1 **Title:** Living in the concrete jungle: carnivore spatial ecology in urban parks

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ABSTRACT

People and wildlife are living in an increasingly urban world, replete with unprecedented human

densities, sprawling built environments, and altered landscapes. Such anthropogenic pressures

can affect multiple processes within an ecological community, from spatial patterns to

interspecific interactions. We tested two competing hypotheses, human shields versus human

competitors, to characterize how humans affect the carnivore community using multi-species

occupancy models. From 2017-2020, we conducted the first camera survey of city parks in

Detroit, Michigan, and collected spatial occurrence data of the local native carnivore community.

Our 12,106-trap night survey captured detected data for coyotes (*Canis latrans*), red foxes

(*Vulpes vulpes*), gray foxes (*Urocyon cinereoargenteus*), raccoons (*Procyon lotor*), and striped

skunks (*Mephitis mephitis*). Overall occupancy varied across species ($\Psi_{coyote}=0.40$, $\Psi_{raccoon}=0.54$, $\Psi_{red\ fox}=0.19$, $\Psi_{striped\ skunk}=0.09$). Contrary to expectations, humans did not

significantly affect individual occupancy for these urban carnivores. However, co-occurrence

between coyote and skunk only increased with human activity. The observed positive spatial

association between an apex and subordinate pair supports the human shield hypothesis. Our

findings demonstrate how urban carnivores can exploit spatial refugia and coexist with humans

in the cityscape.

Keywords: occupancy, city, distribution, community structure, camera survey, Detroit, human

shield, coyote, overlap

INTRODUCTION

Cities are highly heterogeneous landscapes of risk and reward, borne of unique

interactions between anthropogenic and ecological processes (Alberti et al., 2003; Liu et al.,

2007). As urbanization and land cover conversion rates continue to increase worldwide, cities

have emerged as a new and unique habitat for wildlife. By 2050, over half of the global human

population will live in a city while urban development is projected to grow by 120 million

hectares globally by 2030 (Mcdonald et al., 2018; United Nations, 2018). Cities can be a source

or a sink for mammal species, a duality driven by both increases in availability of food sources

and risks of mortality (Bateman, & Fleming, 2012; Lepczyk et al., 2017; Lamb et al., 2020). For

example, cougars (*Puma concolor*) in an urban-wildland system in Colorado successfully

exploited anthropogenic food sources, yet faced a 6.5% increase in mortality risk in developed

areas (Moss et al., 2016). Wildlife responses to the built environment are unsurprisingly driven

by humans themselves and their induced modifications to landscapes through food provisioning,

artificial habitat and light, and roads (Clucas, & Marzluff, 2011; Riley et al., 2014; Gaston et al.,

2017).

Anthropogenic pressures affect wildlife communities from intraguild interactions down

to behavioral shifts in individual species. Perturbations to higher trophic levels can have

cascading impacts on ecosystem processes, which underscores the need to understand how

carnivores respond to human activities (Terborgh, 2010; Ripple et al., 2014b). A study in the city

of Chicago found that raccoons (*Procyon lotor*) comprised a larger relative proportion of the

mesopredator community in urban compared to rural sites, irrespective of patch size (Prange, &

Gehrt, 2004). Individual species responses to human activity are varied and depend on each

species' life history traits and behavioral tolerance of human encounters. Cottontail rabbits

(*Sylvilagus floridanus*) in an urban area were more vigilant at sites where coyotes were absent,

suggesting humans are a third "player" in a predator-prey-human system (Gallo et al., 2019).

Evidently, urban systems produce a suite of complex and synergistic changes to ecological

communities.

Despite evidence that human activity induces complex responses in urban wildlife, there

is a dearth of studies that quantify these effects, particularly for terrestrial carnivores. A meta-

analysis of urban ecology studies found that only 10.2% of 244 studies quantified large mammal

responses to urbanization and only 6% of all urbanization metrics employed in these studies

explicitly considered humans (Moll et al., 2019). Worldwide population declines and range

contraction in carnivores highlight the urgency to assess how spaces dominated by humans alter

interactions within ecological communities (Ceballos, & Ehrlich, 2002; Ripple et al., 2014a).

We leveraged a North American carnivore guild comprised of coyotes, raccoons, red

foxes, gray foxes (*Urocyon cinereoargenteus)*, and striped skunks to investigate how human

activity influences spatial ecology within the community. We implemented the first camera

survey of city parks in Detroit, Michigan from 2017-2020 to study the city's carnivores. By

directly measuring human activity and not proxies of human pressure such as housing density,

we explicitly disentangled the effects of humans on wildlife from those related to the built

environment.

In characterizing human effects many relationships may occur on carnivore communities.

We underscore two pervasive theoretical frameworks in the literature with distinct expectations

for mammalian community response to fine-scale human activity, but recognize these hypotheses

are not mutually exclusive (Figure 1). The human shield hypothesis (HSH) argues that humans

differentially exert top-down pressure on the apex (hereafter dominant) predator in the system,

indirectly benefitting the subordinate competitors and facilitating greater spatial overlap between

humans and subordinate species (Shannon et al., 2014; Moll et al., 2018). Anthropogenic

pressure is known to mediate intraguild interactions (Berger, 2007; Muhly et al., 2011; Gallo et

al., 2019). For instance, red foxes (*Vulpes vulpes*) have been shown to exploit highly developed

core urban areas as spatial refugia to avoid their dominant coyote (*Canis latrans*) competitors

(Moll et al., 2018). A contrasting approach frames humans as competitors (HCH), asserting that

anthropogenic pressure affects multiple species irrespective of their trophic level or dominance

hierarchy (Chapron, & López-Bao, 2016; Farris et al., 2017). According to HCH, human

presence is functionally similar to antagonism from another competitor in the guild, resulting in

increased vigilance, competitive exclusion, and spatial avoidance across the entire community

(Clinchy et al., 2016; Gallo et al., 2019; Suraci et al., 2019).

Here, we addressed the following questions to test whether effects from anthropogenic

pressures on urban carnivores align with expectations of the HSH or HCH: 1) how do humans

influence space use of individual carnivore species? 2) how are pairwise interactions affected by

human activity within a competing carnivore guild?

With HSH, subordinate mesopredators will exploit the spatial refugia created by human

top-down pressures on dominant predators and spatially overlap with humans at the park scale

(Geffroy et al., 2015; Moll et al., 2018). We categorized raccoon, red fox, and skunk as

subordinate based on body size, trophic level, and known antagonistic interaction with coyotes,

which we categorized as dominant (Fedriani et al., 2000). First, for individual species we

expected human activity to reduce dominant carnivore occupancy and concurrently increase

subordinate carnivore occupancy (Berger, 2007; Muhly et al., 2011). Second, for pairwise

interactions we expected human activity to increase dominant-subordinate and subordinate-

subordinate carnivore species pair conditional occupancy (Smith et al., 2018).

Conversely, with HCH humans can function like a superior competitor, reduce the niche

space and thus spatially displace carnivores regardless of whether they are dominant or

subordinate (Everatt et al., 2019). First, for individual species we expected human activity to

reduce both dominant and subordinate carnivore occupancy (George, & Crooks, 2006). Second,

for pairwise interactions we expect human activity to reduce both subordinate-dominant and

subordinate-subordinate carnivore conditional occupancy (Magle et al., 2014).

MATERIALS & METHODS

Study Area

We surveyed the carnivore community at 24 urban parks throughout Detroit, a ~ 370 km²

city in southeastern Michigan, USA using remotely triggered cameras (Figure 2). Parks sampled

as part of our study represent 51% of the total area of the green space in city parks (City of

Detroit, 2015). The Detroit River runs along the city's southern boundary and the Rouge River

runs through the southwestern districts including an automotive manufacturing plant. Over the

last 70 years, Detroit has experienced a substantial population decline, dropping from 1.8 million

residents at the height of its industrial era in 1950 to approximately 673,000 residents in 2016

(U.S. Census Bureau, 2016). Current human population density is 1,819/km compared to 2,374/

km found in the smaller mid-western city of Milwaukee, Wisconsin. The number of empty lots

peaked at roughly 120,000 vacant lots (33% of total parcels) and 48,000 abandoned buildings

(13% of parcels) in 2010 (Detroit Residential Parcel Survey, 2010; Raleigh, & Galster, 2015).

Over time, many empty lots have progressed through early successional stages and have even

developed enough vegetative cover to support small mammal populations, a key prey source for

urban carnivores (Bateman, & Fleming, 2012).

Camera Survey

We conducted a 3-year, non-invasive survey by installing motion-triggered trail cameras

(Reconyx© PC 850, 850C, 900, 900C) throughout city parks during the fall-winter season in

Detroit (November 2017-March 2018, November 2018-February 2019, November 2019 – March

2020). We deployed 39 stations across 23 city parks in 2017, 41 stations across 24 parks in 2018,

and 36 stations at 23 parks in 2019. The same parks were sampled across 2017-2020, with the

exception of 2018 where a new site was added. We selected parks to ensure representation of

ecological and anthropogenic features such as park size, vegetation cover, distance to water,

trails, and built infrastructure such as visitor pavilions and playgrounds. Site selection for camera

placement within parks was based on animal sign such as tracks, scat, or natural trails to improve

detection of carnivores and their prey. Unbaited cameras were placed approximately 0.5 m from

the ground on trees >10 cm in diameter, following standard protocol for mesocarnivore camera

trap studies (Cove et al., 2012). Camera settings were set to high sensitivity, with three images

captured per trigger at 1s intervals, and 15s delay between triggers. For parks with > 1 camera

station, the average distance between cameras was 1,416 m, while the average distance between

parks was 3,200 m.

After camera retrieval, at least two members of the Applied Wildlife Ecology Lab at the

University of Michigan classified images to species and confirmed accuracy. Any unresolved

photos were classified as "unknown" and removed from the analysis. We implemented a 30-

minute quiet period to account for pseudoreplication and improve independence for analysis,

given some animals tend to remain in front of the camera and trigger it multiple times. Domestic

dogs and cats were excluded from the analysis as we could not differentiate between feral

animals who form part of the local carnivore community and those which were temporarily

roaming from their owners. Focal species in this study are relatively common in the eastern

United States and comprise a guild that is hierarchically structured, ideal for investigating the

effects of human presence on the space use of a carnivore community in urban environments.

Modeling Carnivore Occupancy

Camera trap data was formatted for occupancy analysis by generating weekly detection

histories (i.e. presence '1' or absence '0' of each species at each camera location) using the R

package 'camtrapR' (Niedballa, 2016). We used a Bayesian multi-species occupancy modeling

approach and fit a series of candidate models to test hypotheses about anthropogenic effects on

individual carnivore species and intraguild interactions (Rota et al., 2016). The latent occupancy

state (Ψ) was modeled as a multivariate Bernoulli random variable (MVB), where $Z_i = \{Z_{i1}, Z_{i2},$

$Z_{i3}, Z_{i4}\}$ represents the 4-dimensional vector of binary detection data for the four focal carnivores

(Dai et al., 2013). Each occupancy state represents possible scenarios, i.e. Ψ_{1111} denotes all four

species are present, Ψ_{0000} denotes all carnivores are absent.

Equation 1 $Z \sim MVB(\Psi_{1111}, \Psi_{1110}, \Psi_{1100}, \Psi_{1000}, \Psi_{1010}, \Psi_{1001}, \Psi_{1011}, \Psi_{0111}, \Psi_{0100}, \Psi_{0110}, \Psi_{0101},$

$\Psi_{0010}, \Psi_{0011}, \Psi_{0001}, \Psi_{0000})$

Interaction parameters for were included in the model to calculate individual occupancy

estimates as well as conditional probabilities for each species. Conditional probabilities reflect

occupancy estimates given the presence of a competitor (i.e. occupancy estimate of red fox,

given the presence of coyote). We modeled natural parameters (f_1, f_2, f_3, f_4, f_{12}, f_{13}, f_{14}, f_{23}, f_{24},

f_{34}) as linear functions to obtain the probability of each community state, where each subscript

denotes one of the four species: 1=coyote, 2=raccoon, 3=red fox, 4=skunk, following derivations

of (Rota et al., 2016). The number of grey fox detections was insufficient for inclusion in the

occupancy models and were excluded from the analysis (n=9 detections at 1 site) (Mackenzie et

al., 2002).

The detection process was modeled as a function of covariates including park area (km^2)

(AREA), number of trap nights (TN), camera type (CAM), and NDVI as a measure of vegetation

density (VEG); occupancy was modeled as a function of human detections per trap night

(HUM), distance to school (km) (DSCH), year (YR), AREA, and NDVI. Top models were

selected with an information theoretic approach using Akaike's Information Criterion (AIC) to

identify the model with the lowest ΔAIC and greatest weight (*w*) (Mackenzie, & Bailey, 2004).

Models were run using the *unmarked* package in Program R; model fit was assessed using

residual sum of squares (RSS) with the parametric bootstrap function 'parboot' (Fiske, &

Chandler, 2011; R Core Team, 2017). We assessed the effects of human activity on carnivore

occupancy using the HUM covariate coefficient estimate (β_{HUM}) from the model with the lowest

ΔAIC. A negative β_{HUM} signifies that humans decreased individual species or conditional

pairwise occupancy, while a positive β_{HUM} indicated that human activity increased these

occupancy estimates. We calculated the 95% confidence interval for each β_{HUM} to determine

whether it was a strong predictor of occupancy and concluded that intervals overlapping zero

were poor predictors and thus did not affect occupancy.

RESULTS

Our 12,106-trap night survey yielded detections of coyotes (n=220), raccoons (n=1,496),

red foxes (n=88), grey foxes (n=11), and striped skunks (n=38) in a highly urbanized landscape

from 2017-2020. The proportion of sites occupied (uncorrected for imperfect detection) varied

by species (Table 1). We recorded 1,103 human detections at 25 parks, resulting in a naïve

occupancy estimate of 0.64 based on the proportion of occasions where humans were present

across our study period.

Species Response to Human Activity

Contrary to expectations of both HCH and HSH, human activity did not significantly alter single

species occupancy estimates for any of the four focal carnivore species (Figure 3A). Human

β_{HUM} coefficients derived from the top performing model for individual species occupancy were:

coyote (β_{HUM}=-0.13, 95% CI:-11.6, 11.3), raccoon (β_{HUM}=-1.3, CI:-3.9, 1.3), red fox (β_{HUM}=1.5,

CI:-1.5, 4.5), and skunk β_{HUM}=-2.9, CI:-14.8, 8.9). Other environmental variables were strong

predictors of individual species occupancy. For example, DSCH increased occupancy for

raccoons (β_{DSCH}=0.001, CI:0.0008, 0.0012). VEG and AREA were negative predictors for red

foxes, while they were positive and negative predictors for coyotes, respectively (Table 2)

Pairwise Intraguild Interaction Response to Human Activity

Human activity altered how urban carnivores use space with respect to their intraguild

competitors. The inclusion of HUM as a covariate for all individual and pairwise interaction

occupancy estimates greatly improved model inference, demonstrating fine-scale measures of

human activity are informative in explaining carnivore occupancy. Human coefficient estimates

for coyote-raccoon (β_{HUM}=4.8, CI:-6.2, 15.8), coyote-red fox(β_{HUM}=8.7, CI:-2.6, 20.0), raccoon-

red fox (β_{HUM}=-3.9, CI:-11.3, 3.5), raccoon-skunk (β_{HUM}=-0.12, CI:-0.4, 0.2), red fox-skunk

(β_{HUM}=-0.2, CI:-1.0, 0.6), overlapped zero, signaling that humans were weak predictors of

conditional occupancy for these species pairs. However, human activity significantly increased

the likelihood that skunks would occupy an area where coyotes were present (β_{HUM}=9.0, CI:8.7,

9.2) in support of the human shield hypothesis with intraguild interactions between dominant and

subordinate species pair (HSH, Figure 3B).

DISCUSSION

Our study provides necessary insights into how human activity affects space use in the

carnivore community in Detroit parks. Common proxies for human activity derived from

landscape-level metrics of urbanization such as housing density, percent impervious surfaces, or

road density may not capture the resolution necessary to determine fine-scale consequences for

wildlife (Tablado, & Jenni, 2017). The inclusion of indices of direct human activity is therefore

needed in future urban ecology studies to disentangle the effects of humans from the built

environment (Nickel et al., 2020). Further, the design of parks and urban green spaces should

include considerations of how human presence shapes animal communities to adequately balance

the needs of people and wildlife.

Contrary to our expectations, humans did not influence single species occupancy, a result

which neither supports HSH or HCH. Our hypothetical framework hinged on either a positive or

negative effect of humans on urban carnivore space use. However, our observed lack of effect

for individual species may reflect an alternate hypothesis wherein humans do not directly

influence space use at a fine scale, likely as a result of heightened behavioral plasticity in urban

adapters (Lowry et al., 2013). Key resources such as den sites and prey availability may be

intrinsically concentrated in urban green spaces, given that they are essentially habitat fragments

embedded in an urban matrix, thus funneling carnivores into parks regardless of human activity

(Marzluff, 2005). Our results are consistent with a growing body of evidence that underscores

the importance of urban greenspaces to ensure long-term persistence carnivore community

(Gallo et al., 2017).

We found an influence of human activity altering intraguild interactions for only one

species pair. Spatial interaction between coyotes and skunks increased significantly with human

activity, indicating that humans effectively shield skunks from coyotes consistent with HSH. As

the smallest carnivore in our study, they face antagonism from coyotes ranging from interference

competition to direct killing (Fisher, & Stankowich, 2018). To date, there has been little evidence

of skunks spatially avoiding coyotes, thus we present a novel example of how skunk spatial

ecology is mediated by human activity (Prange, & Gehrt, 2007; Ritchie, & Johnson, 2009). The

long-term effects of such increased spatial overlap are unknown between this species pair. If

humans continue to shield skunks from dominant competitors, the result is a net positive for

skunks as coexistence is facilitated. Alternatively, if the interaction strength between humans and

coyotes weakens, yet skunks continue to use humans as a shield, they could potentially be lured

into more frequent antagonistic interactions with coyotes and face increased mortality risk, akin

to an ecological trap (Robertson, & Hutto, 2006; Bateman, & Fleming, 2012). Carnivores may

leverage the temporal niche dimension to avoid competitive exclusion, though our study did not

explore this aspect of urban carnivore ecology and represents a fruitful future direction.

If humans function as shields and facilitate spatial overlap in the carnivore community,

then urban areas could serve as key refugia in cities and increase co-existence in an otherwise

highly competitive guild. Paradoxically, the human shield hypothesis indicates that urbanization

does not inherently result in biodiversity loss at the patch scale, given that subordinate species

can exploit refugia (Moll et al., 2018; Lewis et al., 2019). However, biodiversity loss due to

urbanization at both the landscape and global scale remains a concern for conservation efforts

(Mcdonald et al., 2013; Mcintyre, 2014; Lewis et al., 2015).

In addition to wild carnivores, domestic dogs and cats were commonly detected and often

without human company. Human affiliates such as dogs and cats are widely recognized as

having significant detrimental effects on wildlife (Lenth et al., 2008; Vanak, & Gompper, 2009;

Loss et al., 2013). Despite this, the distinction between free roaming, feral, or simply temporarily

off leash remains unresolved in our study system. As a result, we were unable to determine

whether these human affiliates were true long-term members of the local carnivore assembly and

thus were excluded from the analysis. Leashed dogs sometimes harass and injure wildlife,

including some of the focal species in this study (Hughes, & Macdonald, 2013). However, how

these antagonistic interactions determine the composition, structure, and distribution of carnivore

communities in urban spaces is not well understood. Because dogs are one of the most widely

distributed terrestrial carnivores, filling this knowledge gap should be a key consideration for

future studies to better inform natural resource managers seeking to mitigate their effects on

wildlife (Gehrt et al., 2010).

Our study provides insight into the intraguild interactions of an urban carnivore

community in a mid-sized city whose population has declined over the last 70 years.

Homogenization patterns expected in urban systems do not necessarily scale down to smaller

cities (Collins et al., 2002). Moreover, the historical trajectory and relationship between

population decline, housing vacancy, and vegetation varies by city (Schwarz et al., 2018).

Notably, this emigration of people from the city of Detroit is complex and tied to various

historical socioeconomic biases (Xie et al., 2018). Further, we recognize that how people are

distributed in the city and who has access to green spaces is not equitable and a consequence of

discriminatory housing and city planning policies that impact a myriad of ecological processes

(Watkins, & Gerrish, 2018; Schell et al., 2020). This economic and racial segregation of

neighborhoods introduces a bias to our understanding human-wildlife interactions in cities

(Alberti et al., 2020). The location, maintenance level, and surrounding characteristics of parks

are also unequally distributed in cities, this inequity can potentially attract or deter carnivore

species and confound the interpretation of our results (Elliott et al., 2019; Huang et al., 2020).

Further studies are needed to disentangle urban carnivore coexistence patterns and resource

availability from socioeconomic factors driven by racial disparities and environmental injustices

(Wilson et al., 2008).

Finally, our study could inform how natural resource managers and city planners

approach urban design and offer opportunities for collaboration with ecologists. Given that urban

carnivores seek spatial refuge from human activity hotspots, future park designs could

incorporate wildlife zones where the use of walking trails diverts human foot traffic around

rather than through important habitat (Hess et al., 2014). Urban planners are thus tasked with

promoting access to natural areas for the public, while still conserving habitat for wildlife. City

parks are an important resource for urbanites and provide recreational, cultural, psychological

and physiological benefits to visitors (Soga, & Gaston, 2020). Therefore, finding a balance

between the wellbeing of people and wildlife is a fundamental challenge of the 21st century

(Chawla, 2015; Rigolon, 2016; Liu et al., 2017).

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537   **Table 1** Summary of 2017-2020 DMP camera survey including total and average number of trap

538   nights, camera stations, parks, detections for all species, as well as number and proportion of

539   parks occupied by each species (i.e., naïve occupancy).

Detroit Camera Survey 2017-2020	Total
Trap Nights	12,106
Avg. Trap Nights Per Camera	96
Camera stations	49
Parks	26
Number of Detections	
Human	1,103
Coyote	220
Red Fox	88
Grey Fox	11
Raccoon	1,496
Skunk	38
Domestic Dog	600
Domestic Cat	439
Number of Parks Occupied (Proportion)	
Human	25 (0.96)
Coyote	16 (0.62)
Red Fox	7 (0.27)
Grey Fox	2 (0.08)
Raccoon	19 (0.73)
Skunk	6 (0.23)
Domestic Dog	24 (0.92)
Domestic Cat	23 (0.88)

548   **Table 2** Summary of candidate multispecies occupancy models with covariates including year

549   (YR), park area (km^2) (SIZE), human detections per trap night (HUM), distance to school (km)

550   (DSCH), and NDVI (VEG) as a measure of vegetation density. Dot models (.) denote null (i.e.

551   constant) detection (ρ) or occupancy(ψ). Akaike's Information Criterion (AIC), delta AIC, AIC

552   model weight (*w*), and model goodness of fit residual sum of squares (RSS *p-value*) are listed.

Model	Equation	K	AIC	ΔAIC	*w*	RSS *p-value*
3	ρCoy (VEG); ΨCoy (AREA+VEG+HUM), ρRac (.); ΨRac (DSCH+HUM), ρFox (VEG); ΨFox (AREA+VEG+HUM), ρSku (.); ΨSku (HUM), ρCoy-Rac (.); ΨCoy-Rac (AREA+HUM), ρCoy-Fox (.); ΨCoy-Fox (AREA+VEG+HUM), ρCoy-Sku (.); ΨCoy-Sku (AREA+HUM), ρRac-Fox (.); ΨRac-Fox (VEG+HUM), ρRac-Sku (.); ΨRac-Sku (HUM), ρFox-Sku (.); ΨFox-Sku (HUM)	36	3356.85	0.00	0.74	< 0.01
1	ρCoy (.); ΨCoy (AREA+VEG), ρRac (.); ΨRac (DSCH+HUM), ρFox (.); ΨFox (AREA+VEG), ρSku (.); ΨSku (.), ρCoy-Rac (.); ΨCoy-Rac (AREA+HUM), ρCoy-Fox (.); ΨCoy-Fox (AREA+VEG), ρCoy-Sku (.); ΨCoy-Sku (AREA), ρRac-Fox (.); ΨRac-Fox (VEG+HUM), ρRac-Sku (.); ΨRac-Sku (DSCH), ρFox-Sku (.); ΨFox-Sku (DSCH)	29	3359.52	2.67	0.19	< 0.01
2	ρCoy (NDVI); ΨCoy (AREA+VEG), ρRac (.); ΨRac (DSCH), ρFox (NDVI); ΨFox (AREA+VEG), ρSku (.); ΨSku (.), ρCoy-Rac(.); ΨCoy-Rac (AREA), ρCoy-Fox(.); ΨCoy-Fox (AREA+VEG), ρCoy-Sku(.); ΨCoy-Sku (AREA), ρRac-Fox(.); ΨRac-Fox (VEG), ρRac-Sku(.); ΨRac-Sku (.), ρFox-Sku(.); ΨFox-Sku (.)	26	3363.63	6.78	0.026	< 0.01

Figure Legends

Figure 1. Conceptual framework for the effects of humans on (1) individual carnivore species

and (2) pairwise intraguild interactions under two hypotheses: humans as shields (HSH) and

humans as competitors (HCH). HSH1: Human reduce dominant carnivore occupancy and

increase subordinate carnivore occupancy. HSH2: Increased conditional occupancy for

dominant-subordinate and subordinate-subordinate species pairs. HCH1: Humans reduce

occupancy for both dominant and subordinate carnivore species. HCH2: Reduced conditional

occupancy for dominant-subordinate and subordinate-subordinate species pairs.

Figure 2. Study area – City of Detroit, Michigan. Shaded green polygons represent the 24 city

parks in the Detroit Metro Parks system included in the analysis while black dots denote camera

stations in the study.

Figure 3. Human effects on A) Individual carnivore species and B) Pairwise intraguild

interactions using β coefficient estimates for the human trap night (HUM) covariate and 95%

confidence intervals shown from top model. Asterisk denotes significant effect with interval not

overlapping 0.

581   Figure 1

590   Figure 2

606   Figure 3