

**Influence of Spatial and Temporal Use of Resources by a Top Predator on Use of Resources  
by Co-occurring Species of Mesopredators and Prey**

by

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## Abstract

Use of resources by a species can be influenced by interactions with co-occurring species. Use of both space and time can be altered to putatively reduce interspecific competition or risk of predation. I used occupancy modeling to measure the influence of competition with the coyote (*Canis latrans*) on co-occurring mesopredators. Similarly, the influence of use of space by coyotes was analyzed in the context of a race for space between two species of prey with differing characteristics. I did not detect support for competitive interactions between coyotes and mesopredators. I suggest that differential use of prey and high availability of prey may reduce the need for differential use of resources among these predators. I found evidence for contrasting responses of prey to use of space by coyotes. I propose that traits related to mobility and reproductive output may influence the outcome of the race for space between predators and prey.

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## Chapter 1: Influence of Intraguild Competition From Coyotes (*Canis latrans*) on Spatial and Temporal Use of Resources in a Community of Mesopredators

### Introduction

According to the mesopredator release hypothesis, top predators should negatively influence intermediate predators (mesopredators) in natural communities (Soule et al. 1988, Sieving 1992, Estes 1996, Terborgh et al. 1999, 2001). Specifically, top predators may impact mesopredators either directly through intraguild predation (interference competition, Polis and Holt 1992; Holt and Polis 1997; Palomares and Caro 1999) or indirectly through use of a common, limited resource (exploitative competition, Holt et al. 1994; Linnell and Strand 2000). Theoretical studies provide strong support for purported competition among predators (Soule et al. 1988; Sieving 1992; Estes 1996; Terborgh et al. 1999; 2001) and empirical research suggests that competition among terrestrial mammalian predators may be common (Palomares and Caro 1999; Donadio and Buskirk 2006). However, several studies have reported a lack of support for negative interactions between species of predators that are expected to compete, which has drawn skepticism about appropriateness of the mesopredator release hypothesis across ecological systems (Wright et al. 1994; Litvaitis and Villafuerte 1996; Gehrt and Clark 2003). Thus, further study is required to elucidate the nature and strength of competitive interactions among carnivores. Unfortunately, comprehensive studies of competition among predators have been hampered by difficulties associated with research on such wide-ranging and secretive species (Fedriani et al. 2000).

One putative means of overcoming the limitations associated with studying the mesopredator release hypothesis and competition among predators in general, may be to focus on selection of resources, rather than abundance of competitors. Mesopredator release hypothesis

traditionally has focused on the effect of abundance of top predators on abundance of mesopredators (Crooks and Soule 1999; Rogers and Caro 1999; Henke and Bryant 1999). However, selection of resources by mesopredators also can be altered through competition with a top predator and such changes may have an equal or more negative effect on populations of mesopredators than simply changes in abundance (Schmitz et al. 1997; Werner and Peacor 2003). Therefore, selection of resources may be a solid alternative for measuring competition within a community of predators, while simultaneously overcoming limitations associated with estimating abundance of such hard-to-study species.

Selection of resources can be defined as a disproportionate use of resources by a species relative to availability, typically in an attempt to maximize fitness (Boyce and McDonald 1999; Manly et al. 2002). In theory, resources are selected in a manner that maximizes benefits, such as energetic gain, while minimizing costs associated with predation and competition (Hirzel and Le Lay 2008; McLoughlin et al. 2010). Among predators, competition for resources typically is related to dietary overlap where abundance of shared prey is the limiting factor (Mills and Biggs 1993; Palomares and Caro 1999; Donadio and Buskirk 2006). For mesopredators, selection of resources spatially, temporally, or both may reflect this tradeoff between acquisition of food and exploitive or interference competition with a top predator. Specifically, mesopredators can putatively decrease competitive interactions with top predators by using an area where top predators are rare (Palomares and Caro 1999; Durant 2000), or a time when activity of top predators is low (Johnson et al. 1996; Arjo and Pletcher 1999). Thus, differences in temporal or spatial selection between resources with and without top predators provide indirect support for the mesopredator release hypothesis and competition among predators.

With removal of larger predators and natural expansion of geographic range, the coyote

(*Canis latrans*) is believed to have assumed a top-predator role and to exert competitive pressure on communities of mesopredators (Hill et al. 1987; Lovell et al. 1998; Gompper 2002; Laliberte and Ripple 2004). Studies have elucidated negative correlations between populations of mesopredators and abundance of coyotes, suggesting that competitive interactions with coyotes may limit the number of mesopredators (Crooks and Soule 1999; Rogers and Caro 1999; Henke and Bryant 1999). Additionally, selection of spatial resources by some mesopredators such as foxes, tends to support selection against coyotes (Thompson and Gese 2007; Fedriani et al. 2000; Sovada et al. 1995; Gosselink et al. 2003; Farias et al. 2005) and competition from coyotes is a leading cause of mortality in some populations of foxes (Ralls and White 1995; Nelson et al. 2007). However, spatial overlap is common between coyotes and other mesopredators such as bobcats (*Lynx rufus*; Fedriani et al. 2000; Neale and Sacks 2001; Thornton et al. 2004), raccoons (*Procyon lotor*; Gehrt and Prange 2006; Gehrt and Clark 2003), and striped skunks (*Mephitis mephitis*; Gehrt 2005; Prange and Gehrt 2007), which suggests that competition with coyotes may be reduced among non-canid mesopredators. Given the growing geographic range and abundance of coyotes across North American communities (Hill et al. 1987; Laliberte and Ripple 2004), greater insight into the influence that exploitative and interference competition with coyotes has on mesopredator communities is needed (Gompper 2002).

In this study, I measured the influence of use of resources by coyotes on spatial and temporal selection of resources by a community of mesopredators, including bobcats, red foxes (*Vulpes vulpes*), gray foxes (*Urocyon cinereoargenteus*), raccoons (*Procyon lotor*), and Virginia opossums (*Didelphis virginiana*). I predicted that each of these species would demonstrate either spatial or temporal selection (or both) against resources used by coyotes.

## Methods



### *Study Sites*

To investigate selection of resources in communities of predators, 13 study sites were surveyed for carnivores as part of a larger state-wide biodiversity inventory (J.B. Grand, Auburn University, *unpublished data*). Surveyed sites included state parks and wildlife management areas in Alabama. Ecoregions contained within these sites included the Interior Plateau, Ridge and Valley, Southeastern Coastal Plains, Southwestern Appalachians, Southeastern Plains, and Piedmont (Griffith et al. 2001).

For each study site, I superimposed a grid consisting of points spaced 250m apart. I defined a potential sampling unit as a point and the area contained within 125m of that point. Using ArcGIS 9.2 (Environmental Systems Research Institute, Inc., Redlands, CA) and the National Land Cover Database (2001), I categorized the resulting potential sampling units into one of 33 types of land cover based on the majority type of land cover contained within each unit. A stratified random-sampling design was used to select 10% of available units for survey where stratification was based on category of land cover. Specifically, categories of land cover were surveyed proportional to availability within the 13 study sites.

### *Field Surveys*

To estimate selection of resources by predators, presence-absence data for species were collected during August-December 2008-2010. I obtained samples of predators using non-invasive, infrared, digital trail cameras (RapidFire™ PC85, Reconyx, Inc., Holmen, WI) equipped to run for a 72-hour survey. At each sampling unit, one camera was placed either at the center or 100m from center. I administered commercially available scents (Caven's™, Minnesota Trapline Products, Pennock, MN) 2-3m in front of each camera. Cameras were programmed to take photographs at 2-minute, time-lapse intervals, and when triggered by the

internal motion sensor, for the entire 72-hour survey. I identified species captured in digital images. Time of detection was recorded using the timestamp function; thus, providing a history of detection for each surveyed unit.

### *Attributes of Microhabitat*

Because I expected that spatial use of resources by a species may be influenced by attributes of microhabitat, I collected site-specific measurements on vegetation at each camera including canopy cover, density of downed-woody debris, and understory visibility. These data were collected only during surveys conducted in 2009 and 2010. I estimated percentage canopy cover using point-quarter sampling (Brower and Zar 1977) by calculating the ratio between distance from camera to the nearest tree that provided the greatest canopy cover and distance over which the canopy of that tree extended. This ratio was obtained in each of four quadrants (northwest, northeast, southwest, southeast) from the camera. An index of downed-woody debris was calculated by measuring distance from camera to the first debris  $\geq 4.0$ cm in diameter encountered along each cardinal direction. To index understory visibility, a modified density board was used (Nudds 1977). At distances of 10, 15, and 20m in each cardinal direction, a visibility count of 56 8cm squares on a 128 by 64cm rectangular profile board was conducted. For all three vegetative characters, measurements along the four directions per quadrant were averaged to create an index for vegetation at each camera.

### *Occupancy Modeling*

Because I anticipated that my methods (camera surveys) would provide imperfect rates of detection, I used occupancy analysis to examine patterns in selection of resources and associations between top predator and mesopredators (MacKenzie et al. 2002; 2004; 2005; MacKenzie and Royle 2005). The value of occupancy modeling is that this approach recognizes

that detection of species rarely is perfect and adjusts estimates of use of resources to account for such imperfections. Specifically, occupancy analysis allows the probability of use ( $\psi$ ) of a resource to be estimated based on the history of detection (or the observed record of presence-absence), while simultaneously accounting for probability of detection ( $p$ ; or the probability that a species will be detected when present) of a species at resources. Both  $\psi$  and  $p$  are estimated by conducting multiple surveys, or sampling occasions, over space or time, assuming unchanging use of the resource during sampling. When sampling units are smaller than the home range of the species investigated, as in this study,  $\psi$  should be interpreted as the probability of use of a resource rather than occupancy of a resource (Kendall and White 2009).

In occupancy analysis, probability of detection ( $p$ ) is  $< 1$ , even when a species uses a resource. Detection of a species during any sampling occasion will take one of three forms: resource is used and species is detected, resource is used but species is not detected, or resource is not used. The probability that a species will use the resource and is detected is equal to the proportion of resources used ( $\psi$ ) multiplied by the probability of detection ( $p$ ), or  $\psi \times p$ . In contrast, the probability that a species will use the resource but not be detected is  $\psi \times (1-p)$ . The probability that a species does not use a resource is equal to  $1 - \psi$ .

Additionally, use of, and detection at, a resource may vary as a function of environmental variables such as attributes of resource or co-occurrence of other species (MacKenzie et al. 2002; 2004). In occupancy analysis, estimates of use and detection of resources can be calculated while incorporating such covariates using the logistic model (MacKenzie 2006):

$$\theta_i = \frac{\exp(\beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \dots + \beta_k x_{ik})}{1 + \exp(\beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \dots + \beta_k x_{ik})}$$

Where  $\theta$  equals the parameter of interest (either  $\psi$  or  $p$ ) at the  $i$ th resource or sampling occasion, respectively,  $x$  represents the covariate values for the  $i$ th resource or sampling unit, and  $\beta$  equals the estimates of coefficients for  $k$  covariates.

### *Constructing Spatial and Temporal Models*

I constructed two series of occupancy models; one focused on spatial selection of resources and the other on temporal selection of resources within species. For my evaluation of spatial selection of resources, the resource was each sampling unit. I obtained the multiple-sampling occasions of a sampling unit needed to estimate probabilities of detection within this analysis by dividing the 72-hour survey for each sampling unit into three 24-hour periods. Divisions were made mid-day, when least activity occurred. Each period was considered to be an independent sampling occasion during which presence of a species was counted only once when detected. I expected that spatial use of resources would vary with attributes of macrohabitat and microhabitat in relation to species-specific preferences for habitats. To account for selection of macrohabitat, I reclassified the 33 types of land cover used to designate majority land cover for each sampling unit into 8 broader classes of habitat in an effort to generalize types of habitats and obtain reasonable samples at each class of habitat. The classes of agriculture, coastal, developed, hardwoods, mixed, pine, riparian, and scrub were use as covariates of occupancy. Similarly, the vegetative characteristics of understory visibility, percentage canopy cover, and density of downed-woody debris also were evaluated as covariates of occupancy to account for selection of microhabitat. In addition, I also expected detection to vary with environmental variables associated with weather specific to each sampling occasion. Therefore, I obtained data for temperature, wind speed, and precipitation for each occasion from the nearest weather station (average distance 24km, range 3-80km). I also considered the effect of number

of days since the camera was deployed on probability of detection, anticipating that as time progressed, species might be more likely to encounter the bait or that deterioration of bait might influence rates of detection.

In my evaluation of temporal selection of resources, the resource to be used was a 3-hour period during any date (i.e., 8 time blocks/day: 0000-0300, 0300-0600, 0600-0900 h CDT, etc.). Thus,  $\psi$  was the probability of use of a given block of time by the carnivore. Under this temporal framework, I obtained multiple sampling occasions by building a history of detection using spatial replicates of presence-absence of species across sampling units during each 3-hour block on each calendar day. Species detected at multiple sampling units within a 3-hour block were counted only once. Similar to the effect of preferences of habitat on spatial selection of resources, species-specific patterns of activity may influence temporal selection of resources. To account for this effect, I considered each 3-hour block for inclusion as covariates of occupancy in models. I also considered the effect of average temperature during each temporal block on occupancy. I expected that ability to detect a species during a given 3-hour block may vary according to attributes of habitat of the sampling unit; therefore, I considered the eight classes of macrohabitat as covariates of detection in this temporal analysis.

#### *Predicting Coyote Resource Use*

To estimate the influence of the coyote on use of resources in a community of mesopredators, I created a model that predicted probability of use for any resource (sampling unit or temporal block) where a coyote was not detected. To build the spatial model of use of resources by coyotes, I used a combination of univariate tests (using a single variable in the occupancy model) and ecological reasoning to determine which covariates of occupancy and detection could be influential to spatial use of resource by coyotes. All variables that were

significant at  $\alpha = 0.05$  level in univariate analyses or believed to be important on ecological grounds were then combined to form a global model. I then analyzed and evaluated the global model and all submodels using an AIC framework and calculated the probability of use of each resource using multimodel inference. Specifically, model-averaged predictions were obtained for each resource via a summation of the product of the probability of use predicted by each model and the AICc weight of that model (Anderson et al. 2000; Burnham and Anderson 2002). The same procedure was used to construct a variable for probability of use by a coyote under the temporal framework. Model-averaged predictions were used to predict probability of use for all resources (sampling units or time blocks) when a coyote was not detected; if a coyote was detected at the resource, then probability of use was recorded as 1.0.

#### *Modeling the Influence of Use of Resources by Coyotes*

To evaluate the influence of use of resources by coyote on the other species of mesopredators, I constructed an occupancy model for each species for both spatial and temporal analyses. Each model contained the predicted probability of use of resources by coyotes as a covariate of occupancy. However, observed associations between coyotes and mesopredators may be driven by similarities or differences in selection for specific attributes of resources, rather than avoidance of competitors. For example, even if mesopredators were avoiding coyotes, observed associations could be positive if both species select the same resource (Gilpin and Diamond 1984; Peres-Neto et al. 2001; MacKenzie et al. 2004). Therefore, to investigate the influence of presence-absence of coyotes on use of resources by mesopredators after accounting for selection of resources, each species-specific spatial model included as covariates of occupancy all classes of macrohabitat (and variables of microhabitat if univariate analyses indicated they were important to the species). Similarly, each species-specific temporal model

contained all blocks of time to account for patterns of activity of species. Species-specific models also contained those covariates of detection that were significant in preliminary univariate analyses or were believed to be important to the species. A single-species approach to occupancy was used for these analyses, as opposed to the co-occurrence analyses of species (MacKenzie et al. 2004), because preliminary analyses indicated that the latter method typically failed to converge (unpublished data; MacKenzie et al. 2004). Additionally, I only examined the effect of presence-absence of coyotes in a global model, rather than attempting to find a potentially more parsimonious submodel or averaging of models, because my goal was to estimate effects of competitors while accounting for selection of resources. I used the statistical package R (R Development Core Team 2005) and the unmarked package (Fiske and Chandler 2010) to conduct modeling analyses.

## Results

During the 3 years of surveying, I collected data for 446 sampling units across 13 study sites. This was 958,300 digital images, of which 7,938 captured species of interest (<1%). I detected coyotes at least once at 77 of 446 sampling units (17.3%). I did not detect bobcats at sampling units designated as agricultural or coastal. Because rates of detection can only cannot be calculated where a species is detected at least once, I removed these 25 units from analysis. We detected bobcats at 17 of the remaining 421 units (4.0%). For raccoons, opossums, and foxes, I used data from 360 sampling units (second and third seasons) because of the importance of attributes of microhabitat to selection of resources by the species. Raccoons were detected at 117 (32.5%) and opossums at 120 (33.3%) of these sampling units. Neither species of fox was detected at sampling units designated as riparian; therefore, I removed all riparian sites (20 sites) from analysis of foxes. Because of the small number of red foxes detected (3 of 340 sampling

units, 0.009%), I combined detections of red foxes with those of gray foxes and constructed models to incorporate both species. I believe this was appropriate because both species of foxes were expected to respond similarly to competition from coyotes (Gosselink et al. 2003).

Combined, I detected foxes at 31 (9.1%) of the remaining sampling units.

### *Spatial Analysis*

In preliminary univariate analyses of probability of spatial use by coyotes, covariates of detection for minimum temperature ( $-0.051$ ,  $SE = 0.011$ ,  $p = <0.001$ ) and day of survey (2<sup>nd</sup> Day:  $0.582$ ,  $SE = 0.293$ ,  $p = 0.047$ ) had a significant influence on detection of coyotes. No variable for microhabitat was a significant predictor of spatial selection of resources by coyotes in univariate analysis ( $p \geq 0.064$ ). My global model for predicting occupancy by coyotes, therefore, included these covariates of detection, and eight covariates of occupancy (each habitat class). Analyses suggested that the best model describing spatial use of resources by coyotes, among those considered, included covariates of occupancy for coastal + developed + hardwoods + mixed types of habitats and covariates of detection for minimum temperature and 2<sup>nd</sup> day. However, the Akaike weight of this model was only 0.017, supporting use of model-averaging. Compared to the weight of  $4.82 \times 10^{-7}$  for the null model, this best model was 35,269 times better. Our model-averaged predicted probability of spatial use of resources by coyotes (for those sampling units where coyotes were not detected) ranged from 0.381 to 0.581.

In preliminary analyses of use of resources by mesopredators, I detected the following microscale covariates of occupancy to be significant predictors of spatial use of resources: for foxes, understory visibility ( $0.078$ ,  $SE = 0.037$ ,  $p = 0.035$ ); for raccoons, understory visibility ( $0.065$ ,  $SE = 0.027$ ,  $p = 0.016$ ) and canopy cover ( $1.85$ ,  $SE = 0.812$ ,  $p = 0.023$ ); and for Virginia opossums, canopy cover ( $2.23$ ,  $SE = 0.625$ ,  $p < 0.001$ ). Therefore, I only used data from 2009



and 2010 in subsequent analyses for these species. For detection of mesopredators, the following variables were significant: for foxes, average temperature ( $-0.087$ ,  $SE = 0.022$ ,  $p < 0.001$ ); for raccoons, day of survey (2<sup>nd</sup> Day:  $0.444$ ,  $SE = 0.213$ ,  $p = 0.037$ ); and for Virginia opossums, day of survey (2<sup>nd</sup> Day:  $0.450$ ,  $SE = 0.219$ ,  $p = 0.040$ ; 3<sup>rd</sup> Day:  $1.045$ ,  $SE = 0.233$ ,  $p < 0.001$ ). No microscale covariate of occupancy or detection had a significant influence in the occupancy model for bobcats (all  $p \geq 0.174$ ).

The effect of use of resources by coyotes on spatial use of resources by mesocarnivores, after accounting for selection of resources by species, was not significant for any species (all  $p \geq 0.151$ ). Additionally, estimates of the effect were small and positive for most species, counter to predictions; bobcats, foxes, and raccoons were  $6.34$  ( $0.51 - 78.85$ ; 95% CL;  $p = 0.151$ ),  $1.74$  ( $0.29 - 10.31$ ;  $p = 0.540$ ), and  $2.85$  ( $0.43 - 19.09$ ;  $p = 0.280$ ) times as likely to use a spatial resource used by coyotes. The estimated effect on spatial use of resources by Virginia opossums was also non-significant, but slightly negative. Virginia opossums were  $1.43$  ( $0.23 - 2.15$ ;  $p = 0.534$ ) times as likely to use to resources that were not used by coyotes.

### *Temporal Analysis*

In preliminary analysis of probability of temporal use of resources by coyotes, 3-hour blocks from 0900 to 1800 h CDT (day) were not significantly different from each other (partial likelihood ratio test;  $p = 0.289$ ). Similarly, blocks from 1800 to 0900 (night) were not significantly different from each other for predicting occupancy by coyotes ( $p = 0.717$ ). However, there was a significant difference between day and night ( $1.96$ ,  $SE = 0.372$ ,  $p < 0.001$ ). Therefore, I reduced the eight 3-hour blocks into two 12-hour blocks (day and night). Average temperature during each block of time also had a significant effect on probability of temporal use of resources by coyotes ( $-0.085$ ,  $SE = 0.017$ ,  $p < 0.001$ ). Analyses also indicated that pine, scrub,

and riparian habitats were not significantly different from each other (partial likelihood ratio test;  $p \geq 0.3$ ); that agriculture, hardwoods, and mixed-forest habitats were significantly different from the other classes ( $p \leq 0.04$ ), but not from each other ( $p \geq 0.3$ ); and that coastal and developed habitats were significantly different from all other classes of habitats ( $p < 0.001$  and  $0.004$ , respectively). Therefore, my global, temporal-occupancy model included variables of occupancy for the two time blocks (night vs. day) and average temperature, and a detection variable for the four grouped habitats (agriculture + hardwoods + mixed, coastal, developed, other). Analyses suggested that the best model describing temporal use of resources by coyotes, among those considered, included covariates of occupancy for blocks of time and average temperature of blocks of time and covariates of detection for the four grouped habitats. The Akaike weight of this model was 0.99, and I based predictions on this best model rather than using multi-model inference. Weight of the null model was  $3.21 \times 10^{-19}$ , making the best model  $3.08 \times 10^{18}$  times better. The predicted probability of temporal use of resources by coyotes (for those temporal resources where coyotes were not detected) ranged from 0.018 to 0.808.

Preliminary analyses indicated that macrohabitat had a significant effect only on detection for the Virginia opossum and the most-parsimonious grouping of those classes was group1: agriculture, pine, mixed, scrub, and coastal ( $p \geq 0.3$  for test of significance within group); group 2: developed and riparian ( $p = 0.630$  for test of significance within group), and hardwoods ( $p < 0.001$  for test of significant difference from other groups).

My analyses indicated that the effect of use of resources by coyotes on temporal use of resources by mesocarnivores, after accounting for patterns of activity for each species, was not significant for any species (all  $p \geq 0.147$ ). The bobcat was the only species to exhibit a large association with use of resources by coyotes; bobcats were less than 0.001 ( $<0.0001 - 112.57$ ;

95% CL;  $p = 0.147$ ) times as likely to use a temporal period also used by a coyote. Estimates of the effect were small and negative for the other species; foxes, raccoons, and Virginia opossums were 0.871 (0.10 – 7.25;  $p = 0.898$ ), 0.612 (0.10 – 3.77;  $p = 0.597$ ), and 0.692 (0.21 – 2.25;  $p = 0.541$ ) times as likely to use a temporal resource used by coyotes.

## Discussion

Theory predicts that exploitive or interference competition with top predators, or both, will negatively impact mesopredators and may force these species to adjust spatial or temporal use of resources to putatively reduce the costs associated with such competitive interactions. In this study, I measured the influence of use of spatial and temporal resources by a purported top predator, the coyote, on use of the same resources by bobcats, foxes, raccoons, and Virginia opossums. I predicted that spatial or temporal use of resources by mesopredators would be less likely if those resources also were used by coyotes. I observed little evidence for an effect of coyotes on spatial use of resources by mesopredators, as estimates of selection for such resources were non-significant and positive (with the exception of the Virginia opossum, for which the estimated effect was negative, but still non-significant), which contradicts my prediction. Similarly, there was little evidence for an effect of coyotes on temporal use of resources by mesopredators; estimates of selection for such resources were non-significant for all species. However, the estimated effect of temporal use of resources by coyotes on use of resources by bobcats was large, suggesting that the effect might have been statistically significant with larger samples and could be biologically important.

Lack of support for a negative association between spatial and temporal use of resources by a top predator and mesopredators could be due to several factors. For example, the lack of association may be related to differential use of prey by predators or high availability of shared

prey. Effective partitioning of prey can serve to diminish both the interference and exploitative competition that smaller-bodied predators experience from top predators (Koehler and Hornocker 1991; Palomares and Caro 1999; Heithaus 2001). If mesopredators can minimize competition for a shared prey by switching to alternative prey, costly interactions from top predators should be less common, and the need for mesopredators to use different spatial or temporal resources from top predators would be abated. Although literature is lacking on the dietary habits of predators within Alabama, differential use of prey frequently occurs among these species in other regions (Litvaitis 1981; Cypher 1993; Neale and Sacks 2001; Azedo et al. 2006). Likewise, whereas interspecific competition among predators is typically most frequent and intense when shared resources are limited, top predators are often more tolerable of mesopredators as availability of prey increases (Koehler and Hornocker 1991; Palomares and Caro 1999; Heithaus 2001). Thus, avoidance of spatial and temporal resources used by coyotes may be limited because of a combination of differential use of prey and high availability of prey, reducing the need for negative associations in use of resources.

Prey partitioning may also explain why we determined that bobcats were the only mesopredator to display a large negative association in temporal use of resources with the coyote (albeit non-significant). Body size of predators typically is correlated with use of prey; predators of similar size are expected to display greater dietary overlap (Rosenzweig 1966; Gittleman 1985). Of all the mesopredators considered here, the bobcat is the most similarly sized predator relative to the coyote. Whereas body size may enable the other smaller mesopredators to readily partition prey with coyotes (i.e, by targeting smaller species), coyotes and bobcats both feed on deer and lagomorphs (as well as rodents), although typically in different proportions (Gese and Grothe 1995; Neale and Sacks 2001; Thorton et al. 2004). This overlap may require bobcats to

use the same space as coyotes to capture similar prey, but direct contact with the larger predator likely is undesirable (Anderson 1986; Wilson et al. 2010). By using similar spaces but at different times, bobcats may be able to reduce competitive interactions as a result of direct contact with coyotes, while still obtaining access to shared prey. However, because the power of my measured effect of use of resources by coyotes remains low, I cannot be certain of the strength of this temporal relationship.

I acknowledge a second, albeit opposing, explanation to my observed (or lack thereof) patterns in use of resources by predators. Where poor environmental conditions lead to low availability of prey, patches within a landscape may not contain the necessary dietary resources to fulfill energetic needs of mesopredators, even when prey are partitioned. Instead, mesopredators are forced to compete for those few prey that remain available by congregating at patches with the highest availability of prey, even under threat of interspecific competition with larger predators such as the coyote (Sergio et al. 2003; Wilson et al. 2010,). This type of congregation would explain the observed (albeit non-significant) positive spatial association between coyotes and mesopredators. However, given the large geographic area and time-scale surveyed here, as well as the detection of a large proportion of prey by our cameras (unpublished data), the likelihood that low availability of prey is to blame seems doubtful.

My results hint at the possibility that coyotes in the communities we examined may not serve the moderating role of a top predator as suggested by the mesopredator-release hypothesis. The lack of significant negative association between predators suggests that none of the mesopredators avoided coyotes in space or time, as would be expected if coyotes were dominant competitors. Although coyotes have been considered as top predators elsewhere (Crooks and Soule 1999; Rogers and Caro 1999; Henke and Bryant 1999), previous studies may have

occurred where differences in regions or communities resulted in lower availability of prey or a reduced ability for mesopredators to effectively partition prey from coyotes. If this supposition is the cause for the variations in results among sites, it would support the growing body of evidence suggesting that community stability, including those likely to experience release of mesopredators, depends on both top-down and bottom-up forces (Wilmers et al. 2006; Elmhagen and Rushton 2007).

As conservation and management strategies have begun to consider the important link between top predators and release of mesopredators (Ritchie and Johnson 2009), especially in relation to coyotes (Gompper 2002), the value of understanding competition among predators is great. Here, I failed to detect support of competitive interactions among predators that were expected to compete and suggest that partitioning and availability of prey may be responsible. While the mesopredator-release hypothesis may accurately describe the dynamics of some communities, my results hint that other variables may influence the strength and frequency of competitive interactions among predators.

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## Chapter 2: Traits of Prey That Influence Use of Space Within Predator-prey Relationships

### Introduction

Use of space within a landscape by an individual is believed to be dictated largely by efforts to maximize fitness. For most species, fitness primarily is governed by the need to acquire resources and to avoid predation (Lima and Dill 1990; Lima 1998). Given that areas with high availability of resources often impart the greatest risk of predation, use of space by prey constitutes a balance between maximizing acquisition of resources and minimizing the likelihood of encountering a predator (Lima and Dill 1990; Sih 1992; Hugia and Dill 1994; Molvar and Bowyer 1994; Bleich et al. 1997; Nicholson et al. 1997; Werner and Peacor 2003; Lima and Steury 2005; Bell et al. 2009). However, for predators, the sought-after resource is prey. Therefore, predators attempt to use space that provides the greatest likelihood of capturing prey, typically areas where abundance of prey is greatest, or potentially where prey are more vulnerable to predation (Burger et al. 2004; Honer et al. 2005; Lima 2002; Veit et al. 1993). As prey seek to avoid predators while predators seek to find prey, the ensuing two-player game becomes a predator-prey space race in which predators and prey must spatially respond to actions of each other to eat or avoid being eaten (Sih et al. 1998; Lima 2002, Sih 2005).

Within this predator-prey space race, responses of both species shape spatial associations between predator and prey (Sih 1984; Lima 2002; Bell et al. 2009). For example, when predators outmaneuver efforts of prey at spatial avoidance, predator and prey will be positively associated and occur together more often than expected by chance. Where this occurs, the predator is believed to win the race. When response of prey dominates and prey win the race by successfully avoiding the predator, the spatial association between the two will be negative, as predator and prey will occur together less often than expected by chance (Sih 2005).

Although multiple efforts have been made to model dynamics of this race (Sih 1984; Hugie and Dill 1994; Mitchell and Lima 2002; Rosenheim 2004), few models have addressed how traits of the species involved might influence which species successfully responds to the other and wins the race (Sih 2005; Bell et al. 2009). However, Sih (2005) suggested that traits related to costs and benefits of responding to the opposing species may strongly influence how a species reacts and, thus, the outcome of the race. For example, if one species is less mobile than the other, relative energetic cost of movements in reaction to the other species may outweigh benefits of such movements. Consequently, the more mobile species may be able to outmaneuver the less mobile species and win the space race (Sih 2005). Other behavioral traits that may spatially anchor a species, such as denning, nesting, mating, territories, or parental care (Sih 2005; Thomson et al. 2006; Thaker et al. 2011) similarly may increase the costs of responding spatially, giving the unanchored species the advantage in the predator-prey space race (Sih 2005). Smaller territory or home range, for example, may serve as a spatial anchor by conveying a cost in terms of energetics, unfamiliarity of new terrain, or intraspecific competition, if a response to actions of the other species would require movement outside of the established home range. However, while the influence of such traits on spatial associations makes theoretical sense, few empirical tests have been conducted in regards to such predictions.

Here, I investigate how differences in traits of prey influence the outcome of the predator-prey race. Specifically, I measured patterns of spatial association between a predator, the coyote (*Canis latrans*), and two species of prey that display distinct characteristics, the white-tailed deer (*Odocoileus virginianus*) and the eastern cottontail (*Sylvilagus floridanus*). White-tailed deer and eastern cottontails exhibit contrasting traits in terms of mobility and sizes of home range (Smith 1991; Chapman et al. 1980). Being of large body size, white-tailed deer are accustomed

to traveling greater distances than eastern cottontails in search of resources. Similarly, size of home ranges of white-tailed deer are 60 to 520 times larger than that of eastern cottontails. Thus, energetic costs related to mobility are likely far less for white-tailed deer than for eastern cottontails, and deer are less likely to be spatially anchored by smaller home ranges.

I hypothesized that character traits related to mobility and size of home range of prey, relative to the common predator, would dictate the outcome of the predator-prey space race. I predicted that 1) the spatial association between white-tailed deer and coyotes would be negative (white-tailed deer would win the space race) because the high mobility and large home range of deer relative to coyotes should facilitate avoidance of coyotes by deer; 2) the spatial association between eastern cottontails and coyotes would be positive (eastern cottontails would lose the space race) because the low mobility and small home range of cottontails relative to coyotes should hinder avoidance of coyotes by cottontails; and 3) owing to differences in mobility of prey, the spatial association between white-tailed deer and coyotes would be significantly different than the spatial association between eastern cottontails and coyotes.

## Methods

### *Study Sites*

To investigate patterns of spatial association between the coyote and the two species of prey of interest, white-tailed deer and eastern cottontails, 13 study sites were surveyed across Alabama as part of a larger state-wide biodiversity inventory (J.B. Grand, Auburn University, *unpublished data*). Surveyed sites encompassed state parks and wildlife management areas. Ecoregions contained within these properties included the Interior Plateau, Ridge and Valley, Southeastern Coastal Plains, Southwestern Appalachians, Southeastern Plains, and Piedmont (Griffith et al. 2001).



For each study site, I superimposed a grid consisting of points spaced 250m apart. I defined a sampling unit as a point and the area contained within 125m of that point. Using ArcGIS 9.2 (Environmental Systems Research Institute, Inc., Redlands, CA) and the National Land Cover Database 2001, I categorized all of the resulting sampling units into one of 33 types of land cover based on the majority type of land cover contained within each unit. A stratified random-sampling design was employed to select 10% of the available units for survey where stratification was based on category of land cover. Specifically, categories of land cover were surveyed proportionally to availability within the 13 study sites.

#### *Attributes of Habitats*

Observed spatial associations between species should be shaped by avoidance of predators by prey and pursuit of prey by predators. However, observed associations also may be driven by similarities or differences in selection for specific attributes of habitats. For example, if predator and prey are positively associated with each other (occur together more often than predicted by chance), they could simply be selecting for similar habitats rather than the association being a result of predators doing a better job at finding prey than prey are at avoiding predators (although such patterns may be part of predator-prey co-evolution). In fact, even if prey are succeeding in avoiding predators, observed associations can be positive if both predator and prey select for the same habitat (Gilpin and Diamond 1984; Peres-Neto et al. 2001; MacKenzie et al. 2004). Therefore, to investigate the influence of space use of predator on space use of prey after accounting for selection of habitat, I included attributes of habitats as covariates in analyses. I reclassified the 33 types of land cover used to designate majority land cover into six broader classes of habitats and assigned the appropriate class to each sampling unit. These classes included agriculture, hardwoods, mixed, pine, riparian, and scrub.

### *Field Surveys*

To investigate spatial associations between predator and prey, presence-absence data were collected during August-December 2008-2010. We sampled for coyotes, white-tailed deer, and eastern cottontails using non-invasive, infrared, digital trail cameras (RapidFire™ PC85, Reconyx, Inc., Holmen, WI) equipped to run for a 72-hour survey. At each sampling unit, one camera was placed either at the center or 100m from center. We administered commercially available predator lures (Caven's™, Minnesota Trapline Products, Pennock, MN) 2-3m in front of the camera. Although these lures were designed to target predators, we were able to also generate relatively high capture rates for non-predator species such as white-tailed deer and eastern cottontails (*unpublished data*). Cameras were programmed to take photographs at 2-minute intervals, and when triggered by the internal motion sensor, for the duration of the 72 hour survey. Time of detection was recorded using the timestamp function; thus, providing a history of detection for each surveyed unit.

### *Occupancy Modeling*

Because I anticipated that my methods (camera surveys) would give rise to imperfect rates of detection, I used analysis of occupancy to examine patterns of selection of resources patterns and associations between predator and prey (MacKenzie et al. 2002; 2004; 2005; MacKenzie and Royle 2005). The value of occupancy modeling is that this approach recognizes detection of species rarely is perfect, and adjusts estimates of use of resources and occupancy to account for such imperfect detections. Specifically, analysis of occupancy allows the probability of use ( $\psi$ ) of a resource to be estimated based on the history of detection (or the observed record of presence-absence) while simultaneously accounting for probability of detection ( $p$ ; or the probability that a species will be detected when present) of a species at sampled resources. Both

$\psi$  and  $p$  are estimated by conducting multiple surveys, or sampling occasions, over space or time, assuming unchanging use of a resource during sampling. When sampling units are smaller than size of the home range of the species investigated, as is the case in this study for white-tailed deer and coyotes,  $\psi$  should be interpreted as the probability of use of resources, rather than occupancy of resources (Kendall and White 2009).

In occupancy analysis, probability of detection ( $p$ ) is less than one even when species use a resource. Detection during any sampling occasion will take one of three forms: resource is used and species is detected, resource is used but species is not detected, or resource is not used. The probability that a species will use the resource and is detected is equal to the proportion of resources used ( $\psi$ ) multiplied by the probability of detection ( $p$ ), or  $\psi \times p$ . In contrast, the probability that a species will use the resource but not be detected is  $\psi \times (1-p)$ . The probability that a species does not use a resource is equal to  $1 - \psi$ .

Additionally, use and detection at a site may vary as a function of environmental variables such as attributes of resources or co-occurrence of other species (MacKenzie et al. 2002; 2004). In analysis of occupancy, estimates of use of resources and detection can be calculated while incorporating such covariates using the logistic model (MacKenzie et al. 2006):

$$\theta_i = \frac{\exp(\beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \dots + \beta_k x_{ik})}{1 + \exp(\beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \dots + \beta_k x_{ik})}$$

Where  $\theta$  equals the parameter of interests (either  $\psi$  or  $p$ ) at the  $i$ th resource or sampling occasion, respectively,  $x$  represents the covariate values for the  $i$ th resource or sampling unit, and  $\beta$  equals the coefficient estimates for  $k$  covariates.

### *Constructing Species-Specific Models*

To account for imperfect detection in my analysis of spatial associations between predator and prey, I built species-specific models of occupancy to estimate probability of

occupancy by a species at each sampling unit where that a species was not detected. To obtain the multiple sampling occasions necessary to estimate probabilities of detection, I divided each 72-hour survey from each sampling unit into three 24-hour blocks. Divisions were made mid-day, when the least amount of activity occurred. Each temporal block was considered as an independent sampling occasion during which presence of a species was counted only once when detected. I expected use of resources to vary with attributes of habitats and I also expected detection to vary with environmental variables associated with weather. Therefore, I obtained data for temperature, wind speed, and precipitation for each survey from the nearest weather station (average distance 24km, range 3-80km). I also considered the effect of number of days since the camera was activated, anticipating that as time progressed, either species might be more likely to encounter the bait or that deterioration of bait could influence rates of detection.

To build each species-specific model, I examined the influence of each covariate of detection in univariate analyses. All variables of detection that were significant at  $\alpha \leq 0.05$  level were included in a global model. This model also included all variables of occupancy (classes of habitats) because I wanted to account for similarities and differences in species-specific preferences in habitat. I then fit all submodels of that global model using an AIC framework and calculated the probability of use of each sampling unit by a given species using multimodel inference. Specifically, the model averaged predictions for probability of use of each sampling unit equaled the sum of individual predictions of models weighted by the AICc weight for that model (Anderson et al. 2000; Burnham and Anderson 2001).

### *Modeling the Spatial Association*

Once I obtained the species-specific probability of use of each sampling unit, I was able to estimate spatial associations of predator and prey. I constructed a new occupancy model for

the predator, whereby occupancy by coyotes of a given sampling unit was a function of probability of use by white-tailed deer and eastern cottontails at each sampling unit. Specifically, if a prey was detected at a sampling unit, then the probability of use of that sampling unit was 1.0; if the species was not detected, then the probability of use equaled the model-averaged prediction for the probability of use. As above, this model also included all variables for occupancy of habitats to estimate the association between coyote and white-tailed deer or eastern cottontails after accounting for any effects of selection of habitats. The model also included those variables of detection we determined were significant predictors of detection of coyotes in univariate analyses. We used a single-species approach to occupancy as opposed to the co-occurrence analysis of species (MacKenzie et al. 2004) because preliminary analyses indicated that the latter method typically failed to converge (unpublished data; MacKenzie et al. 2004). Additionally, I chose to model the predator-prey relationship from the point of view of the coyote because doing so facilitated the testing of my prediction that spatial associations with coyotes would be different between white-tailed deer and eastern cottontails (prediction 3). For testing prediction 3, I compared the model for coyotes that contained separate probabilities of use for white-tailed deer and eastern cottontails with a second model for coyotes that contained a single variable describing the probability of use by either species of prey. This probability was calculated using the formula (equation 1):

$$\hat{\psi}_{prey} = 1 - (1 - \hat{\psi}_{deer})(1 - \hat{\psi}_{cottontail})$$

As above, this probability was incorporated at each sampling unit where neither species of prey was detected, and a value of 1.0 was used where either species was detected. I used a partial-likelihood ratio test to determine if the more complicated two-prey model was a significant improvement over the simpler, single-prey model, and thereby test if the effect of use by white-

tailed deer on use of habitats by coyotes was significantly different from the effect of use by eastern cottontails. I used the statistical package R (R Development Core Team 2005) and the unmarked package (Fiske and Chandler 2010) to conduct all modeling analyses.

## Results

During my study, I collected usable data from 420 sampling units across 13 study sites. Coyotes were detected at least once at 67 (16%), white-tailed deer at 140 (33.3%), and eastern cottontails at 22 (5.2%) of those units.

### *Constructing Species-Specific Models*

In construction of each species-specific model of occupancy, the following variables influenced ( $p \leq 0.05$ ) probabilities of detecting species (summarized in Table 1): for coyotes, minimum temperature ( $\beta = -0.052 \pm 0.013$ ;  $\pm$  SE,  $p < 0.001$ ) and number of days from start of survey (2<sup>nd</sup> Day:  $\beta = 0.623 \pm 0.315$ ,  $p < 0.048$ ); for white-tailed deer, maximum temperature ( $\beta = -0.044 \pm 0.009$ ,  $p < 0.001$ ); and for eastern cottontails, no variable significantly influenced probability of detection ( $p \geq 0.211$ ). I constructed species-specific global models that included each variable that influenced probability of detecting a species and the six classes of habitats as covariates to occupancy. Analyses suggested that the best model for describing spatial use of resources by coyotes included covariates of occupancy for coastal + developed + hardwoods + mixed habitats and covariates of detection for minimum temperature and 2<sup>nd</sup> day. For white-tailed deer, the best model included no covariate for occupancy and maximum temperature for detection, while the best model for eastern cottontails contained the mixed-forest habitat and no covariate of detection. The Akaike weights for these best models were 0.017, 0.132, and 0.132 respectively, supporting use of model-averaging. Relative to weights in null models, the best models for the coyote, white-tailed deer, and eastern cottontail were 35,269 (weight of null

model =  $4.82 \times 10^{-7}$ ),  $2.3 \times 10^6$  (weight =  $5.73 \times 10^{-8}$ ), and 1.57 (weight = 0.084) times better.

Model-averaged predictions estimated that probability of use for those sampling units where species went undetected ranged from 0.341 to 0.435 for coyotes, 0.598 to 0.705 for white-tailed deer, and 0.070 to 0.167 for eastern cottontails. Using equation 1, probability of use of sampling units by either species of prey ranged from 0.648 to 0.748.

### *Modeling the Spatial Association*

Our analysis indicated that use of resources by white-tailed deer was not significantly associated with occupancy by coyotes ( $p = 0.147$ ). However, the large estimated effect ( $\beta = -1.43 \pm 0.984$ ), coupled with my relatively limited number of detections of coyotes, suggest that my test may suffer from low power and the effects could be biologically important. Estimates indicate that sampling units without white-tailed deer were 4.17 (0.61 - 28.75; 95% CL) times as likely to have coyotes as sampling units with deer (Table 2). Similarly, use of resources by eastern cottontails was not significantly associated with occupancy by coyotes ( $p = 0.142$ ). Again, the large estimated effect ( $\beta = 1.28 \pm 0.869$ ) and limited number of detections of coyotes and eastern cottontails suggest that my test may suffer from low power and effects could be biologically important. Estimates indicate that sampling units with eastern cottontails were 3.60 (0.65 - 19.75) times as likely to have coyotes as sampling units without eastern cottontails. In testing prediction 3, the partial-likelihood ratio test comparing the model with variables for both use of resources by white-tailed deer and eastern cottontails with a model that contained a single, combined variable for use of resources by prey was significant ( $\chi^2 = 3.816$ ,  $p = 0.05$ ), indicating that the more complex model was superior and that use of sampling units by deer and cottontails had significantly different associations with use of habitats by coyotes.

### Discussion

The outcome of the predator-prey space race likely is influenced by traits of the species involved. Relative mobility between predator and prey is believed to influence how species respond to each other within a space race (Sih 2005). When the mobility of prey is equal to or greater than that of the predator, prey should be able to spatially respond and avoid areas of high likelihood for encounters with predators. For less mobile prey, however, spatial response to a mobile predator requires greater effort on the part of the prey, leaving the predator with an advantage. In comparing the relationship between a predator and two species of prey of differing levels of mobility, my evidence supports this tendency. Specifically, the spatial associations between each of the two prey (white-tailed deer and eastern cottontails) and the common predator (coyote) were significantly different from each other (prediction 3). Such differences in spatial association suggest that traits of the prey may influence how prey respond to predators and, thus, the outcome of the predator-prey space race.

As a large-bodied species capable of long-distance travel and relatively large home ranges (Smith 1991), the mobility exhibited by white-tailed deer should enable the use of spatial avoidance of predators such as coyotes. The benefits to fitness (i.e., reduced rates of predation, reduced levels of stress) of shifting use of space to avoid encounters with coyotes likely are greater than the energetic costs of movement accrued by white-tailed deer. Likewise, large home ranges may allow white-tailed deer to reduce risks of predation through shifts in use of space while remaining within the familiarity of their home range. For white-tailed deer, and other mobile prey, low costs of movement should make spatial avoidance a viable solution to risks of predation, and can give the prey the edge in predator-prey races. Although results here are non-significant (albeit with low power and large size of effect), I observed a negative trend in spatial association between white-tailed deer and coyotes after accounting for species-specific



preferences in habitat, a relationship supported by other studies (Lingle 2002). The observed association tends to suggest (with statistical caution) that white-tailed deer are likely to use space not being used by coyotes; thereby, reducing predation by coyotes and winning the race with coyotes.

Conversely, the small body and minuscule home range (relative to coyotes) that describes the eastern cottontail suggests that limited mobility would make spatial avoidance of a predator less likely. Being less than 7% the size of coyotes (Bekoff 1977; Chapman et al. 1980), the energetic costs for eastern cottontails to move far enough to spatially avoid coyotes likely outweigh the benefits of avoiding coyotes. Likewise, the small home ranges of eastern cottontails make an individual cottontail vulnerable to predation by coyotes throughout its range, and spatial avoidance would require the individual to leave its established home range to avoid encounter with coyotes. My examination of the spatial association between eastern cottontails and coyotes again revealed a non-significant (with low power and large effect of size) trend, whereas in this case, the association was positive. Unlike the more mobile white-tailed deer, this association may suggest that eastern cottontails use the same space as coyotes, and are losing the predator-prey space race.

Of course, I cannot be certain that the observed difference in spatial associations between the two predator-prey pairs were due to difference in size and rates of movement of the prey. Besides factors related to mobility and size of home range, response of prey to use of space by predators may be influenced by reproductive behaviors that affect the cost-benefit tradeoff of avoiding predators. For species that have relatively few offspring and require large investments in parental care, such as the white-tailed deer, spatial avoidance of a predator increases the probability that young will survive. For the parent, reproductive fitness requires surviving long

enough to maximize production of viable offspring, an effort that is enhanced by avoiding predation at an early age. Consequently, such trends may be reversed for species bearing multiple precocial offspring such as the eastern cottontail. Because many young are produced at once, loss of a few to predation is not detrimental to reproductive success. Likewise, the need for long-term survival in adults is reduced because several litters can be reared after only a few reproductive seasons. Such species may benefit more by concentrating efforts toward reproduction rather than accruing the costs associated with spatial avoidance of predators. Although I could not discern whether differences in reproductive traits played a role in shaping the predator-prey associations in this study, the patterns detected here would support such predictions.

I acknowledge the possibility that the spatial associations of this study are the results of population-level processes rather than behavioral responses between predator and prey. For example, if coyotes were highly effective at capturing white-tailed deer but less effective at capturing eastern cottontails, I might expect to see the same patterns in use of space (small populations of white-tailed deer and large populations of eastern cottontails in areas used by coyotes). However, I believe this is unlikely because behavioral responses typically occur at more rapid rates than population-level processes. Likewise, expansion of the geographic range of coyotes into Alabama is a relatively recent event (Hill et al. 1987; Lovell et al. 1998), making it doubtful that enough time has passed for coyotes to reduce populations of white-tailed deer.

Use of space by predators and prey can be influenced by several factors besides the availability of resources. I demonstrate here that traits, such as mobility, size of home range, and possibly reproductive behavior, may influence how prey spatially respond to predators. Although I did not investigate how traits of predators might influence the predator-prey race,

trends are fully expected to be similar. Any trait of either predator or prey for which a cost for fitness is accrued due to spatial movement may affect ability of a species to spatially respond to the other and influence the outcome of a predator-prey race. Further research on additional traits in other prey, as well as in predators, could greatly benefit our understanding of use of space by species within the context of scenarios associated with the predator-prey space race. Such traits could be incorporated in efforts to model use of space by species, a valuable tool for conservation and management endeavors.

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Table 1: Estimated size of effect, standard error, and  $p$ -values as calculated from univariate modeling of each variable of detection ( $p$ ). Variables that approached a significant level of effect ( $\alpha \leq 0.05$ ) were selected for use in subsequent models and are denoted in **bold**.

Variable	Coyote		Deer		Rabbit	
	Estimate (SE)	$p$ -value	Estimate (SE)	$p$ -value	Estimate (SE)	$p$ -value
Maximum Temperature*	-0.036 (0.012)	0.002	<b>-0.044</b> <b>(0.009)</b>	<b>&lt;0.001</b>	0.020 (0.021)	0.360
Average Temperature*	-0.052 (0.013)	<0.001	-0.044 (0.009)	<0.001	0.002 (0.023)	0.910
Minimum Temperature*	<b>-0.052</b> <b>(0.013)</b>	<b>&lt;0.001</b>	-0.031 (0.009)	<0.001	< -0.001 (0.020)	0.976
Precipitation	-0.024 (0.023)	0.301	-0.031 (0.020)	0.118	-0.071 (0.074)	0.340
Maximum Wind Speed	0.033 (0.025)	0.172	0.013 (0.020)	0.505	-0.070 (0.056)	0.211
Average Wind Speed	0.058 (0.044)	0.183	-0.030 (0.040)	0.458	-0.105 (0.100)	0.293
2 <sup>nd</sup> Day of Survey	<b>0.623</b> <b>(0.315)</b>	<b>0.048</b>	-0.137 (0.235)	0.558	< -0.001 (0.558)	0.999
3 <sup>rd</sup> Day of Survey	0.453 (0.319)	0.156	-0.286 (0.240)	0.234	0.280 (0.529)	0.597

\*To avoid confounding effects, I selected the most statistically significant measurement of temperature when multiple measures were significant ( $\alpha \leq 0.05$ ).



Table 2: Estimated size of effect, standard errors, odds ratios, and  $p$ -values of all variables of occupancy ( $\Psi$ ) and detection ( $p$ ) included in the model used to estimate spatial associations between coyotes, white-tailed deer, and eastern cottontails.

Type	Variable	Estimate	SE	Odds Ratio	p-value
$\Psi$	Probability of use for White-tailed Deer	-1.427	0.984	0.240	0.147
$\Psi$	Probability of use for Eastern Cottontails	1.277	0.869	3.586	0.142
$\Psi$	Agriculture	1.806	1.197	6.086	0.131
$\Psi$	Hardwoods	1.761	0.854	5.818	0.039
$\Psi$	Mixed	1.803	0.893	6.068	0.044
$\Psi$	Pine	0.948	0.928	2.581	0.307
$\Psi$	Riparian	1.182	0.999	3.261	0.237
$\Psi$	Scrub	-1.402	1.140	0.246	0.219
$p$	Minimum Temp	-0.053	0.013	0.948	<0.001
$p$	2 <sup>nd</sup> Day	0.657	0.322	1.929	0.039