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Top Down Effects and Resource Selection by Coyotes in South Carolina

Alex Jensen
ajense2@clemson.edu

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TOP DOWN EFFECTS AND RESOURCE SELECTION BY COYOTES IN SOUTH CAROLINA

A Dissertation
Presented to
the Graduate School of
Clemson University

In Partial Fulfillment
of the Requirements for the Degree
Doctor of Philosophy
Wildlife and Fisheries Biology

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by
Alex Joseph Jensen
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Accepted by:
Dr. David Jachowski, Committee Chair
Dr. Michael Childress
Dr. Cathy Jachowski
Dr. John Kilgo

ABSTRACT

Top predators play important roles in functioning ecosystems, including regulating the populations of prey species and competing with other predators. However, in the face of global change, many top terrestrial predators have declined in both range and abundance, making room for some smaller predators to expand into new niches. Coyotes (*Canis latrans*) in North America are a prime example of this – they have rapidly expanded their range in the last 120 years, raising concerns about their impacts on both domestic and wild species. In eastern North America, research has centered around their effects on white-tailed deer (*Odocoileus virginianus*), which are an important game species and particularly vulnerable to coyotes during the first few weeks of life. Despite efforts by governments and citizens to kill coyotes across much of their new range, they are now established, and managers are looking for ways to quantify and reduce their effects on native species. Critical questions remain about variability within coyote populations and how exactly they respond to temporary foods on the landscape. To address these questions, we studied coyote spatial and community ecology in the Piedmont region of South Carolina, USA. In Chapter 1, we used GPS data to investigate variability in habitat selection and movement. At the population level, coyotes avoided risky areas (i.e., open and developed habitat), especially during risky times. However, we found differences across seasons, behavior states, and sexes, highlighting the importance of both extrinsic and intrinsic factors in predicting movement. In Chapter 2, we quantified coyote diet, focusing on the summer months when fawns were available. Coyotes largely switched to temporarily available foods during the summer and fall, suggesting that alternative foods (i.e., summer fruits) could buffer predation on fawns. In addition, using genetics, we found that most of the individuals in our population switched to these temporary foods, indicating that targeted removal would likely not decrease fawn mortality. In Chapter 3, we investigated whether coyotes changed their foraging tactics for different foods and also described coyote movement surrounding fawn predation events. We compared foraging patterns for fawns, blackberries, and small mammals and found relatively few differences in *when* and *how* coyotes moved, yet differences in *where* they foraged. Linking fawn predation events to coyote GPS data showed that coyotes tended to move relatively fast and linearly prior to killing a fawn, then would quickly move away from the kill site and rest for several hours. In Chapter 4, we broadened our investigation into top-down effects by using a field manipulation to test how coyotes influenced smaller carnivore scavenging behavior, relative to other hypothesized factors. We found that coyotes only directly influenced bobcat behavior, while forest structure (particularly understory cover) seemed to modulate risk from coyotes, highlighting the complexity of interactions among carnivores. Taken together, our findings highlight that 1) coyotes have diverse, yet context-dependent top-down effects and that 2) temporary foods shape their behavior and diet (particularly in the summer). More broadly, our findings suggest that habitat management which promotes alternative foods and accounts for human shields may be a viable strategy to influence the behavior of large-herbivore predators. Generalist carnivores will likely continue to thrive in the Anthropocene, necessitating continued research into their effects on other species and management strategies to best coexist.

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CHAPTER ONE

UNDERSTANDING INTRA-SPECIFIC VARIABILITY IN THE MOVEMENT OF AN ADAPTABLE PREDATOR

ABSTRACT

There is increasing recognition that niche variation within populations has important ecological and evolutionary implications, yet the challenges associated with tracking animals have made variation in movement ecology largely unexplored. Variation in movement, both among and within individuals, fundamentally leads to variation in the resources and risks that individuals experience. Multiple factors could explain variation in movement, including changes in the environment through time (e.g., seasons), intrinsic factors (e.g., sex, territorial status), and individual personality. However, the relative importance of each of these sources is unknown and likely context dependent. To address this gap in knowledge, we used fine-scale GPS data to quantify the habitat selection and movement of 60 coyotes in South Carolina, USA. At the population level, coyotes avoided areas where risk from humans would be greatest (open and developed areas), but more so during the riskiest times, suggesting that they exhibit risk-sensitive foraging. When we compared habitat selection across behavioral and demographic factors, we found the most differences among behavior states, suggesting that preferred habitat for highly mobile species can shift on the scale of minutes to hours. We also found differences between males and females, where males selected tree cover more strongly and had consistently greater variability in habitat selection. Contrary to our expectations, we found little variation in habitat selection across territorial statuses but did find that non-residents seemed to exhibit more burst-like movement. In general, we found little evidence for consistent differences among individuals, but there was relatively high repeatability of behaviors during the summer, perhaps due to a boon of temporarily available foods (fawns and fruits). Ultimately, variation within individuals seemed to be comparable in magnitude to the variation across individuals. Taken together, our findings suggest that risk from humans underpins coyote behavior, and some (but not all) intrinsic factors explain variability in movement. We also found that movement strategies are season and behavior-state dependent, highlighting the importance of movement decisions across multiple temporal scales. Future research should try to explicitly link these sources of movement variability to measures of fitness, like resource acquisition and mortality.

INTRODUCTION

When, how, and where animals move has important consequences for individuals and communities (Nathan et al. 2008, Costa-Pereira et al. 2022). The movement decisions that individuals make influences the resources they encounter as well as the risk they are exposed to, with many species needing to balance both demands (Holbrook and Schmitt 1988). Therefore, it is implicit that variability in movement, both within individuals (through time) and among individuals, would have fitness consequences. While traditional movement studies often report differences across seasons, these are often from population-level estimates, which mask any differences across demographic groups and among individuals (Spiegel et al. 2017, Muff et al. 2020). A better understanding of these sources of movement variation is important because intra-population variability in other domains (e.g., diet) has been shown to have ecological and evolutionary implications comparable to differences across species (Araújo et al. 2011, Bolnick et al. 2011).

Some intra-population variability in movement can be expected with predictable changes in life history. For example, during the mating season, male mammals often move to optimize access to females, as exemplified by brown bears and fat dormice (*Ursus arctos, Glis glis*; Ściński and Borowski 2008, Krofel et al. 2010). Juvenile animals can also have distinctive movements, including large exploratory movements like dispersal (Dobson 1982) or little movement in the case of ungulate neonates (Schwede et al. 1992). For territorial species, patterns of movement over weeks or months can help us detect and quantify movement states like residency and transiency (Morin and Kelly 2017). However, robustly quantifying differences in movement across multiple segments of the population requires a large sample size, which can be logistically challenging for some taxa (e.g., carnivores).

Individual variation in movement can manifest through differences among individuals (Bastille-Rousseau and Wittemyer 2019, Muff et al. 2020) and differences within individuals in different contexts (Stuber et al. 2022). By measuring a given individual’s movement in different contexts, we can quantify the degree to which they exhibit repeated behavior – their spatial personality (Spiegel et al. 2017). Although personality research was traditionally concerned with quantifying differences among individuals along dimensions such as boldness and activity, we embrace a broader definition which includes behaviors such as movement and habitat selection (Stuber et al. 2022). If individuals in populations exhibit spatial personalities, this would likely have important ecological consequences like increasing intra-specific spatial niche partitioning and population niche breadth (Araújo et al. 2011). However, we need a better understanding of the temporal scale at which spatial personalities show up. Individuals may behave consistently across seasons or consistently across finer temporal scales. For example, an individual selecting habitat similarly, when both resting and moving (Roever et al. 2014), could be evidence of a spatial personality if other individuals behave differently. Quantifying variability in movement at these fine scales (minutes and hours) is important because it likely reflects decision making, and our understanding of why individuals make different decisions remains poor.

Thus, variability in movement can arise from a variety of factors, including extrinsic factors like season and intrinsic factors like demography and individual identity. Variability could manifest across multiple temporal scales, multiple behavioral scales, or in how animals move (e.g., speed) in addition to where they move (e.g., habitat selection). Yet, without quantifying variability across all of these factors for a single population, we cannot understand the relative importance of each of these. Quantifying these factors requires standardized fine-scale data measured across the year, on enough individuals to have a representative sample from each demographic group of interest, which has yet to be attempted to our knowledge.

To fill this gap in knowledge, we studied the movement ecology of coyotes (*Canis latrans*) in South Carolina, USA. Coyotes are a medium-sized carnivore native to the western two-thirds of North America, only becoming established in the southeastern United States (US) in the last 30-40 years (Hody and Kays 2018). Coyotes are now the largest predator across most of this region and are of high interest to managers due to their realized and potential impacts on other wildlife (Gompper 2002, Kilgo et al. 2010). Past research in the southeast has reported differences in where and how coyotes move across seasons (Youngmann et al. 2022) and among residents and transients (Chamberlain et al. 2021, Webster et al. 2022), which we build on by investigating how additional factors such as time of day and personality influence movement.

Most of our objectives were concerned with where coyotes moved, and we first quantified habitat selection at the population level to serve as a baseline (objective one). Here we hypothesized that extrinsic factors such as seasonal variation in resources or risk would influence selection (Ellington et al. 2020, Figure 1.1). For example, pulses of temporarily available foods such as white-tailed deer fawns (*Odocoileus virginianus*; Chapter 2) could cause unique movement during the summer (Youngmann et al. 2022). There is also strong top-down pressure from human hunters, particularly during the daytime in deer hunting season. Thus, we predicted coyotes would exhibit less risky behavior (e.g., staying under tree cover) during times when risk from humans is greatest. We then quantified differences in selection across intrinsic factors (objective two), including sex, age, size, territorial status, and behavior state, so that we could see how each of these factors contributed to selection in the overall population. Objective three was similar to objective two, except we analyzed how movement metrics (time spent in each behavior state and speed) varied across these intrinsic factors. For example, we predicted that males would move more during mating season (Krofel et al. 2010) or engage in riskier behavior given they were more likely to die in our study area (unpublished data). We predicted that non-residents would move more and be relegated to riskier areas (e.g., along paved roads; Morin and Kelly 2017). We also hypothesized that morphology could influence coyote movement, with larger and heavier coyotes able to defend, and therefore forage and travel in territories that are safer and with more resources.

Lastly, to better understand spatial personality, we quantified the amount of variation in selection within individuals for our fourth and fifth objectives. In objective four, we compared the variation across intrinsic factors (e.g., males and females) to the variation in selection within an individual in different contexts (behavior states and seasons). This allowed us to quantify the relative importance of these subgroups and an individual's identity in regard to total variability in selection. In general, we predicted that coyotes would collectively shift their behavior across seasons (Ellington et al. 2020), such that individual variability would be relatively large. For objective five, we quantified the repeatability of individual decisions associated with habitat selection (Nakagawa and Schielzeth 2010). We hypothesized that repeatability would be a function of resource availability, such that coyotes would behave most similarly during the summer and fall when temporary foods are available (Chapter 2). Collectively, our study provides novel insight into the factors that explain variability in the movement of a generalist carnivore and highlights how this flexibility likely influences fitness through mitigating risk and increasing access to important resources.

METHODS

Study Area

We tracked the movement of GPS collared coyotes across a ~400 km^2 area primarily within McCormick, Greenwood, Saluda, and Edgefield counties in rural South Carolina, USA. This area was representative of the Piedmont physiographic region, with gently rolling hills (120-180 m elevation) and a humid subtropical climate (Griffith 2010). Most of the land was privately owned and covered by loblolly pine (*Pinus taeda*) plantations in various successional stages. There were pastures and fields intermittent throughout the landscape, including planted forage plots for game species. Hardwoods dominated in drainages. Paved road density was relatively low, though there were networks of dirt access roads on most properties. Potential coyote food items included deer, rabbits, small mammals, persimmon (*Diospyros virginiana*), and blackberry (*Rubus allegheniensis*; Chapter 2). Hunting was a popular recreational activity, especially during turkey season in April – May and deer season from October – December. Coyotes arrived in this area in the 1990s and are viewed by many locals as a threat to populations of game species (particularly white-tailed deer). These attitudes, combined with year-round unlimited legal harvest, put coyotes at risk of being shot throughout the year (60% of deaths are from gunshots; unpublished data), but mortality risk is particularly high during deer hunting season.

Data collection and cleaning

We captured coyotes on ~60 km^2 of private land in the center of our study area during the winter months of 2018-2019, 2020, and 2021 (three capture seasons). With help from a professional trapper, we set Minnesota MB 550 foothold traps (Minnesota Trapline Products, Pennock, MN) on dirt roads that had signs of coyote activity (i.e., tracks and scat). We immobilized coyotes using a catchpole and electrical tape wrapped around their muzzle and ankles. We then took body measurements, collected samples (ear punch, hair, blood), ear tagged, estimated age (based on tooth wear; Maher 2002), determined sex, weighed, and fit a GPS-collar around their neck (Vectronic Aerospace, Berlin, Germany; model: VERTEX Light). We only put GPS-collars on individuals if the collar was < 5% of their weight. The average handling time was 25 minutes. All capture and handling procedures were approved by Clemson University IACUC permit no. AUP 2018-031 and USDA Forest Service permit no. USFS 2018-031.

We programmed our GPS-collars to collect data for ~15 months before dropping off automatically. We set the default fix rate to 7 hours but increased it to 30 minutes during three three-week periods (~1000 GPS points per period) from February 8 – February 28, May 13 – June 2, and October 10 – October 30. We chose these windows to capture key biological and ecological processes we predicted would influence movement; including coyote mating and relatively limited food in February (Chapter 2), coyote pup rearing and peak fawn birth in May (Kilgo et al. 2012), and coyote dispersal and deer hunting season in October. We tested GPS accuracy by placing two collars set to 30-minute fix intervals in mature forest and an open field within our study site. We tested each collar in both habitat types and compared locations to a known GPS location taken using the waypoint averaging function on a handheld GPS. We found a nominal difference in GPS error between habitat types (1-2m) and the average GPS error was 23m.

We cleaned each three-week period of 30-minute data (‘dataset’; n = 155) following recommendations by Avgar et al. (2016). Most (n = 144) of the datasets were complete (full 21 days of data), and the remaining 11 datasets averaged 17.2 days in length (all > 10 days). We removed missed GPS fixes and visualized each dataset to look for erroneous fixes. When there were step length outliers (typically > 2000 m) we inspected the GPS track and removed a fix if it led to improbable movement (i.e., two long steps in a row that returned the coyote near the first GPS point). We removed an average of 1.3 fixes per dataset. When there was more than one consecutive missing fix (n = 9 datasets), we split the dataset into multiple subsets of consecutive fixes (bursts) to meet the requirements of integrated step selection analysis. However, if there was just one consecutive missing fix (n = 206) we imputed that fix by averaging the coordinates of the previous and next fix. The average number of steps per dataset was 989 (range = 491-1008).

Classifying data according to our hypotheses

To test our hypothesis that variation in selection and movement was attributable to underlying territorial status (objectives 2-4), we classified datasets as either resident, transient, or biding. From a social status perspective, resident coyotes are typically part of a pack while transients are typically alone and looking for a territory. However, recent research on coyotes in the Southeastern US has shown that there seems to be a third “biding” state. These coyotes may be territory holders, but their movement is characterized by extraterritorial excursions and overlap with nearby resident home ranges (Morin and Kelly 2017). Given territorial status has been shown to be dynamic (Morin and Kelly 2017, Ellington et al. 2020), we primarily used space use patterns during each three-week period to classify each dataset. First, we used the movevis package (Schwalb-Willmann et al. 2020) to create animations of each dataset to get a sense for how the coyote was moving. From this first step, it was often clear when the coyote was exhibiting residency or transiency based on whether they had a defined home range (Figure 1.2). However, to remain objective, we classified the dataset as resident when we observed the repeated use of a relatively small area and their 95% minimum convex polygon (MCP) was < 25 km^2 (n = 103, typical MCP = 10-15 km^2). We classified the dataset as transient when the coyote rarely (if ever) returned to the same area and their MCP was > 75 km^2 (n = 29, average MCP = 181 km^2). We confirmed these classifications by viewing their movement before and after each period. When we were uncertain how to classify the dataset (n = 23), we counted the number of extraterritorial excursions and classified the dataset as resident if there was one extraterritorial excursion and their MCP was < 50 km^2 and as biding if there was more than one extraterritorial excursion and their MCP was > 25 km^2. Ultimately, we classified 106 datasets as resident, 29 as transient, and 20 as biding.

To test our hypothesis that behavioral state would influence movement and selection, we used hidden Markov models and the momentuHMM package (McClintock and Michelot 2018) to classify each step into a behavior state (Figure 1.2). For each dataset, we compared two-state (encamped and moving) with three-state models (encamped, foraging, and traveling). For the two-state model, we characterized initial parameters for encamped behavior with short step lengths (e.g., mean ± standard deviation = 100 m ± 100 m) and a wide turn angle concentration (0.1), while we characterized moving behavior with longer step lengths (e.g., 500 m ± 500 m) and a narrower turn angle concentration (0.7). For the three-state model, we characterized initial parameters for encamped behavior with short step lengths (e.g., 50 m ± 50 m) and a wide turn angle concentration (0.1), foraging behavior with intermediate step lengths (e.g., 400 m ± 300 m) and an intermediate turn angle concentration (0.3), and traveling behavior with long step lengths (e.g., 1000 m ± 500 m) and a narrow turn angle concentration (0.7). We used the retryFits function (n = 10) to increase the odds of finding the true distributions if we chose incorrect initial parameters. We compared the fit of the two-state and three-state models using AIC_c (Burnham and Anderson 2002) and found that the three-state model was best for all 155 datasets (ΔAIC was typically between 10 – 100). We then used the Viterbi algorithm to classify each step as encamped, foraging, or traveling (Michelot et al. 2016).

We also hypothesized that sex, age, mass, and size could be important. For age, we classified each dataset as either from an adult (≥ two years) or a juvenile (< two years). We primarily used our field assessment to classify their age (Maher 2002), but we also obtained precise ages for 15 dead individuals using Matson’s laboratory (cementum annuli tooth analysis). Ages were not static – we reclassified individuals as adults during seasons we believed them to be ≥ two years old if we captured them when they were 1.5

years old. For size, we added together our measurements of the left hind foot (tip of toenail to end of hock) and skull width (at widest part) because we thought these measurements were least likely to be biased by measurer identity.

Objective one: population-level habitat selection

We compared where coyotes moved to where they could have moved using integrated step selection analysis (iSSA; Avgar et al. 2016; Figure 1.2). We generated 20 available steps for each used step (average total steps = 20,740) using the amt package (Signer et al. 2019). The available step lengths were drawn from a gamma distribution and the available turn angles were drawn from a von mises distribution. Since the step lengths and turn angles for each available step were drawn from the full dataset (not behavior state specific), often several of the available steps were much longer than the used step (particularly while encamped and foraging). However, if these available steps ended outside of a territorial animal's home range, those areas were likely not truly available (Ruprecht et al. 2021). Therefore, for datasets which we classified as resident, we removed all available steps that ended > 200 m beyond the MCP created from that dataset (average removed steps = 274, 1.4% of available steps). We never removed more than 10 available steps from the associated used step.

We then extracted spatial data from the endpoint of each used and available step by interfacing with Google Earth Engine using the rgee package (Aybar et al. 2020; Figure 1.2). We hypothesized that land use/land cover (LULC) and paved roads would influence coyote step selection. For LULC, we used the 10 m resolution Dynamic World dataset, which contains near-real-time measures of LULC cover probability (scale = 0 – 1; Brown et al. 2022). We extracted the tree cover, bare cover, and built cover LULC classes (the grass cover, crops cover, shrub and scrub cover classes were all negatively correlated with trees [< -0.8)]). For LULC we extracted the mean value during each three-week period. We also created a distance to paved road raster using the TIGER roads dataset (scale = meters; US Census Bureau 2022).

Because we were interested in variation at the behavior state level (see objective two), we fit three global iSSAs for each of our 155 datasets yielding 465 models in total. We hypothesized that coyote step selection would interact with time of day, so we included three pairwise interaction terms between time of day and tree cover, built cover, and distance to road (Table 1.1), using the amt package to categorize the timestamp at the end of each step as day or night. To quantify the relative strength of each spatial variable on coyote habitat selection at the population level, we calculated the mean estimate and the mean standard error for each estimate for each spatial variable for each season. If the mean estimate ± the mean standard error did not overlap zero, we considered that variable to be significant at the population level.

Objective two: how intrinsic factors influence habitat selection

Next, we used results from our iSSA to test our hypotheses about variation in selection across intrinsic factors. Our response variables were the estimates from each of the seven spatial variables in our previous objective (e.g., tree cover), while our predictor variables were the intrinsic factors we hypothesized would predict variation (territorial status, behavior state, age, sex, mass, size). First, we tested for multicollinearity among our variables by calculating the variance inflation factor (VIF) of a global additive model. We found low collinearity (all < 2.08) and acceptable Pearson's correlation between size and mass (0.63), therefore we retained all of our candidate predictor variables. We fit separate generalized linear mixed models for each season (n = 21 = 7 spatial variables x 3 seasons) because we were most interested in differences in selection within seasons, rather than changes in selection among seasons (which we would expect; Ellington et al. 2020). Individual was a random effect and the reference categories for our categorical variables were resident, encamped, female, and juvenile. We considered predictor variables with estimate absolute values 2x > than their standard error to be significant (Ellington et al. 2020).

Objective three: how intrinsic factors influence movement

For this objective, we tested for differences across intrinsic factors, except in the context of how coyotes moved rather than habitat selection. We quantified two movement metrics which we used as separate response variables: 1) the percentage of time coyotes spent in each behavior state and 2) the average step length while in each behavior state. Like objective two, we used generalized linear mixed models to compare the relative importance of our predictor variables (season, territorial status, age, sex, mass, size) on the percent of time coyotes spent in each behavioral state and average step length. We fit separate global models for each behavior state (three for each analysis) and considered variables with 95% confidence intervals not overlapping zero to indicate significant differences (for our categorical variables) or significant relationships (for our continuous variables).

Objective four: comparing variation in selection among and within individuals

For this objective, we compared consistency in selection among groups we hypothesized would have similar selection (e.g., males, encamped individuals) to consistency in selection within individuals. In step one, we used the standard errors from each of our seven spatial variables (e.g., tree cover) from our iSSA (objective two) as our response variables and season, sex, territorial status, behavior state, mass, and size as our predictor variables in generalized linear mixed models. We found significant differences across season, sex, territorial status, and behavior state (based on 95% confidence intervals not overlapping zero), so we focused on those coyote variables for our comparison. In step two, we defined variation within an individual as the mean standard deviation derived from the iSSA for that individual (an average from 21-84 values depending on how many datasets we had from a given individual). We then calculated the overall mean across individuals (within individual variation) for each season, sex, territorial status, and behavior state, then compared those values to the mean across similar individuals (from step one) by calculating the percent difference.

Objective five: quantifying repeatability of selection in our population

In addition to comparing variation across and within individuals, we also wanted to quantify consistency in selection in our population using a repeatability metric.

Repeatability is a standardized way to estimate personality in a population, where low repeatability (~0) indicates all individuals behave similarly at a given time yet collectively different through time and high repeatability (~1) indicates all individuals behave consistently different from each other through time; Nakagawa and Schielzeth 2010). We calculated repeatability in selection of the response variables from our iSSA (e.g., tree cover), both across and within seasons. We had 3-12 measures for each individual, and therefore three measures within seasons for each individual (one measure for each behavior state). We used the following formula:

$$r = \frac{s^2_{among}}{s^2_{among} + s^2_{within}}$$

where r is repeatability, s^2_{among} is the variance among individuals and the s^2_{within} is the variance within individuals. We used the rptR package (Stoffel et al. 2017) to calculate r and 95% confidence intervals using 1000 bootstraps.

RESULTS

We put GPS-collars on 76 coyotes across our three capture seasons, however due to mortality (n = 10), collar failure (n = 5), or failure to retrieve the collar (n = 1), we had useful data from 60 coyotes (Table A1.1). From these 60 coyotes, we collected 155 seasonal datasets (62 winter, 55 summer, 38 fall). We classified 102 (66%) of these datasets as from juveniles and 53 as from adults, while 104 (67%) of these datasets were from females and 51 were from males. We classified 106 of these datasets as from residents (68%), 20 (13%) as from biders, and 29 (19%) as from transients.

Objective one: population-level selection

At the population level, tree cover and built cover were the only significant variables (Figure 1.3). Coyotes selected for greater tree cover during all seasons, but only significantly so during the fall (average estimate ± average standard error = 0.827 ± 0.613). We also found an effect from the interaction with time of day, where coyotes were less likely to select for tree cover at night, but only significantly so during the summer and fall (-0.316 ± 0.296, -0.886 ± 0.633). Similarly, coyotes avoided built cover during all seasons, but only significantly so during the summer and fall (-0.557 ± 0.451, -0.723 ± 0.706).

Objective two: how intrinsic factors influence habitat selection

We found more nuance when we quantified variation in selection across segments of the population (Figure 1.4, Table A1.2). We found that seasonal differences in tree cover selection could likely be explained by weaker selection while foraging in the winter (estimate and 95% confidence intervals = -0.14 [-0.27 : -0.01]) and traveling in the summer (-0.16 [-0.29 : -0.03]), compared to when coyotes were encamped. Indeed, behavior state was the most important variable overall when explaining variation across individuals – it was a significant factor in 13/21 of our models. For example, we found relative avoidance of bare cover while foraging in the summer (-0.07 [-0.13 : -0.01]) and traveling in the winter and fall (-0.23 [-0.32 : -0.13]; -0.15 [-0.22 : -0.07]). Coyotes also selected for less tree cover while traveling at night during every season (Table A1.2). We found little difference in avoidance of built cover across behavior states, except that coyotes avoided it less while traveling during the fall (0.69 [0.15 : 1.23]) and summer at night (Table A1.2). Territorial status was less important in our models (significant in 5/21 models), and there was less consistency in its effects across seasons. For example, we found that transients selected for greater tree cover (0.25 [0.03 : 0.46]) and bare cover (0.14 [0.02 : 0.26]), but only in the winter. We also found that biders selected for areas further from roads in the winter (0.21 [0.02 : 0.40]), but less so at night (-0.32 [-0.52 : -0.12]). Collectively, we found that behavior state, then territorial status, were important factors that influenced selection, though the significance of these effects varied across season and time of day.

Sex and mass had minor effects on selection, while we found no effect from age or size (Figure 1.4, Table 1.1). Sex was a significant predictor in 4/21 models, all of which were related to tree cover. We found that male coyotes selected for greater tree cover than females, but only in the winter (0.31 [0.08 : 0.53]) and fall (2.90 [1.37 : 4.43]), and less so at night during these seasons (-0.28 [-0.50 : -0.06], -2.97 [-4.51 : -1.44]). Mass was a significant predictor in two models related to built cover, which indicated that larger coyotes avoided built cover more in the fall (-0.54 [-0.99 : -0.09]), though less so at night (-0.58 [0.19 : 0.96]).

Objective three: how intrinsic factors influence movement

On average, coyotes spent 54.6% of their time encamped, 25.8% foraging, and 19.7% traveling (Figure 1.5). Their average step length was 23 m while encamped (0.05

km/h), 181 m while foraging (0.36 km/h), and 640 m while traveling (1.28 km/h; Figure 1.5). We found that season and territorial status explained variation in both of these measures, while sex, age, mass, and size did not. During the fall, coyotes spent more time encamped (one hour on average; estimate and 95% confidence intervals = -5.03 [-8.06 : -2.01]) and traveled more (45 minutes on average; 3.25 [0.37 : 6.13]) compared to winter (Figure 1.5). Across seasons, biders and transients foraged for 1-2 hours longer (5.75 [2.73 : 8.76], 2.94 [0.034 : 5.53], respectively), but traveled for 1-2 hours less (-4.39 [-8.17 : -0.61], -5.81 [-9.10 : -2.52]), compared to residents. Regarding step length, we found that transients stepped further (+ 67 m) than residents while foraging (68.34 [36.156 : 100.52]), while both biders and transients stepped further (+ 72 m and + 139 m, respectively) than residents while traveling (95.25 [13.57 : 176.92], 136.91 [66.66 : 207.16]). Thus, biders and transients spent less time traveling than residents, but perhaps move just as much by traveling further during each step.

Objective four: comparing variation in selection among and within individuals

We found that variability in selection differed by season, behavior state, territorial status, and sex (Figure 1.6bc). Compared to within-individual variation, variation across individuals was generally slightly lower while encamped and foraging (by 15-30%). By contrast, variation across individuals was greater while traveling during the winter and the fall (by 90-278%), but slightly lower in the summer (by 10%). Compared to within-individual variation (and females), males had greater variation in selection (by 55-200%). Overall, biders had greater variation than residents or transients.

Objective five: quantifying repeatability of selection in our population

We found that there was lower average repeatability across seasons (estimate and 95% confidence intervals = 0.083 [0.031 : 0.156]) than within seasons (Figure 1.6a). Repeatability was lower in the winter (0.160 [0.049 : 0.299] and fall (0.187 [0.038 : 0.357]) compared to summer (0.301 [0.137 : 0.454]). These results suggest that there are not consistent individual differences in selection, but rather the population collectively changes their behavior across seasons. However, there appears to be greater within-individual consistency in selection across behavior states during the summer, compared to winter and fall.

DISCUSSION

Most studies of animal movement ecology are hindered from investigating intra-population variation in movement decisions by small sample sizes or course data. Here, we used 155 fine-scale (30-minute) GPS datasets from 60 coyotes to test how extrinsic (season, time of day), and intrinsic (e.g., sex, territorial status) factors influence movement and habitat selection. Despite our study area being relatively rural, avoiding risk from humans seemed to shape movement, and coyotes were more likely to be in risky places during less risky times. Overall, we found the most variation in selection across behavior states, in line with past studies highlighting the importance of accounting for behavior (Roever et al. 2014, Ellington et al. 2020). However, we found the most consistent differences between males and females, perhaps explained by differences in how males forage or how they patrol their territories. We also found little evidence for spatial personalities in our population, perhaps a function of behavioral plasticity across seasons. Collectively, our results support the notion that a mean-field approach (only deriving population-level estimates) can mask important intra-population differences in the movement ecology of wild animals (Muff et al. 2020, Stuber et al. 2022).

Risk from humans shapes population-level habitat selection

Like other studies on carnivore behavior, avoiding risk seemed to be a major determinant of coyote step selection. Risky areas in our system are likely in open areas during the daytime (where hunters have sightlines; Stankowich 2008, Gaynor et al. 2021) and near human development (including paved roads). Coyotes seemed to be sensitive to this dynamic landscape of risk; they selected for tree cover throughout the year, but only significantly so during the fall (when risk from being shot by deer hunters is greatest). Similarly, they primarily selected tree cover during the day (though only significantly more so in summer and fall), which suggests they are also sensitive to how risk changes at the diel scale. Indeed, although coyotes generally avoided built cover and paved roads, they were more tolerant of them at night. These findings align with a step selection analysis on African lions (*Panthera leo*) and pumas (*Puma concolor*) – these carnivores also tolerated anthropogenic risk more during the nighttime in two very different human-dominated landscapes (Nisi et al. 2021). This study and ours support the notion that humans are a major determinant of animal movement (Tucker et al. 2018, Doherty et al. 2021), but that animals have strategies to coexist (Carter et al. 2012, Gaynor et al. 2018).

Here we show that coyotes generally avoided risky areas (i.e., open habitat, built cover), but relaxed this avoidance during less risky times.

Context-specific variability in habitat selection

Although risk seemed to underpin coyote behavior, they tolerated more risk while moving (particularly while traveling), perhaps to obtain food. Indeed, out of the 18 contexts where we quantified selection for built cover or roads (three seasons with three behavior states each), coyotes only relaxed their avoidance while traveling in the summer and fall. More generally, we found that the strength, and in one case, direction, of selection depended on the behavior state coyotes were in (Roever et al. 2014, Ellington et al. 2020). For example, coyotes tended to select tree cover more strongly while encamped (especially during the day). They also switched to avoiding bare cover while foraging and traveling in some seasons despite selecting for it while encamped. It is worth a reminder here that tree cover was significantly negatively correlated with relatively rare (but potentially important) foraging habitat for coyotes – grass cover, crop cover, and shrub and scrub cover. Certain foods, like small mammals and blackberries, are more available in open habitats like these in our study area (unpublished data), which may explain why coyotes were more apt to be in these habitats while moving. However, this explanation would only be partially aligned with a study in Canada, which also found that coyotes were more likely to be moving (as opposed to encamped) in open habitat, but only during the day (Ellington et al. 2020).

We found greater consistency in selection across territorial status relative to behavior states. We only found differences in selection among territorial statuses during the winter, when transients selected for greater tree cover and bare cover, and biders selected to be further from roads. During the winter, coyotes are pairing up and mating, which may explain why transient and bider coyotes (who are presumably alone) select habitat differently during this season. We were surprised that transients and biders did not select habitat closer to paved roads, because non-resident coyotes are sometimes relegated to the interstitial spaces between resident territories (Sacks et al. 1999, Morin and Kelly 2017); and we anecdotally noticed highways acting as de facto territory boundaries and observed several transient coyotes moving along highway corridors. We were particularly interested in how selection was related to territorial status, given a growing recognition of its relevance to important population-level processes, including dispersal and survival (Morin and Kelly 2017, Zepeda et al. 2021). Ultimately, we found greater consistency in selection across territorial statuses than another study in the southeast comparing habitat selection between residents and transients (Webster et al. 2022). However, we used a different modeling approach and a different suite of habitat variables, which could explain the discrepancy.

Males generally selected for greater tree cover than females, perhaps due to risk aversion or different foraging behavior. We found this somewhat surprising, given that males died at around twice the rate of females in our study area (unpublished data), and thus we expected them to exhibit riskier behavior, such as spending *less* time under tree cover. Males did spend less time under tree cover during the night (compared to during the day), particularly during the fall, suggesting they may be cognizant of when risky places become less risky. This sex-based difference in tree cover selection could also be driven by differential foraging tactics – in our study area, males are more omnivorous in the winter and carnivorous in the fall (Chapter 2). Male and female diets are most similar in the summer, which matches our step selection findings here. A large proportion of the carnivory in the fall is likely from scavenging deer carcasses (Chapter 2), which aligns with a finding that an attraction to puma kills was mainly driven by resident male coyotes (Ruprecht et al. 2021). More broadly, finding differences in selection by sex is not surprising (Ściński and Borowski 2008, Krofel et al. 2010, Nisi et al. 2021), but it is intriguing that tree cover was the only variable where we found any significant differences in selection. More work is needed to understand this consistent pattern for tree cover in light of otherwise similar selection between the sexes.

Patterns in how coyotes move across the landscape

Coyotes in our system spent similar amounts of time in each behavior state when compared with previous studies on coyotes and other medium-large mammals. We found that coyotes spent just over half of their time encamped (~55%), on par with coyotes along an urbanization gradient in Chicago (57-62%; Ellington and Gehrt 2019), yet more than coyotes in a Canadian National Park (31-40%; Ellington et al. 2020). Similar to our study, fishers and African elephants (*Pekania pennanti; Loxodonta cyclotis and 24fricana*) spent 44-63% of their time encamped (Roever et al. 2014, Beirne et al. 2021, Hance et al. 2021). However, only the other coyote studies also used a three-state model (encamped, foraging, traveling; as opposed to two-state), with the Chicago study most closely matching our findings. We found that coyotes spent 26% of their time foraging, compared to 21-25% in Chicago and 28-33% in Canada. This left 20% of the day for traveling in our study, compared to 19-20% in Chicago and 32-36% in Canada. Although our study area is quite rural, there are several ecological or methodological explanations for why our results match the Chicago study more closely. First, coyotes may spend more time encamped to avoid people in Chicago and our study area. Second, they may spend more time moving in Canada because prey density is lower. Finally, a similar fix rate in Chicago (15 minutes) and our study (30 minutes) vs. less frequent in Canada (two hours) could influence behavior state classification (Ellington et al. 2020).

Variation in movement (time in each behavior state and step length) was explained by season and territorial status. Our findings that coyotes were encamped less and traveled more in the fall could reflect increased exploratory or dispersal movements but would also likely put coyotes at greater risk of death given our fall data window (October 10-30) aligns with deer hunting season, when the majority of our coyotes die (unpublished data). Other studies have also found an effect of season on behavioral state partitioning, but these effects were driven by environmental factors not relevant in our system (snow or rainy seasons; Ellington et al. 2020, Beirne et al. 2021). Counterintuitively, we found that biders and transients spent less time traveling than residents, though they also stepped further while traveling. This suggests that they may travel more in bursts, perhaps to avoid encountering resident coyotes or humans (Farhadinia et al. 2020). One potentially important factor we were unable to investigate is group size and membership, as these factors have been shown to influence elk and woodpecker movement (*Cervus canadensis*, *Picoides borealis*; Haydon et al. 2008, McKellar et al. 2015). Future research on social carnivores should investigate how these factors influence individual movement.

Comparing variation in selection across and within individuals

Our individual modeling approach allowed us to compare variation across intrinsic factors to selection within individuals. Under most circumstances, variation in selection was lower for a given subset of the population (e.g., encamped coyotes, coyotes in the summer) compared to the average variation within individuals. Yet variation was particularly high when coyotes were traveling in the winter and fall, and for male coyotes. Relatively high variation in selection while traveling makes intuitive sense as coyotes are moving over larger distances and therefore likely to encounter and wider range of habitat conditions. The fact that we did not see this pattern in the summer again suggests that some unique characteristic of summer leads to convergence in habitat selection (Chapter 2).

We were surprised to find consistently high variation for males, a pattern which held across each territorial status. These findings suggest a new line of evidence in support of greater male variability (GMV; Darwin 1871), which has been found for morphological and cognitive traits in a variety of mammalian species (Halsey et al. 2022). For example, male red deer are more variable in size (Clutton-Brock et al. 1982), male chimpanzees have larger variation in brain structure (DeCasien et al. 2020), and male humans exhibit larger variation across a variety of traits (Forde et al. 2020, He and Wong 2021). There are fewer studies on GMV in the animal behavior domain, however a recent meta-analysis found no evidence of widespread GMV across a suite of personality-like behaviors (Harrison et al. 2022). This suggests that coyotes are one of the few mammals where behavioral GMV is present or perhaps habitat selection is fundamentally different as a behavior than personality. In our context, this could mean that males exhibit greater variability in selection as a result of defending home ranges from other males, or perhaps courting females. Combined with our findings on males selecting more tree cover, it seems that males and females in our population move somewhat differently.

Repeatability of selection

When considering individual behavior across seasons, we found that repeatability was relatively low (0.08) compared to other studies. The average repeatability from reviews of spatial behavior was 0.67 (Stuber et al. 2022) and 0.37 across a broad suite of behaviors (Bell et al. 2009). There are at least two possible explanations for the relatively low repeatability we found. First, Stuber et al. (2022) found that juveniles had significantly lower average repeatability (~0.37) compared to adults (~0.75), which is not surprising as adult behavior may become more canalized with experience (Reader 2015), and it may partially explain our relatively low repeatability, as 66% of our datasets were from juveniles. Second, the fact that repeatability was 0.2-0.3 within seasons (more in line with these reviews) may indicate that individual repeatability is simply very weak across seasons for coyotes in our system. This suggests that individuals in our population collectively change their behavior across seasons, though they are more consistent with themselves in their selection within seasons. Intriguingly, repeatability was greatest during the summer, which aligns with when important temporary foods (fawns and blackberries) are available (Chapter 2), and therefore may reflect relatively high consistency in selection associated with foraging for these foods.

Conclusions

Variation within populations is fundamental for evolution, yet we are just beginning to incorporate intra-specific variability into animal movement ecology (Spiegel et al. 2017). Here, we used a robust fine-scale dataset from coyotes to quantify where and when we see consistency in movement across a population of a generalist predator. We come away with several key findings. First, we found that risk from humans seemed to have a strong and multi-pronged effect on coyote movement, such that they avoided risky areas (open habitat and development), especially during times that humans are most threatening (daytime and deer hunting season). This suggests that coyotes have behaviorally or evolutionarily responded to the very high mortality risk across the southeast (Kilgo et al. 2010, Morin and Kelly 2017), which will likely make future generations even more afraid of humans. Second, when we quantified variability across multiple demographic, behavioral, and morphological dimensions, two factors stood out. In line with previous work (Roever et al. 2014), we found the most variability in selection across behavior states, likely a function of how coyotes used different habitats for different activities (e.g., tend to move more in open habitat). We also found that males were both different and more variable in their movement than females, the latter of which represents rare evidence of greater male variability in a behavioral context. Third, we found the variability in selection within an individual and the variability in selection across individuals seem to contribute comparably to the total variability in selection within our population. At the same time, we found relatively little evidence of spatial personalities in our population, seemingly due to the population collectively changing their behavior across seasons and behaviors. This suggests that nearly all individuals in our population converge on similar strategies, which may ultimately mean that spatial personalities may be not as important (or more difficult to detect) in generalist species.

There is increasing recognition that individual animal movement can scale up to influence ecological processes (Abrahms et al. 2021, Costa-Pereira et al. 2022), yet still much to learn about how and where this occurs. Fundamentally, movement influences fitness through changing the resources and risk that individuals encounter. Although we quantified variability in movement across multiple temporal scales, intrinsic factors, and individuals, we were unable to directly link movement decisions to fitness. Future studies could use our framework to quantify how movement influences resource acquisition, mating opportunities, and survival (Gigliotti et al. 2020).

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TABLES

Table 1.1. An overview of our movement and resource selection objectives and results for coyotes in South Carolina, USA. For the movement objective, we found that there were differences across seasons and territorial status, which we indicate with a “✓″. Our reference categories for our coyote variables were winter, resident, encamped, female, and adult, therefore an effect indicates a significant difference from the reference. In our selection objective, we analyzed each response variable three times (once for each season), which is why there are up to three “✓″.

Movement objective		**Significant results from hypotheses**						
response variables	*description*	*season*	*territorial status*	*behavior state*	*sex*	*age*	*mass*	*size*
time in behavior state	Proportion of time coyotes spent in each behavior state (encamped, foraging, traveling)	✓	✓	NA	none	none	none	none
step length	The distance between consecutive GPS points (every 30-minutes)	✓	✓	NA	none	none	none	none
Selection objective		*season*	*territorial status*	*behavior state*	*sex*	*age*	*mass*	*size*
response variables	*description*							
tree cover	Likelihood that a given 10 m^2 raster cell is covered by trees. From Dynamic World	NA	✓	✓✓	✓✓	none	none	none
bare cover	Likelihood that a given 10 m^2 raster cell is covered by bare ground. From Dynamic World	NA	✓	✓✓✓	none	none	none	none
built cover	Likelihood that a given 10 m^2 raster cell is covered by built infrastructure. From Dynamic World	NA	none	✓	none	none	✓	none
distance to road	Distance to the nearest paved road in meters. From Tiger Roads	NA	✓	✓	none	none	none	none
tree cover at night	Interaction between tree cover and time of day (day or night)	NA	✓	✓✓✓	✓✓	none	none	none
built cover at night	Interaction between built cover and time of day (day or night)	NA	none	✓	none	none	✓	none
distance to road at night	Interaction between distance to road and time of day (day or night)	NA	✓	✓✓✓	none	none	none	none

FIGURES

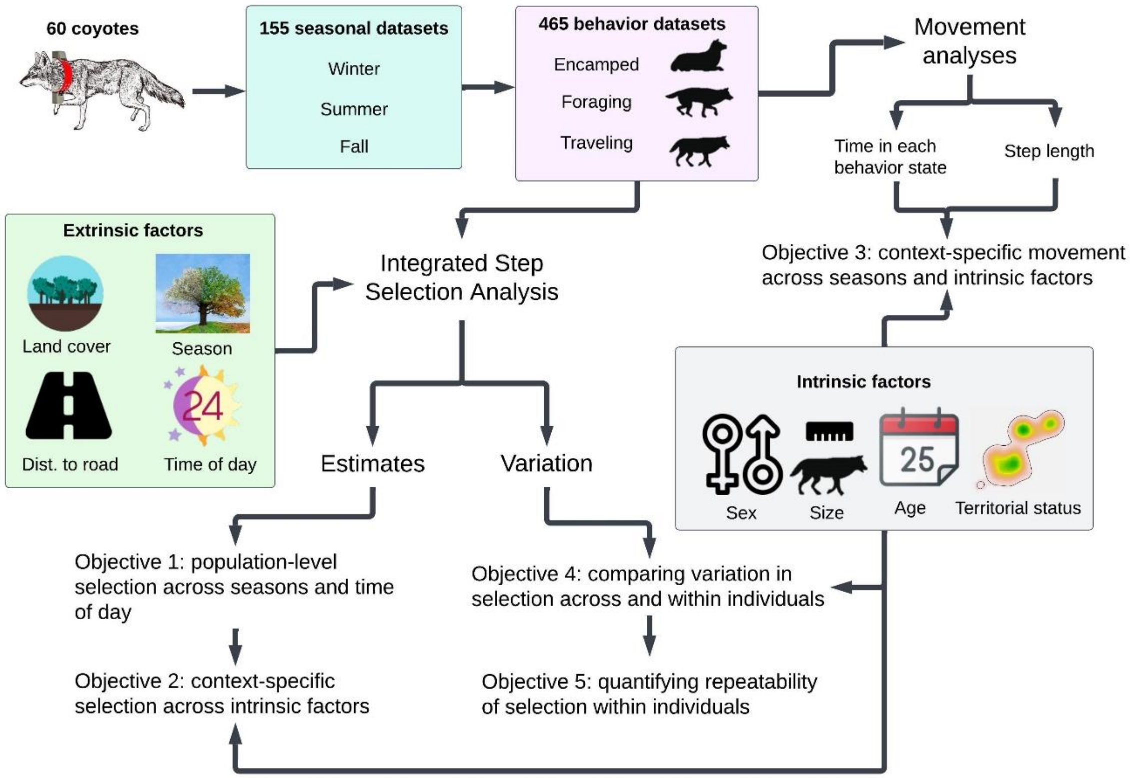

Figure 1.1. Conceptual diagram of our data structure and analyses of coyote movement in South Carolina, USA. Our observation unit was the movement of an individual coyote during a specific year-season while engaged in one of three behavior states. This approach allowed us to test how extrinsic and intrinsic factors were related to selection, variability around selection, and movement.

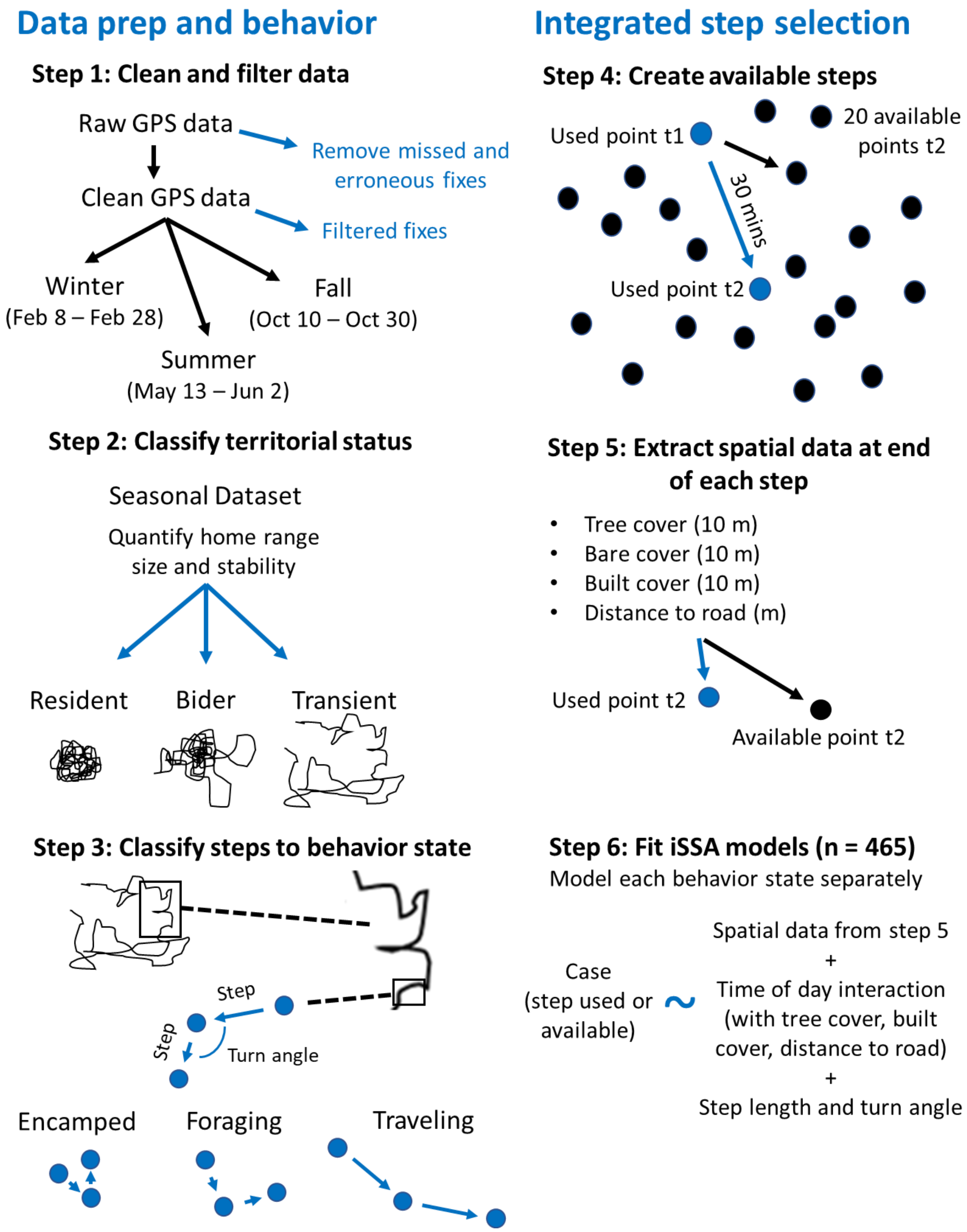

Figure 1.2. Workflow used to analyze step selection and movement by coyotes in South Carolina, USA. In the left column, we show the steps we took to classify our datasets by behavior and in the right column how we performed an integrated step selection analysis.

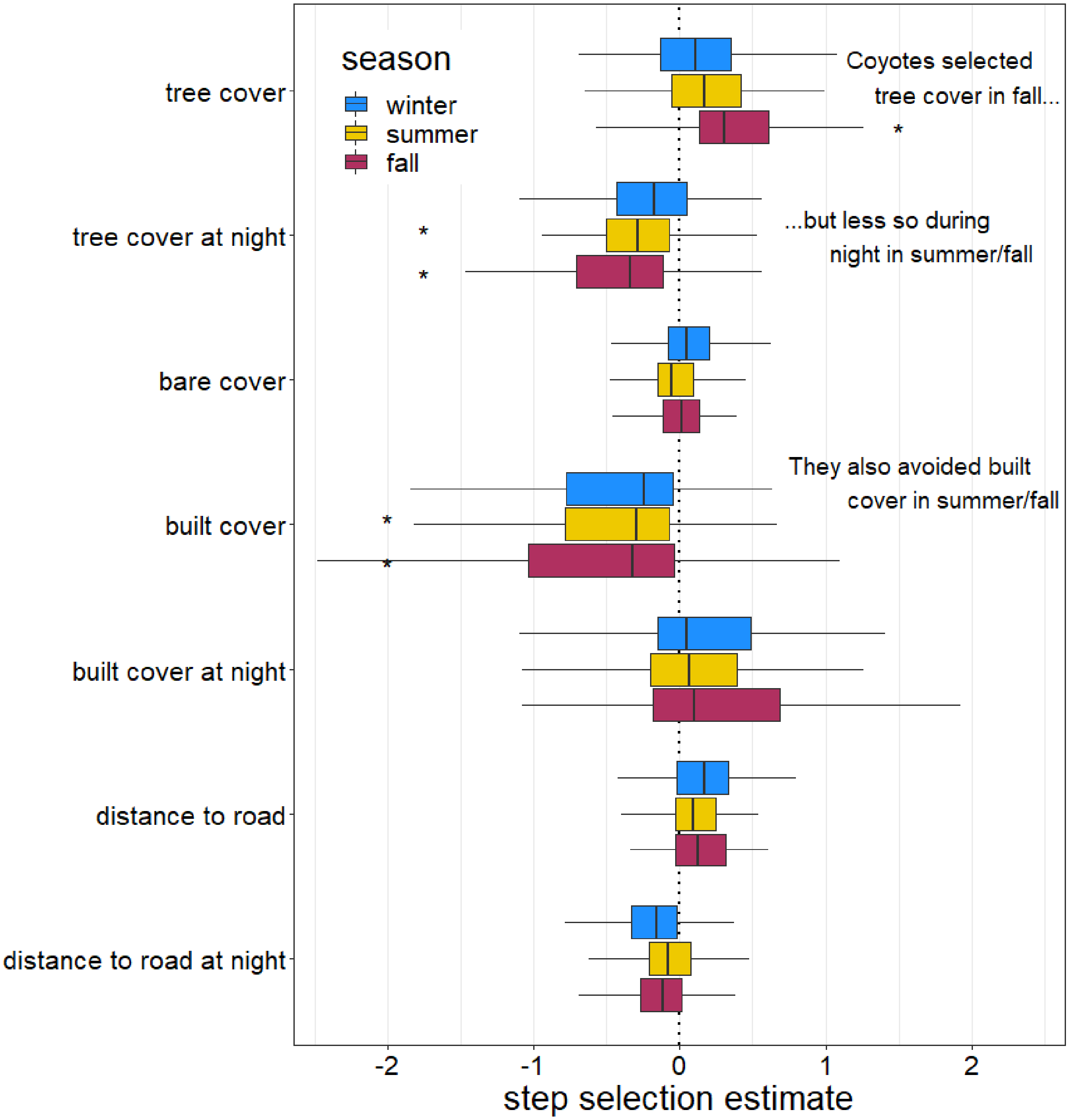

Figure 1.3. Population-level integrated step selection analysis model estimates across seasons for coyotes in South Carolina, USA. We considered mean estimates to be significant if their mean standard errors did not overlap zero, which we indicate by including text about those variables (tree cover, tree cover at night, and built cover). Note that the estimates 'at night' are in reference to during the day, not in reference to the estimate of that variable during nighttime.

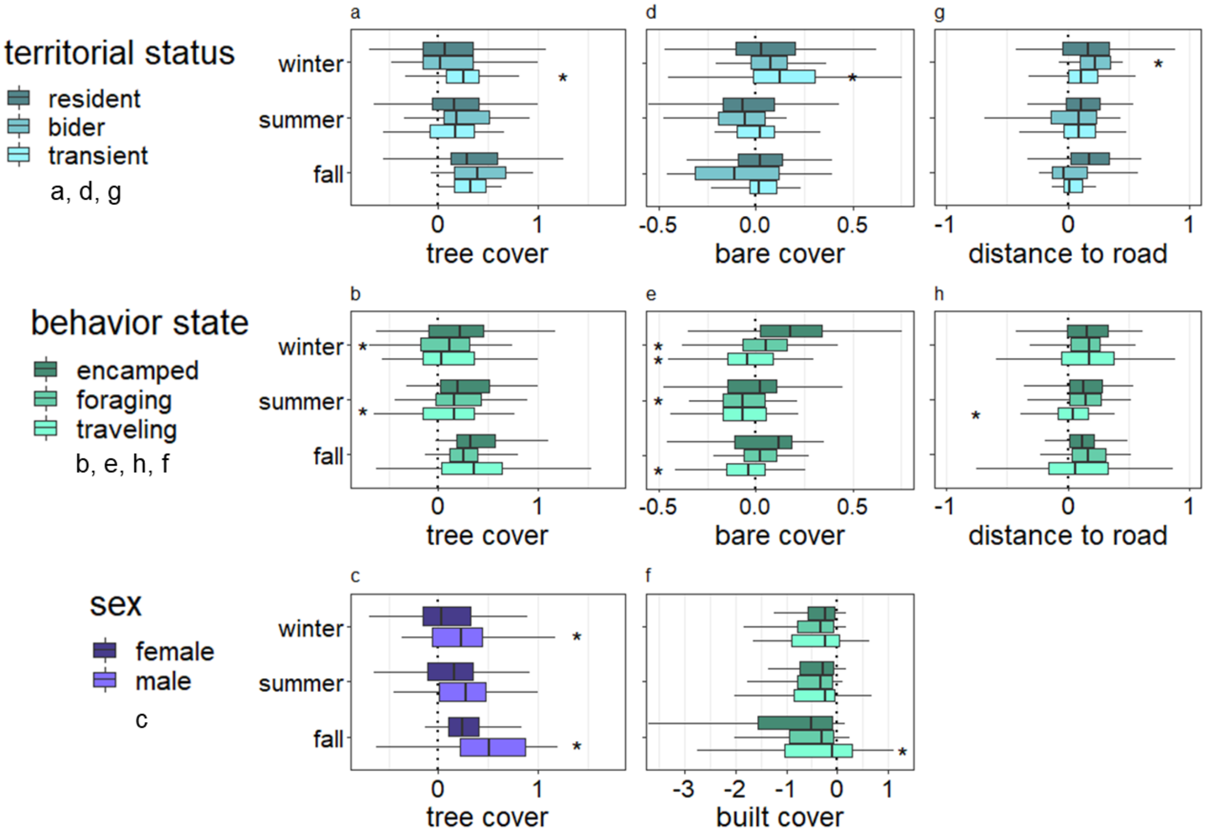

Figure 1.4. Integrated step selection analysis estimates broken down by territorial status (blue), behavior state (green), and sex (purple) for coyotes in South Carolina, USA. We only show variables where we found a significant difference from the reference category during at least one season (indicated with a *). The reference category for territorial status was resident; behavior state was encamped; and sex was female.

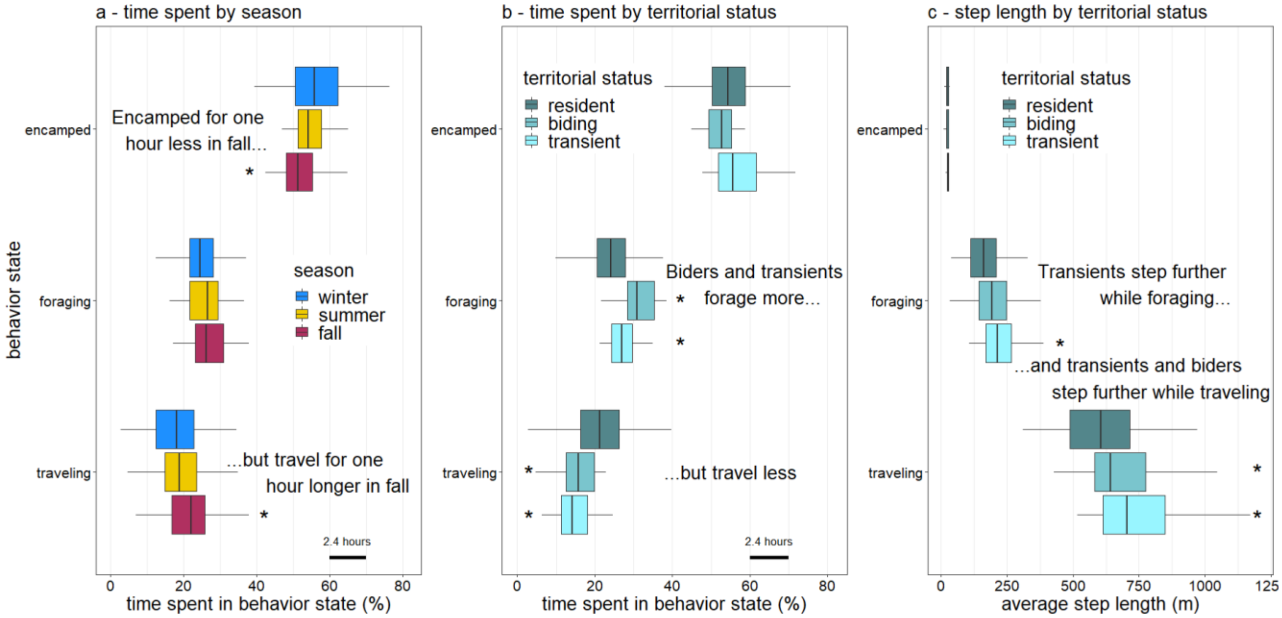

Figure 1.5. We quantified variation in movement across season, behavior state, and residential state for coyotes in South Carolina, USA. We show the average time coyotes spent in each behavior state (a), with boxplots filled by season. In (b) we show similar data, except by territorial status, not season. In (c) we show the average step length during each behavior state, with boxplots filled by territorial status. The reference categories are encamped and resident; we added text and * to summarize significant differences across seasons or territorial status.

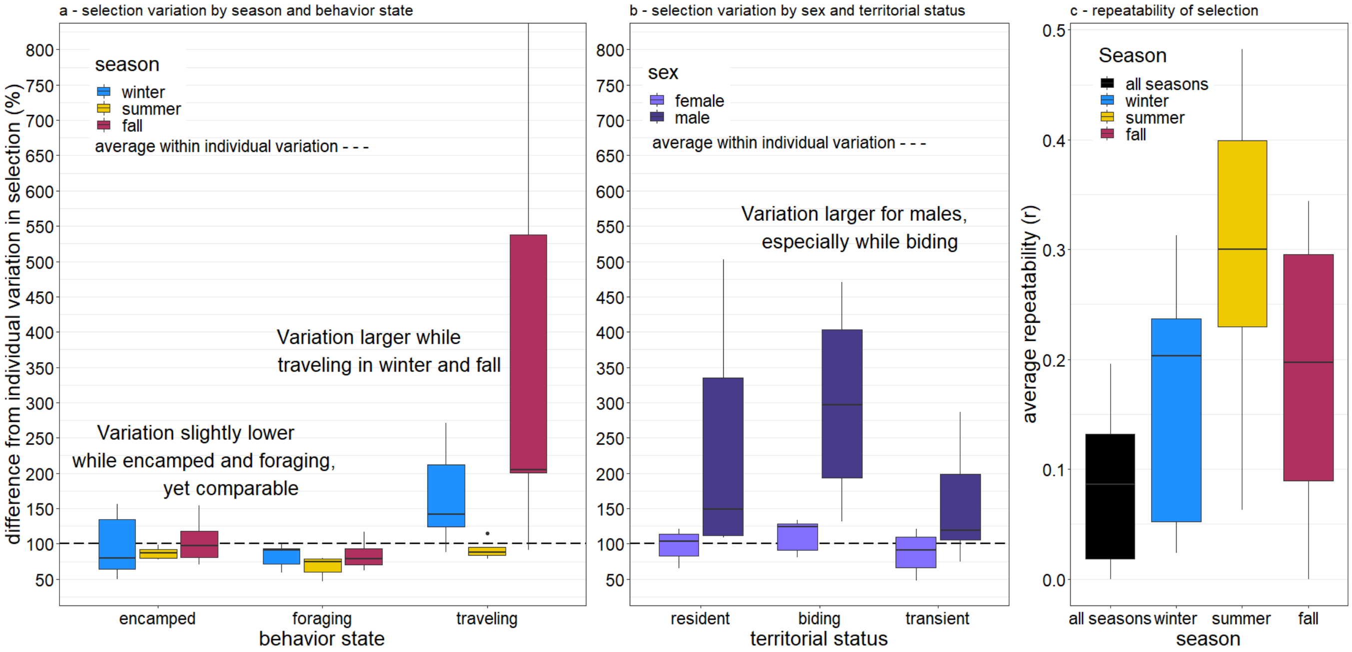

Figure 1.6. Measures of repeatability and variation in selection for coyotes in South Carolina, USA. In (a) we show the average repeatability in selection across all seasons, as well as within each season. In (b) and (c) we compare the average variation in selection within individuals (the dashed lines at 100%) to the average standard deviation across individuals during each season-behavior state combination (b) and sex-territorial status combination (c). The averages are based on the standard deviation of the seven spatial variables we used in our analyses.

CHAPTER TWO

RESOURCE PULSES SHAPE THE NICHE OF AN ADAPTABLE CARNIVORE

ABSTRACT

Applying models of predator-prey dynamics to natural systems remains a challenge, particularly when resources vary in their availability across space and time. Resource pulses are not only an important ecological phenomenon but can also be used to quantify how adaptable predators respond to changes in food availability. We quantified how coyotes collectively and individually responded to seasonal fluctuations in small mammal availability and a pulse of fawns and blackberries across three years, using 540 genetically screened scats (333 individually identified); small mammal and blackberry surveys; and 84 marked fawns. Temporarily available foods (fawns, blackberries, and persimmons) were major components of coyote diet in the summer and fall, likely releasing predation pressure on small mammals in the summer and increasing intra-specific competition. Coyote diets mostly tracked small mammal availability, but they appeared to optimally forage for young fawns during the first half of summer. However, a subsequent decline in fawn availability and a pulse of blackberry availability seemed to jointly reduce fawn consumption. Male and female coyote diets were very similar in the summer and most individuals ate temporarily available foods (including fawns), which suggests targeted removal by managers is unlikely to impact deer predation. Rather, our results suggest that provisioning alternative foods through modified forest and farming practices could reduce consumption of herbivore prey by generalist carnivores and should be a topic for future experimental studies. More broadly, our results highlight a need to better integrate measures of spatial and temporal resource pulses in future studies of predator prey dynamics.

INTRODUCTION

Despite decades of theoretical and experimental research into how predators respond to changes in food availability (i.e., functional responses and prey switching; Solomon 1949, Holling 1956), how well these models fit natural systems remains poorly understood (Abrams and Ginzburg 2000, Miller et al. 2006). This is partly because natural systems are often complex, making it challenging to track the various factors which can influence predation, including predator density, competition, and the availability of key food items (Miller et al. 2006). Moreover, there is mounting evidence that adaptable species are context-dependent foragers, who can engage in both opportunistic foraging and active searching (Prugh 2005, Panzacchi et al. 2008, Rayl et al. 2018), and therefore do not fit into the traditional specialist or generalist dichotomy.

Prey switching studies typically track fluctuations in food availability across annual or seasonal timescales (e.g., Randa and Yunger 2004, Almeida et al. 2012), yet studying pulses of temporarily available foods (hereafter 'temporary' foods) represents a promising alternative approach (Popa-Lisseanu et al. 2007, Yang et al. 2008). The temporal availability of these foods – e.g., birth pulses of vulnerable young and seasonal fruits – is often predictable, and therefore we might expect predators to actively search for them. However, evidence in support of this with young vertebrate prey is mixed: predators actively searched for songbird nests and ungulate neonates in some studies (Pelech et al. 2009, Rayl et al. 2018) but appeared to incidentally encounter them in others (Svoboda et al. 2019, Bowersock et al. 2021, Ruprecht et al. 2021b). Unfortunately, studies on ungulate neonate predation are often of limited use for understanding prey switching because they are habitat-selection based (i.e., they do not quantify actual predation; Suraci et al. 2022) and often do not quantify alternative food availability. Studies also often have limited predator sample sizes, precluding their ability to compare differences in behavior across individuals.

A deeper understanding of prey switching behavior also requires quantifying intra-population variability in diet. In addition to variation across segments of the population (e.g., comparing male and female diets), variation across individuals (i.e., individual specialization) is a widespread, historically underappreciated, and evolutionarily important source of variation in populations (Bolnick et al. 2003, Araújo et al. 2011). Individual specialization has generally been shown to reduce intra-specific competition (Huss et al. 2008, Araújo et al. 2011), though what proportion of populations converge on temporary, highly profitable foods (Popa-Lisseanu et al. 2007), thus increasing intra-specific competition, is relatively unknown. Understanding individual responses to availability of highly profitable foods would be particularly useful for top carnivores, given the stabilizing effects they can have on systems (Rooney et al. 2006, Araújo et al. 2011) and their impacts on important game species and livestock (Ripple et al. 2014).

Thus, we can move our understanding forward by tracking how a top predator responds to resource pulses. To this end, we studied how coyotes (*Canis latrans*) collectively and individually responded to fluctuations in food availability in the southeastern United States (Figure 2.1). Coyotes in this system are an excellent focal species for several reasons: 1) they are highly adaptable and known to exploit temporary foods (Jensen et al. 2022; 2) they are the largest carnivore across most of this system and thus not subject to the complexity of top-down effects from other predators (aside from humans); and 3) they are of high interest to managers (Kilgo et al. 2010), having just arrived in the last 50 years (Hody and Kays 2018). Indeed, coyotes seem to be particularly effective white-tailed deer fawn (*Odocoileus virginianus*) predators in the southeast (Kilgo et al. 2019), leading to wide-scale persecution of coyotes across the region. Critically, fawns are primarily susceptible to coyote predation for the first three-six weeks of the fawn's life (Kilgo et al. 2012, Nelson et al. 2015), representing a highly nutritious, yet ephemeral, food on the landscape. Thus, the diversity of foods that coyotes eat (including fruit, small mammals, rabbits, birds, and insects; Schrecengost et al. 2008, Cherry et al. 2016), has raised the question of whether these foods, if abundant enough, could reduce predation on fawns during this window of vulnerability (Schrecengost et al. 2008, Kelly et al. 2015). Although these studies concluded that other foods cannot reduce fawn predation, they did not track availability.

Understanding individual variability in fawn predation could also inform current coyote management. Although even intensive coyote removal seems to have marginal effects on fawn survival (Kilgo et al. 2014, Gulsby et al. 2015), what proportion of the population is responsible for killing fawns has remained an open question. If patterns exist, they might parallel coyote predation on sheep, with territorial breeding pairs, especially the males, being primarily responsible (Sacks et al. 1999). However, if all (or most) coyotes kill fawns, then removing a territory holder could increase fawn predation through an influx of immigrants vying for the vacant territory (Knowlton et al. 1999).

Our overall goal was to quantify how coyotes responded to changes in food availability at multiple temporal scales. First, we described seasonal dietary patterns for our coyote population (objective one), then tested how coyotes responded to seasonal changes in small mammal availability (objective two). We chose small mammals for this objective because they are available year-round and are a staple food for coyotes across their range (Jensen et al. 2022). We hypothesized that coyotes would either track the availability of small mammals across seasons, or exhibit selectivity for them, wherein consumption would remain stable even when availability declined. Although other studies have reported selection for small mammals by coyotes (though only in arid regions; Windberg and Mitchell 1990, Hernández et al. 2002), we predicted that coyotes would not in our study because there would be more profitable (temporarily available) food items. Third, we focused on summer diets when deer fawns and blackberries were large components to their diet and tested the hypothesis that coyotes would exhibit dietary switching as a function of fine-scale variation in their availability (objective three; Figure 2.1). We predicted that coyotes would exhibit selectivity for fawns, but only the availability of young neonates as opposed to total fawn availability (Kilgo et al. 2012, Nelson et al. 2015). We also predicted that there would be no temporal lag in how long it took coyotes to respond to availability because of how behaviorally plastic they are (Newsome et al. 2015, Jensen et al. 2022). Lastly, we tested the hypothesis that dietary variation was attributable to sex and individual (objective four). We predicted that males would be more carnivorous than females (Sacks et al. 1999, Ruprecht et al. 2021a) and that individual dietary specialization would be lowest when temporary foods were available (Tatler et al. 2019). We hypothesized that genetic distance could influence diet, where individuals more distantly related to the rest of the population would have more divergent diets (Sacks et al. 2008). Collectively, our study represents one of the most comprehensive studies of carnivore diet to date, with ecological implications for how predators track resource pulses and management implications for widely persecuted carnivores like coyotes and their large herbivore prey.

METHODS

Study area

We collected scats across ~15,000 acres (61 km^2) of private land in McCormick County, South Carolina (Figure 2.2). Our study area was representative of the Piedmont physiographic region, with a humid subtropical climate, mild winters (typically 3-13° C), and gently rolling hills (120 -180 m elevation; 40). Most of the land was covered by loblolly pine (*Pinus taeda*) plantations in various successional stages. There were pastures and fields intermittent throughout the landscape, including planted food plots for game species. Midstory and understory plants that coyotes might eat included persimmon (*Diospyros virginiana*), blackberry (*Rubus allegheniensis*), and muscadine (*Vitus rotundifolia*). Other potential coyote prey included deer, wild pigs (*Sus scrofa*), eastern cottontails (*Sylvilagus floridanus*), and small mammals. Hunting occurred throughout the study area, including deer season from October – December. Human density was generally low (< 100 people per km^2), yet human-induced coyote mortality was common (typically from being shot).

Scat survey study design

We collected scats during three survey periods throughout the year from summer 2019 through summer 2021 (seven total survey seasons). We chose our survey periods to capture potentially important differences in food availability and coyote life history throughout the year. We sampled from mid-January through mid-March (winter) when colder temperatures were associated with limited food availability and coyote mating season. We sampled from early May through mid-July (summer) to represent a period when vulnerable fawns and blackberries were available and when many adult coyotes are rearing pups. We sampled mid-October through mid-December (fall) to capture the period when hunters legally harvest deer and potentially leave carcasses or offal for scavenging and when juvenile coyotes typically disperse. During each season we surveyed ~16 km of dirt roads broken up into 7-15 transects distributed across our study area (Figure 2.2). We used GPS data from collared coyotes to help inform the location of our transects because we wanted to maximize our chances of collecting scats from collared individuals (Appendix S1: Section S1).

Scat collection

We typically surveyed transects using off-road vehicles (ATV or UTV). During the first survey of each season, we collected relatively fresh scats and cleared the transect of old scats so that we could more accurately age scats found during the next survey. We surveyed transects every 14 days in the winter and fall, and every 4-7 days in the summer (when heat and humidity degrade DNA faster). Each time we found a carnivore scat we estimated its age in days, recorded its GPS location, and assigned a field species ID. We used size, shape, apparent contents, and context clues (i.e., tracks) to assign a species ID (Elbroch 2003), and included a confidence level of low, medium, or high for our ID (Morin et al. 2016). We also pulled off a pea-sized amount of fecal material from the exterior and placed it in 1.4mL of DETs buffer (Stenglein et al. 2010), which preserves DNA. We placed the remainder of the scat in a plastic bag and froze it for later dietary analysis.

Genetic screening

We used the samples we preserved in DETs buffer to conduct species identification (SID) of the scat depositor using polymerase chain reactions (PCR). First we extracted the DNA from the samples using the Qiagen QIAmp Fast DNA Stool Mini Kit (Qiagen, Valencia, CA, USA) in a laboratory dedicated to low quantity DNA sources and included an extraction negative in each batch. We then conducted SID PCR with a carnivore primer multiplex (De Barba et al. 2014), which is designed to amplify the mitochondrial DNA of whichever carnivore species' DNA is present. We included a PCR- and a PCR+ (gray wolf, *Canis lupus*) on each PCR plate. We used the Applied Biosystems 3130xl ABI capillary machine (ABI) and GeneMapper 6 to analyze the lengths of the amplified DNA fragments and determine the species of origin (sensu Stenglein et al. 2011). We determined that samples with peaks in fluorescent intensity ≥ 100 only at known coyote fragment lengths were deposited by coyotes. There were also 40 samples which had peaks at coyote (≥ 1000 fluorescent unit intensity) and another carnivore (with peaks between 100 - 500), which we passed on to individual ID (see *Objective four*) and determined that successful amplification meant the sample was deposited by coyotes.

Scat content analysis

We quantified coyote diet by isolating the solid material in each coyote scat and identifying it visually. Although genetic approaches to identify food items are becoming more common (i.e., metabarcoding; de Sousa et al. 2019), we elected to use visual identification for two reasons. First, our objectives focused on a core group of easy to visually identify dietary items. Second, we needed to be able to differentiate age classes of deer. We dried the frozen scats in an oven at 85° C for 48 hours, which desiccated them and killed any parasite eggs. We then washed them on a stack of five progressively fine metal sieves (6.3mm, 2mm, 500µm, 63µm, 1.25µm; Advantech Manufacturing, New Berlin, Wisconsin, USA; Newark Wire Cloth Company, Newark, New Jersey, USA), which isolated the solid material (e.g., hair, bone, seeds, feathers). We then air dried the samples for ≥ 72 hours, then separated the contents into material type (hair, bones, feather, vegetation, insect, or other). We used a combination of technical manuals on mammal hair (Moore et al. 1974, Teerink 1991), hair reference slides, and online sources to identify the contents of each sample.

We quantified the amount of the following 11 categories in each sample: deer, wild pig, rabbit, small mammal, other mammal (i.e., armadillo, carnivore, unknown mammal), bird, insect, blackberry, persimmon, other fruit and vegetation (i.e., apple, cherry, grass/leaves/pine needles/bark), and other (i.e., anthropogenic and unknown). In addition, each category received an ID confidence score from 1-3, where 3 was high confidence, 2 was medium confidence, and 1 was low confidence. Most of the confidence “1” items were mammals so we moved those to the “unknown mammal category” and put the others in “other vegetation” or “other”. To differentiate fawns from adult deer during the summer, we measured the width of five hairs from three < six-week-old fawns and three adults from our field site. We determined that hairs < 70 micrometers were likely from fawns, hairs > 90 micrometers were likely from adults, and hairs 70-90 micrometers were ambiguous (Ward et al. 2018). Therefore, for each summer sample with deer hair, we measured three randomly selected deer hairs and used the average width to classify the sample as either fawn, adult, or ambiguous. In addition, if a sample from the summer was classified as ambiguous based on hair width but we found small hooves in the sample, we reclassified that sample as fawn.

After identification, we estimated the percent volume of the sample made up by each category on a scale of 0-5, where 0 was not present, 1 was < 2% (trace), 2 was 2-25%, 3 was 26-50%, 4 was 51-75%, and 5 was 76-100% (Prugh 2005). We converted scores of ‘1’ to ‘0’ for all food items (Prugh 2005), and also scores of ‘2’ to ‘0’ for grass/leaves/pine needles/bark since sometimes these items are collected inadvertently. Because it can be beneficial to compare multiple metrics of carnivore diet when possible (Bojarska and Selva 2012), we also corrected for digestibility using values from side-striped jackal feeding trials (*Lupellela adusta*, Atkinson et al. 2002, reported in Loveridge and Macdonald 2003. We multiplied each food item's estimated volume (0-5) by the appropriate correction factor, using the medium mammal correction factor for deer and wild pigs because Atkinson et al. (2002) did not include ungulates in their feeding trials.

Objective one: Overall and seasonal patterns in coyote diets

We calculated the % weighted occurrence by summing all of the scaled (0-5) or digestion-corrected (0-31.5) occurrences for a given food item during a given time period of interest (i.e., season) and dividing by the total sum of the occurrences for all food items in that time period (Prugh 2005), where X is whether or not food item i is present in sample s (0 or 1) and Y is the scaled or digestion-corrected amount:

% weighted occurrence of food item $i = \frac{\sum_s^S X_{is} Y_{is}}{\sum_i^I XY}$

Objective two: Small mammal consumption relative to seasonal availability

We evaluated support for our hypotheses of whether coyote consumption of small mammals reflected seasonal changes in small mammal availability by measuring small mammal activity at baited cameras (hereafter "sm cameras") concurrent with scat survey seasons. We deployed 30-32 sm cameras from fall 2019 through summer 2021 (six survey seasons, no sm cameras in summer 2019). We describe our methods in detail in Appendix S1: Section S2. Briefly, our setup consisted of a downward-facing camera affixed to the top of metal stake with birdseed gravity-fed from a pipe (Figure 2.2). We counted the number of small mammals in each nighttime photo using TimeLapse 2 (Version 2.2, Greenberg 2021). We summed the number of individuals in each photo for each site, and then averaged those values across all sites for each year-season to obtain a single index of availability for small mammals during each season of our study. We used a generalized linear mixed model to quantify how the availability of small mammals was related to their consumption. Our observation unit was an individual scat, and our response variable was the digestion-corrected weighted occurrence of small mammals. Our predictor variables were the averages from our sm cameras from each year-season, season (winter, summer, fall; winter was the reference category), and site as a random effect. We used a zero-inflated Poisson distribution, fit models with glmmTMB (Brooks et al. 2017), and checked model fit using the DHARMa package (Hartig 2020).

Objective three: Consumption of fawns and blackberries in the summer relative to availability

To investigate the fine-scale dietary response to temporary foods, we quantified the weekly availability of fawns and blackberries in the summer. We used data from a concurrent study of fawn survival in our study area (Appendix S1: Section S3), where we counted the number of alive GPS-collared fawns each day beginning in mid-April and ending in mid-July. To test our hypothesis about the age of fawns, we also estimated availability while accounting for fawns aging out of predation risk after they were 22 or 43 days old (Kilgo et al. 2012, Nelson et al. 2015). Since there were different numbers of fawns captured each year (2019 = 37, 2020 = 27, 2021 = 20), we divided the number of available fawns each day by the total captured each year to create a proportion. We then averaged these daily percentages each week (Monday – Sunday) to create the weekly fawn availability index. We also estimated weekly blackberry abundance in the field beginning in mid-May and ending in mid-July in 2020 and 2021 (Appendix S1: Section S4). Briefly, we counted the number of unripe and ripe blackberries each week at several sites that represented different forest successional stages. Since we did not count blackberries in 2019, we used data from 2020 and 2021 to estimate their availability in 2019 after ensuring that the timing of ripe blackberry availability was similar between years (Figure A2.2, Text A2.4). We used this blackberry data to both test how availability was related to their consumption and the consumption of fawns (Figure 2.1B).

We used generalized linear models to test our hypotheses about how coyotes responded to temporary foods. To match our weekly availability data, we classified each coyote scat as representing consumption during a certain week over the summer. In order to more accurately date when the scat contents were consumed, we subtracted its estimated age from the date we collected it plus another day to account for digestion. Our observation unit was an individual scat, and our response variable was the average percent weighted occurrence of fawns or blackberries during that week. We chose to use this metric because we did not have specific digestibility correction factors for fawns or blackberries.

For fawns, our predictor variables were % available ≤ three-week-old fawns, % available ≤ six-week-old fawns, % available all fawns, ripe blackberry availability, and % weighted occurrence of blackberries consumed that week. For each fawn variable, we created three variations, using availability from that week, the week prior, and two weeks prior (Table A2.1). In order to determine which of these three variations best fit consumption data, we compared them using AIC_c (Burnham and Anderson 2002) and selected the top model. We found that the top model for ≤ three-week-old fawns had a two-week lag, the top model for ≤ six-week-old fawns and all fawns had a one-week lag (Table A2.1). Using these top models, we built 18 models − univariate fawn models, univariate blackberry models, as well as additive and interactive fawn and blackberry models (Table A2.2). For the blackberry analysis, our predictor variables were unripe and ripe blackberry availability, and we tested the same three variations of time lag as the fawn analysis (Table A2.3). The top models for unripe and ripe blackberries had no lag. We compared models using AIC_c, considered models with < 2 delta AIC_c as candidates, and considered variable effects significant if 95% confidence intervals did not overlap zero. We used a zero-inflated Poisson distribution for all models in this objective, included year as a fixed effect, and checked model fit using the DHARMa package (Hartig 2022).

In order quantify the effect that blackberries had on fawn consumption, we compared the difference in fawn availability and consumption during periods before and during peak blackberry availability. First, we calculated the average difference between fawn consumption and ≤ six-week-old fawn availability from April 30 – June 11. We used this number to calculate what fawn consumption would have been without blackberries by adding it to fawn availability during the weeks blackberries were peaking (June 18 – July 9). We then subtracted the actual fawn consumption during the blackberry weeks to find the difference each week. We summed these differences and used the differences in total percent to recalculate the weighted occurrence of fawns in the summer (assuming that fawn remains in a scat equal one dead fawn).

Objective four: Individual variation in coyote diet

For this objective, we evaluated support for our hypotheses that sex and individual identity would influence diet. After completing genetic species ID, samples with peaks in fluorescent intensity ≥ 1000 at known coyote fragment lengths were passed on to individual ID. In addition to these samples, we also passed the gray wolf/dog samples onto individual ID (n = 6) because domestic dog haplotypes are known to occur in coyotes in the southeastern US (Adams et al. 2003). We used a multiplex of 10 nuclear microsatellite loci and two canid-specific sex ID loci (Seddon 2005), using a similar PCR and ABI process as described in *Genetic screening*. We performed two PCRs on each sample before assessing loci amplification success using a Microsoft Access database (Skrbinsek 2016), excluding samples with < 40% loci amplification. We repeated PCR with the rest of the samples 1-4 more times, or until there was consensus at ≥ 7/10 loci (Taberlet et al. 1996). We excluded samples without consensus at the sex loci (not clearly from a male or female).

Next, we grouped samples with each other using their genotypes. Using 89 coyote tissue samples collected from our study area (Appendix S1: Section S1), we calculated that sample genotypes needed to match at ≥ five loci and to meet a probability of identity siblings threshold of < 0.01 as evidence that they came from the same individual (Waits et al. 2001) using GenAlEx 6.5 (Peakall and Smouse 2006). We determined that our gray wolf/dog samples were actually from coyotes if they matched with confirmed coyote samples (n = 4), otherwise we excluded them. When a sample had one allele that did not appear in other samples in that group (n = 16 samples), we considered it a match if all of the following criteria were met:

1. The sample matched the group's reference sample at ≥ 7 loci
2. The sample's sex (male or female) matched the group's sex
3. It was collected near other samples in that group (based on GPS coordinates)

Using this subset of individually identified samples (n = 333), we analyzed variation in diet attributable to season, sex, genetic distance, and individual. Our response variables were the weighted occurrence of deer, small mammals, rabbits, and vegetation during each season. We focused on these food items because they made up 83-91% of weighted occurrence (Figure 2.3). For our sex-related hypothesis, we combined season and sex into a single categorical variable (6 categories) with winter male diets as the reference category. For our genetic distance hypothesis, we calculated the proportion of shared alleles (Bowcock et al. 1994), then computed the average pairwise distance score for the most complete (least missing alleles) sample from each individual and the rest of the reference samples using the memgene package in R (Galpern et al. 2014). We used generalized linear mixed models with a Poisson distribution and fit a global additive model for each food category. We used individual as a random effect and quantified the effect from individual by conducting a likelihood ratio test on the full model and the reduced model without the random effect. We used the DHARMa package (Hartig 2020) to check model fit and considered variables with 95% confidence intervals not overlapping zero to be significant.

We also quantified individual variation in coyote diet across seasons. For each season, we used individuals from whom we collected $\geq$ two scats in that season (winter = 17 individuals, 49 scats; summer = 31 individuals, 104 scats; fall = 22 individuals, 78 scats). We calculated the weighted occurrence of each food category for each individual (using the same formula in *Objective one*) and estimated the variance of each food category within each season by calculating the coefficient of variation (standard deviation divided by the weighted mean). We used these same individual data to calculate individual specialization during each season. We used Roughgarden’s (Roughgarden 1972) metric, which assumes that the total niche width (TNW) is equal to the variation in resource use within individuals (WIC) plus the variation between individuals (BIC), such that $\frac{WIC}{TNW}$ estimates the amount of individual specialization. Values closer to one approach all individuals using the full range of the dietary niche, while values closer to zero indicate lower dietary overlap among individuals (Bolnick et al. 2003). We used the RInSp package (Zaccarelli et al. 2013) to calculate TNW and WIC for each season.

RESULTS

We collected 821 scats during our surveys, of which 540 (66%) were genetically confirmed to be from coyotes. The remaining samples were bobcat (124, 15%), gray fox (15, 2%), red fox (2, < 1%), two species (44, 5%), and unknown (species ID failed; 96; 12%). Overall, we were 73% accurate at identifying coyote scats in the field and 78% accurate identifying bobcat scats (Table A2.4).

Objective 1: Seasonal patterns in coyote diets

The overall weighted occurrence of foods in coyote diets was 26% deer, 18% small mammal, 15% persimmon, 11% other fruit and vegetation, 9% blackberry, 6% rabbit, 4% other mammal, 3% insect, 2% wild pig, 1% bird, 1% other, and < 1% anthropogenic (Figure 2.3). We collected 132 scats in the winter, 206 in the summer, and 202 in the fall (77 on average each survey season). Coyote diets varied substantially among seasons, where small mammals were the most consumed item in the winter, fawns and blackberries were the most consumed items in the summer, and persimmons were a major component in the fall (Figure 2.3). During the summer, fawns made up 26% of coyote diets, deer of ambiguous age were 7%, and adult deer were 2%. Correcting for digestion made mammals more important and other food items (i.e., fruit) less important in coyote diets (Figure 2.3).

Objective 2: Small mammal consumption relative to seasonal availability

With the exception of summer 2021, we found support for the hypothesis that small mammal consumption would track availability (Figure 2.4). Small mammal consumption was positively related to their availability through time (estimate and 95% confidence intervals = 0.15 [0.03 : 0.27]. Relative to winter, small mammals were consumed less in the summer (-0.27 [-0.41 : -0.13]) and a similar amount in the fall (0.05 [-0.20 : 0.29]; Figure 2.4).

Objective 3: Consumption of fawns and blackberries in the summer relative to availability

During the summer, we collected 41 scats in 2019, 75 in 2020, and 90 in 2021. The only candidate model in the fawn analysis was a sub-global model which included an interaction between ≤ six-week-old fawn availability (one-week lag) and consumed blackberries (85% of model weight; Table A2.2). Fawn consumption was positively related to fawn availability (estimate and 95% confidence intervals = 0.37 [0.19 : 0.55]) and negatively related to blackberry consumption (-0.75 [-1.02 : -0.49]), though blackberries primarily had an effect when fawn availability was declining (0.44 [0.18 : 0.69]; Figure 2.5). Thus, we found support for our prediction that younger fawns would primarily be consumed, though our prediction that there would be no lag in response was not supported.

Weekly fawn consumption was 10.2% greater (on average) than weekly fawn availability during the first half of fawning season (April 30 - June 11), then only 2.2% greater while blackberries were available (June 18 – July 9; Figure 2.5C). The difference then rose back up to 10.6% during our last survey week when blackberry consumption became negligible (though our scat sample size was three; Figure 2.5C). If fawn remains in a scat are equivalent to one dead fawn, then fawns being in 26% of scats in the summer would equate to 53 dead fawns (summer sample size 202 * 0.26). However, without a pulse of blackberry availability, fawns would be 28% of scats, equating to 56 dead fawns (a 6% increase in dead fawns).

The only candidate model in the blackberry analysis was the ripe blackberry availability (no lag) model (66% of model weight; Table A2.2). Blackberry consumption was positively related to ripe blackberry availability (0.34 [0.04 : 0.63]); indeed, except for the first week of June, blackberry consumption was commensurate with weekly availability from mid-May through mid-July (Figure 2.5B). Thus, unlike fawns, we found support for our prediction that there would be no lag in response.

Objective 4: Individual variation in coyote diet

We individually identified 333 coyote scats from 117 different individuals. Sixty-one individuals contributed one sample, while the remaining 56 individuals contributed an average of 4.8 samples. There was nearly equal representation among sexes (176 male, 167 female) but unequal representation among seasons (69 winter, 150 summer, 114 fall). There were significant differences in consumption of our focal food items among seasons, which were generally maintained by both males and females (Figure 2.6). Our hypothesis that males would be more carnivorous than females was generally not supported, as they had statistically similar diets in 10/12 of the season food-item combinations we examined. However, males ate 15% more deer in the fall and 13% more vegetation in the winter, compared to females (Figure 2.6). We found no support of an effect from genetic distance on consumption of any of the four food categories.

However, our likelihood ratio tests indicated that including a random effect from individual significantly improved model performance for each food category (all p-values were < 0.001).

We found that most individuals had diverse diets with substantial consumption of the dominant seasonal food items (Figure 2.7). Even with two or three samples from 73% of individuals, we rarely documented individuals eating just one type of food during a season (4% of individuals). In the summer, deer were eaten by 90% (81% for fawns) of individuals, while blackberries were eaten by 65% of individuals. For comparison, deer were eaten by 53% and 68% of individuals during the winter and fall, respectively. In the fall, persimmons were eaten by 82% of individuals. In the winter, small mammals were eaten by 71% of individuals, compared to 48% and 59% of individuals during the summer and fall, respectively. These percentages for the summer and fall were surprisingly high, considering small mammals were 3-4x less important in overall diet compared to winter (Figure 2.3). This was also true for insects in the summer – they were eaten by 39% of coyotes but were only 3-6% of diet. Other than these cases, variability (coefficient of variation) was generally negatively related to the weighted occurrence of a given food during each season (Figure 2.7).

We found support for our hypothesis that temporary foods influenced individual specialization in our population of coyotes. The total niche width (TNW) of the population was similar in summer (0.047) and fall (0.042) yet was 1.7x greater in winter (0.073). However, the within-individual component (WIC) in the summer (0.018) and fall (0.030) made a larger proportion of TNW than in the winter (0.021), such that $\frac{WIC}{TNW}$ (individual specialization) was 0.287 in the winter, 0.390 in the summer, and 0.718 in the fall. Using the fall as an example, these ratios mean that ~72% of the dietary variation in the population can be explained by the variation in the proportion of each food item within an individual’s diet, while ~28% of the variation can be explained by dietary differences across individuals.

DISCUSSION

Understanding how wild predators respond to fluctuations in food availability is key for understanding predator-prey dynamics (Abrams and Ginzburg 2000, Miller et al. 2006) and managing wildlife populations. By tracking coyote diets and the availability of food items, we showed that temporary foods are a key determinant of coyote behavior in our system (Popa-Lisseanu et al. 2007, Yang et al. 2008, Tatler et al. 2019), and that their ability to exploit these foods both directly facilitates, and potentially indirectly reduces, fawn predation. Similar to coyote populations in other portion of their range (Jensen et al. 2022), we showed that small mammal consumption largely reflected availability throughout the year, with the exception of summer, when two important high value food items became available (fawns and blackberries). Fine-scale analysis of summer diet suggests a rapid switching to fawns as they become available, but then a gradual reduction in fawn consumption mid-summer when availability of young (≤ six-week-old) fawns decreased and there was a pulse of blackberry availability. Most individuals in the population converged on temporary foods, suggesting these rapid responses to pulses of high value foods are happening across the population and targeted efforts to remove problem individuals are unlikely to be effective.

Seasonal shifts in diet

Coyote diets are known to vary substantially across seasons (Jensen et al. 2022), though the food items they eat reflect local availability. During the winter, we found that 75-84% of coyote diet was mammals, and they ate 3-4x more small mammals and rabbits during the winter compared with summer and fall. This relatively carnivorous diet in winter likely reflects increased vulnerability of small-medium mammals in sparser understory, lower availability of fruit, and perhaps increased reliance on scavenging deer carcasses (Ruprecht et al. 2021a, Jensen et al. in revision). During the summer, fawns and blackberries were 50-60% of coyote diets, demonstrating a remarkable shift to these temporary foods. Indeed, by building on previous methods to differentiate ungulate age classes in diet, we showed that fawns constituted 75-95% of deer consumption in the summer. Other coyote diet studies in the southeast have also differentiated fawns from adult deer and reported somewhat lower percentages of fawns (60-65%; 27, 28, 49). Coyote diet in the fall was functionally similar to summer (~60% fruit and deer), but persimmons replaced blackberries and it is unclear how coyotes obtained deer. Although it is possible that some of the consumed deer were killed by coyotes (Chitwood et al. 2014), it is likely that most of the deer were scavenged from hunter kills or roadkill (Ruprecht et al. 2021a, Jensen et al. in revision).

Small mammals were a staple food for coyotes, with consumption likely influenced by both apparent fluctuations in their availability and the availability of more profitable foods. Other than the last season (summer 2021), small mammal consumption seemed to be commensurate with their availability measured at our specialized cameras. This finding contrasts with other studies that reported coyote selection for small mammals (Windberg and Mitchell 1990, Hernández et al. 2002), though this may be because those studies were in arid regions where small mammals are a more important part of coyote diet (Jensen et al. 2022). The large mismatch between availability and consumption in summer 2021 may be explained by the dominance of deer and blackberries in coyote diets. Despite relatively high availability of small mammals, coyotes seemed to have focused on the temporary boom of fawns and blackberries, as they did in the two previous summers as well.

Our finding that small mammal availability was greatest in the winter (other than summer 2021) could reflect an important distinction between abundance and availability. Small mammal abundance should be greatest in the summer and early fall, coincident with peak litter production. Therefore, greater small mammal availability during winter as measured by our baited cameras could reflect an increased willingness to feed in the open, and therefore be more available to coyotes. These findings highlight our methodology (and others like it e.g., McCleery et al. 2014) as a potentially attractive alternative to mark-recapture, from an ecological (and logistical) perspective.

Summer dietary switching

By quantifying weekly diets and availability of fawns and blackberries, we showed how a carnivore functionally responds to temporary foods. Past fawn survival studies have shown that there is a window of high vulnerability to coyotes (birth – six weeks; Kilgo et al. 2012, which our results support. Availability which accounted for fawns ‘aging out’ of predation risk after six weeks most closely matched fawn consumption. This was most apparent beginning in June, as consumption declined with availability of ≤ six-week-old fawns and the availability of all fawns (regardless of age) remained relatively high.

Two lines of evidence suggest that coyotes switched their diet to prioritize fawns. First, the largest difference between availability and consumption was during the first three weeks of May, as availability was rising, yet still relatively low. Second, fawn consumption matched availability more closely after a one-week lag, which suggests that coyotes behaviorally responded to fawn availability on the landscape. It is unlikely that this lag is an artifact of sampling because we accounted for the age of the scat and digestion when dating each scat. No previous studies that we are aware of have quantified carnivore diet and food availability at the temporal scale we did here, yet it may be worth comparing our findings to movement studies. One study in Michigan quantified carnivore movement during three periods of varying fawn availability and found that both coyotes and wolves did not select for areas with greater predicted fawn availability (Svoboda et al. 2019). Similarly, coyote movement in New York and Oregon was not found to be related to changes in fawn availability (Boser 2009, Ruprecht et al. 2021b). Thus, these findings seem to contrast with ours, though future research should quantify how important fawns are in coyote diets when there are even fewer vulnerable fawns on the landscape (as we were unable to collect scat samples during April).

Although complicated by the concurrent decline in young fawn availability, we found evidence that blackberries serve to buffer predation on fawns. Blackberry consumption had a strong effect on fawn consumption in our models, and our post-hoc analysis suggests that the effect of blackberries on fawn survival was modest (+ 6%). The only other study on weekly carnivore diets that we could find was from a wolf pack in Minnesota, where the pack ate fawns in early summer but then predominantly ate berries in mid-summer, which appeared to have a direct effect on fawn consumption (Gable et al. 2018). Blackberries would likely reduce fawn predation further if there were more of them or if their peaks in availability were more aligned. Other studies on coyote diet in the southeast have also reported heavy use of blackberries (Schrecengost et al. 2008, Cherry et al. 2016), yet also substantial use of other summer fruits like wild plum and wild grape (Schrecengost et al. 2008, Kelly et al. 2015, Cherry et al. 2016), which we rarely found in scats. Perhaps forest management practices (clearcutting and burning) created ideal conditions for blackberries in our study area, particularly in immature pine stands (5-10 years old, personal observation), while practices at other sites favored wild plum and wild grape. Thus, habitat management which promotes fruit mast (such as not spraying herbicide) may buffer fawn predation to some extent, though there is a need for future experimental work. Similarly, less fawns may be killed if climate change is shifting the timing of blackberry fruiting to be more aligned with fawn availability (the southeast is generally warming; Schwartz et al. 2006), particularly if plant phenological responses outpace changes in mammal birth timing. Indeed, the effects from alternative foods will also likely be a function of how predators behaviorally respond, as we found no evidence for a temporal lag in how coyotes responded to blackberries (unlike fawns, for which we found a one-week lag).

Evidence of close tracking of alternative food items is also relevant in the context of predator management more broadly because previous studies have generally concluded that supplemental or diversionary feeding did not reduce predation on focal prey species (Kubasiewicz et al. 2016). For example, providing supplemental foods to coyotes, gray wolves (*Canis lupus*), and bears did not increase caribou calf survival (*Rangifer tarandus*), though it may have increased moose calf survival (*Alces alces*; Boertje et al. 1992, Lewis et al. 2017, Pugesek et al. 2021). Providing carrion to brown bears (*Ursus arctos*) did not reduce livestock depredation in Slovenia or Canada (Kavčič et al. 2013, Morehouse and Boyce 2017), and supplemental feeding did not reduce duck nest predation in North Dakota (Conover et al. 2005). However, supplemental foods seem to reduce conifer damage by bears in the pacific northwest (Partridge et al. 2001,Ziegltrum 2004). While providing supplemental foods to predators like this is both expensive and logistically taxing (Boertje et al. 1992), habitat management that enhances the availability of naturally occurring seasonal food items is typically feasible; and thus an important line of future inquiry (including experimental manipulations) when the goal is to improve recruitment of large herbivores.

Individual dietary variability

We found evidence for both dietary convergence and divergence in our coyote population. Male and female diets were similar in the summer, when they both switched primarily to eating fawns and blackberries. Though it is possible that some of the fawns were killed by a mate and brought back to the den, our (unpublished) data from GPS collared coyotes indicate that females resumed foraging a few days after giving birth. During the winter, males were more omnivorous than females – vegetation was the second most important food for males after small mammals (fourth most for females). The importance of vegetation for males was somewhat surprising given the lower relative availability and nutritional value of vegetation in winter. By contrast, males were more carnivorous (ate more deer) than females in the fall. This could reflect a greater propensity to scavenge, which would align with a finding that resident male coyotes were the primary demographic scavenging at cougar kills (*Puma concolor*; Ruprecht et al. 2021a). These differences in fall and winter could also be explained by differences in habitat selection or movement rates (Chamberlain and Leopold 2000), which could lead to differences in food encounter rates.

Our individual diet analysis showed that most of the individuals in our population converged on temporary food items (81% ate fawns, 65% ate blackberries, and 82% ate persimmons). The true percentages are likely even greater, considering our limited sample sizes from many individuals. Combined with our sex findings, these results suggest that all (or nearly all) coyotes eat fawns. This has important management implications, namely that killing any one coyote will not necessarily reduce fawn predation more than killing any other coyote. Indeed, there is good evidence that even intensive coyote removal, only marginally (at best) improves fawn survival (Kilgo et al. 2014, Gulsby et al. 2015).

We also found that individual specialization was lowest when fawns and fruits were available. When these items were not available (in the winter), 71% of dietary variation was explained by differences among individuals (compared to 61% in summer and 28% in fall). Indeed, this variation among individuals was so relatively large as to make the total niche width of the population largest in the winter (even though some foods have relatively low availability, e.g., fruits and insects). As we predicted, individual specialization was lower in the summer, but we did not expect it to be lowest in the fall. This suggests that coyotes may be keying into persimmons even stronger than fawns or blackberries, though we were unable to devise a method to quantify persimmon availability to test this. Collectively, these results suggest that the intensity of intra-specific competition is dynamic, and subject to the availability of temporary foods. However, stronger evidence for our conclusions would have come from sample sizes large enough to track the diets of individuals across seasons (Araújo et al. 2011), to see how much changes in availability influenced their diet. Future research should also investigate how individual coyote diet scales up to influence fitness (Balme et al. 2020).

Conclusions

We present evidence that seasonal resource pulses can alter predator foraging behavior and potentially influence predation on an important large herbivore game species. Given the limited success of supplemental foods to reduce predation on wild ungulates and livestock (e.g., Kubasiewicz et al. 2016, Lewis et al. 2017), our findings may be of particular interest to managers looking for indirect ways to influence carnivore behavior. Indeed, for carnivores where even intensive removal efforts are either not effective (e.g., coyotes; Kilgo et al. 2014) or not socially acceptable (Decker et al. 2006), further research into how alternative foods can influence predation on focal species may be warranted.

Our results also suggest that there are other ecological effects stemming from an ability to switch between foods. Although most mammalian carnivores are threatened with extinction (Marneweck et al. 2021), there are several species, either with expanding ranges or of management importance, which have diets that are diverse and regionally varying (e.g., dingoes, golden jackals, raccoons, coyotes; *Canis dingo, Canis aureus, Procyon lotor*; Doherty et al. 2018, Salgado 2018, Lange et al. 2021, Jensen et al. 2022). Flexible diets, and more specifically, their ability to exploit temporary foods, are likely core reasons why these carnivores are not only able to expand into new niches (Popa-Lisseanu et al. 2007), but also maintain high population densities (Caut et al. 2008).

Lastly, we showed how a wild predator functionally responds to changes in food availability at an unprecedented resolution. Our results suggest that most (if not all) coyotes key in on young fawns when available, but that it takes them about one week to respond to changes in fawn availability. In contrast, there was no temporal lag in their response to blackberries, perhaps suggesting that the behavioral response depends on the foraging strategy needed to locate different foods. Although we think our dietary approach represents an important advancement in understanding wild predator behavior in response to resource pulses, integrating spatial data is still needed to quantify if and to what degree predators alter their habitat selection or movement (Lesmerises et al. 2015, Rayl et al. 2018, Ruprecht et al. 2021b). Ultimately, our study is an important step forward in understanding the effects of resource pulses on predator-prey dynamics, with implications for the management of predators and their large herbivore prey.

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TABLES

Table 2.1. Estimates and 95% confidence intervals (CI) from statistical analyses of coyote diets in South Carolina, USA. We only show variables from candidate models for which 95% confidence intervals did not overlap zero.

Response variable	**Predictor variable**	**Estimate**	**Lower 95% CI**	**Upper 95% CI**
Small mammal consumption	1) Seasonal small mammal availability	0.150	0.034	0.266
	2) Summer (relative to winter)	-0.273	-0.415	-0.132
Fawn consumption	1) ≤ Six-week-old fawn availability (FA)	0.369	0.186	0.553
	2) Blackberry consumption (BC)	-0.753	-1.021	-0.485
	3) Interaction (FA * BC)	0.437	0.184	0.690
Blackberry consumption	Ripe blackberry availability	0.340	0.045	0.634

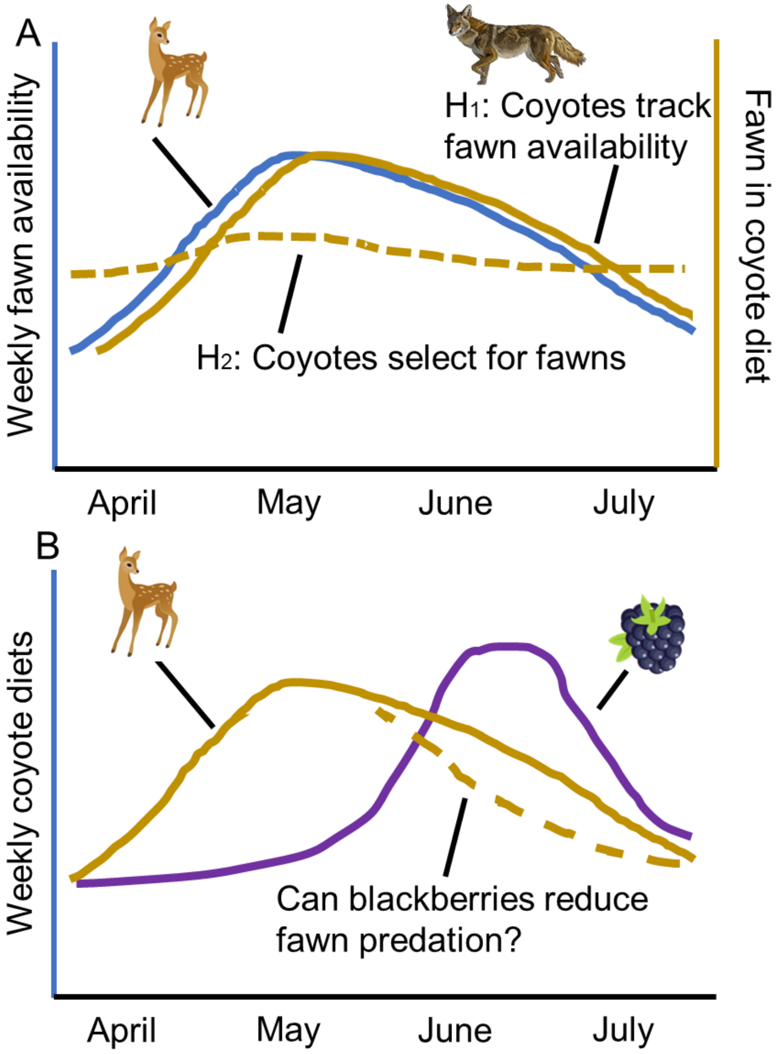

Figure 2.1. Conceptual diagrams of how coyotes could respond to temporary foods during the summer in South Carolina, USA. In panel A we show a pulse of fawn availability and then two hypotheses about how coyotes might dietarily respond. In panel B we show how a pulse of blackberry availability might reduce fawns in coyote diets (and therefore predation on fawns).

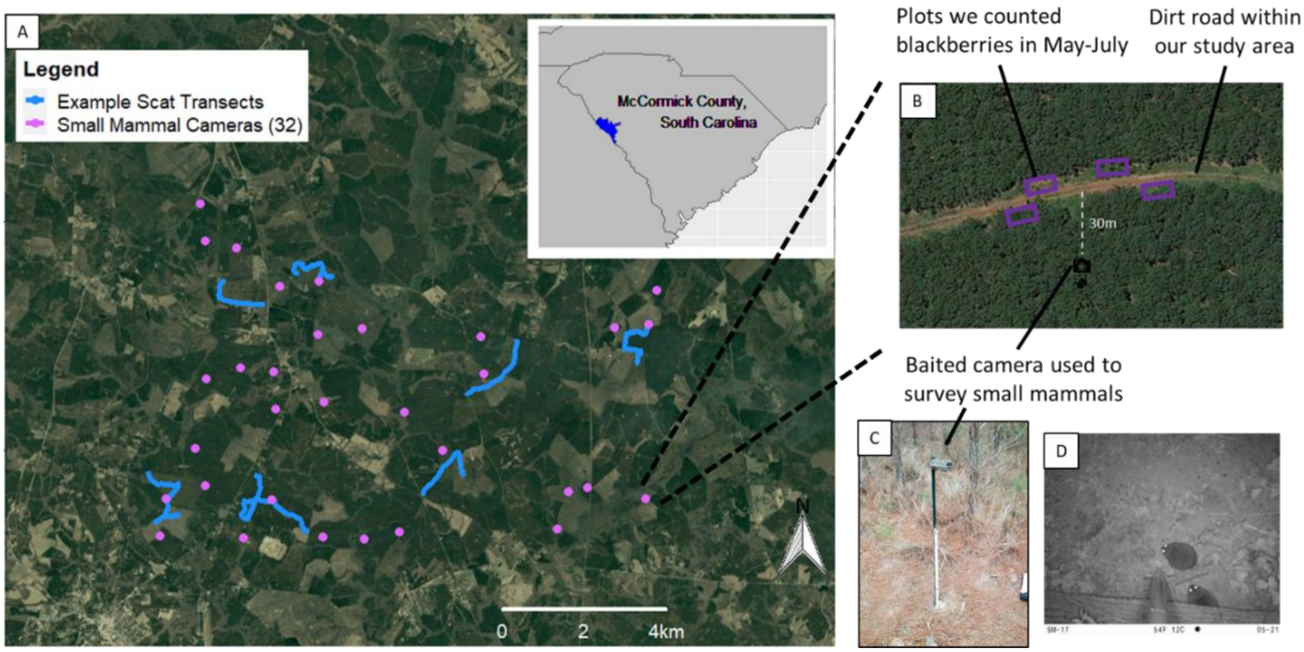

Figure 2.2. Study design for how we collected data on coyote diets and food availability in South Carolina, USA. In the main panel (A), we show an example of how our scat transects were distributed across the landscape during one survey season, as well as the locations of the 32 small mammal cameras. In (B), we zoom in on one of these small mammal camera sites to show a representative example of where the cameras were in relation to dirt roads. We also show an example of where we counted blackberries at several of these sites. In (C), we show the setup we used to survey small mammals, which consists of a downward-facing motion activated wildlife camera attached to a metal stake, to which we lashed a PVC pipe full of 300mL of bird seed. In (D), we show an example photograph of rats taken by a small mammal camera.

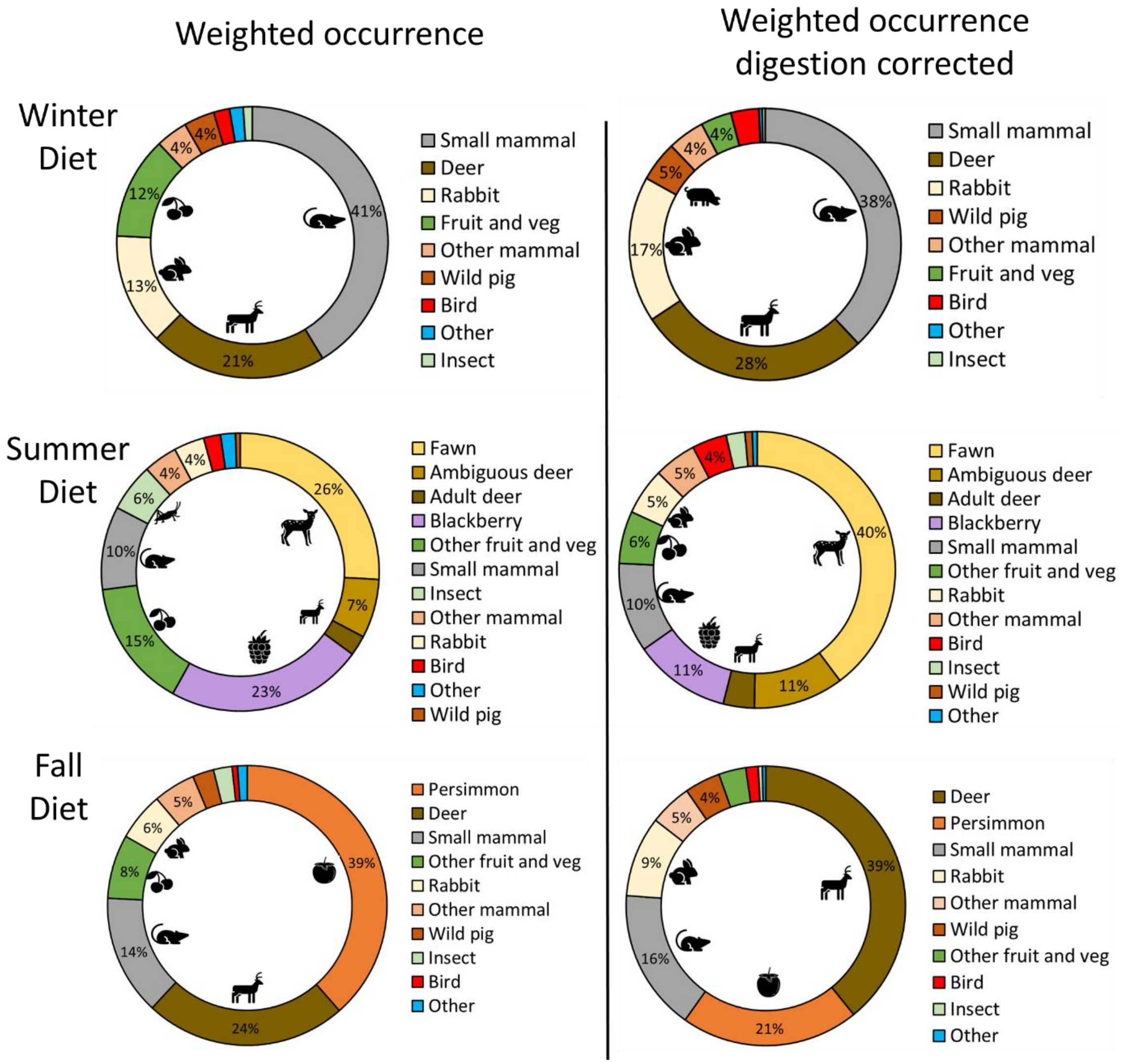

Figure 2.3. Seasonal coyote diets in South Carolina, USA. We calculated diets using weighted occurrence (left column) and weighted occurrence corrected for digestion (right column). We list items in the legends by order of importance in the diet.

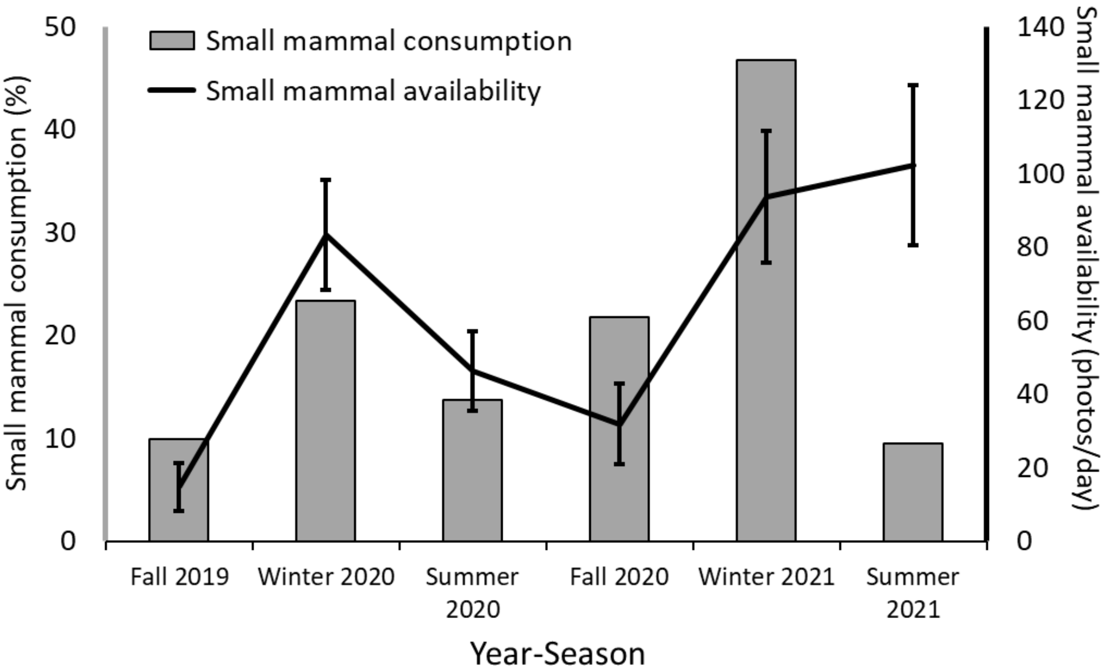

Figure 2.4. Consumption of small mammals by coyotes (bars) compared to small mammal availability (line) in South Carolina, USA. We measured consumption using the average digestion-corrected weighted occurrence from each year-season and we measured availability using the average number of detections of small mammals per day from a special camera array (Figure 2.2). Error bars represent standard error of the mean.

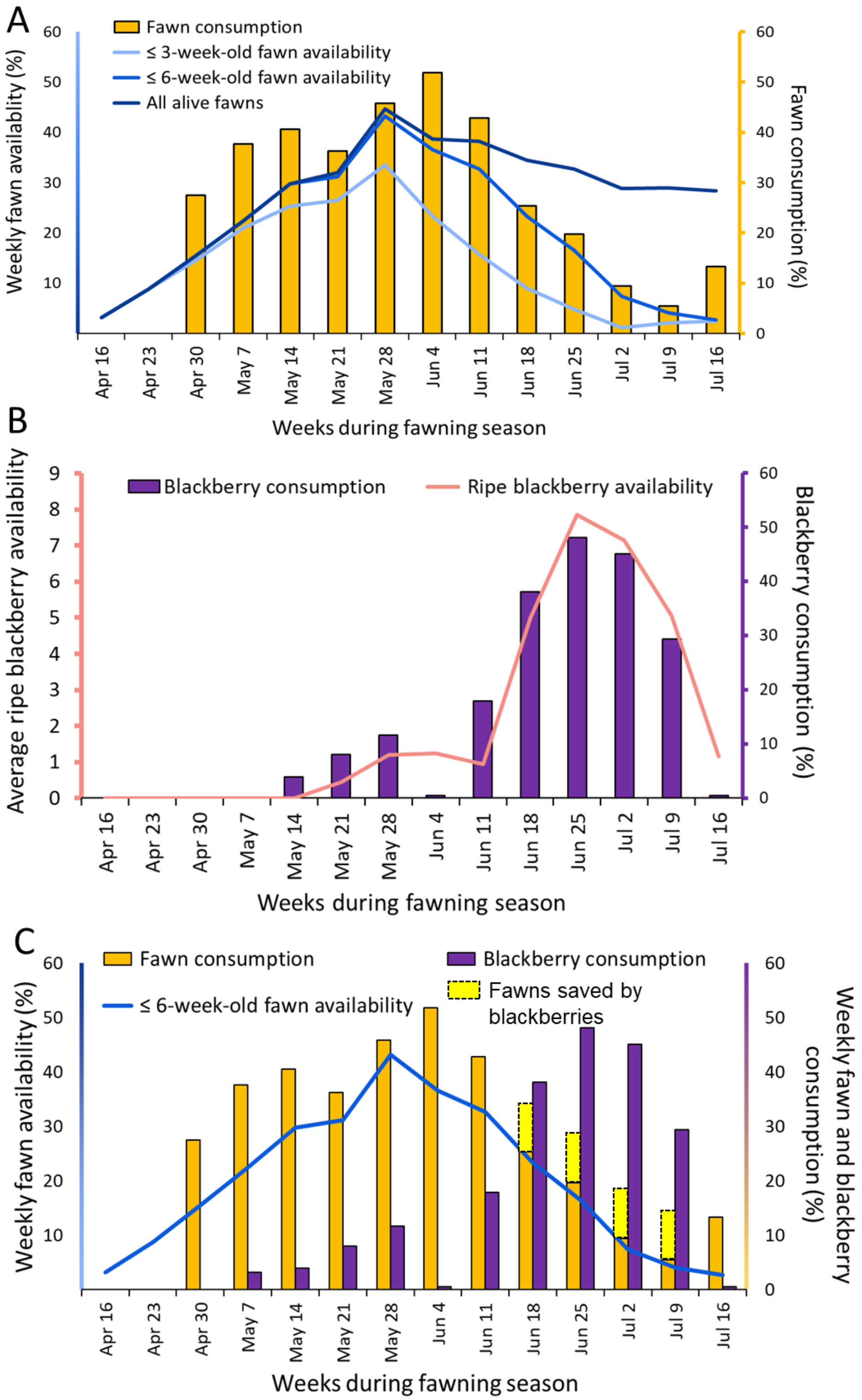

Figure 2.5. Weekly availability and consumption of fawns and blackberries by coyotes during fawning season (April – July) in South Carolina, USA. In panel A we show the average weekly availability of fawns as well their average consumption (weighted occurrence). In panel B we show the average weekly availability and consumption of blackberries. In panel C, we show the estimated effect that blackberries had on fawn consumption.

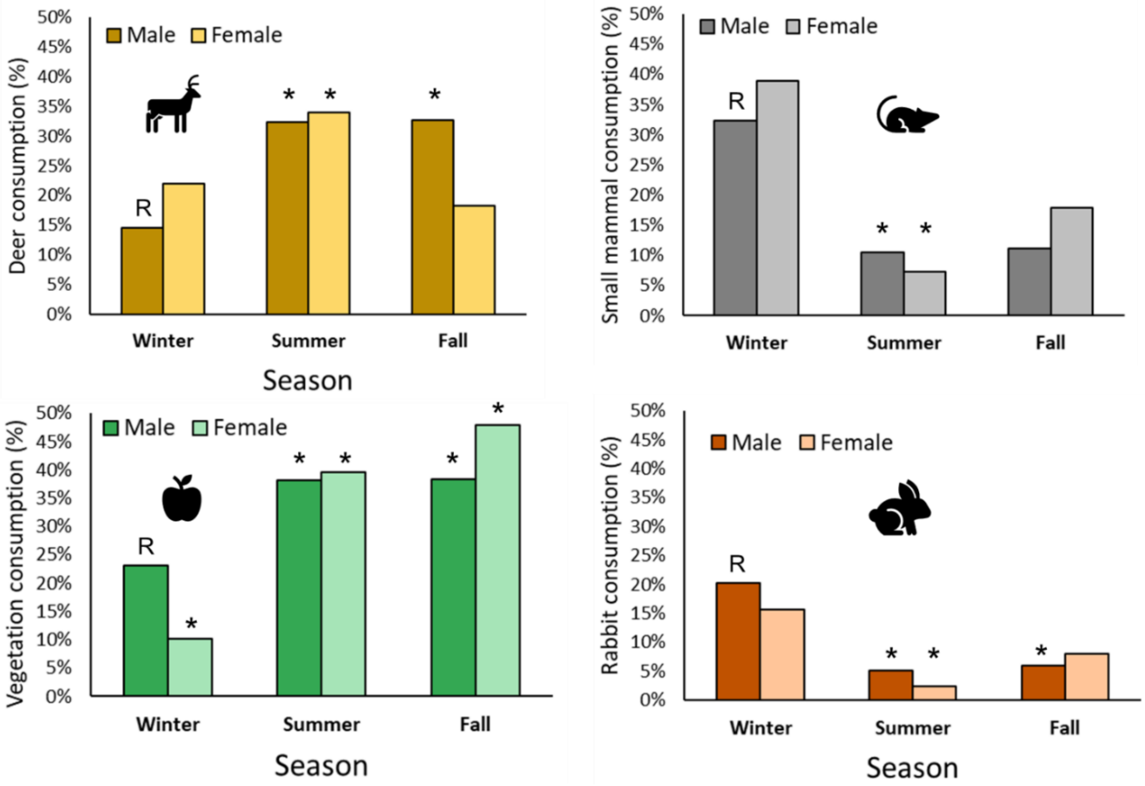

Figure 2.6. Comparisons of deer, small mammal, vegetation, and rabbit consumption (weighted occurrence) by male and female coyotes in South Carolina. All samples used in this analysis were from genetically individually identified scats, which is how we know the sex of the coyote. The R above males in the winter denotes the reference category and the * signifies a significant difference from the reference (95% confidence intervals do not overlap zero).

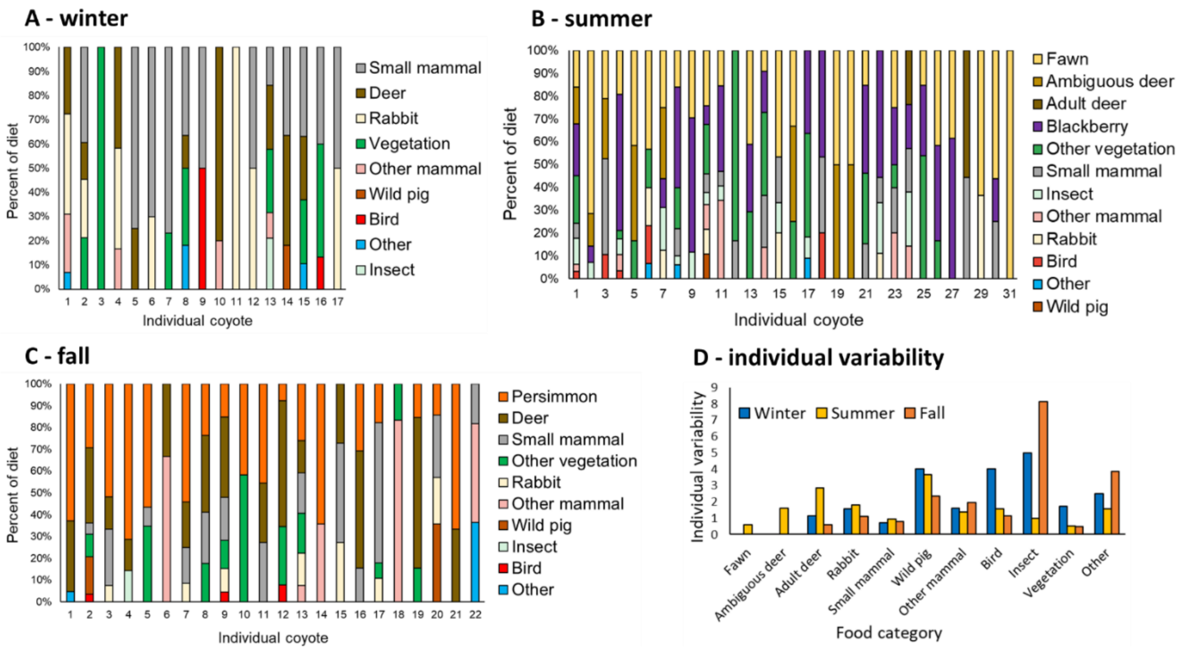

Figure 2.7. Individual variation in coyote diets in South Carolina. In A, B, and C, we show the weighted occurrence of various food items for each individual with ≥ two scats during winter, summer, and fall, respectively. Except for summer (where we show deer age classes consecutively), we ordered the food items by the average weighted occurrence that season. In D, we show the coefficient of variation (standard deviation divided by the weighed mean) across individuals for each category during each season. Larger values indicate more variability among individuals.

CHAPTER THREE

VARIABLE FORAGING TACTICS OF A GENERALIST CARNIVORE REVEALED BY LINKING MOVEMENT TO DIET

ABSTRACT

According to optimal foraging theory, predators should make decisions that maximize their caloric intake while minimizing energetic costs and risk. Yet, this requires knowledge of how predators actually forage, not just what they eat, which can be challenging to acquire. For generalist predators, switching to temporarily available foods could be beneficial but the extent to which they change their behavior to target different foods is unknown. Here, we compared when, how, and where coyotes foraged for fawns, blackberries, and small mammals during three summers in South Carolina, USA. We used genetics to link dietary information to fine-scale movement data from 16 individual coyotes, then quantified movement and habitat selection during a 20-hour window during which they foraged for and consumed the food. We also used fawn mortality data to identify and describe coyote behavior before, during, and after attacking fawns. We found that coyotes seemed to forage for each food item throughout the diel cycle, showing little evidence for food-specific foraging routines and also creating limited temporal refuges for their prey. There were a few differences in how fast and directed coyotes moved, but ultimately energetic costs seemed to be similar among foods when accounting for the time that coyotes spent in those states. However, we did find differences in where coyotes foraged for fawns and blackberries; coyotes avoided tree cover and human development while hunting fawns and had behavior-state-dependent (encamped, foraging, or traveling) selection for blackberries. This suggests that coyotes are making fine-scale decisions about where to forage for different foods, which seem to be partially mediated by risk from humans. Coyotes move far and fast while foraging for fawns, but then spend surprisingly little time at the attack site, instead likely

taking part of it to a homesite. This highlights the novel insight that can be gained from marking predators and their prey in the same system. Although based on small sample sizes, our findings represent an important step towards linking predator behavior to diet and highlight potential ways that managers can influence predator behavior to reduce predation on large herbivores.

INTRODUCTION

Tradeoffs can explain patterns across multiple domains of biology, from physiology to evolution and animal behavior (Cowan et al. 2014). In ecology, a fundamental tradeoff exists between the costs of obtaining a resource and the benefits of said resource (Zera and Harshman 2001). While resources can be many things (e.g., habitat, heat; Abrahms et al. 2021), understanding the tradeoffs predators make when choosing what foods to eat has been an important and foundational part of ecology (Pyke et al. 1977). Indeed, many studies have documented the physiological and ecological implications of variation in predator diet (Costa-Pereira et al. 2022, Shipley et al. 2022), yet few have quantified if and how predator behavior is dependent on the food item. Without understanding the link between predator behavior and foraging tactics, we risk missing important variables (e.g., risk, energetic cost) in our understanding of the tradeoffs involved in making foraging decisions (Gallagher et al. 2017).

Spatiotemporal variation in food availability (or vulnerability) is likely an important predictor of predator behavior in many systems (Abrahms et al. 2021). Food availability can fluctuate across multiple temporal scales, including cyclically across years (e.g., snowshoe hares; Krebs et al. 2016) and seasonally (e.g., wild fruits). These seasonally available foods (or resource pulses) have been shown to have important ecological effects (Yang et al. 2008) and could also serve to test if and how predators change their behavior when a new food becomes available

(Popa-Lisseanu et al. 2007). Optimal foraging theory predicts that predators should switch to foods with larger net energy gains (Macarthur and Pianka 1966), yet even when predator diets clearly shift, it can be challenging to know if this is due to changes in predator foraging behavior or simply changing encounter rates (Brunet et al. 2023). Research on several species of generalist carnivores suggests that they can indeed switch from opportunistic foraging to active searching (Prugh 2005, Panzacchi et al. 2008, Rayl et al. 2018), but these studies do not directly measure predator behavior while hunting for or consuming different food items.

Temperate forests could be an ideal system to study shifts in carnivore foraging because they are productive and contain multiple temporary foods. For example, in the southeastern united states, fruits many wildlife species eat include blackberries (*Rubus spp.*), wild cherries (*Prunus avium*), and wild plums (*Prunus americana*) in the summer and persimmons (*Diospyros kaki*) in the fall. White-tailed deer fawns (*Odocoileus virginianus*) are also functionally a temporarily available food for several carnivore species in the region, including coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and black bears (*Ursus americanus*). Fawns are born in the late spring and early summer and are subject to high predation rates from carnivores during the first three-six weeks of life, though once they grow enough to outrun predators, mortality rates drop precipitously (Kilgo et al. 2012, Nelson et al. 2015). Coyotes are responsible for most fawn mortality across the southeast (up to 80% in one study; Kilgo et al. 2012, 2019), likely contributing to declines in deer populations in some areas (Kilgo et al. 2010) and incentivizing managers to look for ways to reduce predation rates. Coyote removal does not seem to be very effective (Kilgo et al. 2014, Gulsby et al. 2015), but perhaps alternative foods (if abundant enough) could buffer fawn predation. While other research has concluded that this is unlikely to work (Schrecengost et al. 2008, Kelly et al. 2015), we found that coyotes largely switched from fawns to blackberries during the summer (Chapter 2; Figure 3.1A) and therefore may be a viable way of reducing predation on fawns. We also found that there was relatively little intra-individual variation in both diet (Chapter 2) and habitat selection (Chapter 1) across our population in the summer, suggesting that these temporarily available foods induce behavioral convergence. However, without linking diet to space use, we were unable to tell if coyotes were consistently changing their behavior while foraging for different food items.

A better understanding of coyote foraging behavior could reveal habitat management actions which reduce predation on fawns. For example, if coyotes forage in different habitats for fawns and blackberries, then habitat management which promotes blackberries could potentially keep coyotes away from habitat containing fawns. One study in Kenya found that the endangered hartebeest (an ungulate, *Alcelaphus buselaphus lelwel*) selected habitat differently than zebras (*Equus quagga*), creating a refuge when lions were attracted to areas dense with the more common zebras (Ng'weno et al. 2019). There is some evidence that coyotes have food-item specific foraging behavior (Lingle 2000), but this was from an open system (where behavior can be directly observed). One approach that could work in closed systems (i.e., forests) to link carnivore movement to diet is GPS cluster analysis; algorithms can be used to detect clusters of GPS points, which can then be investigated and searched for prey remains (Webb et al. 2008). However, a major shortcoming is that small (portable) food items are harder or impossible to detect with this method (Bacon et al. 2011). Thus, clusters may be adequate for large carnivores who primarily eat large herbivores, but they likely should not be the sole means of estimating the diet of carnivores who also eat small foods (Svoboda et al. 2013, Jansen et al. 2019). Instead, it may be fruitful to use a more inclusive method of assessing carnivore diets (scat analysis) and then link that dietary information to individual movement and habitat use information. While this has been done for black bears (Lesmerises et al. 2015), the authors focused on differences between individuals, still leaving a gap in knowledge around whether foraging behavior differs by food item.

Accordingly, our primary goal was to compare coyote movement and habitat use during a timeframe in the summer where we knew they ate either fawns, blackberries, or small mammals. In general, following adaptable foraging theory, we hypothesized that these foods would require different foraging strategies to find and consume, reflecting effort required and their distribution across the landscape (Figure 3.1). With objective one, we tested whether coyotes shifted when and how they moved throughout the diel period for each of these food items. Although it is well known that many terrestrial predators have feeding or hunting times throughout the 24-hour day (Kohl et al. 2019), no one has yet (to our knowledge) tried to answer if they change their foraging tactics throughout the day to target different foods. We hypothesized that the availability or vulnerability of animal prey would be dynamic while blackberry availability would be static (Figure 3.1B). We predicted that coyotes would be more likely to hunt fawns and small mammals at night when they are more active (unpublished data, Monterroso et al. 2013). Our second objective was to test for differences in how coyotes were moving (speed, directionality, and accelerometer activity) among our three foods items. We hypothesized that coyote movement effort would largely be a function of encounter rate, where more movement would be needed to find cryptic or less dense food items (Lingle 2000). However, according to optimal foraging theory, it would remain worth it (to a point) to forage for these harder to find food items if they represent a larger reward (Figure 3.1C). Thus, we predicted that coyotes would move faster, be more directed, and have greater activity readings when hunting fawns, followed by small mammals, then blackberries. Our third objective was similar, except we tested for differences in habitat use instead of movement parameters. Following optimal foraging theory, we hypothesized that coyotes would forage in habitat that would maximize encounter rates, while minimizing risk (Gaynor et al. 2021). We predicted that coyotes would be more likely to forage for small mammals and blackberries in open habitat (where they are more abundant; unpublished data) but canopy cover would not be significant for fawns (Figure 3.1D). We predicted that coyotes would be more likely to be encamped near humans because it is safer than moving.

Our secondary goal was to take advantage of a novel opportunity to quantify coyote behavior before and after killing fawns. The major downside to our scat-based approach is that we cannot pinpoint precisely when the food was eaten, but by overlaying our coyote GPS data over fawn GPS data during known coyote attacks, we were able to identify several times when a collared coyote killed a fawn. Given this only happened a handful of times, we focused on describing coyote behavior leading up to and after attacking the fawn. Although coyotes can clearly be efficient fawn predators in the eastern US, how they find fawns has remained an open question. Here, we provide the first quantitative look into what coyotes are doing ahead of attacking a fawn. More generally, our study provides a rare opportunity to quantify if and how predator behavior changes in parallel with their diet, with implications for the management of an important game species.

METHODS

Study area

We captured coyotes and collected scats across ~60 km^2 of private land in McCormick County, South Carolina. Our study area was representative of the Piedmont physiographic region, with a humid subtropical climate (hot summers 21-32° C) and gently rolling hills (120-180 m elevation; Griffith 2010). Most of the land was covered by loblolly pine (*Pinus taeda*) plantations in various successional stages. There were also pastures and fields intermittent throughout the landscape, including planted food plots for game species. Understory and midstory plants that coyotes ate included blackberry (*Rubus allegheniensis*) and persimmon (*Diospyros virginiana*; Jensen et al. in prep). Other coyote prey included deer, wild pigs (*Sus scrofa*), eastern cottontails (*Sylvilagus floridanus*), and small mammals. Human density was generally low (< 100 people per km^2), yet there were networks of dirt access roads and human-induced coyote mortality was common (typically from being shot).

Coyote capture and GPS data

We captured coyotes during the winter months of 2018-2019, 2020, and 2021 (three capture seasons). With help from a professional trapper, we set Minnesota MB 550 foothold traps (Minnesota Trapline Products, Pennock, MN) on dirt roads that had signs of coyote activity (i.e., tracks and scat). We immobilized coyotes using a catchpole and electrical tape wrapped around their muzzle and ankles. We then took body measurements, collected a genetic sample from their ear, and fit a GPS-collar around their neck (Vectronic Aerospace, Berlin, Germany; model: VERTEX Light). We only put GPS-collars on individuals if the collar was < 5% of their weight. Average handling time was 25 minutes. All capture and handling procedures were approved by Clemson University IACUC permit no. AUP 2018-031 and USDA Forest Service permit no. USFS 2018-031.

We programmed our GPS-collars to collect GPS data at 30-minute intervals during an eleven-week period from April 19 – July 7 to capture fine-scale movement when fawns were available on the landscape. We tested GPS accuracy by placing two collars set to 30-minute fix intervals in mature forest and an open field within our study site. We tested each collar in both habitat types and compared locations to a known GPS location taken using the waypoint averaging function on a handheld GPS. We found a nominal difference in GPS error between habitat types (1-2m) and the average GPS error was 23m.

Scat surveys and content identification

We refer the reader to Chapter 2 for details on how we conducted scat surveys and quantified food items. Briefly, we surveyed from early May through mid-July in 2019, 2020, and 2021. We conducted surveys on ~16 km of dirt roads each year, using data from our GPS collared coyotes to maximize our chances of collecting scat from tagged individuals. When we encountered a scat we estimated its age, recorded its location, and preserved a pea-sized amount in DETs buffer (Stenglein 2010) to be used for genetic analysis.

We used standard techniques in the lab to isolate and identify the solid food items found in each scat. We first dried scats in an oven, then washed them to isolate solid material present in the scat. We then used a combination of technical manuals on mammal hair (Moore et al. 1974, Teerink 1991), hair reference slides, and online sources to identify the contents of each sample. We quantified the weighted occurrence (Prugh 2005) of 11 different food categories in each sample, but for this study focused on deer fawns, blackberries, rodents, and rabbits (~75% of summer diet). Due to small sample sizes, we combined rodent and rabbit samples together in ‘small mammals’. We distinguished fawns from adult deer in samples by recording the presence of small hooves and comparing the width of deer hair in the sample to the width of hair from known aged deer from our field site (sensu Ward et al. 2018).

Genetic analysis

We identified coyote scats to species using the process described in Chapter 2. Briefly, we conducted a polymerase chain reaction (PCR) designed to amplify whichever carnivore species' mitochondrial DNA is present in the sample (Stenglein et al. 2011). We determined that samples with peaks in fluorescent intensity ≥ 100 at known coyote fragment lengths were deposited by coyotes and samples with peaks ≥ 1000 were considered high-quality and passed on to individual identification. To identify individual coyotes, we amplified 10 nuclear microsatellite loci and two canid-specific sex ID loci 2-6 times from these high-quality samples (until there was consensus at ≥ 7/10 of the non-sex loci; Taberlet et al. 1996). We amplified these same loci twice from each tissue sample (less replicates were needed since tissue is higher quality) in order to match them to scats. We grouped samples (both scats with each other and scats with tissue samples) if they had perfect matches at ≥ five loci using GenAlEx 6.5 (Peakall and Smouse 2006).

Linking dietary data to movement data

In order to link diet to movement and habitat selection, we quantified coyote space use during the period they likely consumed the food found in a focal scat (Figure 3.2). For each scat, we needed concurrent GPS data at 30- or 90-minute fix intervals, so we excluded scat samples that did not meet those criteria (57 samples met these criteria). To ensure that we were capturing movement and habitat use during periods when they likely consumed a given food item, we only used scats where each focal food item was > 50% of the scat (27 samples met this criterion: 14 fawn, 9 blackberry, 4 small mammal). We used our field estimate of the scat's age to visualize corresponding GPS data and determine when the scat was likely deposited (usually within a 30-minute window; Figure 3.2). There is little research on coyote (or other canid) gut passage time, and the most detailed study we could find suggests that the majority of scats are deposited 4-24 hours after the meal is consumed (Draper et al. 2021). This study also found no effect on contents (i.e., the amount of fruit) on gut passage time, so we did not treat food items differently in this regard. Given the uncertainty of when foods were consumed, we did not try to identify when and where foods were consumed, but rather focused on the coyote's movement and habitat use during the window when they likely were hunting for (and consumed) that food. Thus, we used the GPS data from the 4-24 hours prior to estimated deposition (Figure 3.2), which contained 41 (n = 26) or 14 GPS points (n = 1) depending on the fix rate.

Objective one: How do coyotes partition their time while hunting fawns, blackberries, and small mammals?

For this objective, we tested the hypothesis that coyotes would partition their time differently while hunting for different food items (Table 3.1). We took a point-by-point approach for this and the following objectives, which allowed us to decompose coyote movement into behavior states. We classified each step as one of three behavior states (encamped, foraging, or traveling) using hidden Markov models and the momentuHMM package (McClintock and Michelot 2018). Because 'foraging' is a behavior state and a general behavior, we use 'hunting' when referring to the general behavior to reduce confusion in some places. Since there were not enough fixes from the 20-hour window to accurately classify steps, we classified each step in the 20 days surrounding the window (typically 10 days prior and 10 days after) using the Viterbi algorithm (Michelot et al. 2016), then filtered out the fixes outside of the 20-hour window. We partitioned our data by food item, then calculated the proportion of points classified in each behavior state for each 30-minute interval (when our GPS points were taken). We used this data to visualize behavior throughout the day and also split the data into daytime and nighttime fixes using local sunrise (5:30) and sunset (21:30) times from June 1. To test for differences between fawns and blackberries during daytime and nighttime, we used generalized linear models (in the glmmTMB package; Brooks et al. 2017) with the proportion of time spent in the behavior state as the response variable and food item as the predictor. In order to quantify differences between each food item, we ran each model twice with small mammals as the reference category, then again with blackberries as the reference category. We considered differences significant if p was < 0.05.

Objective two: Do coyotes exhibit distinct movement while hunting fawns, blackberries, and small mammals?

For this objective, we tested the hypotheses that coyotes use different hunting strategies for fawns and blackberries (Table 3.1). We compared movement and habitat selection across food items for each behavior state separately (Figure 3.2). For movement, our response variables were speed, absolute turn angle (greater values indicate larger angles and less directed movement), and average accelerometer activity at each point (step). Our accelerometers continuously measured movement of the collar across three axes and recorded the average value for each axis every five minutes. The maximum value was 255 and the minimum was 0. To estimate activity at each GPS point we averaged the three values from five minutes prior to the fix, during the fix, and five minutes after the fix. For each behavior state and response variable combination, we fit two generalized linear mixed models with a gaussian distribution (we log transformed speed and turn angle), food item as the predictor, and individual coyote as a random effect. Like objective one, we fit two models in order to make comparisons between each food item. We considered differences significant if p was < 0.05.

Objective three: Do coyotes exhibit distinct habitat selection while hunting fawns, blackberries, and small mammals?

For habitat selection, we used an integrated Step Selection Analysis (iSSA; Avgar et al. 2016) to test our hypotheses that habitat selection would be dependent on the food item (Table 3.1). We generated 20 available points for each used step using the amt package (Signer et al. 2019), with step lengths drawn from a gamma distribution and turn angles drawn from a von mises distribution. We used separate distributions for each behavior state, drawn from the 20-days worth of values used in the behavior state classification (see objective one). We then interfaced with Dynamic World (Brown et al. 2022) using the rgee package (Aybar et al. 2020) to extract the mean percent tree cover, mean percent grass cover, mean percent shrub and scrub cover, and mean percent built cover. Given Dynamic World is such high resolution (10 m), we also wanted a measure of habitat diversity near each point. To do this, we again calculated mean percent tree, grass, shrub and scrub, and built cover, but extracted them at 50 m resolution to capture a larger area around each point. We then calculated the average of the differences between each resolution’s value for each cover type to estimate the patch diversity. We dropped grass cover and shrub and scrub cover because they were significantly negatively correlated with tree cover (-0.84, -0.83, respectively). We fit separate iSSAs for each food item and behavior state (nine total) and considered selection estimates to be significant if their standard errors did not overlap zero.

Objective four: What do coyotes do before and after killing a fawn?

We also placed GPS collars on white-tailed deer fawns in our study area and were able to identify and describe coyote behavior leading up to and after probably killing several fawns. We captured adult female deer during the winter months of 2019, 2020, and 2021, fitting each with a vaginal implant transmitter (VIT, Advanced Telemetry Systems). These VITs then alerted us when a doe gave birth during the spring or early summer, and we searched for her fawns and placed an expandable GPS collar on them. These collars had a built-in mortality sensor, which alerted us if the fawn had not moved in 8 hours, which we then investigated. We used a combination of field evidence (e.g., fawn buried in soil, width of bite marks) and genetics (e.g., swabs on fawn collars) to identify cases where a coyote was likely responsible for killing the fawn. More details on our capture procedures and mortality investigations can be found in Muthersbaugh (2023). In addition, we saw a GPS collared coyote carrying a fawn on one of our cameras (Figure 3.3), so we were able to estimate when this fawn was killed as well.

To identify cases where a collared coyote likely killed a collared fawn, we visualized our coyote GPS data in relation to each suspected coyote fawn mortality location during a 72-hour window centered on the time we estimated the fawn to have been killed. We estimated when and where the fawn was killed using a combination of the mortality alert and abrupt changes in GPS or accelerometer data from the fawn’s collar. When there was one or more coyotes nearby, we investigated further by visualizing the path of the coyote(s) and fawn to see if the coyotes were in close proximity to the fawn when it died. For the cases where we were confident that a collared coyote was responsible (or at least involved in the fawn’s death), we quantified the coyote’s movement before and after the attack. Before the attack, we focused on the time between the last (more than two-hour) period of encamped behavior and the attack because we thought that would represent a hunting bout. After the attack, we focused on a 12-hour window to represent their behavior after killing a fawn. During both periods, we calculated the percent of GPS points classified as each behavior state (using the same process as described in objective one) and the coyote's average speed.

RESULTS

We tracked 76 coyotes using GPS collars and were able to use scats from 16 of these individuals. We collected 324 scats during our summer surveys, of which 206 (64%) were genetically confirmed to be from coyotes. Of these, 153 were individually identified and 72 of these matched with tissue samples from our captured coyotes. However, we could only use concurrent fine-scale GPS data and samples composed of > 50% of our focal foods, so our final scat sample size was 27. Of these 27, 14 were from female coyotes and 13 were from males.

Objective one: How do coyotes partition their time while hunting fawns, blackberries, and small mammals?

Overall, we found that coyotes spent 35-50% of their time encamped, 20-40% foraging, and 15-45% traveling (Figure 3.4). During the daytime, coyotes partitioned their time similarly while hunting for the three different food items, except that they spent 3-4 more hours encamped for small mammals compared to fawns on average ($p = 0.010$; Figure 3.4). At night, they only spent 18% of their time foraging for blackberries, compared to 38% for small mammals (a difference equating to nearly five hours; $p = 0.014$; Figure 3.4). By contrast, they traveled much less for small mammals at night (13% of their time), compared to both fawns and blackberries ($p = 0.001$; ~40%).

When we descriptively examined their temporal activity, there were some similarities among food items but also some differences. For example, coyotes were the most active for all three foods during the evening and early night hours (Figure 3.4). The largest qualitative differences were during the day, as coyotes were very active for fawns during the early morning and became less active as the day wore on. By contrast, coyotes were moderately active in the morning for blackberries and very active during the early afternoon. Coyote activity for small mammals was more similar to fawns, with high activity in the morning, followed by being encamped in the afternoon.

Objective two: Do coyotes exhibit distinct movement while hunting fawns, blackberries, and small mammals?

In general, we found more differences in movement while coyotes were foraging and traveling compared to while they were encamped (Figure 3.5). For example, we found that coyotes moved faster while foraging for fawns and small mammals compared to blackberries ($p < 0.001$). Coyote foraging and traveling was more directed (straighter turn angles) for small mammals, compared to blackberries ($p = 0.049$ and 0.047, respectively). For activity, we found that coyote accelerometer readings were greater for small mammals while foraging (compared to blackberries; $p = 0.025$) and greater for blackberries while traveling (compared to fawns; $p = 0.049$).

Objective three: Do coyotes exhibit distinct habitat selection while hunting fawns, blackberries, and small mammals?

We found that habitat selection was dependent on the behavior state coyotes were in, and we only found evidence of selection or avoidance while coyotes were hunting fawns and blackberries (Figure 3.6). While encamped for blackberries, coyotes selected for built cover (estimate ± standard error = 0.224 ± 0.194) and avoided diverse patches (-0.135 ± 0.130). Coyotes avoided built cover while foraging for fawns (-0.174 ± 0.127) and avoided diverse habitat while foraging for blackberries (-0.371 ± 0.224). Coyotes also avoided built cover while traveling for fawns (-0.264 ± 0.160), as well as tree cover (-0.191 ± 0.090). However, coyotes selected for diverse patches while traveling for both fawns (0.171 ± 0.071) and blackberries (0.115 ± 0.089).

Objective four: What do coyotes do before and after killing a fawn?

We identified four cases where a GPS collared coyote was likely responsible for (or at least involved) in killing a GPS collared fawn and one case with an uncollared fawn. In general, these scenarios involved the coyote leaving a resting area, typically traveling relatively fast for several hours, attacking the fawn, then returning to a resting area to presumably consume (some of) the fawn (Figure 3.3). During the period leading up to the attack, four of these coyotes were moving relatively fast (0.80 km/hr on average), where we classified 53% of their GPS points as traveling, 23% as foraging, and 25% as encamped (Table 3.2). The other coyote moved a bit slower (0.25 km/hr) and we classified all of her points as foraging. This case was also different in that the coyote was foraging within 200 m of the resting location and was only moving for two hours before encountering the fawn. By contrast, the other four coyotes were moving for four, six, eight, and fifteen hours before encountering the fawn.

In the 12 hours after (presumably) killing the fawn, all five coyotes behaved somewhat similarly (Table 3.2). Their average speed was slow compared to before killing the fawn (0.23 km/hr) and we classified 67% of their points as encamped, 19% as foraging, and 15% as traveling. One coyote moved away immediately after the presumptive attack, then returned for one GPS point, then moved away again and remained encamped for several hours. Apart from this example, the coyotes did not linger at the attack site, and instead moved 0.5-1 km away, perhaps carrying parts of the fawn to share with other pack members (e.g., pups) at a communal location.

DISCUSSION

Generalist predators have options of what they can eat, with each option likely representing variable effort, risk, and caloric benefits. Optimal foraging theory predicts that predators should choose foods with the greatest net benefit (Pyke et al. 1977), yet this requires knowledge of predator foraging behavior, which can be challenging to quantify. Here, we compared coyote movement and habitat use while hunting for three key food items during the summer. We found several differences in *when* and *how* coyotes hunted, yet net energetic costs were likely similar among food items. However, we found the most consistent differences in *where* coyotes hunted when they ate fawns and blackberries, perhaps explained by differences in their distribution across the landscape and the risk involved. Indeed, our novel analysis of encounters between GPS collared coyotes and GPS collared fawns suggests that coyotes exhibit distinct behavior prior to and after killing fawns. Collectively, our findings highlight the importance of decomposing optimal foraging into tradeoffs across multiple dimensions, some of which require knowledge of fine-scale predator behavior.

Low variability in diel activity while hunting for different food items

A growing number of predator-prey studies have highlighted the importance of the temporal domain for understanding predation risk and predator behavior (Kohl et al. 2019, Smith et al. 2019). In line with these studies, we investigated whether coyotes tended to be active at different times for different foods. We found no clear differences in coyote diel activity among food items, though a few patterns did emerge. At night, coyotes foraged more and traveled less for small mammals, perhaps reflecting more tortuous movement associated with hunting these species (Lingle 2000). Indeed, we also found that coyotes were more likely to be encamped for small mammals during the day (compared to fawns), in line with our hypothesis that it may be optimal to hunt for small mammals at night, when small mammals are more active (Monterroso et al. 2013). Our descriptive analysis of behavior during the day suggests that coyotes were more likely to hunt both fawns and small mammals in the morning and fruit during the afternoon. Perhaps this reflects the timeframe when both small mammals and fawns are not very active, making blackberries the optimal choice. By contrast, coyotes were remarkably active during the evening and early night hours for all three foods, which could reflect a period in their circadian rhythm where they are opportunistically foraging (Neale and Sacks 2001). Lastly, although coyotes are typically described as nocturnal or crepuscular from camera data (Higdon et al. 2019, Crawford et al. 2021, Saldo 2022), our behavior-state approach shows that they are no less likely to be foraging or traveling during the day as opposed to night. This suggests that there are not predictable times that serve as a temporal refuge for their prey in our system and more broadly, that GPS data should complement camera data when quantifying diel predation risk. Although we were unable to determine when exactly coyotes encountered different food items, working with a species with less variable gut retention times could make our approach (and others like it, Lesmerises et al. 2015) viable for a precise estimation of consumption times for terrestrial predators.

Comparing coyote movement while hunting for different foods

In relatively flat systems, the energy that predators expend while hunting is primarily a function of how fast they move and how long they move for (Carbone et al. 2007). We found several differences in how coyotes moved when comparing food items, but net energetic costs seemed comparable when considering how long they moved. In general, coyotes moved faster, were more directed, and had greater activity readings when hunting small mammals. This contrasts with our predictions that fawns would require the most effort due to their hiding strategy and lower abundance on the landscape. However, we also found that coyotes traveled much less for small mammals (at night; objective one), suggesting that there is a tradeoff between movement intensity and duration. It is also possible that traveling for small mammals represents directed movement between patches, while traveling for fawns represents searching behavior (see objective four). Of likely greater interest to managers though are differences between fawns and blackberries, as some of our other work suggests that blackberries could buffer predation on fawns (Chapter two). Here we found that coyotes moved faster while foraging for fawns and were more active while traveling for blackberries. Given fawns spend a majority of time inactive and hiding during the 3-6-week period they are most vulnerable to coyotes, perhaps this reflects greater search effort while foraging (Lingle 2000) and more pauses while traveling. Thus, while hunting fawns, foraging seems to be relatively fast and traveling relatively slow, suggesting little functional distinction between them. Ultimately, we found little evidence that there are large differences in how coyotes move while hunting different foods, yet future research should more explicitly integrate energetics into foraging decisions through quantifying encounter rates, handling time, and caloric differences among foods (Carbone et al. 2007).

Key differences in coyote habitat selection while hunting different foods

We found differences in where coyotes hunted fawns and blackberries, which seemed to be mediated by risk from humans. Most notably, we found that coyotes avoided built cover when foraging and traveling for fawns (and we did not find this effect in any other context). One potential explanation for this could be that coyotes try to reduce risk when hunting fawns, as they are already exposing themselves to additional risk by traveling in open habitat. An alternative explanation is that fawns are more abundant away from buildings. However, our unpublished data suggests that does may select birth sites near buildings (Michael Muthersbaugh pers. comm.), in alignment with the human shield hypothesis (Berger 2007), which predicts that large herbivores will select areas closer to humans because their predators are afraid of people (Suraci et al. 2019). In our context, this would likely manifest through doe birth-site selection (Berger 2007), since fawns typically remain relatively close to their birth site during the period they are most vulnerable to predators. We also found that coyotes avoided tree cover and selected diverse habitat while traveling for fawns, which is particularly important because we found that coyotes were disproportionately likely to be traveling when they encountered a fawn (objective four).

Taken together, these findings suggest that open habitat further from human development is most risky for fawns.

In contrast to fawns, coyotes had behavior-state dependent habitat selection for blackberries and no evidence of habitat selection for small mammals. While encamped for blackberries, coyotes selected areas closer to built cover and avoided diverse habitat. Blackberries are unique among our focal foods in that we suspect that the encamped behavior state could represent places and times where coyotes are eating (hunting in a patch), whereas we assume that coyotes need to generally be in the foraging or traveling state to encounter fawns and small mammals. Eating blackberries while encamped would also likely expose coyotes to less risk than moving, perhaps allowing coyotes to feed in areas closer to humans. Interestingly, we found a switch from avoiding diverse habitat while encamped and foraging to selection while traveling for blackberries. This could mean that blackberries are more abundant in a certain type of habitat (our unpublished data suggests this is in young pine stands) but coyotes travel through diverse habitat between patches. Lastly, our small sample size for small mammals (n=4) likely explains the large uncertainty in selection estimates. Our small mammal findings should be interpreted with the most caution in general given the sample size and use of scats containing either rodents or rabbits.

Describing coyote movement prior to and after killing a fawn

Unless predator behavior can be directly observed (i.e., in open habitat), it can be challenging to know what they do before and after a predation event. Using a unique dataset from concurrently GPS collared coyotes and fawns, we were able to quantify and describe coyote behavior before and after killing several fawns. A fawn’s survival strategy during the first several weeks of its life is to hide (Lent 1974), using its spots for camouflage and moving very little. Thus, the four (out of five) coyotes that were moving relatively fast and far prior to encountering the fawn were likely attempting to maximize their chances of encountering a hidden fawn. These results align with an observational study reporting that coyotes engage in specific mule deer (*Odocoileus hemionus*) hunting behavior, where they move relatively fast while cooperatively hunting together as a group (Lingle 2000). Cooperative hunting for mule deer fawns by coyotes has been reported in other western states as well (Hamlin and Schweitzer 1979, Wenger 1981), but it seems like eastern coyotes do not engage in this behavior as frequently (Bekoff and Wells 1986). Indeed, of the five cases where we documented a coyote carrying a fawn (including Figure 3.3), the coyote appeared to be traveling alone each time. We did note one case where one of our focal coyotes began traveling with another collared individual (presumably her mate) soon after killing a fawn, eventually returning to the place where the fawn was attacked together. To be clear, without genetic data that links a specific coyote to a fawn and considering that pack members sometimes travel together, we cannot be certain that our GPS collared individuals were directly responsible for killing the fawn. However, given we only analyzed cases where there was clear spatial overlap during a timeframe when accelerometer readings from the fawn indicated it was likely attacked, we can be nearly certain our focal coyotes were at least involved.

After the attack, we were somewhat surprised to see that coyotes did not linger at the attack site. However, in every case, the fawn’s GPS collar was found near the attack site (and fawn bodies were rarely found generally), suggesting that coyotes quickly dismember fawns, then carry the body to a resting location away from the attack site (we captured multiple photographs of coyotes carrying fawns on our camera traps; Figure 3.3). There are at least two explanations for this behavior. First, perhaps the coyote wants to avoid lingering at the attack site to reduce the odds of another predator (even another coyote) stealing its kill. Second, given fawning season overlaps with pup rearing season, it is likely that many fawns are brought back to a communal location to share with other pack members. Regardless, our findings have important implications for cluster searches and analyses for ungulate neonates (Bacon et al. 2011). Specifically, we did not observe coyote clusters at the site of attack, highlighting that where predators consume portable food items may not be where those foods were encountered. Further, aside from one individual exclusively in the foraging state before attacking the fawn, there seems to be a general pattern of relatively fast traveling, followed by a brief use of the attack area, followed by a prolonged period of encampment up to a kilometer away. In particular, this means that coyotes can be in ‘foraging mode’ while in both the foraging and traveling states. Future studies using cluster analyses to study coyote (or other carnivore) predation on ungulate neonates may find this information useful to estimate where and when attacks took place.

Conclusions

Tracking how predators actually forage for foods − not just quantifying what they eat − is challenging. By linking individual dietary information to movement, we were able to quantify how coyotes hunted for three different food items and we came away with three general conclusions. First, we found relatively few differences in *when* and *how* coyotes hunted fawns, blackberries, and small mammals. Most of the differences we did find were between small mammals and the other two food items, yet net energetic costs associated with how and how much coyotes moved for each food appeared to be similar. Second, we did find differences in *where* coyotes hunted, particularly between fawns and blackberries. This suggests that despite being concurrently available, optimally foraging for these foods requires different habitat use at a fine scale. And management that promotes blackberries or fear of humans could provide spatial refuges for fawns. Third, by integrating GPS data from fawns, we were able to show that coyotes seemed to have a signature of movement in the hours leading up to, during, and after killing a fawn. This represents the first look at how coyotes are finding fawns in a region where they are responsible for killing nearly half of all fawns born (on average; Kilgo et al. 2019). More generally, these interactions show the insight that can be gained from concurrent spatial data on predators and their prey (Kays et al. 2015). Taken together, our results suggest that coyotes do not engage in routine and intentional food-item-specific foraging but adjust their behavior at fine spatial and temporal scales.

Moving forward, advancements in animal tracking will continue to clarify what predators are actually doing on the landscape. For example, video cameras integrated into collars have been used to capture what animals are doing for a short period (Thompson et al. 2012), yet the additional weight currently limits them to large species. Battery technology will also continue to improve, mitigating the tradeoff between fix rate and battery life, such that very high fix frequencies (seconds or minutes) can be used for longer periods. Sample sizes larger than ours will allow researchers to quantify differences across individuals (Lesmerises et al. 2015) and the importance of spatial foraging personalities (Spiegel et al. 2017). Collectively, these advancements will give us a clearer understanding of the trade-offs that predators make when foraging.

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TABLES

Table 3.1. An overview of our analyses and predictions for our three objectives quantifying when, how, and where coyotes moved while hunting fawns, blackberries, and small mammals in South Carolina, USA.

Objective	**Response variable(s)**	**Predictor variable**	**Scale**	**Model example**	**Predictions**
1 (when)	1. Percent of time in behavior state during day 2. Percent of time in behavior state during night	Food item	20-hour window	Percent time ~ food item	Coyotes will be more likely to hunt fawns and small mammals at night
2 (how)	1. Speed 2. Turn angle 3. Activity	Food item	GPS point	Speed ~ food item + coyote ID	Coyotes will move faster, more directed, and greater activity for fawns, followed by small mammals, then blackberries
3 (where)	1. Tree cover 2. Built cover 3. Patch diversity	Food item	GPS point	Case (used or available) ~ tree cover + built cover + patch diversity + coyote ID	Coyotes will be more likely to hunt in open habitat for small mammals and blackberries

Table 3.2. Information about cases where a GPS collared coyote killed a white-tailed deer fawn in South Carolina, USA. We quantified coyote behavior before and after the estimated time of attack. We considered a hunting bout to start after a period of encamped behavior that was at least two hours in duration and we quantified coyote behavior in the 12 hours after the attack. All coyotes except the first individual (Figure 3.3) were associated with a collared fawn, which is how we know how old the fawn was when it died.

Coyote info	**Fawn age at death (days)**	**Estimated attack time**	**Moving duration before attack**	**Behavior before attack**	**Speed before attack (km/hr)**	**Distance from home site to attack site (m)**	**Behavior after attack**	**Speed after attack (km/hr)**
Adult female CFC-46	NA	5-June-2020 07:00	8.5 hours	53% traveling 18% foraging 35% encamped	0.67	900	25% traveling 29% foraging 46% encamped	0.24
Adult male CMC-42	11	5-June-2020 16:00	2 hours	0% traveling 100% foraging 0% encamped	0.25	100	20% traveling 16% foraging 64% encamped	0.25
Adult male CMC-39	14	8-June-2020 08:30	15.5 hours	44% traveling 31% foraging 25% encamped	0.65	761	4% traveling 0% foraging 96% encamped	0.12
Adult female CFC-77	10	5-June-2021 04:30	4 hours	56% traveling 11% foraging 33% encamped	0.74	430	16% traveling 24% foraging 60% encamped	0.33
Adult female CFC-77	16	8-June-2021 00:00	6 hours	62% traveling 31% foraging 8% encamped	1.04	300	8% traveling 24% foraging 68% encamped	0.22
Average	13		7.2 hours	43% traveling 38% foraging 20% encamped	0.70	498	15% traveling 19% foraging 67% encamped	0.23

FIGURES

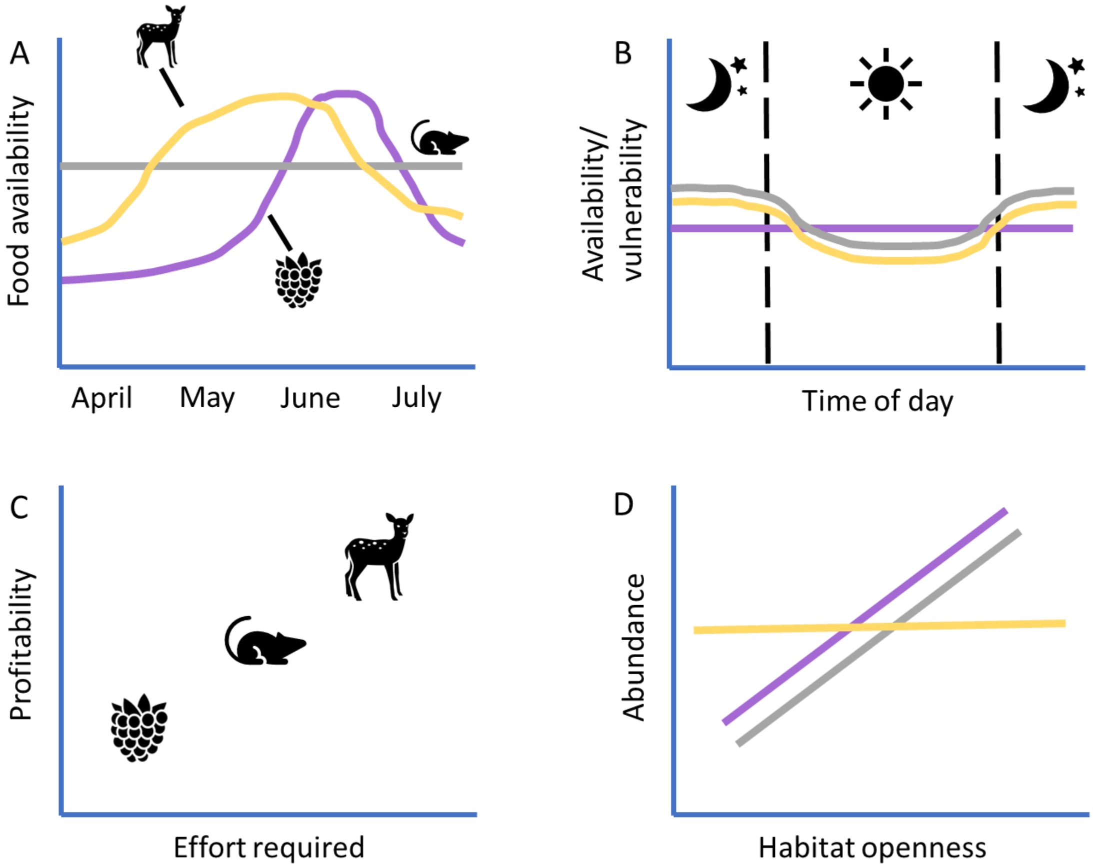

Figure 3.1. Background and hypothesized relationships which explain coyote hunting behavior for three different food items in South Carolina, USA. In A, we show how the availability of fawns (yellow), blackberries (purple), and small mammals (gray) changes throughout the summer, potentially leading to shifts in hunting behavior to target the most profitable foods. In B, we show how we predict that the availability and/or vulnerability of our three focal foods will change throughout the diel cycle. In C, we show how the relationship between effort required to find and potential caloric reward of each of our food items. In D, we show our prediction that habitat openness will predict abundance, but only for blackberries and small mammals.

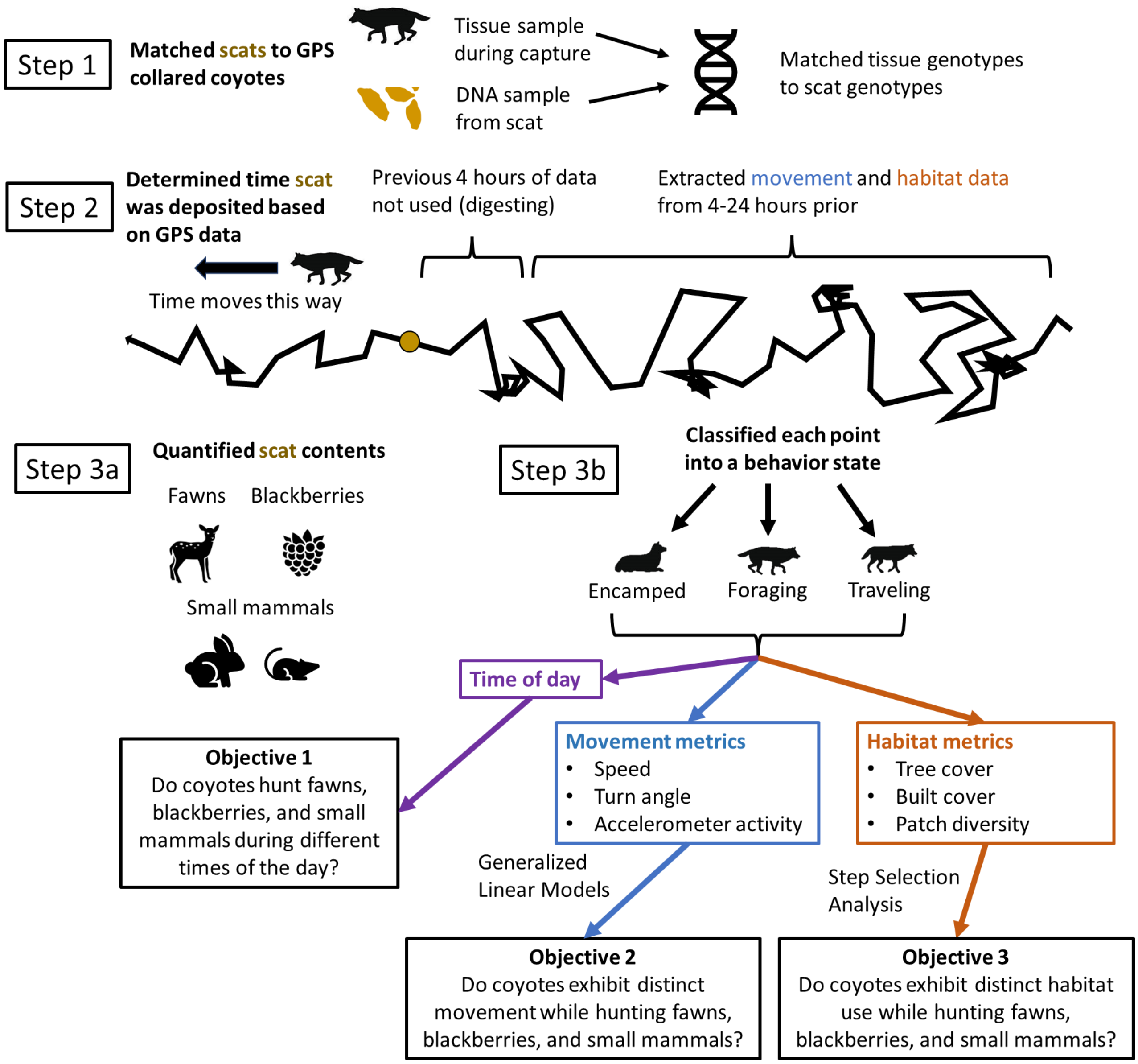

Figure 3.2. Workflow for how we linked diet data from coyote scats to movement and habitat data from GPS collars in South Carolina, USA.

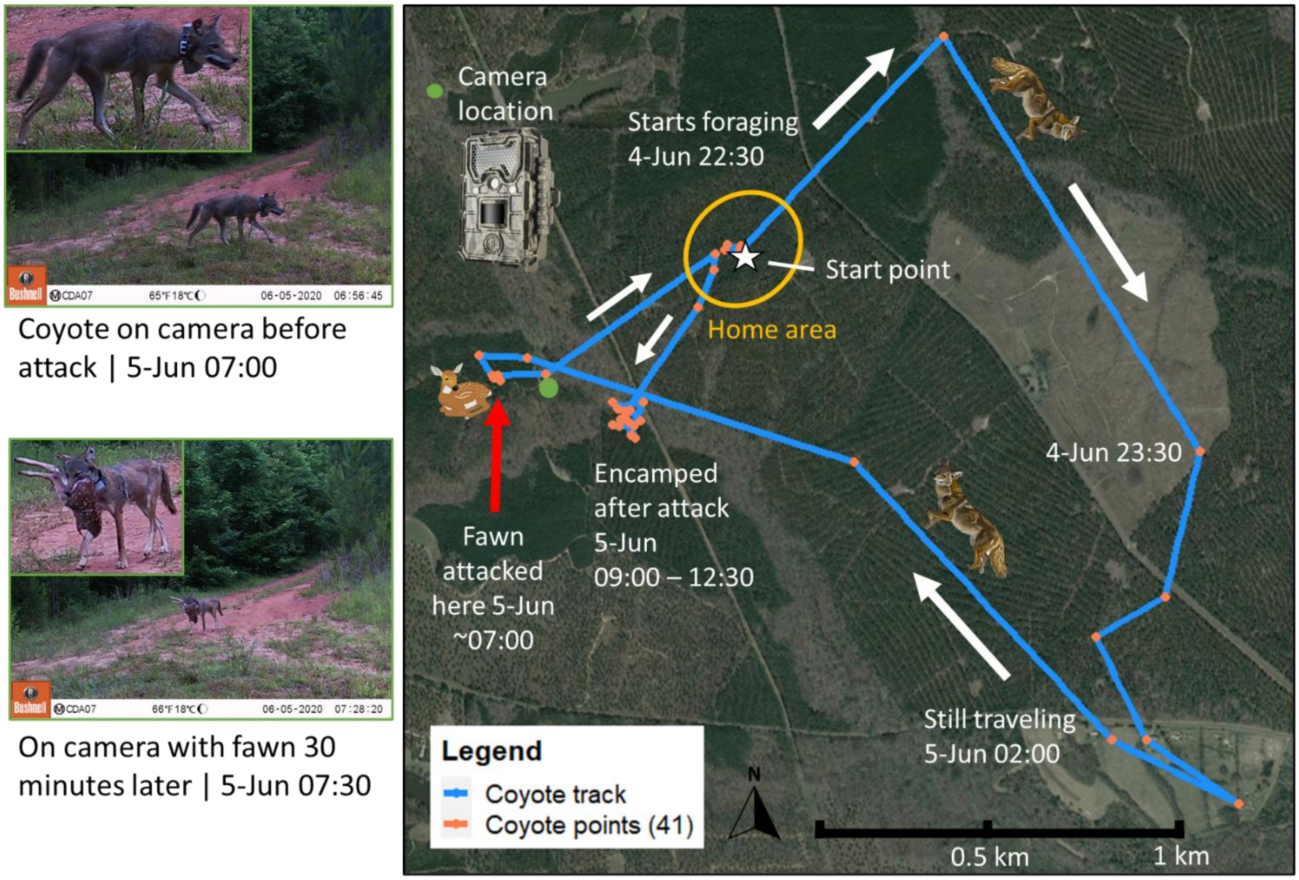

Figure 3.3. Coyote movement before and after killing a fawn in South Carolina, USA. In the main panel, we show the GPS track of an adult female coyote leaving a home area, traveling for several hours, then eventually detected on one of our camera traps (top left). Thirty minutes later she is detected again on the same camera with the hindquarters of a fawn in her mouth, suggesting that she just killed the fawn. She then briefly returns to the home area before being encamped nearby for several hours.

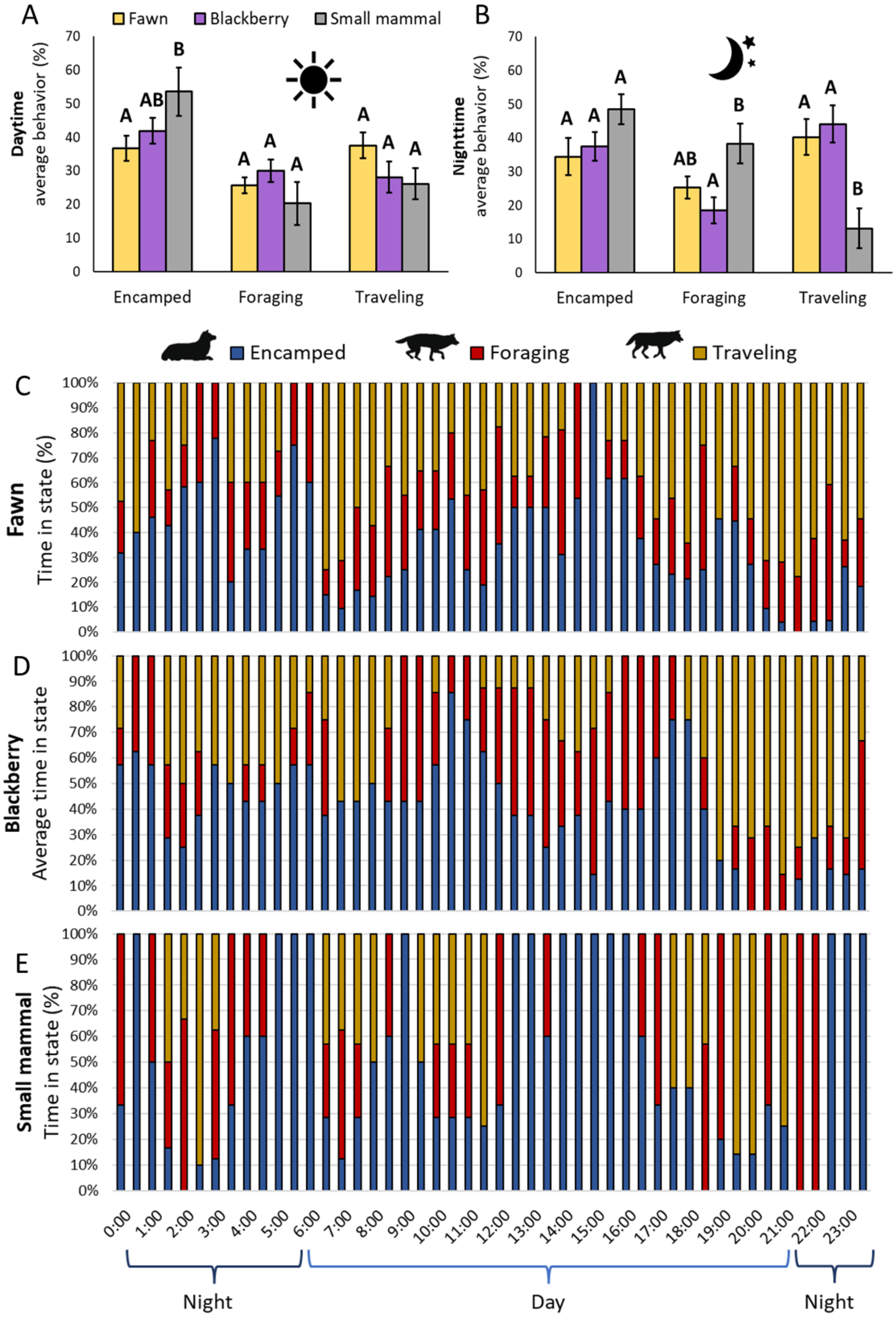

Figure 3.4. Visualizations of when coyotes were in each behavior state when hunting fawns, blackberries, and small mammals across the 24-hour day during summer in South Carolina, USA. In panels A (day) and B (night), we show the average percentage of time (error bars are standard error) coyotes spent in each behavior state, with different letters indicating significant differences ($p < 0.05$) within that triad. In panels C-E, we show the percentage of time coyotes spent in each behavior state every 30 minutes (during each GPS fix).

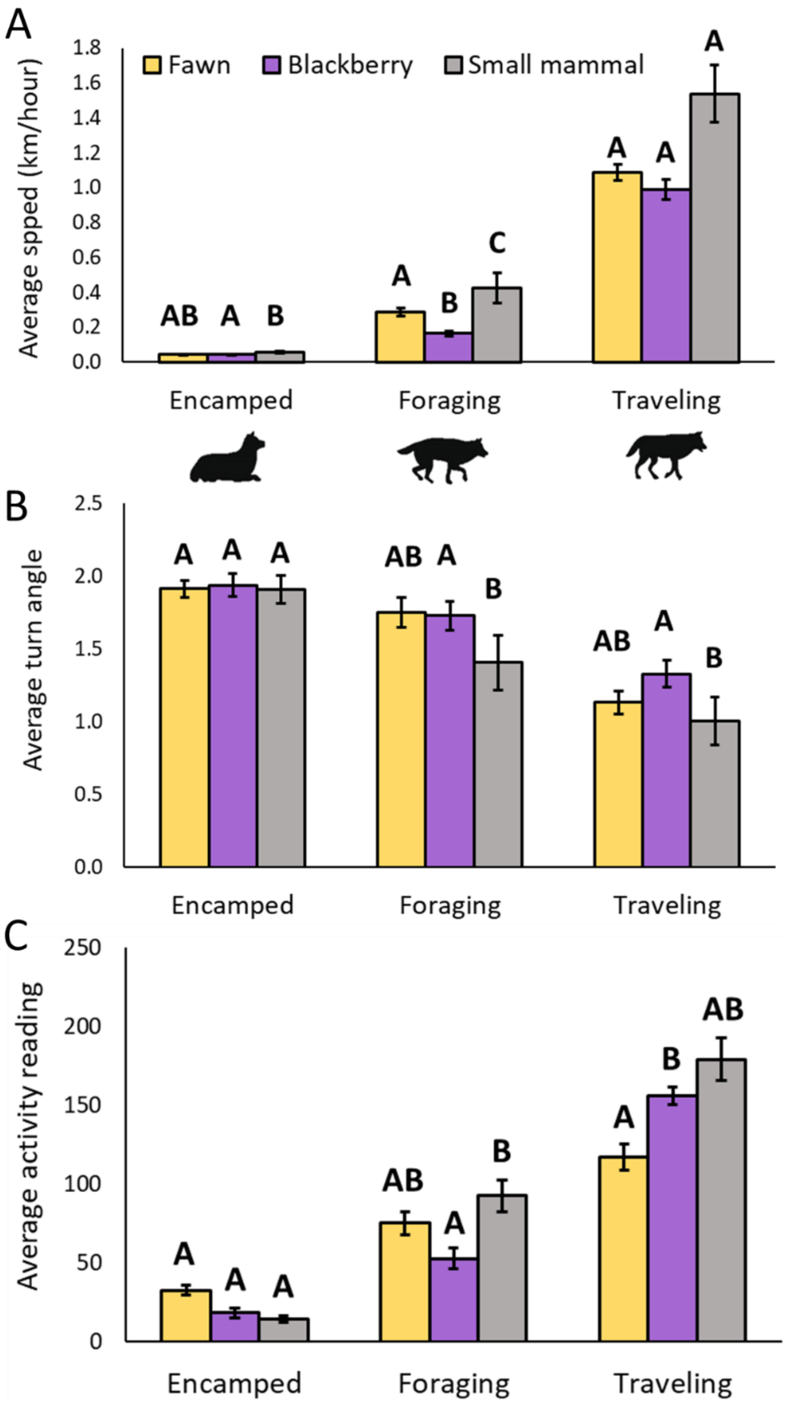

Figure 3.5. Results from how coyotes moved during a 20-hour window when they likely consumed fawns, blackberries, and small mammals in South Carolina, USA. Different letters indicate a significant difference ($p < 0.05$) within each triad. In panel A, we show the average speed (meters per hour) they were traveling during this 20-hour window. In panel B, we show the average turn angle (the angle created between three successive GPS points), and in panel C, we show the average activity reading from a three-axis accelerometer in the collar. Error bars are standard error.

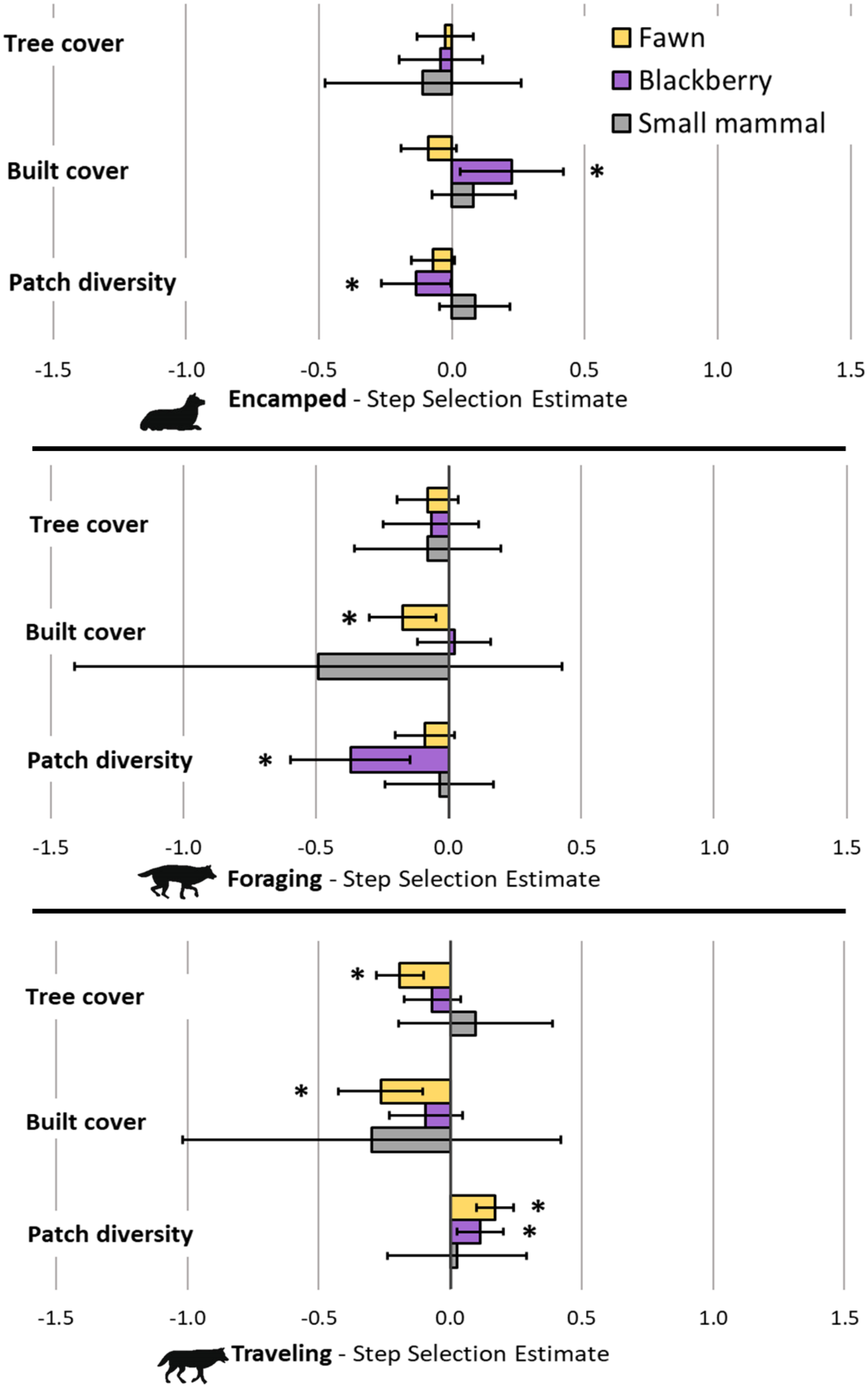

Figure 3.6. Results from an integrated Step Selection Analysis on coyote habitat use during a 20-hour window when they likely consumed fawns, blackberries, and small mammals in South Carolina, USA. The bars are the step selection estimates for each habitat variable and the error bars are the standard errors of those estimates. Bars on the right of the center line indicate selection, while bars on the left indicate avoidance. We use an asterisk to indicate cases where the standard error does not overlap zero.

CHAPTER FOUR

RISK FROM A TOP PREDATOR AND FOREST STRUCTURE INFLUENCES SCAVENGING BY SMALLER CARNIVORES

ABSTRACT

Large carcasses often attract multiple carnivore species, so subordinate carnivores must weigh the reward of a profitable meal with the risk of being attacked by dominant carnivores. These risk-reward tradeoffs are likely influenced by a variety of factors, including scale-dependent risk from dominant carnivores (e.g., short- vs. long-term risk) and the amount of carcass remaining. In the southeastern United States, human hunters provision a large amount of white-tailed deer carrion, which appears to be an important food source for coyotes (a novel top predator), but we know little about how coyotes influence the scavenging behavior of smaller carnivores. In this study, we evaluated the relative importance of risk from coyotes, vulture activity, forest structure, and remaining food on bobcat, gray fox, raccoon, and opossum scavenging by deploying 71 deer carcasses within a managed forest in South Carolina during January 2020 and 2021. We found that coyotes only had direct effects on bobcat behavior, suggesting that competition for carcasses was greatest between these two species. However, the relative importance of long- vs. short-term risk from coyotes was dependent on the stage in the scavenging process. Effects from forest structure were also stage-dependent, where tree density and age were related to carcass discovery for bobcats and raccoons, while minimal understory cover facilitated bobcat, gray fox, and opossum scavenging, despite short-term risk from coyotes. Vulture activity appeared to serve as a cue for gray foxes to discover carcasses. Ultimately, we found that risk from coyotes had species-specific and context-dependent effects on smaller carnivore scavenging. This represents some of the first direct evidence of how coyotes change smaller carnivore behavior in a region where coyotes are a novel top predator. However, forest

structure (particularly understory cover) seemed to mediate risk from coyote, highlighting how habitat can influence predator-predator interactions. Future research should also investigate these interactions during other times of the year and try to quantify the ecological effects from human provisioned carcasses on populations and communities.

INTRODUCTION

Aggression between carnivores is typically greatest when species are similarly sized, closely related, or consume the same foods (Ritchie and Johnson 2009). Larger carnivores are often dominant, though other factors such as group size and weapons are also important (Palomares and Caro 1999, Allen et al. 2016). There is also mounting evidence that top-down effects on subordinate carnivores are not consistent across space and time (Haswell et al. 2016, Jachowski et al. 2020), highlighting a need to better understand the mechanisms which govern these interactions. Predator-prey theory suggests that risk and risk-responses are scale dependent; the risky places hypothesis predicts that prey species will avoid places with high long-term predation risk (i.e., habitat where predators often hunt; Laundré et al. 2001), whereas the risky times hypothesis predicts that prey behavior should be most altered when predators are nearby (Creel et al. 2008). Moreover, environmental factors such as vegetative cover or human activity can mediate prey risk, creating refuges or ecological traps (Weldon and Haddad 2005, Berger 2007). A better understanding of when predator-prey theory applies to predator-predator interactions is needed.

Many carnivores are facultative scavengers, though large carcasses can be “hotspots” of encounter risk among carnivores (Sivy et al. 2017). Scavenging was traditionally viewed by ecologists as a “free meal”, because it requires little handling time and can have large caloric benefits (Wilson and Wolkovich 2011). However, recent research has shown that large carcasses can be fatal attractants for subordinate carnivores if dominant carnivores catch them there (Sivy et al. 2017). Although carcasses can be risky places, subordinate carnivores can likely mediate that risk by visiting carcasses during less risky times (Swanson et al. 2016). Carnivores have been shown to increase vigilance at carcasses in response to sympatric predators (Atwood and Gese 2008, Kautz et al. 2021), but very few studies have directly tested how predation risk influences carrion consumption. Understanding how subordinate carnivores navigate this risk-reward trade-off is one important facet of understanding the ecological effects of carrion on the landscape (Ruprecht et al. 2021).

Carrion can become available through multiple means and is increasingly acknowledged as a substantial proportion of many carnivore species' diets (Prugh and Sivy 2020). Large carnivores provision large herbivore carrion, as do humans, the latter often through hunting or vehicle collisions (Wilson and Wolkovich 2011, Pereira et al. 2014). A global review found that 79 vertebrate species ate carrion from big game hunters (Mateo-Tomás et al. 2015), and in the United States (US) alone, an estimated 625,000,000 kg of carrion is left in the field by hunters every year (Oro et al. 2013). This is at least comparable to the amount of carrion provisioned by large carnivores, which is estimated to be 42.2 kg/km^2/yr (Prugh and Sivy 2020) or ~415,000,000 kg/yr in an area the size of the US.

In the southeastern US, white-tailed deer hunting (*Odocoileus virginianus*; hereafter 'deer') is a common recreational activity during the fall, resulting in a large amount of carrion available to scavengers. In 2020, there were 197,893 deer harvested in South Carolina alone (2.4 deer/km^2; South Carolina Department of Natural Resources 2021). Indeed, most studies on coyote (*Canis latrans*) diet in the Southeast have reported a spike in deer consumption coincident with hunting season, often large enough to make deer the most consumed food item during the fall (e.g., Schrecengost et al. 2008, Kelly et al. 2015, Swingen et al. 2015, Ward et al. 2018). Coyotes likely acquire deer through multiple means, including finding hunter-killed (or crippled) deer before the hunter can, and scavenging from carcass dump sites or field-dressed deer. Importantly, coyotes have only become established across the Southeast in the last 30-50 years (Hody and Kays 2018) and have been shown to be a substantial source of fawn mortality (Nelson et al. 2015, Kilgo et al. 2019). Therefore, although hunters generally perceive coyotes as an invasive, problematic species in the Southeast, they are likely supplementing coyote diets with a profitable, low-effort food source.

Apart from humans, coyotes have no predators across most of the eastern US, making scavenging less risky relative to where they coexist with large carnivores (Sivy et al. 2017, Ruprecht et al. 2021). However, coyotes could be a source of risk for smaller carnivores intending to scavenge. Across their range, coyotes suppress and kill multiple fox species, and will also sometimes kill bobcats (*Lynx rufus*, Fedriani et al. 2000, Moehrenschlager et al. 2007, Nelson et al. 2007). However, coyotes and bobcats appear to share less niche space relative to coyotes and foxes, including metrics like dietary overlap, habitat use, and temporal activity (Thornton et al. 2004, Witczuk et al. 2015, Rich et al. 2018). Coyotes seem to suppress raccoon (*Procyon lotor*) populations in some contexts (Sargeant et al. 1993, Crooks and Soule 1999), but not others (Gehrt and Prange 2007). Since coyotes have become established in the southeastern US, there has been relatively little research on their interactions with smaller carnivores. So far, a study in Mississippi found that gray foxes (*Urocyon cinereoargenteus*) avoided coyote core areas but overlapped considerably with full coyote home ranges (Chamberlain and Leopold 2005), and a similar pattern was found between bobcats and coyotes in Florida (Thornton et al. 2004). This suggests that scavenging on carrion in places with high coyote activity would be most risky, while carrion in places with lower coyote activity would be less risky.

In this study we evaluated support for multiple hypotheses that might influence the detection and consumption of deer carcasses by bobcats, gray foxes, raccoons, and opossums (*Didelphis virginianus*). We hypothesized that risk from a top predator (coyotes) would be important, but short-term risk and long-term risk might not have parallel effects. We also thought that vulture activity (i.e., flying) could serve as a cue for carnivores, especially given vultures often find carcasses quickly (Turner et al. 2017). Forest structure could influence the probability or speed in which carnivores detect carrion, through being correlated with carnivore abundance (Nelson et al. 2007) or their ability to detect visual and olfactory cues. Vegetative cover could influence perceived risk (Flores-Morales et al. 2018, Prugh and Sivy 2020), which may be highest from coyotes in open habitat given their cursorial foraging strategy. Lastly, the amount of carrion remaining likely influences the time spent consuming carrion. We approached our analysis by decomposing the scavenging process into multiple steps: 1) how long it took our focal species to arrive (objective one); 2) how much time they spent at carcasses (objective two); and 3) how much time they spent feeding (objective three). For the most part, we used the same hypotheses for each step of the scavenging process (Table 4.1), so that we could quantify when each factor was important. By testing multiple hypotheses in a multi-predator system, we were also able to determine if coyotes have species-specific effects on smaller carnivores.

METHODS

Study Area

Our study area was in the Piedmont region of western South Carolina, characterized by a humid subtropical climate, mild winters, and gently rolling hills (Griffith 2010). Various Native American tribes lived in the region during the period of European colonization, likely including the Yuchi, Westo, Chickasaw, Apalachee, Yamassee, and Savanna Peoples (Gallay 2002, Cobb and Depratter 2012, Native Land 2022). As late as the early 1700s, much of the land was a savannah community, including native grasses and bison (*Bison bison,* McCormick County Chamber of Commerce 2021). During the 1800s, much of this land was converted to cotton fields and our study area still contains a plantation house where slaves lived and worked. The dominant land cover changed again in the 1900s, this time to forest, which mostly consisted of managed loblolly pine (*Pinus taeda*) plantations in various stages of succession. Hardwoods dominated in drainages, including white oak (*Quercus alba*), southern red oak (*Q. falcata*), and hickory (*Carya* spp.). Understory vegetation included blackberry (*Rubus allegheniensis*), muscadine (*Vitus rotundifolia*), and fennel (*Eupatorium* spp.). Pastures and fields were intermittent throughout the landscape, including food plots for game species. The majority of deer hunting occurred during rifle season in October, November, and December.

We deployed deer carcasses across ~15,000 acres (61 km^2) of private land in McCormick County, South Carolina (Figure 4.1). Potential scavengers included coyote, red fox (*Vulpes vulpes*), gray fox, domestic dog (*Canis familiaris*), bobcat, striped skunk (*Mephitis mephitis*), raccoon, opossum, wild pig (*Sus scrofa*), turkey vulture (*Cathartes aura*), black vulture (*Coragyps atratus*), American crow (*Corvus brachyrhynchos*), and birds of prey (*Accipitridae spp.*). Black bears (*Ursus americanus)* were rarely seen in the study area. The average temperature was 11° C (52° F) during our first survey period (January 2020) and 8° C (47° F) during our second survey period (January 2021). It rained 1-3 cm during three days in January 2020 and five days in January 2021.

Study Design

We stratified carcass deployment locations based on coyote activity. We primarily used data from an established camera array in our study area (Saldo et al. 2023, In press) to estimate coyote activity (Section S1). The array consisted of ~90 unbaited cameras deployed on dirt roads, each ~1 km apart (Figure 4.1). For each camera array site, we counted the number of photos of coyotes from the year prior to carcass deployment and divided by the number of days each camera was active (photos/day). In order to capture a gradient of coyote activity, we evenly stratified each camera site into low, medium, and high activity using quantile breaks in ArcMAP 10.7 (ESRI, Redlands, CA, USA). We randomly chose an equal subset from each category, avoiding placing sites next to each other when possible. Once we arrived at the camera, we deployed each carcass 250 m away in a random direction, while ensuring the carcass was in the same habitat type as the camera.

Carcass Deployment

In early January 2020 and 2021 (immediately after deer hunting season) we collected unwanted portions of deer carcasses (bones, guts, hides) from local deer processers. We chose this timing because we wanted to be representative of deer hunting season (October – December) while limiting the availability of other carcasses on the landscape. While a whole deer carcass is representative of some carrion, we wanted to simulate the leftovers from field-dressed deer or those left at carcass dump sites, while also standardizing the amount of carcass at each site. We placed 15-16 kg of deer carcass into a 1 m x 0.5 m cage made of metal garden fencing and secured the cage to a tree with wire (Figure 4.2), or with 1-2 metal 1 cm diameter corkscrew anchors driven into the ground. We used garden fencing with 5 cm x 7.5 cm cells because we wanted scavengers to be able to feed from the carcass without being able to pull out large portions and feed off camera. We attempted to diversify the type of carcass in each cage (e.g., guts and bones), but 26 of 75 cages were only filled with a single type. We placed a motion-activated wildlife camera (Bushnell, Overland Park, KS, USA) ~5 m away and set it to take three photos per trigger with a one-minute delay between triggers (Figure 4.2). We left carcasses out for a minimum of 21 days, and most sites were deployed for at least 28 days. We deployed 35 sites in January 2020 and 40 sites in January 2021. However, we censored two sites from each year from all analyses due to various issues (i.e., burned by fire, batteries died < 7 days after deployment), therefore we used 71 sites in our analyses unless specified otherwise.

Photo Processing

We processed photos using TimeLapse2 (Greenberg 2020). For each photo we recorded the species and the amount of carcass remaining relative to when it was deployed (> 75%, 75-50%, 50-25%, < 25%, bones and hide, or unknown/moved). For our focal species (bobcat, gray fox, raccoon, opossum) we also recorded their behavior (head up, head down not feeding, head down feeding, unsure). We defined ‘head up’ as any photo where the top of the neck was parallel with or raised above the top of the back. For quality control, each photo received a certainty score (100% sure, fairly confident, or unsure), and all photos not tagged as 100% sure were checked by the first author.

Objective 1: Time until arrival at the carcass

We quantified how long it took our focal species to arrive at the carcasses (if they showed up at all). We jointly modeled two response variables: 1) whether or not the species was detected, and 2) the time until the species arrived (defined as the time difference between the deployment date-time and first detection in hours) or the hours until the site became non-operational. Although our modeling approach accounted for variation in deployment time, we still wanted our sites to be representative, so we censored any sites where the focal species was never detected and that were deployed < 15 days (species-dependent censored site range = 6-10).

We hypothesized that short-term and long-term risk from coyotes could influence time until arrival. For short-term coyote risk, we used the time from deployment until coyotes arrived. We chose to use time until arrival rather than some other metric from the carcass sites (e.g., total time spent by coyotes) because we wanted to test if and when coyotes discovered sites influenced how long it took our focal species to arrive. For long-term coyote risk, we used the camera array and an inverse-distance weighted approach to quantify coyote activity from the previous year. Specifically, we counted the number of coyote photos taken in May, June, October, and November of the previous year by each camera in the array and divided by the number of days the camera was operational (coyotes/day). We used data from these months due to photo processing constraints (over three million photos were collected throughout the study), and because we wanted to capture coyote activity during key biological periods throughout the year (May and June = pup rearing, October and November = dispersal). To decide which array cameras would represent which carcass sites, we used ArcMAP to visualize a 1 km buffer around each carcass site and used up to three of the closest array cameras within that buffer (Figure A4.1). We distance-adjusted each coyote/day value by subtracting the distance (in km) from the carcass site from one, then multiplied that distance by coyotes/day so that closer array cameras were adjusted less. We then averaged these adjusted values for each carcass site:

$$\bar{X}\, {}^{coyotes}\!/_{day_i} \times w_i$$

where w_i = one minus the distance from camera site i to the carcass in km.

We also hypothesized that vulture activity and forest structure could influence time until arrival. We counted the number of vulture photos taken at each carcass site between the hours of 4pm and 9am, which is when carnivores would likely be cuing into vulture activity, based on exploratory analyses of diel activity (85-95% of focal species detections were during nocturnal or crepuscular hours). Given this time period only represents a portion of the day (~3 hours) when the typically diurnal vultures were active, we tested if crepuscular vulture activity was representative of total vulture activity. We used data from 2021 (38 sites) to test for a correlation between the subset of crepuscular photos we used and all vulture photos and found a moderate correlation between the two datasets ($R^2 = 0.618$). Accordingly, we proceeded with crepuscular vulture activity as representative of vulture activity at the carcass sites. We divided the number of vulture photos at each site by the days the site was operational to standardize between sites. For vegetative structure, we measured several variables while deploying the carcass. To approximate stand age, we measured the circumference (at 1.5 m off the ground) of the five closest trees of the type that dominated the stand (usually loblolly pines), then averaged these five values. For tree density, we counted the number of trees (of the dominant species) within a 5 m radius of the carcass. We only counted the dominant species because we wanted to capture the management phase the stand was in, and midstory hardwoods would have confounded this in some stands. For understory cover, we viewed a Robel pole (Robel et al. 1970) from 10 m away from the carcass in the four cardinal directions and averaged those four values.

We used time until event (cox proportional hazard) models to test our hypotheses. We tested for collinearity between our four predictor variables and found no pair with Pearson's > |0.55|. We centered and scaled each predictor variable, then fit 13 models for each of our focal species (Table A4.1). In addition to univariate and global models, we included subglobal models which captured combinations of variables we hypothesized could be important. For example, we included a 'forest structure' model, with stand age, tree density, and understory cover. We also included a model with an interaction between stand age and vulture activity, because we thought that vulture activity might be particularly influential at younger sites (with no or little canopy). We used the survival package (Therneau and Grambsch 2000) in R (R Core Team, Version 4.4.1 2021) to fit our models and check model assumptions. We found that raccoons had one model and opossums had two models that violated cox proportional hazard assumptions, so we excluded those models.

We used an information theoretic approach (AIC; Burnham and Anderson 2002) to determine relative support for our hypotheses. We ranked models using AIC_c and the MuMIn package (Barton 2009) and determined that any model within 2 delta AIC_c of the top model (unless ranked below the null model) would be considered a competitive model (Burnham and Anderson 2002). For competitive models, we determined variable significance if 95% confidence intervals did not overlap zero. When there were multiple competitive models containing the same variable, we reported statistics from the top ranked model.

Objective 2: Time spent at the carcass

For this analysis, we calculated the total time our focal species spent at each site. We grouped photos of the same species at the same site into *detection events* if they were separated by < 30 minutes (Ridout and Linkie 2009), then recorded the duration of a detection event as the time between the first and last photo. We recorded events consisting of one trigger as one minute in duration because of the one-minute delay between triggers. Our response variable was the sum of the duration of each species' detection events at each site divided by the days the site was operational. We hypothesized that several variables could influence time spent at the carcasses (Table 4.1). For long-term coyote activity, stand age, tree density, and understory cover, we used the same measures as previously described. For short-term coyote activity, we calculated the minutes spent by coyotes and divided by the days the carcass site was operational.

We used generalized linear models followed by AIC model selection for this analysis. We tested for collinearity between our four predictor variables and found none with Pearson's > |0.52|. We compared the fit of different distributions on our global models with six combinations for each species: Poisson and two types of negative binomial models, along with either zero inflation or no zero inflation specified. We found that a negative binomial distribution was always best, but only raccoons needed the zero inflation term. Therefore, we carried these distributions into each species' model structure. In addition to the global model, we built nine other models for each of our focal species (Table A4.2). We used a similar combination of models as objective one, with the addition of an interaction between short-term coyote activity and understory cover, because we thought that risk from coyotes might be particularly high at sites with more cover. We included a logoffset term to account for the number of days each carcass site was operational. We checked model fit using the DHARMa package (Hartig 2020) and used the same AIC_c and variable rules as previously described.

Objective 3: Percent of time spent feeding on the carcass

We calculated the percentage of time our focal species spent feeding during each detection event (see *Objective two*) by counting the number of photos where the animal was feeding with its head down and dividing by the total photos during that detection event. Therefore, our response variable was the proportion of photos where the animal was feeding during the detection event. We hypothesized that the same variables from *Objective two* would be important, with the addition of the amount of carcass remaining (Table 4.1). We used the same measures of long-term coyote activity, stand age, tree density, and understory variables as previously described. We quantified short-term risk by summing the cumulative minutes spent by coyotes at that carcass site in the previous seven days (prior to that detection event). We chose seven days because we found that average coyote activity dropped incrementally from the day of discovery to day five, and we added two days to account for lingering scent. For carcass remaining, we used the state of the carcass as described in *Photo Processing* and converted this to an ordinal variable (5 = > 75% remaining, 4 = 75-50%, 3 = 50-25%, 2 = < 25%, 1 = bones and hide only). We excluded events where the carcass state was classified as “unknown/moved” (n = 1 for each species).

To test how these variables influence time spent feeding, we used a similar analytical approach to *Objective two* (generalized linear models), with the difference being our observational unit was detection events rather than sites. We decided to not include gray foxes or raccoons in this analysis because they were only detected feeding in 3/30 and 3/35 detection events, respectively. None of our variables had pairwise correlations > |0.61|. We used a binomial distribution because our response variable had an upper limit of one.We fit 14 models for each species (Table A4.3), which included a random effect of carcass siteand weights for the number of photos in the detection event , but were otherwise similar to previous analyses in structure, function, AIC$_c$, and variable rules.

RESULTS

We collected useful data from 71 deer carcasses deployed across our study area in January 2020 and January 2021 (Figure 4.1). Vultures and coyotes were detected most frequently, followed by our focal carnivores and wild pigs (Figure A4.2). We also detected domestic dogs, American crows, red-tailed hawks (*Buteo jamaicensis*), golden eagles (*Aquila chrysaetos*), and owls.

Objective 1: Time until arrival at the carcass

We detected coyotes at nearly all sites not censored from this analysis (91%), followed by opossums (46%), bobcats (40%), raccoons (26%), and gray foxes (19%; Figure 4.3). For the sites where they did arrive, coyotes were typically the first to arrive (average days until detection ± standard error = 5.93 ± 0.57), followed closely by opossums (6.05 ± 1.11), whereas gray foxes (10.00 ± 2.25), raccoons (10.06 ± 1.63), and bobcats (10.23 ± 1.74) took longer to arrive at the carcasses.

Our bobcat analyses had three competitive models (Table A4.1). Bobcats arrived faster at sites with greater long-term coyote activity (hazard ratio = 2.766) and when the tree stand was younger (hazard ratio = 0.637; Table 4.2). Our gray fox analysis had three competitive models (Table A4.1), and gray foxes arrived faster at sites with more vulture activity (hazard ratio = 1.545; Table 4.2). Our raccoon analysis had four competitive models (Table A4.1), and raccoons arrived faster at sites with greater tree density (hazard ratio = 1.361; Table 4.2). For our opossum analysis, there were three competitive models (Table A4.1), yet 95% confidence intervals overlapped zero.

Objective 2: Time spent at the carcass

Totaled across all sites, we found that coyotes spent 4.3x more time (133.9 hours) at the carcass sites compared to opossums (31.1), which spent much more time than bobcats (4.0), gray foxes (2.8), and raccoons (1.6; Figure A4.2). Coyotes also spent the most minutes per operational day at the sites (average minutes ± standard error = 8.4 ± 2.4), followed by opossums (3.4 ± 0.8), gray foxes (1.0 ± 0.6), bobcats (0.7 ± 0.3), and raccoons (0.6 ± 0.3).

The bobcat and gray fox analyses were informative, while the raccoon and opossum analyses were not. For bobcats, there was one competitive model (Table A4.2). Long-term coyote activity had a positive effect on bobcat activity, where bobcats spent 10 additional seconds at the carcasses for each additional photo/day of coyotes from nearby cameras (Figure 4.4). For the gray fox analysis, there were two competitive models related to habitat (Table A4.2). Although gray foxes spent little time at the carcasses to begin with, they spent 10 less seconds at the carcasses for every two-unit increase in understory cover, though this effect was primarily present when cover was relatively low (Figure 4.4). The null model was the top model for the raccoon analysis (Table A4.2). For opossums, there were four competitive models (Table A4.2), yet all 95% confidence intervals for their estimates overlapped zero.

Objective 3: Time spent feeding on the carcass

We recorded 695 coyote detection events, 150 opossum events, 56 bobcat events, 35 gray fox events, and 30 raccoon events. Bobcat detections lasted the longest on average (average minutes ± standard error = 13.8 ± 3.8), followed closely by opossum (13.1 ± 1.5) and coyote (11.6 ± 0.9). Gray fox (4.8 ± 2.0) and raccoon (3.1 ± 0.8) detections were shorter. Notably, many of the detection events for each species were one minute long (our minimum possible event time length) – 73% for raccoons, 59% for bobcats, 57% for gray foxes, 50% for coyotes, and 46% for opossums. Averaged across all sites, our focal species were detected feeding in < 10% of the photos within a detection event; bobcats were feeding in 9.8% ± 3.5% of photos, the same as opossums (9.8% ± 3.5%), followed by coyotes (8.4% ± 1.7%), raccoons (5.8% ± 3.3%), and gray foxes (5.5% ± 4.4%).

For the percent of bobcat photos feeding analysis, the short-term coyote activity * understory interaction model was the only competitive model (Table A4.3). Bobcat feeding was jointly influenced by negative effects from coyote activity and understory cover (Table 4.2, Figure 4.5). Coyote activity was most influential, as bobcat feeding was greatest at low levels of coyote activity and lowest at high levels of coyote activity. However, minimal understory cover facilitated bobcat feeding, even at high levels of coyote activity (Figure 4.5). For opossum feeding, there was also only one competitive model: carcass remaining * understory cover interaction model (Table A4.3). Opossums feeding had a strong positive association with the amount of carcass remaining, but particularly when understory cover was high (Figure 4.5). However, when there was little carcass remaining, the effect of understory reversed and little understory was associated with more feeding.

DISCUSSION

Our findings provide additional support for the notion that dominant carnivores have scale-dependent and species-specific effects on subordinate carnivore behavior (Jachowski et al.

2020), which are mediated by vegetation structure (Gigliotti et al. 2021). Out of the four smaller carnivores we studied, only bobcats seemed to be influenced by coyotes, suggesting that competition is greatest between these two similarly sized species. Additionally, how coyotes and forest structure influenced smaller carnivore behavior was dependent on which step in the scavenging process we were assessing. The diversity of facultative scavengers we detected, combined with the high intensity of carcass use by coyotes across both space and time, support the notion that carcasses act as point sources of competition (Prugh and Sivy 2020). Ultimately, we show that coyotes have context-specific effects on smaller carnivore behavior and suggest behavioral strategies for how these smaller carnivores coexist with this novel large carnivore in our system.

How coyotes influenced scavenging

Bobcats arrived faster and spent more time at carcasses where long-term coyote risk was greater, perhaps because they aimed to claim and defend the carcass. Although coyotes and opossums spent more total time at the carcasses, bobcats had the greatest percentage of detection events > 30 minutes in duration (18%), suggesting they were defending the carcass in these cases. Bobcats have been shown to engage with and “win” most direct encounters with coyotes at carcasses, even though they are a smaller species (Allen et al. 2016). We did record two instances where a bobcat clearly defended a carcass from a coyote, but there were not enough of these interactions to analyze. Another plausible explanation is that bobcat and coyote density was spatially correlated, potentially since both species share small mammals as important parts of their diet throughout the year (Koehler and Hornocker 1991, Neale and Sacks 2001). Indeed, dietary overlap is likely greatest in the winter when food availability is lowest (Cherry et al.

2016), meaning that carcasses would have been a valuable resource for both species. Therefore, increased dietary overlap may be the underlying explanation driving these relationships we found.

Short-term coyote risk reduced the time bobcats spent feeding, perhaps because putting their head down and feeding would reduce their ability to detect a coyote. Coyotes may have had similar effects on gray foxes and raccoons, as 4/6 of their total feeding events occurred when recent coyote activity was zero and the other two occurred when recent coyote activity was relatively low. Dominant carnivores in Alaska (wolves and wolverines; *Canis lupus*, *Gulo gulo*) had similar effects on subordinate carnivores (coyotes and red foxes), where the dominant species spent 2x more time feeding on carcasses (Klauder et al. 2021). In Montana, beta (but not alpha) coyotes reduced time feeding on carcasses in the presence of wolves (Atwood and Gese 2008). Although coyotes apparently reduced bobcat feeding intensity , it is possible that bobcats were able to compensate for this loss of food by eating a similar amount of food over a longer time period. Perhaps this also explains why bobcats spent the most time at the carcasses per detection event.

Long-term and short-term coyote risk only had significant effects on bobcats, which suggests that competition for carcasses was greatest between these two species. Indeed, risk from coyotes best explained bobcat behavior at every step of the scavenging process, and our results suggest that a combination of fear and proactive defense may be driving these responses. While coyotes can kill bobcats (Fedriani et al. 2000), a recent meta-analysis reported that 74% of studies did not find evidence for interference competition between bobcats and coyotes, and it was less likely to be found in forested habitat (like ours; Dyck et al. 2022). Therefore, it seems that coyotes influence bobcat behavior, but the outcomes of direct interactions are context dependent. In summary, we demonstrate the importance of investigating species-specific patterns in response to risk from a top predator through multiple measures, both in terms of predation risk (short-term and long-term risk) and through decomposing the multi-step behavioral response to resources in the environment (e.g., detection, investigation, consumption).

How forest structure influenced scavenging and mediated risk

Forest stand structure (tree age and density) influenced bobcat and raccoon time until arrival. Bobcats arrived faster at carcasses within younger tree stands, which is likely where bobcats are more abundant in the Southeast (Chamberlain et al. 2003, Little et al. 2018). This also supports our hypothesis that prey availability is one of the mechanisms that explains bobcat time to arrival, because small mammals and rabbits (bobcat primary prey) were most abundant in young pine stands (unpublished survey data). Raccoons arrived faster at carcasses where tree density was greater, which may likewise be related to habitat selection. Although raccoon habitat selection is often scale and season dependent, in the winter raccoons seem to select hardwoods and to some extent immature pines (which tended to have denser trees in our study area; Chamberlain et al. 2003, Byrne and Chamberlain 2011). It is possible that risk from coyotes is one of the mechanisms driving selection of denser forests by raccoons, as there are more options for climbing to escape predators. Future studies should try to quantify a baseline measure of scavenger abundance or density near carcass sites, so that these effects can be disentangled from characteristics of the site which facilitate discovery.

Understory cover was an important factor in several analyses, and seemed to mediate risk from coyotes in some cases. Although gray foxes spent relatively little time at carcasses to begin with, they spent more time at sites with very minimal understory cover. We posit that gray foxes were more comfortable at carcasses with longer sightlines, which would allow them to detect dominant carnivores more quickly. Of our focal species, gray foxes were likely at the highest risk of predation by coyotes, considering coyote-specific mortality is well documented (e.g., Fedriani et al. 2000) and we observed gray foxes killed by coyotes in our study area. This may also explain why we did not detect red foxes at our carcasses, despite them being present in our study area (Saldo et al. 2023, In press) − predation risk from coyotes may be even greater for red foxes (Levi and Wilmers 2012). We also found that bobcats fed more when understory cover was minimal. Importantly, this effect interacted with short-term coyote risk, where minimal understory cover facilitated bobcat feeding, even when coyote risk was high. Similarly, understory cover interacted with the amount of carcass remaining for opossum feeding, yet here we found that minimal understory cover only facilitated feeding when there was little carcass remaining (and had the opposite effect when there was more carcass). Perhaps this suggests a risk-reward tradeoff, where opossums are willing to engage in riskier behavior when there is a lot of food, but less willing when there is little food. Regardless, these findings again highlight the complex relationship between understory cover and subordinate carnivore behavior.

Past research has explored how vegetative structure can mediate predation risk. At the landscape scale, increased vegetative cover has been associated with facilitating coexistence between carnivores, presumably by reducing encounter rates with top predators (Janssen et al. 2007, Nelson et al. 2007). However, at smaller scales, reduced vegetative complexity has been shown to benefit subordinate carnivores. For example, cheetah survival was greater in areas of low vegetative complexity, partially because large predators could ambush them in more complex habitats (Gigliotti et al. 2020). In a scavenging context, an ideal carcass for a subordinate carnivore might be in open habitat (to better detect predators), but still relatively close to cover (for escape), which would parallel risk-sensitive forage selection by ungulates (Creel et al. 2008, Stears and Shrader 2015). Collectively, we show that forest structure had divergent effects on subordinate carnivore scavenging depending on the context.

How vulture activity influenced time until arrival

Gray foxes arrived faster at sites with more vulture activity, which could mean gray foxes were cuing in on vulture activity. Although gray foxes were nocturnal (and vultures were diurnal), it is possible they were attentive to vulture activity during crepuscular periods. Vultures discovered sites quickly and were the most detected taxa (on average) during 26 of the 30 days we monitored carcasses. Therefore, even though gray foxes slowly discovered sites during the first two weeks after deployment, vulture activity would have likely remained high enough to serve as a cue throughout this time period. Vulture activity was also a top model for raccoon and opossum time until arrival (with the same effect direction), but 95% confidence intervals overlapped zero. This suggests that these two species may have also been cuing into vulture activity, though not as strongly as gray foxes. Our results somewhat contrast with an experimental study, also in South Carolina, which found that carnivores did not arrive faster at sites where vultures were not excluded compared to sites where they were (Hill et al. 2018). However, other studies have found results in line with ours and suggested explanations. In addition to simply locating carcasses (large carnivores and have been shown to cue in to vulture activity; Houston 1979), small carnivores may be cuing in because vultures can tear open carcasses for them (Cortés-Avizanda et al. 2012). Alternatively, given how quickly vultures can discover carcasses, their activity may serve as an indication of a fresh carcass, which could mean that a coyote (or another dominant carnivore) has yet to discover it. Thus, cuing into vultures may ultimately be another coexistence strategy for subordinate carnivores when sympatric with a dominant carnivore.

Limitations

We used a standardized approach to quantify scavenging during a single season, which leaves our results subject to at least two limitations which require further investigation. First, although field manipulations can be a powerful approach to understand complex systems, it can be challenging to know how representative the experimental conditions are (Smith et al. 2020). Providing and monitoring carcasses is an established method in scavenging research, though carcasses are not often placed in a metal cage like ours were. Scavengers seemed to have no trouble feeding from the carcass through the cage (as intended), though they may have fed more if the cage was not present. The size of the carcass has been shown to have a powerful effect on who scavenges and for how long (Moleón et al. 2015, Turner et al. 2017), so we wanted to avoid this confounding variable while reducing the ability of scavengers to move the carcass out of view. Second, scavenging frequency by facultative scavengers has been shown to vary throughout the year, typically peaking in winter when other foods are most limited (Pereira et al. 2014, Turner et al. 2017). Therefore, quantifying scavenging behavior primarily in January likely represented the period of highest potential competition. Future research should compare scavenging dynamics during other parts of the year when other foods are more abundant as well as try to quantify scavenger density.

Conclusions and implications

We draw several conclusions from the results of our study likely of interest to ecologists. First, when considering the full scavenging process, forest structure was often more important for smaller carnivores scavenging than risk from coyotes. We showed that understory cover influenced both bobcat and opossum feeding, likely mediating the risk-reward tradeoff associated with scavenging. We also found that gray foxes spent more time at carcasses with less understory cover and racoons potentially selected dense forests as a proactive antipredator strategy, though future work should try to account for how habitat influences baseline focal species density. Second, although coyotes may influence the behavior of all of our focal species, we only found direct evidence that bobcats were cognizant of risk from coyotes. Indeed, risk from coyotes best predicted bobcat behavior at every step of the scavenging process, but not at the same risk scale. Specifically, short-term risk did not seem to be important until bobcats were actually feeding. Third, the relatively low frequency of feeding by all carnivores suggests that many detections represented investigatory behavior, amplifying the importance of measuring consumption in scavenging research. Moving forward, quantifying carnivore responses to risk using multiple measures will continue to add nuance to how they weigh the risks and rewards of scavenging (Ruprecht et al. 2021). Collectively, our results support an emerging body of literature showing effects from top carnivores are complex and context-dependent (Haswell et al. 2017, Jachowski et al. 2020).

Coyotes have various ecological roles across their range, and we highlight how they change smaller carnivore behavior in a region where they are a novel top predator. Indeed, as coyotes have expanded their range, ecologists have been interested in the extent to which they can functionally replace wolves (Gompper 2002, Benson et al. 2017). We show how short-term risk from coyotes in our study area reduced scavenging by a smaller carnivore, just like short-term risk from wolves reduced scavenging by coyotes in other areas (Atwood et al. 2008, Klauder et al. 2021). However, in addition to having negative effects, large carnivores can also benefit other carnivores (including coyotes) by provisioning them with carrion (Prugh and Sivy 2020, Ruprecht et al. 2021). Yet coyotes would likely only serve this provisioning role in areas where they kill adult ungulates, which occurs in the northeastern portion of their newly expanded range (Benson et al. 2017), but is less common in the southeastern portion (except see Chitwood et al. 2014). Thus, coyotes would primarily have negative top-down effects on other carnivores in systems such as ours. In areas where coyotes do kill adult ungulates regularly, future studies should investigate the extent to which coyotes facilitate scavenging opportunities for smaller carnivores.

Perhaps human hunters in the eastern US have somewhat filled the lost large carnivore carcass-provisioning role, though likely in a manner more temporally and spatially constrained (Wilmers et al. 2003). The speed of discovery and time spent by coyotes at our carcasses suggests that hunter (or vehicle collision) provisioned carcasses are a profitable and low-risk food for coyotes in areas without larger carnivores. Given human-food subsidies have been shown to change carnivore behavior and improve their fitness (Oro et al. 2013, Newsome et al. 2015), future studies should try to quantify how the effects from human-provisioned carcasses scale up to influence population dynamics and community assemblage.

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TABLES

Table 4.1. Descriptions and significant results for seven variables we hypothesized would influence carnivore detection and consumption of deer carcasses in South Carolina, USA. ↑ indicates a significant positive effect, ↓ a significant negative effect, . no effect, and NA indicates that variable was not used in that analyses.

Hypothesis	**Description**	Time until arrival				Time spent at carcass				% Time feeding	
		Bobcat	*Gray fox*	*Raccoon*	*Opossum*	*Bobcat*	*Gray fox*	*Raccoon*	*Opossum*	*Bobcat*	*Opossum*
Long-term coyote risk	An estimate of nearby coyote activity derived from a passive camera array (unit = average coyote photos/day)	↓	.	.	.	↑	.	.	.	.	.
Short-term coyote risk	Coyote activity at the carcass site (unit = varies depending on the analysis)	.	.	.	.	.	.	.	.	↓	.
Vulture activity	Vulture activity at the carcass site during crepuscular periods (unit = photos/day)	.	↓	.	.	NA	NA	NA	NA	NA	NA
Tree stand age	The average circumference of the five nearest trees of the dominant type (unit = centimeters)	↑	.	.	.	.	.	.	.	.	.
Tree density	The number of trees (of the dominant type) within a 5 m radius of the carcass (unitless integer)	.	.	↓	.	.	.	.	.	.	.
Understory cover	The average index from four Robel pole measurements (unitless, possible values = 1.0 – 16.0)	.	.	.	.	.	↓	.	.	↓	↓↑
Carcass remaining	The amount of carcass remaining (unitless, possible values = 1 – 5)	NA	NA	NA	NA	NA	NA	NA	NA	.	↑

Table 4.2. Estimates and 95% confidence intervals (CI) from statistical analyses of bobcat, gray fox, raccoon, and opossum activity at deer carcass sites in South Carolina, USA. We only show variables from competitive models for which 95% CIs did not overlap zero. Note that effects from the time until arrival analyses are from hazard estimates, which, in this context, increase if sites are discovered quicker.

Analysis	**Species**	**Variable**	**Hazard estimate**	**Lower 95% CI**	**Upper 95% CI**	**Hazard ratio**
Time until arrival	Bobcat	long-term coyote activity	1.018	0.353	1.682	2.766
		stand age	-0.451	-0.837	-0.064	0.637
Time until arrival	Gray fox	vulture activity	0.435	0.040	0.831	1.545
Time until arrival	Raccoon	tree density	0.308	0.032	0.584	1.361
			Linear model estimate	**Lower 95% CI**	**Upper 95% CI**	
Time spent at carcass	Bobcat	long-term coyote activity	0.370	0.124	0.616	NA
Time spent at carcass	Gray fox	understory cover	-3.197	-5.397	-0.997	NA
Percent time spent feeding	Bobcat	short-term coyote activity*understory cover	6.157	1.522	10.792	NA
		short-term coyote activity	-4.199	-11.209	2.811	NA
		understory cover	-4.835	-10.448	0.777	NA
Percent time spent feeding	Opossum	carcass remaining*understory cover	-0.445	-0.780	-0.110	NA

FIGURES

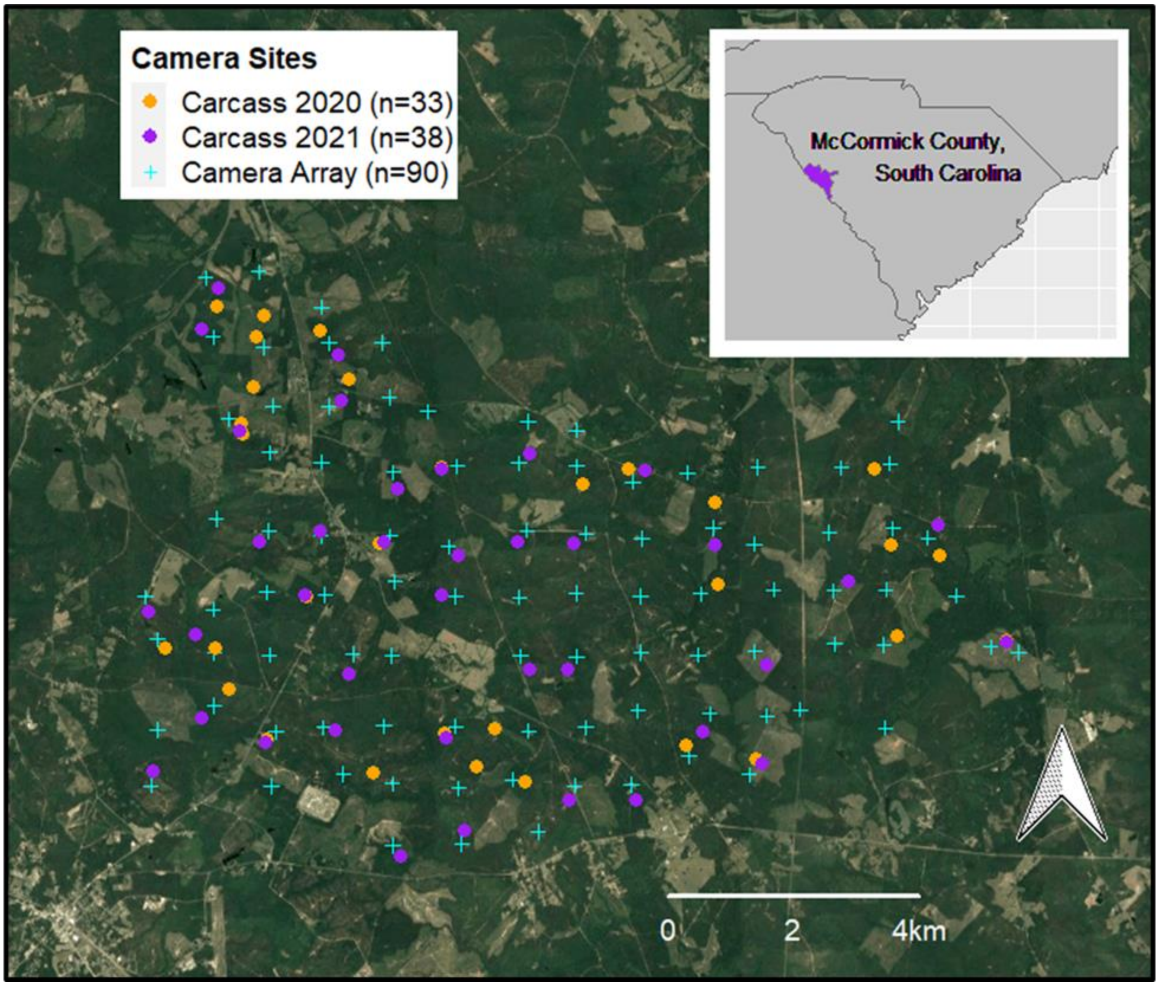

Figure 4.1. Location of our study area in McCormick County, South Carolina, USA. Most of the land was managed loblolly pine plantations in various stages of succession. We show the distribution of 71 carcasses we deployed in January 2020 (orange, n = 33) and January 2021 (purple, n = 38), as well as the 90 passive cameras in an array (cyan), which we used to estimate long-term coyote risk at the carcass sites.

Figure 4.2. An example of how deer carcasses were deployed and monitored in South Carolina, USA, to quantify scavenging activity: (a) the 1 m x 0.5 m (metal garden fence) cage containing 15-16 kg of deer carcass secured to a tree with wire and wire clips, (b) the placement of the camera relative to the carcass, and (c) a GPS-collared coyote feeding from the carcass.

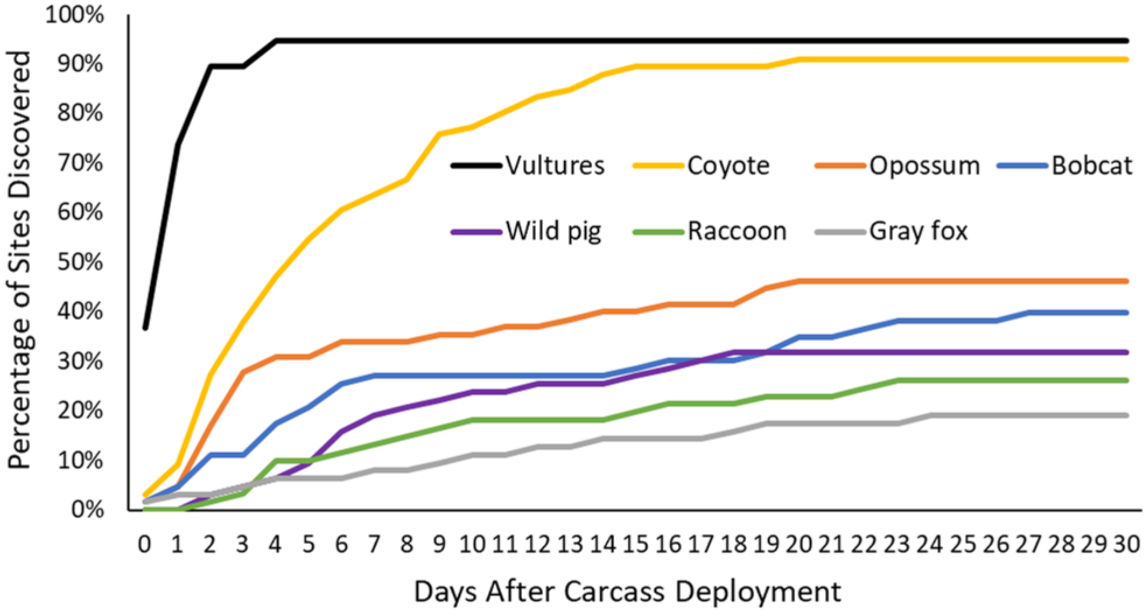

Figure 4.3. Site accumulation curves for various scavenging vertebrates visiting carcass sites in South Carolina, USA. Day “0” is photos from the day the carcass was deployed. The vulture data was derived from 2021 data (n = 38 sites), while the rest of the species’ data was derived from 2020 and 2021 (n = 61-66 sites depending on the species; see methods in Objective 1).

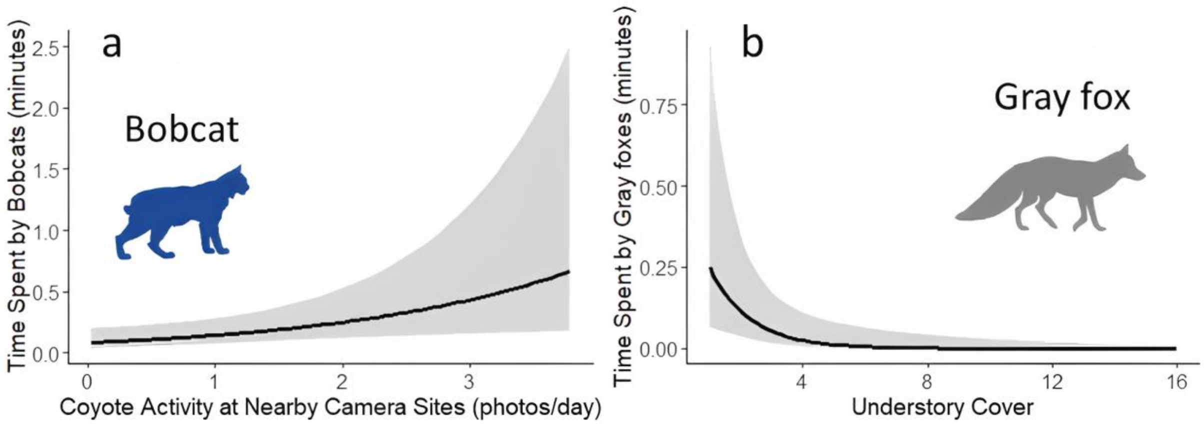

Figure 4.4. Significant effects on time spent at deer carcasses by bobcats and gray foxes in South Carolina, USA. In (a) we show time spent by bobcats vs. coyote activity at nearby cameras (long-term coyote risk), and (b) time spent by gray foxes vs. understory cover.

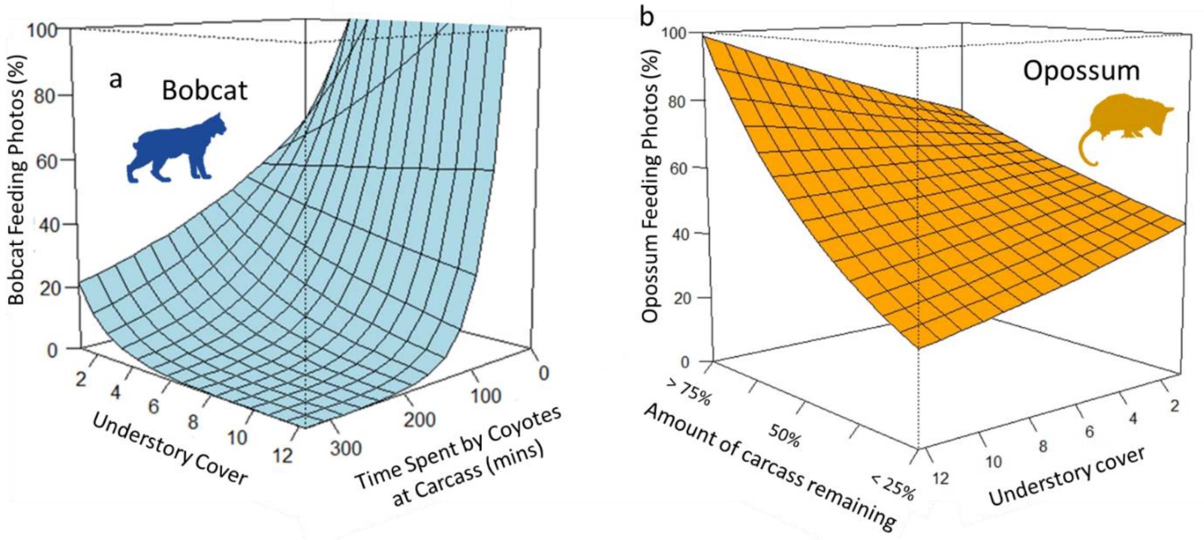

Figure 4.5. Significant effects on bobcat and opossum feeding on deer carcasses in South Carolina, USA. In (a) we show an interaction between time spent by coyotes at the carcass site within the last seven days and understory cover on bobcat feeding. In (b) we show an interaction between the amount of carcass remaining and understory cover.

APPENDICES

Appendix A1

Supplemental information for Chapter 1

Table A1.1. Samples sizes for GPS data from coyotes in South Carolina across multiple factors.

		Sex		Age		Residence status		
	Total	Males	Females	Juveniles	Adults	Residents	Biders	Transients
Individuals	60	22	38	NA	NA	NA	NA	NA
Seasons (datasets)	155	51	104	102	53	106	20	29
Winter	62	20	42	42	20	45	6	11
Summer	55	19	36	40	15	33	9	13
Fall	38	12	26	20	18	28	5	5

Table A1.2. Model results from integrated step-selection analyses on coyotes in South Carolina. We show the average estimates for each variables, yet results are bolded and highlighted if they are significantly different than the reference class for territorial status (resident), behavior state (encamped), sex (female), and age (adult). We also sum the number of these significant values for each row and column.

variable	**season**	territorial status			behavior state			sex		age		morphology		total significant
		resident	bider	transient	encamped	foraging	traveling	female	male	adult	juvenile	mass	size	
tree cover at night	winter	-0.24 (0.25)	-0.33 (0.47)	-0.14 (0.25)	-0.17 (0.19)	-0.20 (0.19)	**-0.33 (0.43)**	-0.15 (0.24)	**-0.41 (0.34)**	-0.18 (0.22)	-0.26 (0.30)	-0.01 (0.06)	0.00 (0.06)	6
	summer	-0.30 (0.26)	**-0.54 (0.47)**	-0.18 (0.24)	-0.20 (0.26)	-0.34 (0.22)	**-0.38 (0.40)**	-0.32 (0.31)	-0.32 (0.27)	-0.27 (0.25)	-0.34 (0.31)	-0.03 (0.05)	-0.04 (0.05)	
	fall	-0.99 (0.67)	-0.45 (0.35)	-0.89 (0.68)	-0.35 (0.30)	-0.42 (0.30)	**-1.95 (1.28)**	-0.34 (0.33)	**-2.07 (1.30)**	-1.21 (0.78)	-0.59 (0.50)	0.49 (0.40)	0.70 (0.39)	
built cover at night	winter	0.28 (0.59)	-0.21 (1.31)	0.22 (0.62)	0.07 (0.37)	0.33 (0.49)	0.27 (1.13)	0.27 (0.57)	0.12 (0.91)	0.20 (0.52)	0.24 (0.75)	-0.11 (0.17)	0.01 (0.15)	2
	summer	0.17 (0.51)	0.40 (0.77)	0.03 (0.60)	-0.01 (0.49)	0.21 (0.46)	**0.31 (0.76)**	0.16 (0.56)	0.19 (0.62)	0.08 (0.47)	0.21 (0.62)	-0.01 (0.11)	-0.02 (0.10)	
	fall	0.47 (0.72)	0.29 (0.78)	-0.05 (1.04)	0.52 (0.60)	0.45 (0.63)	0.15 (1.08)	0.38 (0.62)	0.33 (1.10)	0.55 (0.86)	0.19 (0.69)	**0.58 (0.20)**	-0.06 (0.20)	
distance to road at night	winter	-0.17 (0.25)	**-0.48 (0.37)**	-0.12 (0.27)	-0.08 (0.22)	-0.17 (0.20)	**-0.34 (0.37)**	-0.16 (0.25)	-0.26 (0.31)	-0.21 (0.22)	-0.19 (0.30)	-0.05 (0.05)	-0.01 (0.04)	3
	summer	-0.07 (0.22)	-0.08 (0.28)	-0.06 (0.26)	-0.02 (0.23)	-0.07 (0.20)	**-0.12 (0.29)**	-0.04 (0.25)	-0.11 (0.26)	-0.07 (0.25)	-0.07 (0.25)	0.01 (0.03)	-0.01 (0.03)	
	fall	-0.10 (0.24)	-0.25 (0.28)	-0.09 (0.28)	-0.09 (0.23)	-0.16 (0.21)	-0.12 (0.31)	-0.11 (0.24)	-0.14 (0.32)	-0.11 (0.25)	-0.13 (0.28)	0.01 (0.05)	-0.08 (0.05)	
total significant		Ref	2	0	Ref	0	6	Ref	2	Ref	0	1	0	

Appendix B

Supplemental information for Chapter 2

Table A2.1. Hypotheses and models we used to determine which variation of each fawn age class variable would be used in the main analysis of coyote diets in South Carolina. We compared three models for each fawn age class: availability from that week, the week prior, and two weeks prior. We compared models using AIC_c and bolded the top model for each age class.

Variable	Hypothesis	Model	Description
≤ Three-week-old fawns	Three-week fawn availability	Scat fawn ~ % ≤ 3 fawn	Linear response to ≤ three-week-old fawn availability
	Three-week fawn availability one-week lag	Scat fawn ~ % ≤ 3 fawn L1	Linear response to ≤ three-week-old fawn availability from the week prior
	Three-week fawn availability two-week lag	**Scat fawn ~ % ≤ 3 fawn L2**	**Linear response to ≤ three-week-old fawn availability from two weeks prior**
≤ Six-week-old fawns	Six-week fawn availability	Scat fawn ~ % ≤ 6 fawn	Linear response to ≤ six-week-old fawn availability
	Six-week fawn availability one-week lag	**Scat fawn ~ % ≤ 6 fawn L1**	**Linear response to ≤ six-week-old fawn availability from the week prior**
	Six-week fawn availability two-week lag	Scat fawn ~ % ≤ 6 fawn L2	Linear response to ≤ six-week-old fawn availability from two weeks prior
All fawns	All fawn availability	Scat fawn ~ % fawn	Linear response to all fawn availability
	All fawn availability one-week lag	**Scat fawn ~ % fawn L1**	**Linear response to all fawn availability from the week prior**
	All fawn availability two-week lag	Scat fawn ~ % fawn L2	Linear response to all fawn availability from two weeks prior

Table A2.2. Results from AIC_c model selection on fawn consumption by coyotes from April – July in South Carolina. We based inference on models with delta $AIC_c < 2$ (bolded).

Number	**Model**	**K**	**LogLik**	**AICc**	**Delta**	**Weight**
1	**Six-week-old fawn (one-week lag) * blackberry consumption + year**	**6**	**-269.15**	**552.9**	**0.0**	**85%**
2	Three-week-old fawn (two-week lag) * blackberry consumption + year	6	-271.1	556.7	3.8	13%
3	Three-week-old fawn (two-week lag) + blackberry consumption + year	5	-274.8	561.9	9.1	1%
4	All fawn (one-week lag) * blackberry consumption + year	6	-273.8	562.2	9.34	1%
5	Six-week-old fawn (one-week lag) + blackberry consumption + year	5	-274.9	562.2	9.4	1%
6	Blackberry consumption + year	4	-277.4	565.2	12.3	0%
7	All fawn (one-week lag) + blackberry consumption + year	5	-276.7	565.8	12.9	0%
8	Null	1	-285.2	574.5	21.6	0%
9	Year	3	-284.0	576.1	23.3	0%
10	Three-week-old fawn (two-week lag) + year	4	-283.1	576.5	23.7	0%
11	Six-week-old fawn (one-week lag) + year	4	-283.2	576.6	23.7	0%
12	Blackberry availability + year	4	-283.4	577.2	24.3	0%
13	Three-week-old fawn (two-week lag) + blackberry availability + year	5	-282.8	578.0	25.1	0%
14	Six-week-old fawn (one-week lag) + blackberry availability + year	5	-282.8	578.1	25.2	0%
15	All fawn (one-week lag) + year	4	-283.9	578.2	25.3	0%
16	All fawn (one-week lag) + blackberry availability + year	5	-283.3	579.0	26.2	0%
17	Three-week-old fawn (two-week lag) * blackberry availability + year	6	-282.7	579.9	27.1	0%
18	All fawn (one-week lag) * blackberry availability + year	6	-283.3	581.1	28.2	0%

Table A2.3. Hypotheses and models we used to determine which variation of blackberry availability would be used in the main analysis of coyote diets in South Carolina. We compared six models for each blackberry ripeness, which included availability from that week, the week prior, and two weeks prior, as well as linear and quadratic responses to each of those three variations. We compared models using AIC_c and bolded the top model for each ripeness category.

Variable	**Hypothesis**	**Model**	**Description**
Unripe Blackberries	**Unripe blackberry availability**	**Scat Blackberry ~ Avg. Unripe BB**	**Linear response to unripe blackberry availability**
	Unripe blackberry availability one-week lag	Scat Blackberry ~ Avg. Unripe BB L1	Linear response to unripe blackberry availability from a week prior
	Unripe blackberry availability two-week lag	Scat Blackberry ~ Avg. Unripe BB L2	Linear response to unripe blackberry availability from two weeks prior
Ripe Blackberries	**Ripe blackberry availability**	**Scat Blackberry ~ Avg. Ripe BB**	**Linear response to ripe blackberry availability**
	Ripe blackberry availability one-week lag	Scat Blackberry ~ Avg. Ripe BB L1	Linear response to ripe blackberry availability from a week prior
	Ripe blackberry availability two-week lag	Scat Blackberry ~ Avg. Ripe BB L2	Linear response to ripe blackberry availability from two weeks prior

Table A2.4. Summary of carnivore scat identification in South Carolina. We compare our field species identification with the species identification using genetics (DNA fragment analysis). (a) is a true negative, (b) is a false positive, (c) is a false negative, and (d) is a true positive. We were more likely to falsely identify a coyote scat as a bobcat in the field – 65% of scats we identified as bobcat in the field were from coyotes, and 17% of scats we identified as coyote in the field were from bobcats. We based our table layout on Morin et al. 2016 Bias in carnivore diet analysis resulting from misclassification of predator scats based on field identification.

Coyote		Predicted (field identification)			Accuracy 73% $^{(a+d/(a+b+c+d))}$	
		Not a coyote (negative)	Is a coyote (positive)	Total		
Actual (genetic species identification)	Not a coyote (negative)	45^{a}	96^{b}	141	True negative rate 32% $^{(a/(a+b))}$	False positive rate 68% $^{(b/(a+b))}$
	Is a coyote (positive)	90^{c}	450^{d}	540	False negative rate 17% $^{(c/(c+d))}$	True positive rate 83% $^{(d/(c+d))}$
	Unclear (failed and multispecies)	28	112	140		
	Total	163	658	821		

Bobcat		Predicted (field identification)			Accuracy 78%	
		Not a bobcat (negative)	Is a bobcat (positive)	Total		
Actual (genetic species identification)	Not a bobcat (negative)	499	59	558	True negative rate 89%	False positive rate 11%
	Is a bobcat (positive)	93	31	124	False negative rate 75%	True positive rate 24%
	Unclear (failed and multispecies)	118	22	140		
	Total	710	111	821		

Table A2.5. Results from AIC$_c$ model selection on blackberry consumption by coyotes from April – July in South Carolina, USA. We based inference on models with delta AIC$_c$ < 2 (bolded).

Number	**Model**	**K**	**LogLik**	**AICc**	**Delta**	**Weight**
1	Ripe blackberries (no lag) + year	4	-253.5	517.2	0.0	70.5%
2	Unripe blackberries (no lag) + year	4	-255.7	520.4	3.2	14.6%
3	Year	3	-256.6	521.3	4.0	9.2%
4	Null	1	-259.1	522.2	5.0	5.7%

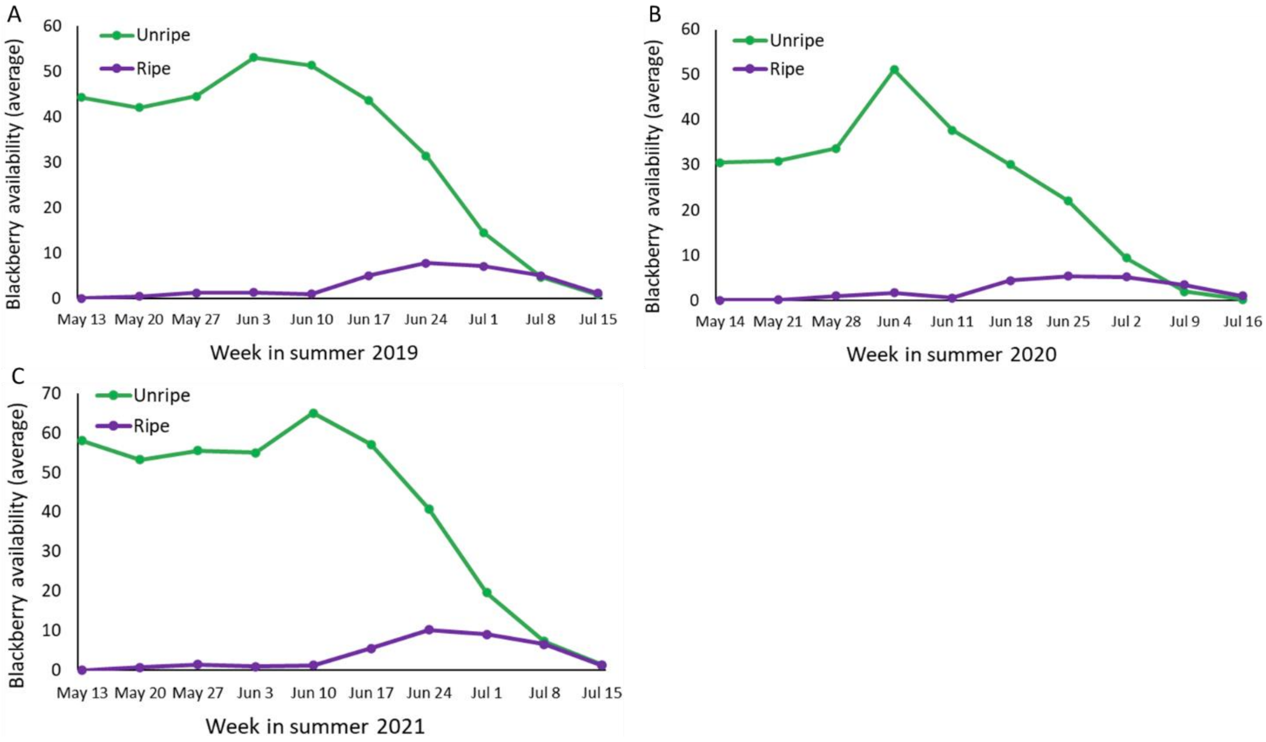

Figure A2.1. Weekly summer unripe and ripe blackberry availability data in South Carolina. We only counted blackberries in 2020 and 2021, so the weekly counts for 2019 are the average for each week from the following two years.

Text A2.1. Description of methods used to capture and monitor the movement of coyotes in McCormick County, South Carolina.

We captured coyotes using Minnesota MB 550 foothold traps (Minnesota Trapline Products, Pennock, MN) set on dirt roads that had signs of coyote activity (i.e., tracks and scat) during December 2018, January – March 2020, and January 2021. We immobilized coyotes using a catchpole and electrical tape wrapped around their muzzle and ankles. We fit a GPS collar (Vectronic Aerospace, Berlin, Germany; model: VERTEX Light) on individuals if the collar was < 5% of their weight. The average handling time was 25 minutes. All capture and handling procedures were permitted by Clemson University IACUC permit no. AUP 2018-031 and USDA Forest Service permit no. USFS 2018-031. We programmed our GPS collars to collect data for ~15 months before dropping off automatically. The default fix rate was 7 hours, which generally changed to 30 minutes during three three-week windows from February 8 – February 28, April 19 – July 7, and October 10 – October 31.

We used this GPS data to inform where our scat transects were to maximize the chance that we would pick up scats from collared individuals. We first mapped the dirt roads in our study area and then each season randomly selected 100 points along roads in this layer using ArcMap 10.3 (ESRI, Redlands, CA). We added a 0.5 km buffer to each of the random points, then overlayed each coyote's GPS points from the month prior to beginning surveys (e.g., for winter we used December points) and counted the number of GPS points within each nearby buffer. We chose the two randomly selected points that had the most GPS points within their buffer to represent that coyote (the second was a backup). Each of these selected points represented a transect, and when necessary, we chose additional random points to distribute our transects relatively evenly across the study area. Once in the field, we selected 1-3 km of road (the transect) that would maximize our chances of detecting scats (i.e., dirt road with bare ground) while still including the selected point.

Text A2.2. Description of methods used to estimate seasonal small mammal availability.

Each of the sm cameras was associated with a non-baited camera in a passive array (Figure 1), and we stratified locations to represent the diversity of vegetative complexity in our study area (i.e., successional stages). Locations of the sm cameras remained the same between seasons. At each site, we deployed a downward-facing motion-activated Bushnell wildlife camera (models Trophycam Aggressor or CORE; Bushnell, Overland Park, Kansas, USA) attached to a metal stake, to which we lashed a 2.5cm diameter PVC pipe full of bird seed (Figure 1). The camera was ~1m off the ground and set to take three photos per trigger with a one-minute delay between triggers. Additional settings included "IR" = low, sensor level = normal, and "NV shutter" = high. We initially filled the pipe with 300mL of bird seed, then (if necessary) refilled it back up to ~300mL of seed when we returned to check the camera after one week.

In order to facilitate photo processing, we only examined photos taken at night for 15 days. At many sites, daytime photos of grass and shadows permeated the dataset, and we were most interested in the activity of crepuscular and nocturnal rodents, so we filtered out photos taken from 9:00 – 15:59. In addition, to standardize between sites, we only processed the filtered photos from the first six days after the camera was first set out and the first nine days after the first camera check (which were the days most likely to have bait present). We visually assessed and then recorded the number of animals present in each photo using TimeLapse 2 (Version 2.2, Greenburg 2019). We categorized a small mammal as either a mouse, rat, vole, or shrew. We noted whether bait was present in each photo and found no consistent differences between the number of small mammal photos when bait was present and when it was not.

Text A2.3. Description of methods used to capture and monitor the survival of white-tailed deer fawns in McCormick County, South Carolina.

We captured white-tailed deer does in January – April of 2019, 2020, and 2021 using dart guns and rocket nets. We fit each doe with a GPS collar and vaginal implant transmitter (VIT). When the does gave birth (sometime April – July), the VIT would alert us. We would then track to the does location, locate the newborn fawns, and place expandable GPS collars on the fawns. If the fawn did not move for 4-6 hours, the GPS collar would send a mortality alert, which we would investigate.

Text A2.4. Description of methods used to estimate blackberry availability during the summer in McCormick County, South Carolina.

In 2020, we classified our 32 small mammal sites (see *Objective 2*) into four classes of vegetation (mature pines, immature pines, clearcut, mixed pine and hardwood), then randomly chose one site from each class to count blackberries at. Once at the site, we set up four 3 m x 1 m plots, in which we counted blackberries each week (Figure 1). We chose the plot locations by walking along the road for up to 50 m or until we saw a (usually unripe) blackberry, then sticking four flags in the ground to delineate the plot. At each plot we used a hand counter to tally the number of not-ripe (green and/or red) and ripe (fully dark purple) blackberries within each plot. In order to create a weekly index from this data, we averaged the counts of the four plots from each site, then averaged those four numbers across the four sites. In 2021, we used eight total sites (two from each habitat class) and counted a group of four every other week. We then interpolated the missing weeks (except the first and last week) for each site by averaging the counts from the week prior and the following week. We averaged weekly counts across all sites to create the weekly index for 2021. Since we did not count blackberries in 2019, we combined our 2020 and 2021 count data to represent 2019. We first examined the blackberry data from 2020 and 2021 to ensure they were similar; we found that unripe blackberries peaked the first week of June in 2020 and the second week of June in 2021, but ripe blackberries peaked the fourth week of June both years (Supplemental figure 1). We deemed these trends similar enough to combine, so we averaged the counts for each week across years.

Appendix D

Supplemental information for Chapter 4

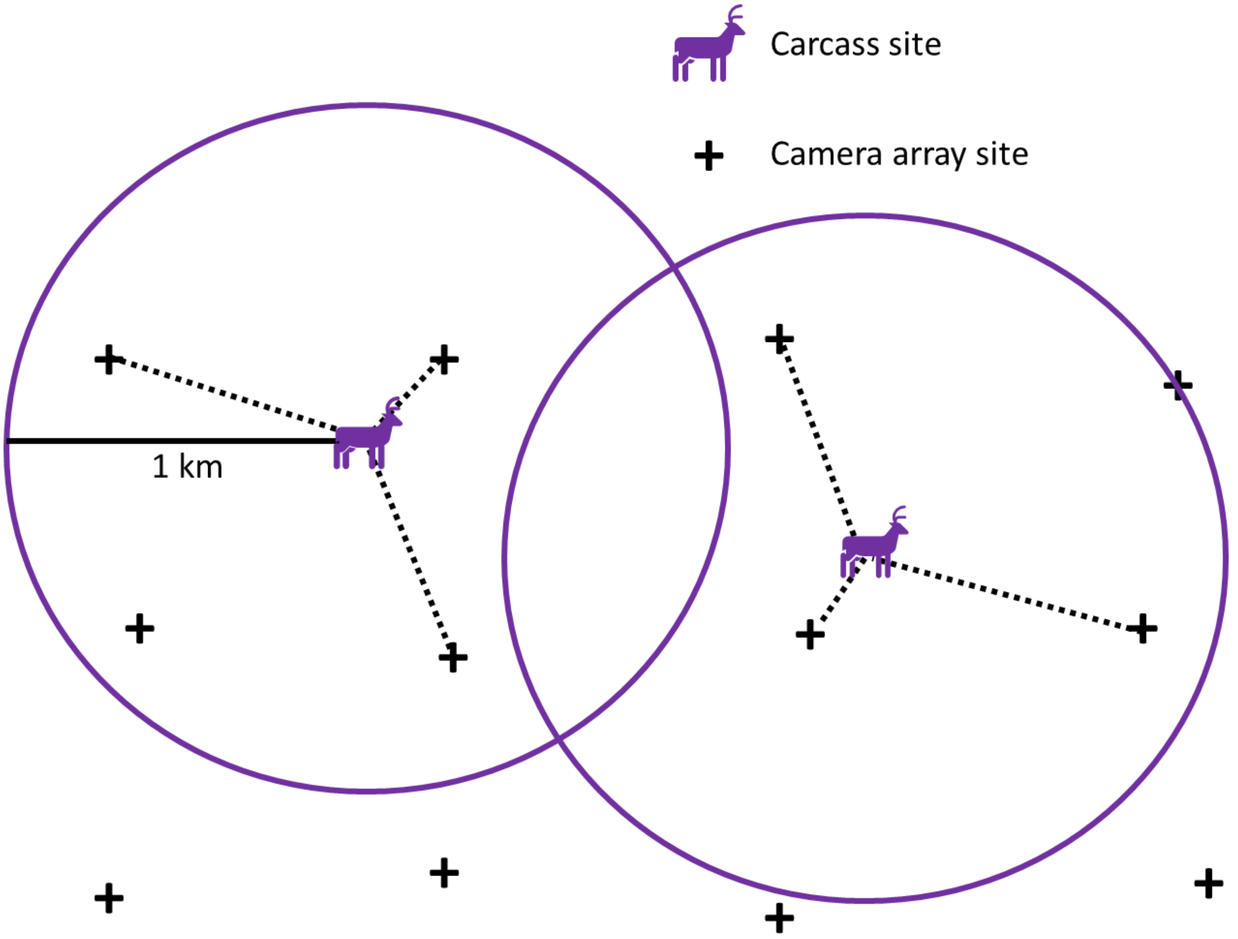

Figure A4.1. A diagram of how we selected which camera array sites to represent long-term coyote activity at a given carcass site (deer) in South Carolina, USA. We visualized a 1 km buffer around each carcass site (circles), then selected the three closest array cameras within that buffer. We then measured the distance (dotted lines) from each of those selected cameras to the carcass to adjust the coyote activity value by the inverse-distance (closer cameras were weighted more heavily).

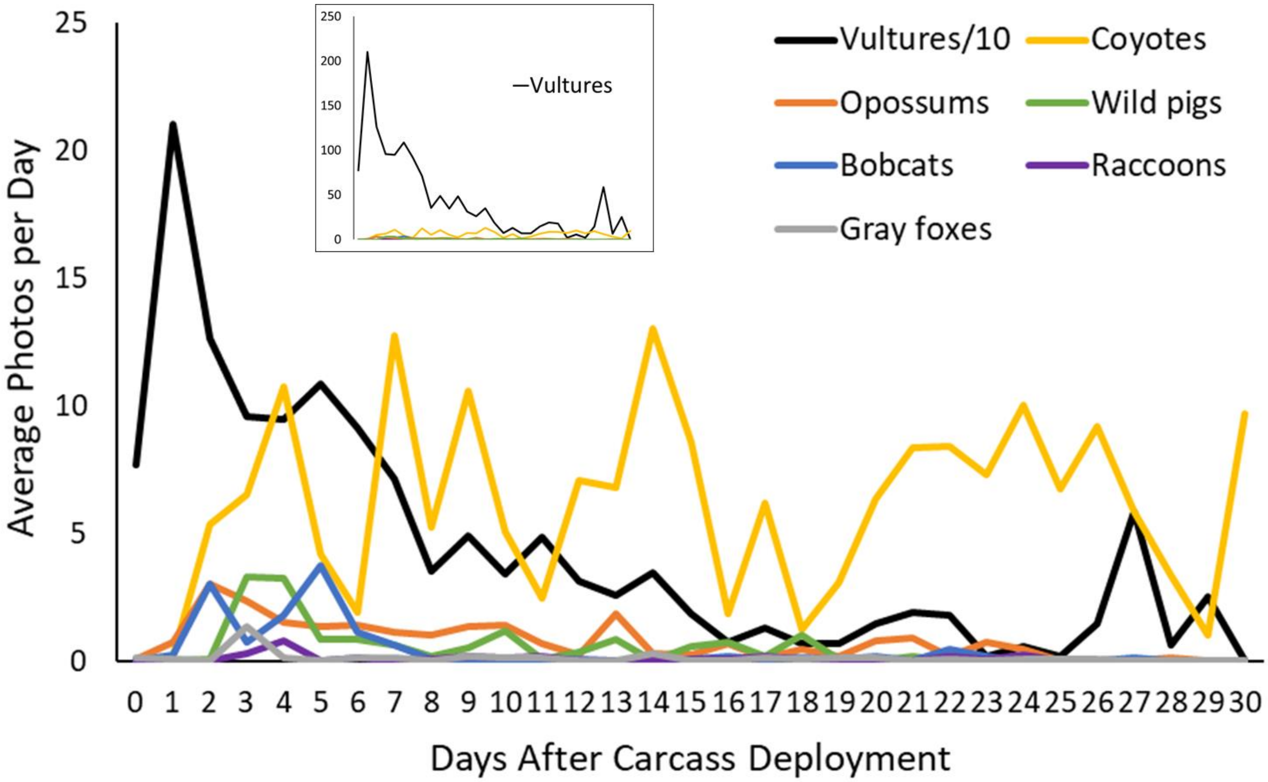

Figure A4.2. The average number of photos taken of several common scavenging vertebrates in South Carolina, USA, for each day after the carcass was deployed. Day "0" is the day the carcass was deployed. The vulture data is the average number of photos from only the sites deployed in 2021 (n = 38), including daytime photos. The main chart shows the vulture data divided by 10 (for easier visualization of the other species), while the inset chart shows the vulture data not divided.

Table A4.1. Results from AIC$_c$ model selection on time until arrival (cox proportional hazard) models for bobcats, gray foxes, raccoons, and opossums. We based inference on models with delta AIC$_c$ < 2 (bolded, unless ranked below null model).

Bobcat time until arrival	Number	Model	K	LogLik	AICc	Delta	Weight
	1	**long-term coyote activity**	**2**	**-96.23**	**194.64**	**0.00**	**34.74%**
	2	**stand age**	**2**	**-96.92**	**196.01**	**1.37**	**17.48%**
	3	**long-term coyote activity + short-term coyote activity**	**3**	**-95.98**	**196.48**	**1.85**	**13.79%**
	4	long-term coyote activity + short-term coyote activity + vulture activity	4	-95.10	197.29	2.65	9.22%
	5	stand age + tree density + understory cover	4	-95.52	198.13	3.50	6.05%
	6	null	1	-99.44	198.89	4.25	4.14%
	7	vulture activity + stand age + vulture activity*stand age	4	-96.10	199.29	4.65	3.39%
	8	vulture activity	2	-98.79	199.75	5.12	2.69%
	9	understory cover	2	-98.98	200.13	5.50	2.22%
	10	understory cover + tree density	3	-97.96	200.44	5.80	1.91%
	11	tree density	2	-99.29	200.76	6.12	1.63%
	12	short-term coyote activity	2	-99.32	200.81	6.17	1.59%
	13	long-term coyote activity + short-term coyote activity + vulture activity + stand age + tree density + understory cover					

Gray fox time until arrival	Number	Model	K	LogLik	AICc	Delta	Weight
	1	**vulture activity**	**2**	**-46.50**	**95.40**	**0.00**	**33.21%**
	2	null	1	-48.23	96.47	1.07	19.48%
	3	understory cover	2	-47.31	97.03	1.63	14.72%
	4	tree density	2	-48.21	98.81	3.41	6.03%
	5	long-term coyote activity	2	-48.23	98.85	3.45	5.91%
	6	short-term coyote activity	2	-48.23	98.86	3.46	5.89%
	7	stand age	2	-48.23	98.87	3.47	5.87%
	8	tree density + understory cover	3	-47.11	99.56	4.16	4.16%
	9	vulture activity + tree density + vulture activity*tree density	4	-46.38	101.76	6.36	1.38%
	10	long-term coyote activity + short-term coyote activity	3	-48.22	101.78	6.38	1.37%
	11	long-term coyote activity + short-term coyote activity + vulture activity	4	-46.46	101.93	6.53	1.27%
	12	stand age + tree density + understory cover	4	-47.04	103.07	7.67	0.72%

	13	long-term coyote activity + short-term coyote activity + vulture activity + stand age + tree density + understory cover	7	-45.33	119.46	24.06	0.00%

Raccoon time until arrival	Number	Model	K	LogLik	AICc	Delta	Weight
	1	**tree density**	**2**	**-69.15**	**140.55**	**0.00**	**22.64%**
	2	**vulture activity**	**2**	**-69.24**	**140.74**	**0.19**	**20.55%**
	3	**null**	**1**	**-70.64**	**141.29**	**0.74**	**15.63%**
	4	**stand age + tree density**	**3**	**-68.45**	**141.70**	**1.15**	**12.74%**
	5	stand age	2	-70.47	143.19	2.64	6.03%
	6	short-term coyote activity	2	-70.52	143.29	2.74	5.75%
	7	long-term coyote activity	2	-70.61	143.47	2.92	5.25%
	8	understory cover	2	-70.62	143.48	2.94	5.22%
	9	vulture activity + tree density + vulture activity*tree density	4	-68.80	145.31	4.76	2.09%
	10	long-term coyote activity + short-term coyote activity + vulture activity	4	-68.84	145.40	4.86	2.00%
	11	long-term coyote activity + short-term coyote activity	3	-70.49	145.77	5.23	1.66%
	12	long-term coyote activity + short-term coyote activity + vulture activity + stand age	5	-68.69	148.45	7.90	0.44%

Opossum time until arrival	Number	Model	K	LogLik	AICc	Delta	Weight
	1	**stand age**	**2**	**-114.91**	**231.96**	**0.00**	**31.51%**
	2	**vulture activity**	**2**	**-115.48**	**233.11**	**1.15**	**17.75%**
	3	**null**	**1**	**-116.80**	**233.61**	**1.65**	**13.80%**
	4	stand age + tree density	3	-114.79	234.02	2.06	11.26%
	5	tree density + understory cover	3	-115.36	235.17	3.22	6.31%
	6	long-term coyote activity	2	-116.63	235.40	3.44	5.64%
	7	tree density	2	-116.78	235.71	3.75	4.83%
	8	short-term coyote activity	2	-116.80	235.75	3.79	4.73%
	9	long-term coyote activity + short-term coyote activity + vulture activity	4	-115.28	237.49	5.53	1.99%
	10	long-term coyote activity + short-term coyote activity	3	-116.63	237.70	5.74	1.79%
	11	long-term coyote activity + short-term coyote activity + vulture activity + stand age + tree density + understory cover	7	-112.52	240.68	8.72	0.40%

Table A4.2. Results from AIC_c model selection on time spent at carcasses by bobcats, gray foxes, raccoons, and opossums. We based inference on models with delta AIC_c < 2 (bolded, unless ranked below null model).

Bobcat time spent at carcass	**Number**	**Model**	**K**	**LogLik**	**AICc**	**Delta**	**Weight**
	1	**long-term coyote activity**	**2**	**-109.18**	**224.73**	**0.00**	**46.33%**
	2	long-term coyote activity + short-term coyote activity	3	-109.14	226.90	2.17	15.65%
	3	stand age	2	-110.44	227.25	2.52	13.12%
	4	null	1	-112.11	228.40	3.67	7.39%
	5	tree density + understory cover	3	-110.39	229.40	4.67	4.48%
	6	understory cover	2	-111.63	229.64	4.91	3.97%
	7	tree density	2	-111.86	230.08	5.36	3.18%
	8	short-term coyote activity	2	-112.01	230.38	5.66	2.74%
	9	long-term coyote activity + short-term coyote activity + stand age + tree density + understory cover	6	-107.40	230.64	5.91	2.41%
	10	short-term coyote activity + understory cover + short-term coyote activity*understory cover	4	-111.06	233.07	8.34	0.72%

Gray fox time spent at carcass	**Number**	**Model**	**K**	**LogLik**	**AICc**	**Delta**	**Weight**
	1	**tree density + understory cover**	**3**	**-63.38**	**135.38**	**0.00**	**34.24%**
	2	**understory cover**	**2**	**-64.75**	**135.86**	**0.49**	**26.85%**
	3	short-term coyote activity + understory cover + short-term coyote activity*understory cover	4	-63.43	137.80	2.43	10.18%
	4	short-term coyote activity	2	-66.02	138.40	3.02	7.56%
	5	tree density	2	-66.17	138.71	3.34	6.46%
	6	null	1	-67.64	139.46	4.08	4.45%
	7	long-term coyote activity + short-term coyote activity + stand age + tree density + understory cover	6	-62.19	140.21	4.84	3.05%
	8	long-term coyote activity + short-term coyote activity	3	-65.84	140.30	4.92	2.92%
	6	long-term coyote activity	2	-67.21	140.79	5.41	2.29%
	9	stand age	2	-67.34	141.06	5.68	2.00%

Raccoon time spent at carcass	**Number**	**Model**	**K**	**LogLik**	**AICc**	**Delta**	**Weight**
	1	null	1	-82.65	171.67	0.00	18.17%
	2	short-term coyote activity	2	-81.63	171.88	0.20	16.43%

	3	stand age	2	-81.67	171.97	0.30	15.65%
	4	understory cover	2	-81.94	172.51	0.84	11.94%
	5	long-term coyote activity + short-term coyote activity + stand age + tree density + understory cover	6	-77.32	173.03	1.36	9.23%
	6	long-term coyote activity	2	-82.58	173.79	2.11	6.32%
	7	tree density	2	-82.64	173.91	2.24	5.94%
	8	long-term coyote activity + short-term coyote activity	3	-81.53	174.01	2.34	5.65%
	8	tree density + understory cover	3	-81.55	174.06	2.39	5.51%
	9	short-term coyote activity + understory cover + short-term coyote activity*understory cover	4	-80.42	174.20	2.52	5.15%

Opossum time spent at carcass	**Number**	**Model**	**K**	**LogLik**	**AICc**	**Delta**	**Weight**
	1	**tree density + understory cover**	**3**	**-185.95**	**380.52**	**0.00**	**21.93%**
	2	**understory cover**	**2**	**-187.11**	**380.60**	**0.08**	**21.09%**
	3	**short-term coyote activity + understory cover + short-term coyote activity*understory cover**	**4**	**-185.02**	**380.99**	**0.47**	**17.32%**
	4	**stand age**	**2**	**-187.63**	**381.64**	**1.12**	**12.53%**
	5	long-term coyote activity	2	-188.32	383.01	2.49	6.31%
	6	long-term coyote activity + short-term coyote activity + stand age + tree density + understory cover	6	-183.85	383.54	3.02	4.85%
	7	null	1	-189.68	383.55	3.03	4.83%
	8	short-term coyote activity	2	-188.59	383.55	3.03	4.83%
	9	long-term coyote activity + short-term coyote activity	3	-187.51	383.65	3.13	4.58%
	10	tree density	2	-189.62	385.61	5.09	1.72%

Table A4.3. Results from AIC_c model selection on percent of time spent feeding on carcasses by bobcats and opossums. We based inference on models with delta AIC_c < 2 (bolded).

Bobcat percent time feeding	**Number**	**Model**	**K**	**LogLik**	**AICc**	**Delta**	**Weight**
	1	**short-term coyote activity + understory cover + short-term coyote activity*understory cover**	**4**	**-105.90**	**228.18**	**0.00**	**46.43%**
	2	null	1	-111.03	230.86	2.68	12.13%
	3	long-term coyote activity	2	-109.92	231.07	2.89	10.93%
	4	short-term coyote activity + carcass remaining	3	-108.90	231.56	3.38	8.56%
	5	stand age	2	-110.24	231.70	3.52	7.99%
	6	tree density + understory cover	3	-109.63	233.01	4.83	4.14%
	7	carcass remaining	2	-110.95	233.13	4.96	3.89%
	8	tree density	2	-111.02	233.26	5.09	3.65%
	9	long-term coyote activity + short-term coyote activity + stand age + tree density + understory cover + carcass remaining	7	-104.60	234.20	6.03	2.28%
	10	short-term coyote activity	2	-121.42	254.06	25.89	0.00%
	11	long-term coyote activity + short-term coyote activity	3	-121.42	256.59	28.41	0.00%

Opossum percent time feeding	**Number**	**Model**	**K**	**LogLik**	**AICc**	**Delta**	**Weight**
	1	**short-term coyote activity**	**3**	**-389.69**	**789.80**	**0.00**	**26.56%**
	2	**short-term coyote activity + carcass remaining**	**3**	**-388.92**	**790.43**	**0.63**	**19.37%**
	3	**carcass remaining**	**2**	**-390.33**	**791.08**	**1.28**	**13.99%**
	4	long-term coyote activity + short-term coyote activity	3	-389.68	791.95	2.15	9.07%
	5	null	1	-392.26	792.79	3.00	5.93%
	6	stand age	2	-391.28	792.99	3.19	5.39%
	7	short-term coyote activity + understory cover + short-term coyote activity*understory cover	4	-389.47	793.74	3.94	3.70%
	8	long-term coyote activity + short-term coyote activity + stand age + tree density + understory cover + carcass remaining	7	-386.22	794.03	4.23	3.20%
	9	tree density	2	-392.04	794.50	4.71	2.53%
	10	carcass remaining + understory cover + carcass remaining*understory cover	4	-389.86	794.51	4.72	2.51%
	11	stand age + tree density + understory cover	4	-389.92	794.62	4.83	2.37%
	12	understory cover	2	-392.11	794.64	4.84	2.36%

13	long-term coyote activity	2	-392.21	794.85	5.05	2.12%
14	tree density + understory cover	3	-392.00	796.59	6.80	0.89%

Text A4.1. Description of methods used to capture and monitor the movement of coyotes in McCormick County, South Carolina, USA.

We captured coyotes using Minnesota MB 550 foothold traps (Minnesota Trapline Products, Pennock, MN) set on dirt roads that had signs of coyote activity (i.e., tracks and scat) during December 2018 and January - March 2020. We immobilized coyotes using a catchpole and electrical tape wrapped around their muzzle and ankles. We fit a GPS collar (Vectronic Aerospace, Berlin, Germany; model: VERTEX Light) on individuals if the collar was < 5% of their weight. The average handling time was 25 minutes. All capture and handling procedures were permitted by Clemson University IACUC permit no. AUP 2018-031 and USDA Forest Service permit no. USFS 2018-031. We programmed our GPS collars to collect data for ~15 months before dropping off automatically. The default fix rate was 7 hours, which generally changed to 30 minutes during three three-week windows from February 8 – February 28, May 14 – June 3, and October 10 – October 31.

We used this GPS data to deploy 16 sites in 2020. We used locations from eight resident GPS-collared coyotes (Supplemental Text 1) to visualize 50% (core area) and 95% (home range) minimum convex polygons for each individual. We deployed a carcass in a random location within each core area and in a random location within the home range excluding the core area (n = 16). In 2021, we solely used data from the camera array to stratify our carcass deployments, in order to standardize the distance between the carcass and the nearest camera in the array. Although using two methods (cameras and collared individuals) was not ideal, we only used these data to sample across a gradient of coyote activity – we used a different dataset from the cameras to estimate coyote activity nearby for our analysis.