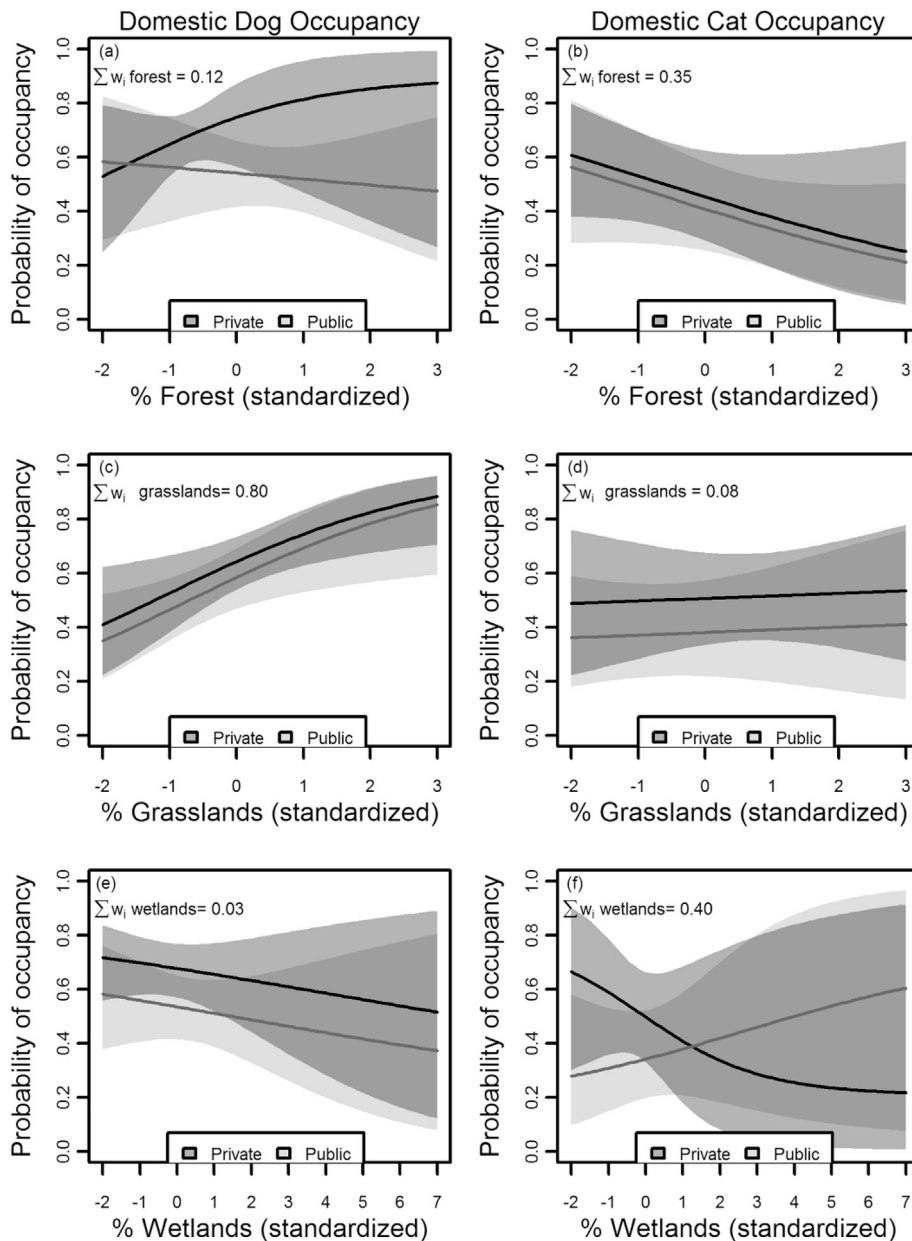


Fig. 3. Domestic dog (left) and domestic cat (right) occupancy over standardized gradients of % forest (a and b), % grassland (c and d), and % wetland (e and f) with summed model weights ($\sum w_i$) for each variable, on public and private land ($\sum w_i$ land ownership = 0.59 for dogs and 0.66 for cats).

vulpes; $\hat{\psi} = 0.26 \pm 0.04$) and gray fox (*Urocyon cinereoargenteus*; $\hat{\psi} = 0.29 \pm 0.03$; Lesmeister et al., 2015), and thus could pose considerable risk to local wildlife across southern Illinois.

Interestingly, cat occupancy declined with increased forest dominance, which correlated with increased fine-scale use by coyotes (*Canis latrans*; Lesmeister et al., 2015). Coyotes are common cat predators (Grubbs and Krausman, 2009) and were ubiquitous in the study area ($\hat{\psi} = 0.95 \pm 0.03$ across camera clusters; Lesmeister et al., 2015). In addition, bobcat (*Lynx rufus*) populations are recovering in southern Illinois and occupancy and survival declined with increasing anthropogenic influences such as roads (Lesmeister et al., 2015; Nielsen and Woolf, 2002). While human density is generally low, human presence is pervasive across the region. Thus, coyotes and bobcats could have positive indirect effects on native prey populations (Crooks and Soule, 1999) through reduced cat occupancy in more forested areas and farther from anthropogenic habitats, but the broad-scale distribution of humans across the landscape still expands the presence of domestic cats across a range of habitats.

Dogs were widespread across the 16-county study area, however differences in occupancy in relation to land cover can result in differential impacts to native species. Native prairies have declined precipitously in the US and grassland wildlife

Table 2

AICc table for top-ranked ($\Delta\text{AICc} < 5$) domestic cat single season occupancy models over three land cover types (forest, grasslands, or wetlands) in relation to anthropogenic features at two different scales (50 ha and 250 ha) in southern Illinois, USA. The detection model structure was $p(\text{year} \times \text{previous detection})$ for all models. Camera-trap data was collected from 357 camera-station clusters across 16 counties, rotating sites from 2008–2010. Top ranked models ($\Delta\text{AICc} < 2$) for full candidate set including all land cover types and anthropogenic covariates are in bold.

Land cover type	Model ^a	ΔAICc	w_i^b	K^c	$-\log\text{Lik}2$	AICc
Forest	$\psi(\text{structures/ha} + \% \text{ forest cover})_{250\text{ha}}$	0	0.14	9	704.92	723.44
	$\psi(\text{land ownership})$	0.88	0.09	8	707.90	724.32
	$\psi(\text{structures/ha} + \text{distance to structure} \times \% \text{ forest cover})_{250\text{ha}}$	1.28	0.07	11	701.96	724.72
	$\psi(\text{structures/ha})_{250\text{ha}}$	1.70	0.06	8	708.73	725.14
	$\psi(\text{structures/ha} \times \% \text{ forest cover})_{250\text{ha}}$	1.82	0.06	10	704.62	725.26
	$\psi(\text{distance to structure} + \text{structures/ha} + \% \text{ forest cover})_{250\text{ha}}$	1.96	0.05	10	704.77	725.4
	$\psi(\text{distance to municipality} + \text{structures/ha} + \% \text{ forest cover})_{250\text{ha}}$	2.07	0.05	10	704.87	725.51
	$\psi(\text{land ownership} + \% \text{ forest cover})_{250\text{ha}}$	2.13	0.05	9	707.05	725.57
	$\psi(\text{distance to structure} + \text{structures/ha} + \text{land ownership} + \% \text{ forest cover})_{250\text{ha}}$	2.55	0.04	11	703.23	725.99
	$\psi(\text{structures/ha} + \text{land ownership} + \text{distance to structure} \times \% \text{ forest cover})_{250\text{ha}}$	2.58	0.04	12	701.11	726.02
	$\psi(\% \text{ forest cover})_{250\text{ha}}$	2.64	0.04	8	709.66	726.08
	$\psi(\text{land ownership})$	0	0.23	8	707.90	724.32
	$\psi(\text{structures/ha})_{250\text{ha}}$	0.83	0.15	8	708.73	725.14
	$\psi(\text{land ownership} + \% \text{ grassland cover})_{50\text{ha}}$	2.10	0.08	9	707.90	726.42
Grassland	$\psi(\text{land ownership} + \% \text{ grassland cover})_{250\text{ha}}$	2.10	0.08	9	707.90	726.42
	$\psi(\text{structures/ha} + \% \text{ grassland cover})_{250\text{ha}}$	2.44	0.07	9	708.24	726.76
	$\psi(\text{distance to municipality} + \text{structures/ha} + \text{land ownership} + \% \text{ grassland cover})_{250\text{ha}}$	2.59	0.06	11	704.14	726.91
	$\psi(\text{distance to structure} + \text{structures/ha} + \text{land ownership} + \% \text{ grassland cover})_{250\text{ha}}$	2.60	0.06	11	704.16	726.92
	$\psi(\text{distance to municipality} + \text{structures/ha} + \% \text{ grassland cover})_{250\text{ha}}$	3.78	0.03	10	707.46	728.1
	$\psi(\text{distance to municipality} + \text{land ownership} + \% \text{ grassland cover})_{250\text{ha}}$	3.81	0.03	10	707.49	728.12
	$\psi(\text{distance to structure} + \text{land ownership} + \% \text{ grassland cover})_{250\text{ha}}$	4.21	0.03	10	707.89	728.53
	$\psi(\text{distance to structure} + \text{structures/ha} + \% \text{ grassland cover})_{250\text{ha}}$	4.56	0.02	10	708.24	728.87
	$\psi(\text{distance to municipality})$	4.80	0.02	8	712.7	729.12
	$\psi(\text{distance to structure} + \text{structures/ha} + \text{land ownership} \times \% \text{ wetland cover})_{250\text{ha}}$	0	0.19	12	697.64	722.55
	$\psi(\text{distance to municipality} + \text{structures/ha} + \text{land ownership} \times \% \text{ wetland cover})_{250\text{ha}}$	0.24	0.17	12	697.88	722.79
	$\psi(\text{land ownership})$	1.77	0.08	8	707.9	724.32
	$\psi(\text{land ownership} \times \% \text{ wetland cover})_{250\text{ha}}$	1.99	0.07	10	703.9	724.54
	$\psi(\text{structures/ha})_{250\text{ha}}$	2.6	0.05	8	708.73	725.14
Wetlands	$\psi(\text{land ownership} + \% \text{ wetland cover})_{50\text{ha}}$	3.28	0.04	9	707.3	725.82
	$\psi(\text{land ownership} \times \% \text{ wetland cover})_{50\text{ha}}$	3.34	0.04	10	705.25	725.88
	$\psi(\text{land ownership} + \% \text{ wetland cover})_{250\text{ha}}$	3.71	0.03	9	707.74	726.26
	$\psi(\text{distance to structure} + \text{land ownership} \times \% \text{ wetland cover})_{250\text{ha}}$	3.73	0.03	11	703.51	726.28
	$\psi(\text{structures/ha} + \text{land ownership} + \text{distance to municipality} \times \% \text{ wetland cover})_{250\text{ha}}$	3.77	0.03	12	701.41	726.32
	$\psi(\text{structures/ha} + \text{land ownership} \times \% \text{ wetland cover})_{250\text{ha}}$	4.1	0.02	11	703.88	726.64
	$\psi(\text{structures/ha} + \text{land ownership} + \text{distance to structure} \times \% \text{ wetland cover})_{250\text{ha}}$	4.36	0.02	12	702	726.91
	$\psi(\text{structures/ha} + \text{land ownership} + \text{distance to structure} + \% \text{ wetland cover})_{250\text{ha}}$	4.4	0.02	11	704.18	726.94
	$\psi(\text{structures/ha} + \text{land ownership} + \text{distance to municipality} \times \% \text{ wetland cover})_{50\text{ha}}$	4.41	0.02	12	702.05	726.96
	$\psi(\text{distance to municipality} + \text{structures/ha} + \text{land ownership} + \% \text{ wetland cover})_{250\text{ha}}$	4.41	0.02	11	704.2	726.96
	$\psi(\text{structures/ha} + \% \text{ wetland cover})_{250\text{ha}}$	4.57	0.02	9	708.6	727.12
	$\psi(\text{structures/ha} + \text{distance to municipality} \times \% \text{ wetland cover})_{250\text{ha}}$	4.74	0.02	11	704.52	727.29

^a Detection model: $p(\text{year} \times \text{previous detection})$.

^b Model weight calculated for models within a single land cover type candidate set.

^c Number of parameters.

species are threatened by fragmentation, degradation and conversion of habitat (Rahmig et al., 2009; Samson and Knopf, 1994). Grassland birds including Henslow sparrow (*Ammodramus henslowii*) could be at particular risk in Illinois (Walk et al., 2010) where high rates of dog occupancy may exacerbate population declines and hinder recovery efforts, although additional research is required to determine specific impacts. Domestic dogs can also negatively impact survival of game species in grassland habitats, depredating white-tailed deer (*Odocoileus virginianus*) fawns (Nelson and Woolf, 1987; Rohm et al., 2007) and wild turkey hens on nests (*Meleagris gallopavo*; Speake et al., 1985), also further decreasing potential recruitment. High rates of dog occupancy on private land in dominant forest areas could negatively impact specialists in those habitats. For example, gray fox populations have declined (Bluett, 2013) and range has contracted in southern Illinois (Lesmeister et al., 2015). Asymmetrical competition among native canids resulting in intraguild killing, spatial displacement from forested areas, (coyotes) and increased exploitative competition in human-associated habitats (red fox) are proposed agents. Thus, interactions with free-ranging dogs could exacerbate cumulative impacts to gray fox populations across the region. However, research specifically evaluating the interactions between dogs and native wildlife within different land cover types is necessary to effectively measure impacts (Young et al., 2011).

The large proportion of southern Illinois occupied by free-ranging dogs was surprising. But perhaps this should be expected considering the rural environment and fragmented mosaic landscape composition (Fig. 1). A meta-analysis of studies of domestic dogs found the human:dog ratio and percentage of owned dogs that were restricted in their movements was generally lower in rural landscapes (Gompper, 2014a) and dog-wildlife interactions peaked along the rural wildland interface

(Butler et al., 2004; Srbeck-Araujo and Chiarello, 2008; Vanak and Gompper, 2010). Agriculture is the dominant land cover (44% of study area), but the region is commonly characterized by relatively high edge density (Heske, 1995; Marini et al., 1995; McDonald et al., 2008). Moreover, approximately 12% of the study area was public lands including the Shawnee National Forest, Crab Orchard and Cypress Creek National Wildlife Refuges, and 21 state-managed parks and natural areas (Lesmeister et al., 2015). These public holdings were generally aggregated but not contiguous, as reflected by patch cohesion and aggregation indices, and are permeated by private inholdings. As a result, anthropogenic influences are pervasive and 90% of the pixels for the predicted landscapes are within 1.75 km of a human structure with a mean dog occupancy rate of 0.33, and 80% of pixels were within 1 km of human structures leaving few areas free of domestic dogs (Fig. 4).

The strong effect of land ownership on overall domestic cat occupancy and dog occupancy in areas with high forest dominance highlights the role human values and local regulations can play in anthropogenic impacts on wildlife. The effect of human behavior on dog occupancy could be considered from an optimistic perspective, as human actions that allow for extensive distribution of dogs can equally affect a decline in occupancy. Human perceptions of risk towards domestic pets

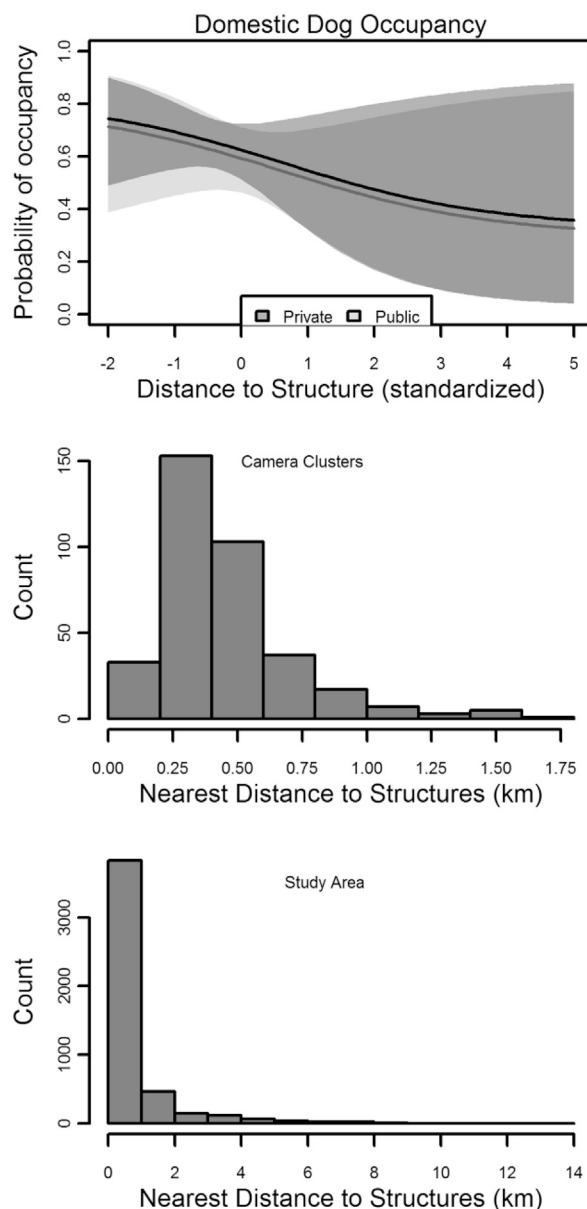


Fig. 4. Model-averaged predicted domestic dog occupancy rates across a standardized gradient of distances to structures (top). Occupancy was estimated using single-season occupancy models for a camera-trap study conducted from January–April 2008–2010, in 16 counties in southern Illinois, USA. Distribution of real minimum distances to structures are shown for all camera trap clusters (middle), and the entire study area (2.06 km × 2.06 km raster pixel resolution).

compared to wildlife are unequal, and perceived risk of pets to wildlife are often underestimated. Gramza et al. (2016) found misperception or underestimation of the risk domestic cats posed to wildlife led to more irresponsible behavior in cat owners. Education and local regulations can be powerful tools in addressing human perceptions and influencing attitudes to reduce potential impacts of domestic dogs and cats (Bellard et al., 2016; Gramza et al., 2016; Parsons et al., 2016). Pet owner education may be particularly effective when targeted in areas with extensive private inholdings and bordering public lands.

The distribution of free-ranging domestic pets across southern Illinois is extensive and threatens wide-ranging potential impacts for native wildlife if left unchecked. However, specific interactions with and impacts to native species are still unknown, which will make changing stakeholder perspectives difficult. There is often heated debate surrounding policy and in addressing concerns about local practices in maintaining free-ranging, owned or subsidized pets (Loss and Marra, 2017; Loyd and Miller, 2010; Wald et al., 2013). Globally, the threats dogs pose are highly underestimated, both by the public and by conservationists (Doherty et al., 2017). Thus, while education of stakeholders including landowners, managers, and pet owners is necessary, it is equally critical that conservationists be armed with defensible evidence of prevalence and impacts of domestic pets for public education and conservation efforts to be effective.

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