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Do coyotes *Canis latrans* influence occupancy of prey in suburban forest fragments?

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Abstract

With the extirpation of apex predators from many North American systems, coyotes *Canis latrans* have become the *de facto* top predator and are ubiquitous members of most ecosystems. Keystone predators aid in maintaining ecosystem function by regulating the mammal community through direct predation and instilling the landscape of fear, yet the value of coyotes regulating systems to this capacity is understudied and likely variable across environments. Since coyotes are common in the Midwestern United States, we utilized camera traps and occupancy analyses to assess their role in regulating the distribution of mammalian herbivores in a fragmented suburban ecosystem. Forest cover was a strong positive predictor of white-tailed deer *Odocoileus virginianus* detection, while coyote occurrence had a negative effect. Coyotes exerted a negative effect on squirrel (*Sciurus* spp.) and eastern cottontail rabbit *Sylvilagus floridanus* occurrence, while urban cover was a positive predictor for the prey species' occurrence. These results suggest all 3 species behaviorally avoid coyotes whereby deer seek denser forest cover and squirrels and cottontails mitigate risk by increasing use of urban areas. Although previous studies reveal limited influence of coyote on the rest of the carnivore guild in suburban systems, we suggest coyotes play an important role in regulating the herbivorous mammals and hence may provide similar ecological benefits in urban/suburban forest fragments through trophic cascades. Furthermore, since hunting may not be allowed in urban and suburban habitats, coyotes might also serve as the primary regulator of nuisance species occurring at high abundance such as white-tailed deer and squirrels.

Key words: camera traps, coyote, deer, rabbit, squirrel, urban wildlife.

The presence of large carnivores elicits behavioral responses in prey that can shape ecosystem function from top-down through trophic cascades (Ripple and Beschta 2004). More formally known as the landscape of fear, predators intimidate, chase, and threaten prey, which in turn, plays a strong role in shaping prey behaviors and physiology (Terborgh and Estes 2010). Through manipulating movements and behavior of keystone herbivores (Fortin et al. 2005), the top-down cascades caused by predators often result in ecosystem services that otherwise are lost (Ritchie et al. 2012). Likewise, apex predators may be necessary to sustain ecosystem function and potentially increase ecosystem resilience (Sala 2006). However, many predators were extirpated from much of their range in North America in the 1900s and have yet to be restored in many areas (Prugh et al. 2009).

Lack of other large carnivores has led to rises in mesocarnivore populations such as coyotes *Canis latrans* which now are the closest

link to an apex predator in many North America systems (Prugh et al. 2009). However, their role as apex predator is not well established because in some cases they may drive trophic cascades similar to large carnivores and in others they do not (Roemer et al. 2009; Cove et al. 2012). Coyotes certainly can alter ecosystems by regulating keystone herbivore populations through neonate predation (Kilgo et al. 2012) and may cause trophic cascades through regulation of other mesocarnivore populations, which alter distributions of their prey (Crooks and Soulé 1999). They are capable of killing adult white-tailed deer *Odocoileus virginianus* (Chitwood et al. 2014), and have a wide dietary breadth that may directly influence ecosystems at many trophic levels (Roemer et al. 2009). However, little data are available on the role of coyotes in behavioral cascades observed in many systems with large carnivores.

Coyotes are generally thought to be a nuisance but could provide valuable ecosystem services at the suburban–wildlife interface. Because large carnivores are persecuted by humans, they often avoid more developed areas and therefore trophic cascades associated with apex predators may be lost in closer proximity to development (Waser et al. 2014). However, coyotes seem to be more resilient to using developed areas than other large carnivores (Gehrt et al. 2009; Cove et al. 2012), and therefore, could potentially foster trophic cascades that are beneficial to other trophic levels in fragmented areas. These effects could be particularly important in areas where white-tailed deer are overabundant and damage understory plant communities by overbrowsing (Cote et al. 2004) but other management strategies such as "hunting for fear" to reduce deer damage are not feasible (Cromsigt et al. 2013). Given the rapid expansion of urban development, the resilience of coyotes to using these areas, and the potential ecosystem service of trophic cascades, investigating the potential for coyotes to serve as a surrogate for large carnivores in this fashion is warranted.

We used camera traps to determine if coyote occurrence altered the probability of detection ($\hat{p}$) and site use (Ψ) of 3 mammal species in forest patches in a fragmented suburban landscape in Central Missouri, USA. Previous literature indicates coyotes are not affected by urbanization (Cove et al. 2012), and may even be attracted to fragmented and urbanized areas (Roemer et al. 2009). Therefore, we hypothesized the probability of detection and site use by deer, both eastern fox squirrels *Sciurus niger* and eastern grey squirrels *Sciurus carolinensis*, and eastern cottontail rabbits *Sylvilagus floridanus* would decrease as coyotes utilize the sites. Either by altering the preys' behavior to avoid coyote occupied sites or by direct mortality from coyote predation, coyote-induced alteration in presence of these prey species would suggest coyotes are encouraging a trophic cascade in these fragmented systems. Alternatively, prey species' habitat selection and site use might be driven by resource availability, despite predation pressure and as such we also aimed to examine this relationship.

Materials and Methods

Study site and camera trapping
We conducted 22 wildlife surveys in public and private forest patches from October 2009 to May 2010 at Longview Lake, Lee's Summit, Missouri (38°54′35″N, −94°28′11″W) and Warrensburg, Missouri (38°45′47″N, −93°44′6″W), USA (Figure 1). The two locations vary in forest connectivity and urban influence—Longview Lake provides more overall forest cover and connectivity, whereas Warrensburg exhibits higher overall urban/forest interface. We randomly selected camera trap locations at distances greater than

500 m apart (mean = 1622 ± 814 m) within forest patches that had variable amounts of suburban influence and left cameras operational for up to 18 days per site. Each site had a single camera trap set on a tree approximately 0.5 m off the ground and aimed at a clearing or along an animal game trail. Camera models were either Reconyx RM45 IR Game Camera (RECONYX, Inc., 3828 Creekside Lane, Suite 2, Holmen, WI, USA) or Moultrie Game Spy 4.0 Camera (EBSCO Industries, Inc., P.O. Box 1943, Birmingham, AL, USA). In some cases, cameras were stolen or failed during the surveys and we accounted for these instances as missing data in our analyses (see section 'Analyses'). Any further camera trapping methods and site-specific information were previously explained in Cove et al. (2012).

Habitat data
To measure landscape features associated with each camera survey site, we used ArcGIS 9.3 (ESRI, 380 New York Street, Redlands, CA, USA) to overlay all camera trap locations onto a digitized land use/land cover map. We calculated site-specific total forest cover (ha) and total suburban/urban land use (ha), by extracting these data from within 250-m radius buffers around each camera trap site. Additionally, we included a variable for location (i.e., Warrensburg or Longview Lake) due to the inherent differences between landscape features at the geographically separate locations.

Data analysis
We compiled all camera trapping records and created binary detection histories (detection = 1, no detection = 0) for each species, for each day of survey effort. For comparisons to other camera trap studies, we used raw detection histories to calculate trap success as the number of independent detections per 100 trap nights (Kelly and Holub 2008). Detection for a species was only considered independent based on the 24-h clock, so multiple records on the same day were still only considered a single detection. Due to difficulties in differentiating between species of squirrels, we pooled the data together and treated them as a single group. Trap nights were calculated as the 24-h period that a single camera was recording images (e.g., 18 days with 1 camera = 18 trap nights).

We then partitioned the detection histories into 3-day sampling units (e.g., 1 = the species was detected in any of the 3 days, 0 = not detected), leading to a maximum of 6 repeat surveys for each site. Six repeated surveys were not always possible if cameras malfunctioned or were stolen, but these missing data can be accommodated in the occupancy models (MacKenzie et al. 2006). To examine how habitat covariates affected our ability to detect a species, we modeled detection probability and then used the covariates with the most support as a constant set when deriving subsequent occupancy estimates. We used the coyote detection and occurrence (use) models from Cove et al. (2012) for predator information. We used the conditional occupancy estimates (ψ-cond) of coyote occurrence for each site to derive a coyote site use (trophic) covariate and assumed any sites with ψ-cond < 0.5 were not used by coyotes during the surveys (Cove et al. 2012). We modeled prey species detection probabilities and occurrence (use) using the same procedures as for coyotes, with the addition of the trophic covariate, and additive models with combinations of cover type and trophic effects for a total of 10 a priori hypotheses (Cove et al. 2012). We hypothesized that coyote site use negatively influences prey site use due to the threat of predation, while increasing urbanization would also have a negative relationship with prey site use due to reduced habitat and increasing human disturbance. We further predicted that forest cover and location
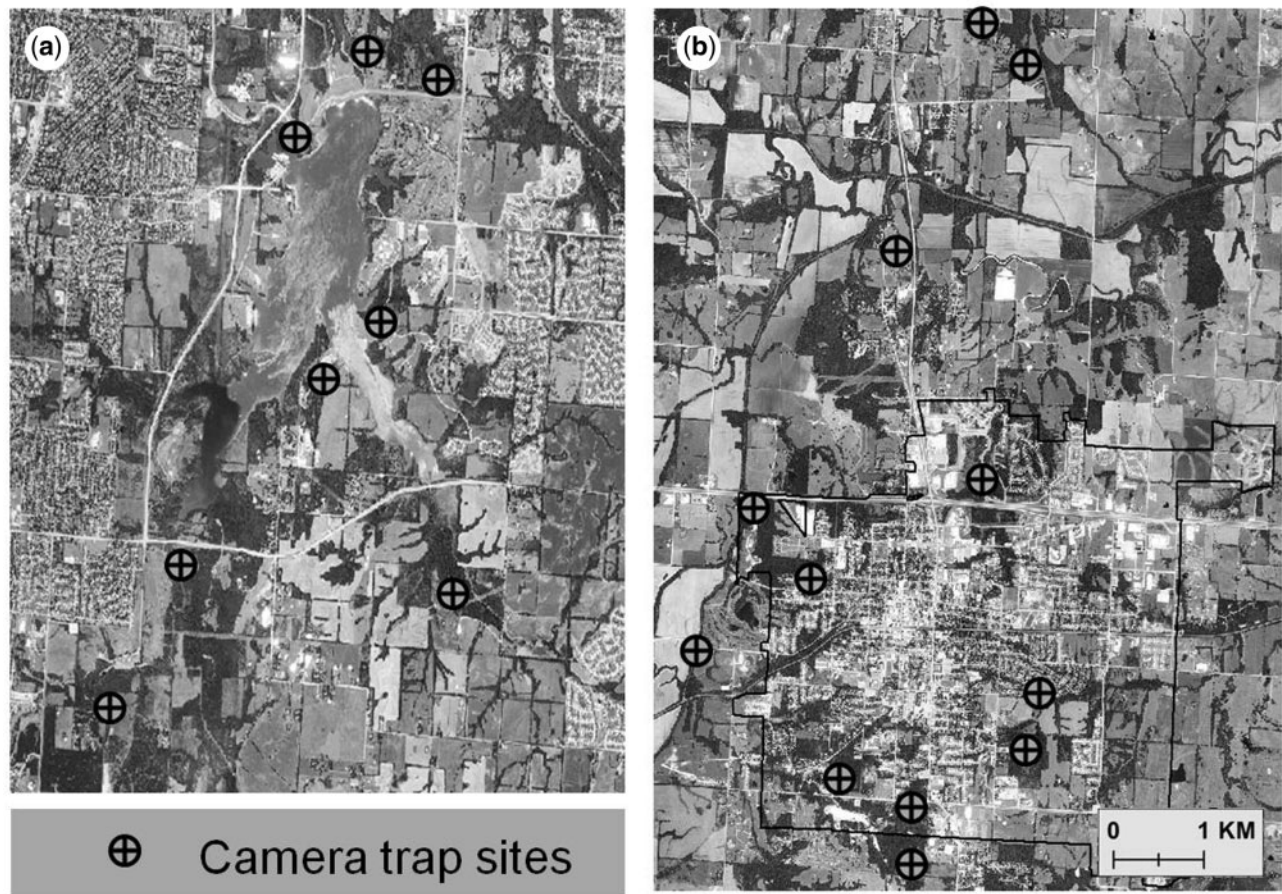
Figure 1. Camera trap sites from the two study areas, (a) Longview Lake, Lee's Summit, MO, USA, and (b) Warrensburg, MO, USA, excluding two camera trap sites from Warrensburg on private lands east of the urban center.

(e.g., differences at landscape scale) have positive relationships with prey site use because these covariates represent increasing natural habitat and connectivity. Although other potential factors influence detection and occurrence, we limited the model development in the context of the modest sample size and parsimony; we considered all a priori hypotheses to be biologically plausible explanations of species occurrence in the urbanizing landscape (Appendix 1).

We developed the single-season occupancy models implemented in program PRESENCE 2.4 (Hines 2009). There are two-species occupancy models that allow the simultaneous estimation of occupancy and interaction factors among species (MacKenzie et al. 2004; Bailey et al. 2009); however, we did not use these models due to the large number of parameters to be estimated and the inappropriateness of the modest sample size. The current analyses are sufficient because we were interested in the effect of coyote site use (over the course of the surveys) on prey, which we incorporated as a trophic covariate in the same framework as Cove et al. (2012) and similar to other occupancy studies utilizing prey as a predictor of predator occurrence (Karanth et al. 2011). The best approximating models were selected based on the Akaike Information Criterion corrected for small sample size (AIC$_c$—e.g., number of sites) and Akaike weights (ω_i). We considered models to be strong if they were contained within an information distance of < 2 ΔAICc, or if they were contained within 95% CI ($\sum \omega_i = 0.95$) and ranked higher than the intercept-only model (Burnham and Anderson 2002). From the subsequent confidence sets, we considered covariates to have strong effects on detection or occurrence if the coefficients were retained in multiple competing models and excluded 0 at the 95% CI.

Results

From 308 trap nights, we detected the 3 main mammal prey species and wild turkeys *Meleagris gallopavo* (Table 1); however, turkey data were too sparse to conduct further analyses. Camera trap success was high for these species compared to previous surveys in the United States (Table 1).

White-tailed deer were detected at all sites, so we modeled detection probability as the parameter of interest as an index of abundance and frequency of utilization since there is an apparent relationship between local abundance/use and detectability (O'Connell and Bailey 2011). Forest cover was contained in 3 of the top competing models and had a significant positive effect on detection for white-tailed deer ($\sum w_i = 0.593$, Table 2). Coyote site use was contained in 2 of the top competing models and had a significant negative effect on deer detection ($\sum w_i = 0.325$, Table 2). Urban cover and location also had positive effects on white-tailed deer detection probabilities but contained less model support.

We report coyote occurrence models and effects from Cove et al. (2012). There were no strong influences of any covariates that we measured on coyote occurrence. Constant detection was the most supported model for squirrels ($P = 0.49 \pm 0.07$ *SE*) and rabbits ($P = 0.45 \pm 0.13$ *SE*); so subsequent occupancy models were

modeled with constant detection for both groups. Squirrel occurrence was significantly affected negatively in relation to site use by coyotes ($\sum w_i = 0.751$, Table 2). Urban cover had a positive but variable relationship with squirrel occurrence ($\sum w_i = 0.572$, Table 2). The constant model was most supported for cottontail rabbit occurrence, but coyote presence and urban cover both had model support with a negative effect from coyote site use and a positive effect of increasing urbanization (Table 2).

Discussion

The ascension of the coyote to the top predator in many systems in the contiguous United States is well documented, but the value of coyote as a potential apex predator shaping behavioral cascades is poorly understood and understudied. Our results indicate that coyotes might play a role in altering the distribution and habitat use of

Table 1. Selected estimates of trap success (detections per 100 trap nights), naïve and mean estimated occupancy (Ψ), and total number of independent detections from wildlife camera trap surveys in the suburban Midwest, USA, conducted October 2009–May 2010

Species	Trap success	Ψ		Independent detections
		Naïve	Mean	
White-tailed deer *Odocoileus virginianus*	27.92	1.00	1.00	86
Squirrel *Sciurus niger* and *Sciurus carolinensis*	19.48	0.55	0.56	60
Coyote *Canis latrans*	7.79	0.45	0.56	24
Cottontail rabbit *Sylvilagus floridanus*	3.9	0.18	0.19	12
Wild turkey *Meleagris gallopavo*	0.97	0.09	–	3

mammalian herbivores similarly to apex predators in other systems, and thus, may encourage similar behavioral cascades in the suburban Midwest, where large carnivores are absent. For deer detection models, a positive relationship between forest cover and negative relationship with coyote occurrence was likely observed because deer avoids coyotes by seeking dense cover associated with forest. This may be the most efficient way for deer to evade predation pressure from coyotes, which used gradients in forest cover and urban area similarly (Cove et al. 2012). Magle et al. (2014) observed a similar trend with urban deer more frequently occurring in areas of dense canopy cover, but the authors did not find a negative effect from coyotes and alternatively observed a positive association between the predator and prey. The authors suggested that the scarcity of quality habitat for both species in the highly urban greater Chicago (USA) area caused this high co-occurrence despite predation pressure. Our results reveal a different effect, which is most likely because the suburban landscape of our study provides sufficiently more quality habitat despite the high levels of fragmentation and urban edge.

Similarly to the large prey (deer), coyotes exerted a strong negative influence on squirrel occurrence; yet contrary to our predictions, the prey was more positively associated with increasing urban area. It is probable that squirrels and cottontails are selecting urban areas to avoid coyotes since they are limited by the predator in forest patches. Kelly and Holub (2008) observed a positive trend between coyotes and squirrels, suggesting coyotes more actively used sites that were used by squirrels. It is likely that squirrels are protected from coyotes in more urban areas than forest fragments and therefore coyotes have a greater impact on squirrel use of forest fragments with limited connectivity to source populations. Moreover, the Virginia (USA) study may have failed to detect this relationship because they surveyed a more forested area with greater connectivity in a protected reserve (Kelly and Holub 2008). Similar to the squirrels in our study, cottontail occurrence was not influenced by forest

Table 2. Model selection statistics for top models with untransformed coefficients of habitat variables and trophic interactions on detection (p) or site use (Ψ) from wildlife camera trap surveys in the suburban Midwest, USA, conducted October 2009–May 2010

Species				Untransformed coefficients of covariates (SE)				
Model	Δ_i	w_i	K	Intercept	Forest	Urban	Location	Coyote
Coyote[a]								
Ψ(.)	0.00	0.405	3	0.212 (0.865)	–	–	–	–
Ψ(forest)	1.27	0.215	4	1.609 (2.922)	1.791 (2.742)	–	–	–
Ψ(location)	1.80	0.165	4	−0.248 (1.044)	–	–	1.374 (1.979)	–
White-tailed deer								
p(forest)	0.00	0.268	3	0.205 (0.197)	**0.432 (0.207)**	–	–	–
p(global)	0.96	0.166	6	0.437 (0.310)	**0.705 (0.247)**	**0.561 (0.242)**	0.555 (0.449)	**−0.924 (0.451)**
p(forest + coyote)	1.04	0.159	4	0.478 (0.280)	**0.439 (0.209)**	–	–	−0.556 (0.397)
p(.)	1.83	0.107	2	0.203 (0.193)	–	–	–	–
Squirrel								
Ψ(urban + coyote)	0.00	0.572	4	2.429 (1.457)	–	1.881 (1.281)	–	−3.864 (2.002)
Ψ(coyote)	2.32	0.179	3	1.339 (0.817)	–	–	–	**−2.145 (1.071)**
Ψ(.)	4.51	0.060	2	0.260 (0.450)	–	–	–	–
Cottontail rabbit								
Ψ(.)	0.00	0.342	2	−0.208 (0.510)	–	–	–	–
Ψ(coyote)	1.80	0.139	3	−1.010 (0.689)	–	–	–	−1.136 (1.261)
Ψ(urban)	1.83	0.137	3	−1.519 (0.602)	–	0.529 (0.577)	–	–

Bolded habitat and trophic interaction coefficients are significant in that the 95% CI excludes 0.

Covariates: forest and urban are the standardized values for the total coverage (ha) of forest and suburban/urban areas within site buffers; location is the binomial term to differentiate between Warrensburg and Longview Lake, Missouri study areas; coyote is the trophic interaction term for coyote site use.

[a]Excerpted from Cove et al. (2012).

cover but tended to be negatively influenced by coyote occurrence and positively by urban cover suggesting they also select urban areas at a greater rate than should be expected to avoid co-occurrence with coyotes. In fact, forest cover was not supported by any of the top models for either of the small prey species suggesting the buffer of urbanization is more effective than forest cover to alleviate predation risk.

Alteration of small mammal site use, and in particular scatter-hording mammals (Jansen et al. 2004), can impact the plant community (Schnurr et al. 2004). The consequences of squirrels and potentially rabbits selecting urban areas could alter plant communities of both environments (Schnurr et al. 2004). For example, squirrels are the main disperser of oak mast (Quercus—acorns) and disproportionate use of urban areas would likely result in disproportionate caching of acorns in those areas. Likewise, herbivory pressure from cottontails may directly impact plant communities and often causing damage to garden and landscaping plants (Barton and Hanley 2013). In these cases, coyotes may be increasing the likelihood of human–wildlife conflicts. However, if deer seek cover in forested areas when in the presence of coyotes, the benefits of the resulting decrease in human–deer conflicts likely outweigh any negative influence on human conflict with the smaller herbivores because deer are the primary concern in most areas (McShea 2012).

Coyotes are mesocarnivores that have been released from predation and interspecific competition with the eradication of large carnivores in the Midwestern United States. As a result, their populations have increased dramatically, which can result in negative effects within the lower trophic guilds as observed in many systems (Prugh et al. 2009). Also, coyotes may have limited importance in the regulation of other mesocarnivore populations in suburban areas (Cove et al. 2012). However, we suggest that in a suburban/urban system, coyotes might be important in regulating abundant pest species (e.g., white-tailed deer, cottontails, and squirrels) through direct predation, but also behaviorally through restoring the landscape of fear in suburban systems. Therefore coyotes may be important members of urban forest ecosystems fostering a diverse plant community by regulating herbivory in an "island" environment.

Camera traps are an invaluable resource to examine predator–prey interactions with relatively low sampling effort. Although we still recommend sampling more sites and increasing the number of trapnights in future surveys for more advanced and robust occupancy analyses (e.g., multiseason, multistate, multispecies—MacKenzie et al. 2006), the current sampling effort was sufficient for our objectives and similar to other camera trap surveys and occupancy analyses (Ordenana et al. 2010 and the references therein). Furthermore, the high detection probabilities for the prey species (per 3-day sampling occasion) suggests that we sampled sufficiently to detect each species during the survey period leading to mean occupancy estimates that are similar to naïve estimates. Our sampling effort was only slightly more than one-third of that from a Virginia camera trap study in a forest reserve (Kelly and Holub, 2008), and yet we detected all 3 prey species of interest with higher trap success in the current fragmented system. Remnant forest patches along the urban/wildland gradient may concentrate wildlife species into smaller areas and increase their observability and intensify predator—prey interactions allowing them to be more easily measured. Similar ideas have been suggested in other studies utilizing camera traps in fragmented systems (Cove et al. 2013) and should be kept in consideration when designing new camera trap surveys where lower camera trapping effort per unit area may be required in fragmented landscapes (e.g., it may be beneficial to sample more sites for shorter time). Allocating variable survey effort based on site connectivity within an occupancy framework allows researchers to allocate trapping effort to minimize uncertainty and more efficiently evaluate habitat associations and trophic relationships among multiple taxa in urban environments.

Our realm of inference is the suburban/urban Midwestern United States, but we believe that the relationships that we examined between prey species and the now dominant coyote are relevant to many urban ecosystems across North America. Crooks and Soulé (1999) observed a positive relationship between coyote presence and passerine bird diversity in southern California; and although Cove et al. (2012) observed no apparent relationship between coyotes and nest predators, we have further explored their effects on herbivorous mammals in that system and reveal that coyotes might be important to maintenance of the native plant community.

Appendix

Appendix 1 Descriptions and expected directions of 10 a priori occupancy models examining habitat variables and trophic interaction effects on site use (ψ) by prey species from wildlife camera trap surveys in the suburban Midwest, USA, conducted October 2009–May 2010

Hypothesis	Model	Structure of model	Expected result
No effects of habitat or trophic interactions on prey site use	$\psi(.)$	β_0	—
Increasing percent forest cover at a site will positively affect prey site use	$\psi(\text{forest})$	$\beta_0 + \beta_1 (\text{forest})$	$\beta_1 > 0$
Increasing percent urban cover at a site will negatively affect prey site use	$\psi(\text{urban})$	$\beta_0 + \beta_1 (\text{urban})$	$\beta_1 < 0$
Landscape differences between the areas will affect prey site use	$\psi(\text{location})$	$\beta_0 + \beta_1 (\text{location})$	$\beta_1 > 0$
Coyote site use will negatively affect prey site use	$\psi(\text{coyote})$	$\beta_0 + \beta_1 (\text{coyote})$	$\beta_1 < 0$
Increasing percent forest cover at a site will positively affect prey site use and coyote site use will negatively affect prey site use	$\psi(\text{forest} + \text{coyote})$	$\beta_0 + \beta_1 (\text{forest}) + \beta_2 (\text{coyote})$	$\beta_1 > 0$, $\beta_2 < 0$
Increasing percent urban cover at a site will negatively affect prey site use and coyote site use will negatively affect prey site use	$\psi(\text{urban} + \text{coyote})$	$\beta_0 + \beta_1(\text{urban}) + \beta_2 (\text{coyote})$	$\beta_1 < 0$, $\beta_2 < 0$
Landscape differences between the areas will affect prey site	$\psi(\text{location} + \text{coyote})$	$\beta_0 + \beta_1(\text{location}) + \beta_2(\text{coyote})$	$\beta_1 > 0$, $\beta_2 < 0$

(continued)

Appendix 1. (continued)

Hypothesis	Model	Structure of model	Expected result
use and coyote site use will negatively affect prey site use			
Increasing percent urban cover at a site will negatively affect prey site use and landscape differences between the areas also affect prey site use	ψ(urban + location)	$\beta_0 + \beta_1$(urban) $+ \beta_2$(location)	$\beta_1 < 0, \beta_2 > 0$
All potential habitat and trophic covariates affect prey site use	ψ(global)	$\beta_0 + \beta_1$(forest) $+ \beta_2$(urban) $+ \beta_3$(location) $+ \beta_4$(coyote)	$\beta_1 > 0, \beta_2 < 0,$ $\beta_3 > 0, \beta_4 < 0$

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