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# ECOLOGY AND IMPACTS OF COYOTES (CANIS LATRANS) IN THE SOUTHEASTERN UNITED STATES

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ECOLOGY AND IMPACTS OF COYOTES (CANIS LATRANS) IN THE  
SOUTHEASTERN UNITED STATES

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A Dissertation  
Presented to  
the Graduate School of  
Clemson University

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

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by  
Cady Rose Etheredge  
December 2013

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Accepted by:  
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## ABSTRACT

Recent coyote (*Canis latrans*) colonization of the southeastern United States has prompted speculation on the top-down effects of a new top predator on systems which have gone without a strong predator presence since the extirpation of the red wolf (*Canis rufus*). This dissertation reports on the results of a series of investigations of the potential impact of coyotes on raccoons (*Procyon lotor*) and other management issues related to coyotes in the Southeast. Chapters 1-3 present indirect field tests of the Mesopredator Release Hypothesis. Chapter 4 presents an overview of the current knowledge of the ecology and potential impacts of coyotes in the Southeast.

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## CHAPTER ONE

### LOCAL SCALE DIFFERENCE OF COYOTE FOOD HABITS ON TWO SOUTH CAROLINA ISLANDS

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**Abstract** - *Canis latrans* Say (Coyote) are a classically regarded generalist predator which has recently established itself in large populations throughout the southeastern United States. To better understand how Coyote food habits in the Southeast may differ on an extremely small spatial scale, a total of 305 Coyote scats were collected from 2009 to 2011 on two islands separated by a 1.4 km – 2.5 km wide stretch of low saltwater marsh on the coast of Georgetown, SC. Diagnostic remains of prey items were identified to the lowest taxonomic level. A multi-response permutation procedure revealed differences in Coyote diet composition between islands ( $A = 0.0090$ ,  $p < 0.0001$ ). Subsequent indicator species analysis revealed a total of four food items that serve to differentiate diet between islands: birds, *Sus scrofa* L. (Wild hog), *Ilex spp.* fruit, and lagomorphs. This study shows how Coyote food habits and their potential ecosystem effects may change dramatically on a very local scale. This may be of particular concern to biologists attempting to utilize published diet studies to inform Coyote management strategies.

## Introduction

*Canis latrans* Say (Coyote) are new invaders of ecosystems across the southeastern United States (Parker 1995) and could have potentially large impacts on community dynamics of southern systems (Kilgo et al. 2012). While the basic ecology of Coyotes has been widely studied in the western United States, the larger body size of eastern Coyotes and extreme plasticity in Coyote behavior makes these studies of limited use in understanding specific food habits of southeastern populations (Schrecengost et al. 2008). Similar to western populations, diets of southeastern Coyotes are comprised largely of rodents, vegetation, and lagomorphs, with the abundance of items such as fruit, domestic animals, livestock, commercial crops, wild ungulates, and birds varying greatly due to prey availability. A number of authors have addressed Coyote diet in regions of the Southeast where Coyotes have been established since the 1930s (e.g., Chamberlain and Leopold 1999, Wagner and Hill 1994, Blanton and Hill 1989, Gipson 1974), but Coyote diet investigations are lacking throughout Georgia and the Carolinas, where coyote populations are still expanding (Schrecengost et al. 2008). Detailed studies of localized food habits are of vital importance to wildlife biologists throughout the region, who can only base management decisions on the best available information (Smith and Kennedy 1983).

Studies investigating differences in the diet of generalist species must compare data from two or more study areas with minimal connectivity between them to ensure diet data collected in an area is representative of that specific area and is independent of the others (e.g., Kamler et al. 2007, Lavin et al. 2003). Animal movement between areas utilized in

such studies may be limited by distance between sites or by some barrier to movement that limits connectivity between study areas. Often, studies investigating the relationship between diet and habitat are coupled with radio-telemetry studies of space use, where animal groups are known to occupy defined areas and movement between areas is known to be limited. Researchers investigating differences in diet without radio-telemetry often use reported home ranges of the target species as a physical-distance proxy for information about movement. For example, Farias and Kittlein (2008) chose sites separated by 15 km to test for differences in the diet of *Lycalopex gymnocercus* Fischer (Pampas fox), which have an average home range size of 0.45 km<sup>2</sup>. Utilizing information on average home range size in this manner only takes into account physical distance between sites. However, areas that are physically close together but have low connectivity between patches (either natural or anthropogenic) should allow for similar comparisons between groups.

The goal of this study was to investigate food habits of southeastern Coyotes in a unique island system. Our goals were to: 1) document Coyote diet on two islands on the coast of South Carolina, 2) test for differences in Coyote food habits between areas in close proximity but with potentially low connectivity between areas, and 3) speculate on what these potential differences in coyote diet might mean for wildlife managers in the Southeastern United States.

### **Field-Site Description**

The Tom Yawkey Wildlife Center Heritage Preserve (TYWCHP) is a 9,700-ha wildlife preserve off the coast of Georgetown, South Carolina, USA. The TYWCHP

consists of Cat, South, and North Islands (Fig. 1.1); Cat and South Islands were the focus of this study. Cat Island is separated from the mainland by the Atlantic Intracoastal Waterway and contains *Pinus palustris* Mill. (Longleaf pine) flatwoods, freshwater bogs, salt and freshwater waterfowl impoundments and planted wildlife openings. Pine flatwoods are burned on a 2-year rotation to prevent hardwood intrusion. Upland areas on Cat Island include a wide variety of dominant plant species, including *Quercus marilandica* Muenchh. (Blackjack oak), *Pteridium aquilinum* L. (Bracken fern), *Vaccinium spp.* and *Gaylussacia spp.* South Island consists mainly of saltwater waterfowl impoundments, maritime forest, and barrier beach with Winyah Bay to the north and the Atlantic Ocean to the east. Upland areas on South Island include mainly maritime forest communities dominated by *Quercus virginiana* Mill. (Southern live oak), *Ilex vomitoria* Sol. (Yaupon), *Juniperus virginiana* L. (Eastern red cedar), *Magnolia grandiflora* L. (Southern magnolia), *Pinus taeda* L. (Loblolly pine), and *Sabal minor* Pers. (Dwarf palmetto). Cat Island is roughly 3 times as large as South Island (4,525 ha and 1,507 ha, respectively), but South Island includes a larger area of managed wetlands (485 ha and 702 ha on Cat Island and South Island, respectively; Dozier, unpublished data). The TYWCHP is recognized as a western hemispheric shorebird preserve and an Audubon Important Bird Area due to large numbers of waterfowl, shorebirds and wading birds utilizing managed wetlands (Hopkins-Murphy 1989).

Both islands contain a variety of mammals, including a host of small mammals species (<200 g), *Sylvilagus floridanus* J.A. Allen (Eastern cottontail), *Didelphis virginiana* Kerr (Virginia opossum), *Procyon lotor* L. (Raccoon), and *Lynx rufus*

Schreber (Bobcat). *Odocoileus virginianus* Zimmermann (White-tailed deer), *Sus scrofa* L. (Wild hog), and *Sciurus carolinensis* Gmelin (Eastern grey squirrel) occupy both islands but are more commonly seen on Cat Island. *Sciurus niger* L. (Fox squirrel) are found on Cat Island. The TYWCHP is managed by the South Carolina Department of Natural Resources (SCDNR) and is closed to hunting and to general public access. White-tailed deer density on both islands averages around 1 deer / 8 ha in upland areas. Approximately 10-16 White-tailed deer and 20 Wild hogs were removed from Cat Island each year of the study period by SCDNR staff. However, carcasses generated by management activities are deposited uncovered at a disposal area on South Island where Coyotes have access to White-tailed deer and Wild hog carrion. The first Coyote was reported on the TYWCHP on Cat Island in 2006.

South Island is separated from Cat Island by a 1.4 km – 2.5 km wide stretch of low saltwater marsh. The marsh is tidally influenced and exposed at low tide. It is characterized by dense stands of *Spartina alterniflora* Loisel. (Salt marsh cordgrass) and *Juncus roemerianus* Scheele (Black needle rush) with thick layers of organic matter and silt. The two islands are connected by a 3.2 km causeway, which is the only road for vehicle traffic between the islands. Coyotes seen travelling between islands on the causeway are targeted by SCDNR staff; 1 coyote was shot on the causeway and 1 was hit by a truck during the study period.

## **Methods**

Coyote scats were collected on transects along roads, dikes, and through beachfront dunes from May 2009 to July 2009 and January 2010 to December 2010.

Seven transects were established on Cat Island and 7 on South Island. All transects were of roughly equal length (2-3 km long). Each transect was travelled by foot, bicycle, or truck at least twice during each season, with seasons defined as winter (Dec-Feb), spring (Mar-May), summer (Jun-Aug), and fall (Sep-Nov). Scats were also collected opportunistically during the course of other field work. Scats were stored in plastic bags at room temperature before processing. Each scat was hand washed with water over a 1-mm mesh screen and air dried. Diagnostic remains of diet items (e.g., dorsal guard hairs, bones, teeth, claws, seeds) were removed and identified to the lowest taxonomic level possible using reference collections at the Campbell Museum of Natural History Clemson, South Carolina and with identification keys (Roest 1986, Moore et al. 1974, Martin and Barkley 1961). Coyote scats were distinguished from those of Bobcat by size and shape (Murie and Elbroch 2005). Plant matter deemed to have been collected incidentally with the sample (oak leaves, pine needles) and not likely purposefully ingested by a Coyote (grass, seeds) was removed from analysis, as were intact, undigested insects that may have been feeding on collected samples.

The proportion of each diet item utilized was calculated as the percent of scats (the no. of scats with a diet item x 100/total no. of scats). Shannon's diversity index was calculated for each island, after which diet items found in <1% of scats for both islands combined were discounted from further analysis. Multi-response permutation procedures (MRPP; Mielke and Berry 2001) were performed with a Sorenson (Bray-Curtis) distance measure to test the null hypothesis of no difference in Coyote diet composition between islands (see Appendix 1). Pairwise chi-squared tests were subsequently used to test for

differences between islands for each diet item. An indicator species analysis (ISA) was also conducted to describe the ability of different diet items to differentiate between islands (Dufrêne and Legendre 1997; see Appendix 2). Significance of the ISA was tested using a Monte Carlo test with 4,999 permutations. MRPP, ISA, and Shannon's diversity indices were conducted with PC-ORD (MJM Software Design, Gleneden Beach, OR); SAS (SAS Institute, Cary, NC) was used for chi-squared tests. A significance level of  $\alpha = 0.05$  was set for all tests.

Relatively small samples (<2 cm in diameter), which might have been confused with Bobcat scat, were left uncollected where they were found. These smaller scats located in the dunes or exposed areas of South Island were often observed for >3 months after, making it difficult to determine when scats were actually deposited. For this reason, and because low samples sizes precluded seasonal or annual comparisons between islands, no attempt was made in this paper to distinguish between seasonal or annual differences in diet.

## **Results**

A total of 106 scats were collected on Cat Island and 199 on South Island, with more scats collected on South Island in 5 of 7 sampling periods (Table 1.1). Forty-four total diet items were identified on both islands combined, with 32 items identified from Cat Island scats and 39 items from South Island. Shannon's diversity indices were similar for each island (Cat Island = 2.44, South Island = 2.46), but MRPP showed a significant difference between coyote diet on the two islands ( $A = 0.0090$ ,  $p < 0.0001$ ). *Sigmodon spp.* (cotton rats) were the most common food item found in Cat Island scats,

followed by birds, vegetation, and *Peromyscus spp.* (deer mice). Birds were the most common item found in South Island samples, followed by cotton rats, vegetation and *Neotoma spp.* (wood rats; Table 1.2). Cat Island samples comprised a larger percent of scats containing Wild hog, lagomorphs, *Diospyros spp.* (persimmon), and soricomporphs, while South Island samples contained more birds, crabs, *Mephitis mephitis* Shreber (Striped skunk), and mustelids (Table 1.2). ISA yielded significant indicator values for three animal groups and one plant genus: birds, lagomorphs, Wild hogs and *Ilex spp.* (Table 1.2).

### **Discussion**

Differences in Coyote diet found in this study may be explained by differing prey availability and habitat types (Morey et al. 2007, Dumond and Villard 2001). South Island includes a larger area of managed wetlands (702 ha, approximately 47% overall area; Dozier, unpublished data) which supports more wading birds and shorebirds (Dozier, Christmas Bird Count unpublished data). Upland areas of South Island are also dominated by *Ilex vomitoria* Sol. (Yaupon) which is commonly found in the diets of mammalian generalists (Miller and Miller 2005). Comparatively more wading bird and shorebird habitat, and an abundance of Yaupon on South Island, could explain a greater percent of scats with bird remains and *Ilex* seeds in South Island samples. Likewise, Wild hog populations are well established on Cat Island, but not South Island (Dozier, unpublished data), and more Cat Island scats contained Wild hog remains. Although no data on distribution and abundance of lagomorphs exist for the TYWCHP, Cat Island has more upland habitat than South Island, most of which is comprised of Longleaf pine



flatwoods with a diverse herbaceous understory that should favor lagomorphs (Yarrow and Yarrow 1999). Differences in habitat structure between the two islands could explain significantly more lagomorphs in Cat Island samples.

Birds, lagomorphs, *Ilex spp.*, and Wild hog were also identified by ISA as being important contributors of overall differences in food habits between the islands.

However, four groups of diet items showed significant differences in percent of scats between islands but were not identified by ISA as important drivers of overall diet. Crab, Striped skunk, and mustelid items were all found more often in South Island samples, but likely not in quantities large enough to influence overall diet (<3% on either island).

Sorciomorphs were also found more commonly in South Island samples and more commonly overall (13.21% and 9.05% on Cat Island and South Island, respectively), but perhaps not enough to be included in ISA.

Despite equal search effort between islands, more scats were located on South Island than Cat Island. This could be due to a larger density of Coyotes on South Island than Cat Island, increased persistence of scats on South Island than those on Cat Island, or increased detectability of scats on South Island than those on Cat Island. No population estimates have been conducted for Coyotes on the TYWCHP and hence a comparison of density between islands is not readily available. Anecdotal evidence does suggest there is increased persistence of scats on South Island, however, where scats are more exposed in open habitats on beach dunes and along dikes. Potential differences in Coyote diet related to season were not assessed because of this uncertainty of when scats were actually deposited (as opposed to when scats were collected). However, if more

scat was found on South Island during the spring and summer seasons because of a shift in Coyote space use from one island to the other, differences in diet between islands could be driven by seasonal availability of food items, and not by habitat differences between islands. The more exposed nature of transects on South Island could also mean that scats were more detectable on South Island than Cat Island.

Many other southeastern Coyote food habit studies have documented rodents and vegetation as major diet items (e.g., Crimmins et al. 2012, Grigione et al. 2011, Smith and Kennedy 1983, Hall 1979), but no other southeastern studies to date have documented such a large avian component in Coyote diet. Several studies have documented low levels of Coyote consumption of songbirds, most of which are listed as unidentified passeriformes (Hoerath 1990, Hall 1979, Michaelson 1975, Gipson 1974). However, Hall (1979) was able to identify 10 different songbird species from recovered flight feathers in scats of Coyotes in Louisiana. No flight feathers were recovered in the present study. Instead, most feathers were downy, white or gray, and lacking any identifiable markings (Scott and McFarland 2010). While a lack of distinguishable marks makes it difficult to determine which bird species or groups Coyotes may be utilizing, it appears that during this study wading birds may have been more likely to be preyed upon compared to other avian taxa (e.g. passerines). Given the relatively larger body size of wading birds than passerines, Coyotes may selectively consume the body of wading birds, avoiding the wings and larger feathers which would have aided in species identification. This likely differs from Coyote consumption of passerines, which may be easier to consume as whole birds, leaving flight feathers and other identifiable remains

deposited in scat. Coyote consumption of wading birds at this study site is also more likely given the large numbers of wading birds utilizing waterfowl impoundments on the TWYCHP each year. Future studies of Coyote diet in coastal areas may be able to utilize stable isotope techniques to distinguish between songbirds, which typically consume terrestrial insects, fruits and seeds, and wading birds, which utilize aquatic prey (e.g., Hilderbrand et al. 1996).

Diet studies of generalist carnivores that rely on identification of items from scat often suffer from biases related to different consumption patterns and assimilation efficiencies of different groups of food items (Marucco et al. 2008, R  he et al. 2008, Andelt and Andelt 1984). For example, carnivores utilizing carcasses of large mammals may consume more meat or organs and less hair or bones than those consuming whole rodents, potentially causing the importance of large mammals in carnivore diets to be underrepresented as remains from meat or organs are less likely to appear in scat compared to hair samples or bone fragments (Marucco et al. 2008). Similarly, no egg shells (either avian or reptilian) were found in this study, despite Coyotes on the TYWCHP being the main predator of Loggerhead sea turtle nests on South Island (Eskew 2012). Coyotes on South Island break open turtle eggs on the beach and lick out the yolk, which leaves no diagnostic remains in scat (Etheredge, personal observation). Even so, other studies have found egg shells in Coyote scat (avian, Wagner and Hill 1994, Litvaitis and Shaw 1980; reptilian, Wooding et al. 1984). Further, no remains of Loggerhead sea turtle hatchlings were documented in the present study, even though Coyotes are a known predator of hatchlings on South Island (Eskew 2012), suggesting

that studies of Coyote diet based on scat sampling may be inadequate to detect the potential for Coyote impacts on some species of special conservation concern.

Coyote impacts on White-tailed deer are particularly concerning for southeastern wildlife managers, and several authors have documented large proportions of deer remains in scats and stomachs (Crimmins et al. 2012, Schrecengost et al. 2008, Blanton and Hill 1989). These findings have suggested that Coyote depredation, particularly on fawns, may have a profound region-wide effect on White-tailed deer populations (Kilgo et al. 2012), at least in areas of very high deer densities (Blanton and Hill 1989). The present study found relatively low frequencies of White-tailed deer (<7% of scats on either island) compared to other studies (40% of scats in December, Schrecengost et al. 2008), which may be a function of lower deer densities on the TYWCHP (Blanton and Hill 1989). This study did not attempt to differentiate between adult deer and fawns, although it is worth noting that Coyotes readily scavenged deer left uncovered at the carcass disposal area on South Island (Etheredge, personal observation).

Differences in food habits documented at such a local scale in this study suggest that diet may differ within a region, and hence that regional generalizations about Coyote diets may be misleading. Landowners and wildlife managers alike should understand that even a study conducted in the same state or county likely does not reflect conditions on their own property. Studies testing predictive hypotheses about Coyote food habits based on habitat types or prey population sizes across the Southeast (e.g. Blanton and Hill 1989) will likely be more useful to managers than smaller scale studies reporting

variation in coyote diet based on season, habitat, or prey availability, which has already been well established for Coyotes.

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**Table 1.1.** Coyote scats collected by season on Cat Island and South Island at the Tom Yawkey Wildlife Center and Heritage Preserve, Georgetown, South Carolina, USA, 2009-2011.

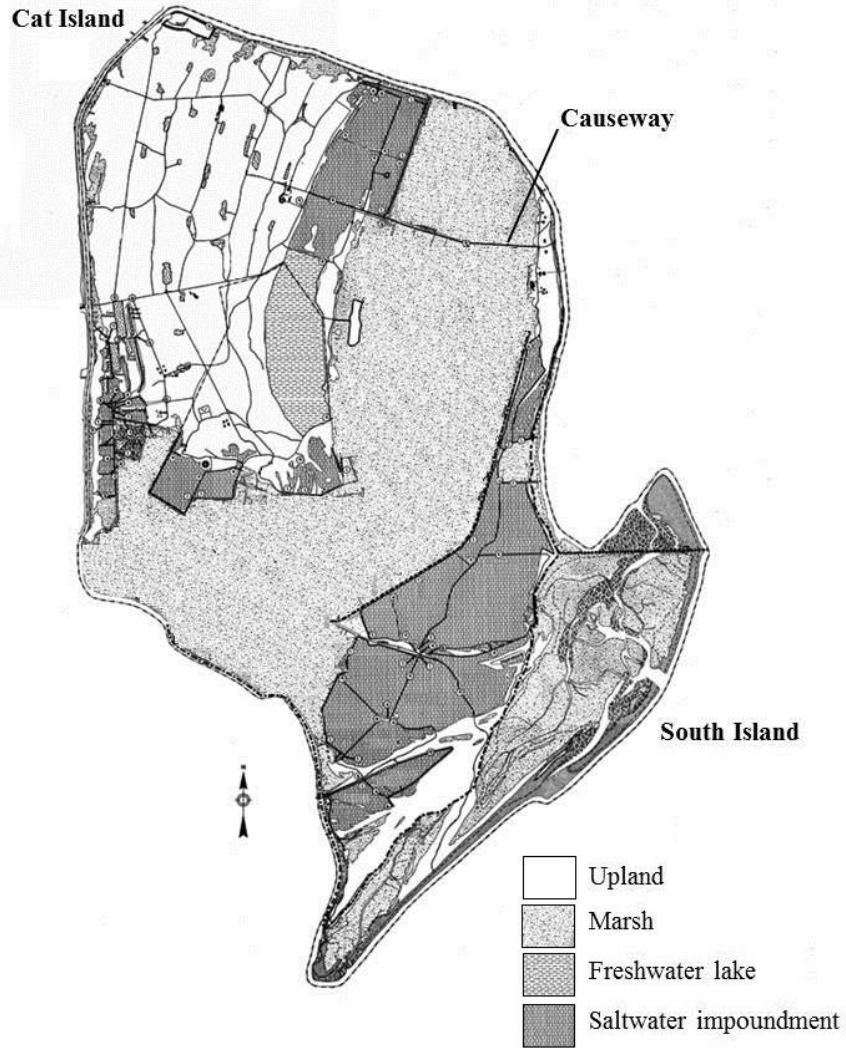
	Spring 2009	Summer 2009	Winter 2010	Spring 2010	Summer 2010	Fall 2010	Winter 2010- 2011	Total
Cat	4	11	36	32	3	15	5	106
South	34	23	50	44	31	13	4	199

**Table 1.2.** Percent of scats, item rank, and indicator values for diet items found in Coyote scats on Cat Island and South Island at the Tom Yawkey Wildlife Center and Heritage Preserve, Georgetown, South Carolina, USA, 2009-2011. Percent of scats is calculated as the no. of scats with a diet item (n) x 100/total no. of scats (N). Indicator values are the observed maximum indicator value for both islands (IV). IV p-values are the result of a Monte Carlo test of significance based on 4,999 randomizations.

Diet item	Cat Island N=106		South Island N=199		Indicator Value	
	% (n)	Rank	% (n)	Rank	IV	p
<b>Small mammals</b>						
<i>Microtus spp.</i>	18.87 (20)	6	13.07 (26)	6	11.1	0.1928
<i>Neotoma spp.</i>	11.32 (12)	10	18.59 (37)	4	12.4	0.1398
<i>Oryzomys spp.</i>	7.55 (8)	11	7.04 (14)	11	3.9	0.1398
<i>Peromyscus spp.</i>	23.58 (25)	4	17.09 (34)	5	13.6	0.2222
<i>Rattus spp.</i>	0.66 (2)	15	3.52 (7)	15	2.4	0.4861
Scuridae	2.83 (3)	14	4.02 (8)	14	2.5	0.7540
<i>Sigmodon spp.</i>	54.72 (58)	1	46.73 (93)	2	29.2	0.2899
Soricidae*	13.21 (14)	8	9.05 (18)	9	7.8	0.3263
<b>Midsized herbivores</b>						
Lagomorpha*	21.70 (23)	5	10.05 (20)	8	14.8	0.005
<b>Large herbivores</b>						
<i>Odocoileus virginianus</i>	3.77 (4)	13	6.03 (12)	12	4	0.4323
<i>Sus scrofa</i> *	14.15 (15)	7	3.02 (6)	16	11.7	0.0018
<b>Mesopredators</b>						
<i>Didelphis virginiana</i>	12.26 (13)	9	7.54 (15)	10	7.5	0.2178
<i>Mephitis mephitis</i> *	0.33 (1)	16	1.51 (3)	18	1	1
Mustelidae*	0 (0)		2.51 (5)	17	2.6	0.1622
<i>Procyon lotor</i>	1.89 (2)	15	1.01 (2)	19	1.2	0.6179
<b>Other</b>						
Aves*	42.45 (45)	2	59.80 (119)	1	37.5	0.0038
Decopoda	1.89 (2)	15	2.51 (5)	17	1.5	1
<i>Diospyros spp.</i> *	2.83 (3)	14	0.50 (1)	20	1.5	0.1322
<i>Ilex spp.</i> *	0.94 (1)	16	10.55 (21)	7	5.2	0.0016
Insecta	7.55 (8)	11	3.52 (7)	15	3.8	0.1660
Reptilia	4.72 (5)	12	3.02 (6)	16	2.9	0.5333
Unknown seeds	7.55 (8)	11	5.03 (10)	13	4.5	0.4663
Vegetation	32.08 (34)	3	31.66 (63)	3	16.9	0.9064

\*Significant difference in % of scats between islands (Chi-square test;  $p < 0.05$ )

**Figure 1.1.** Cat Island and South Island on the Tom Yawkey Wildlife Center and Heritage Preserve, Georgetown, South Carolina, USA.



## CHAPTER TWO

### RACCOON ANTI-PREDATOR RESPONSE TO AN ARTIFICIAL INCREASE IN COYOTE ACTIVITY

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**ABSTRACT** The strength of the a prey individual's anti-predator response (APR) is often related to the strength of the competitive relationship between the two species, whereby stronger APRs are seen when prey encounter cues from predators which more frequently prey on conspecifics. The mesopredator release hypothesis (MRH) predicts strong competitive relationships within predator guilds, with smaller-bodied predators responding to larger ones with the same APRs as seen in traditional predator-prey relationships. This study uses anti-predator behavior to test a portion of the MRH by examining the spatial avoidance of raccoons (*Procyon lotor*) in areas with artificially increased coyote (*Canis latrans*) activity. We mapped home ranges for radio-collared raccoons and created test plots inside 50% and 95% fixed kernel contours to test for differential raccoon responses based on potential tradeoffs between resource availability and predation risk. We used a coyote urine treatment inside to simulate a local increase in coyote activity. We then compared the proportion of locations inside treated and control plots one week before and one week after plot establishment. Raccoons did not

avoid areas of artificially increased coyote activity regardless of habitat variables or plot location inside the home range. Our results suggest that either coyotes do not present a significant threat to raccoons in this study system or that raccoons are unaware of the threat coyotes may pose. Understanding the strength of the competitive relationship between coyotes and other mesopredators is especially important in the southeastern United States, where recent coyote invasions are thought to be changing predator dynamics.

**KEYWORDS** Anti-predator response, *Canis latrans*, mesopredator release hypothesis, *Procyon lotor*.

## **INTRODUCTION**

Prey species often change their behavior under the perceived risk of predation to avoid encounters with predators (Lima and Dill 1990). Prey may be more vigilant or they may forage less in areas where predators are detected, or else they may avoid habitats where predators frequent altogether (Atwood et al. 2009, Nelson et al. 2007, Heithaus and Dill 2002, Durant 1998, Kotler et al. 1993). While these anti-predator responses (APRs) to the potential presence of predators should ultimately lower the risk of injury or death (Lima and Dill 1990), any APR is assumed to represent an energetic tradeoff, where increased vigilance or changes in space use correlate with some cost, such as decreased foraging efficiency or reproductive opportunities (Lima 1998). Predator presence in a particular area may be detected by a variety of mechanisms, including visual identification of the predator, auditory cues, eavesdropping, and the detection of semiochemicals, such as those present in predator urine or scat (Eichholtz et al. 2012,

Vanak et al. 2009, Hunter 2008, King et al. 2008, Scheinin et al. 2006). In particular, prey may use semiochemicals to assess varying levels of potential threat posed by different predator species or individuals (Osburn and Cramer 2013, Cox et al. 2010, Berton et al. 1998, Nolte et al. 1994, Wilson and Lefcort 1993). Differential responses to varying threat levels suggests that APRs to perceived risk are presumably tied to the strength of the competitive relationship between two species (Osburn and Cramer 2013). Rodents, for example, foraged less often and exhibited more defensive behaviors when exposed to scat from predators fed an all-meat diet than scat from those fed a vegetarian diet (Berton et al. 1998, Nolte et al. 1994). Likewise, tadpoles reduced their activity in the presence of chemicals from newts fed tadpoles (Wilson and Lefcort 1993). Kangaroos and goats (*Capra hircus*) both decreased time foraging and consumed less food in the presence of scat from predators fed conspecifics (Cox et al. 2010). Similarly, porcupines (*Erethizon dorsatum*) detected a larger degree of threat presented by urine collected from specialist predators (fisher, *Martes pennanti*) as opposed to that collected from generalists (coyote, *Canis latrans*; Osburn and Cramer 2013). Kangaroos also exhibited greater APRs when presented with semiochemicals derived from familiar, rather than novel, predator species (Parsons et al. 2007).

APRs to perceived risk can also occur as a result of competition within a single guild, similar to the responses of prey under the potential threat of predation. Top predators, for example, may pose a threat to populations of smaller mesopredators in a competitive relationship predicted by the mesopredator release hypothesis (MRH). The MRH not only predicts an inverse relationship in population sizes between predator

species, but also a corresponding APR, whereby smaller-bodied predators avoid larger ones in space or time (Prugh et al. 2009, Sergio et al. 2007, Crooks and Soule 1999). While the MRH is very well supported in a variety of different predator guilds (Ritchie and Johnson 2009, Prugh et al. 2009), it may not accurately describe some systems where the top predator is itself also considered a mesopredator or where a strong competitive relationship between predator species is lacking (Cove et al. 2012). For example, both direct (population level studies; e.g., Levi and Wilmers 2012, Henke and Bryant 1999) and indirect (behavioral studies; e.g., Vanak et al. 2009, Mitchell and Banks 2005, Sargeant et al. 1987) evidence provides strong support for the MRH within the canid family. Clear body size differences dictate competitive relationships between species, with larger-bodied canids suppressing smaller-bodied species (Levi and Wilmers 2012, Berger and Gese 2007, Gosselink et al. 2007, Karki et al. 2007, Mitchell and Banks 2005, Kamler et al. 2003, Sargeant et al. 1987). However, there is conflicting evidence surrounding the relationship between coyotes and other mesopredators not within the Canidae (Cove et al. 2012, Gehrt and Prange 2007, Prange and Gehrt 2007, Gehrt and Clark 2003). Some authors have demonstrated an inverse relationship between population sizes of coyotes and mesopredators in other families (Crooks and Soule 1999, Henke and Bryant 1999, Sargeant et al. 1993, Robinson 1961). However, others have suggested that much of the evidence supporting MRH applications between coyotes and other mesopredators is correlational (Gehrt and Clark 2003), and in some cases may be the result of sampling artifacts (Cove et al. 2012). Other studies have also not found any evidence of interspecific killing or intraguild predation between coyotes and other



mesopredators (Gehrt and Prange 2007, Prange and Gehrt 2007, Gehrt 2005, Chamberlain et al. 1999). Behavioral evidence also offers little support for MRH applications between coyotes and skunks (Prange and Gehrt 2007) and between coyotes and raccoons (Gehrt and Prange 2007).

Understanding the nature of intraguild dynamics as predicted by the MRH can be critical to managers attempting to increase production in populations of ground-nesting prey in particular, where a host of predator species may cause significant egg or hatchling losses (Gehrt and Clark 2003). For this reason, biologists have increasingly called for the inclusion of MRH predicted relationships into predator control programs (Prugh et al. 2009, Barton and Roth 2008, Rayner et al. 2007, Gompper 2002, Rogers and Caro 1998). An understanding of the MRH as it pertains to coyotes and raccoons is particularly important in the southeastern US, where coyotes have recently established themselves as top predators (Parker 1995), and where raccoons are consistently among the most significant nest predators of a wide variety of prey species (e.g., Barton and Roth 2008, Chalfoun et al. 2002, Sargeant et al. 1993).

The purpose of this study is to provide a behavioral test of the MRH by using coyote urine applications to expose raccoons to an artificial increase in coyote activity. If there is a strong competitive relationship between coyotes and raccoons whereby coyotes represent a significant mortal threat to raccoons, we expect raccoons to exhibit a behavioral response by avoiding that area after coyote urine application. If, however, the threat of coyote predation does not outweigh the potential benefits of using a particular

area, we expect to see no change in raccoon use of that area before or after urine treatment.

## **STUDY SITE**

The Tom Yawkey Wildlife Center Heritage Preserve (TYWCHP) is a 9,700-ha waterfowl preserve off the coast of Georgetown, South Carolina, USA. It is managed by the South Carolina Department of Natural Resources and is closed to hunting and to general public access. The TYWCHP consists of a variety of different habitat types, including longleaf pine savannahs, salt and fresh water waterfowl impoundments, freshwater bogs, saltwater marshes, mixed pine and hardwood hammocks, and planted wildlife openings. The first coyote was reported on the TYWCHP in 2006.

## **METHODS**

This study utilizes a Before-After-Control-Impact design to detect changes in space use of focal animals (Manly 2002). Testing periods ( $n=3$ ) were conducted from March 2011 to August 2011 with 2 weeks between each period. Test plots (300 m x 300 m) were divided into 4, 2.25-ha subplots (150 m x 150 m). We randomly assigned each subplot a treatment, such that every plot contained 2 urine treatments, 1 active control, and 1 passive control. For urine treatments, we sprayed coyote urine approximately every 15 m on tree stumps, dead logs, or vegetation close to the ground along a transect covering most of the subplot (Fig. 2.1). In active controls, we walked the same transect pattern without applying urine. We left passive controls undisturbed to test for raccoon

avoidance of human activity as opposed to urine treatments. Urine used in this study was purchased commercially and was collected from coyotes fed a furbearer diet blend composed of 50% poultry, 40% beaver, and 10% cereal grains (Minnesota Trapline Products, Pennock, MN).

Raccoons were captured in box traps (Tomahawk Live Trap Co., Hazelhurst, WI) baited with cat food or fish and placed on dikes, along the sides of waterfowl impoundments, and in wildlife openings. Captured raccoons were anesthetized with Telazol (10mg/kg), fitted with a radio-collar (MOD-125; Telonics Inc., Mesa, AZ), and returned to their site of capture. All procedures were approved by the Clemson University Institutional Animal Care and Use Committee (protocol AUP2009-021) and work was conducted under a South Carolina Department of Natural Resources Scientific Collecting Permit (permit G-09-11).

We used a three element Yagi antenna for bearings and used at least three bearings for triangulation (LOAS, Ecological Software Solutions, LLC, Hegymagas, Hungary) wherever possible. We used biangulation with as close to a 90° intersection as possible in locations where three bearings were not feasible. All bearings used for locations were taken within 15 min of each other. Error ellipses were determined by 25 triangulations of 5 stationary collars placed 200 m away from technicians. Test locations were within 40 m of actual locations, with a 2° angle error. Collars could typically be detected up to 1.5 km away from the receiver; however, we took most bearings <0.3 km away from raccoons. While raccoons are considered to be mainly nocturnal or crepuscular, we regularly saw active raccoons during the course of diurnal field work. In

order to include possible diurnal movements, we located individual raccoons 8 times every 24 hrs (3-hr intervals) for a 7-day period prior to test plot establishment.

At the end of each “before” week, test plots were established as previously described. “After” locations were collected in a similar manner as “before” locations for one week following plot establishment. Only raccoons with  $\geq 20$  “before” locations were used for tests. We calculated fixed kernel home ranges using least-squares cross validation (BIOTAS, Ecological Software Solutions, LLC, Hegymagas, Hungary) for the “before” week of each test animal and established plots in two types of areas within a focal animal’s home range: 1) high use areas (inside the 50% contour) and, 2) low use areas (outside the 50% contour but within the 95% contour). We established as many test plots as possible within a two day period; however, it was not always possible to establish both high and low use plots for every raccoon in each treatment period.

We conducted vegetation surveys at 5 randomly selected points within each subplot at the end of each treatment period. We classified each point as one of the following major habitat types: longleaf pine, mixed pine-hardwoods, freshwater bog, saltwater marsh, field, or other. Because vegetative structure within the subplot could potentially affect raccoon detection of predators (or vice versa), we also measured visibilities at each point. Visibility assessments were conducted as follows: a field technician (raccoon mimic) crouched 1 m off the ground, while another technician (coyote mimic) walked with her hand at her side until the raccoon could no longer see the coyote’s fingers. The distance between the two mimics was then recorded in meters. Distances  $>30$  m were assigned a value of 50 m for ease of analysis. We conducted these

measurements in each of the 4 cardinal directions at each point and then averaged all visibility values across the subplot.

To account for differing numbers of locations achieved for different raccoons in different testing periods, we calculated the proportion of focal raccoon locations inside each subplot during each “before” and “after” week as the total number of focal animal locations inside a particular subplot divided by the total number of focal animal locations for that week. We then performed a simple difference in the “before” and “after” proportions for each focal raccoon in each subplot, which served as our dependent variable in a general linear mixed model to test for treatment effects in the proportion of focal raccoon locations inside individual subplots before and after treatment ( $\alpha = 0.05$ ; SAS proc mixed, SAS Institute, Cary, NC). Fixed and random effects used in the model are given in Table 2.1.

## **RESULTS**

Five male raccoons were radio-collared in February 2011 and 3 were collared in June 2011. Although males were not specifically targeted, Gehrt and Fritzell (1996) have reported a substantial male-bias in live trapping raccoons, and no females were captured during this study. From 27 March 2011 to 20 June 2011, we performed 3 total treatment cycles, each comprising 4 unique plots, for a total of 12 plots constructed overall and 2 to 4 focal raccoons represented in each testing period. Two plots were used to test multiple focal raccoons, such that with 12 established plots we were able to test the response of 16 unique focal animal-plot combinations (1 focal animal in 1 plot; Table 2.2); 9 of these

represent locations inside focal animal 50% contours while 7 of them represent locations outside focal animal 50% contours but within that animal's 95% contour.

Overall use of plots in both the "before" and "after" weeks was low, averaging 0.0521 proportional locations in high use subplots and 0.0182 in low use subplots. Raccoons did not change their proportional use of subplots between "before" and "after" weeks based on treatment, plot position inside or outside of the focal animal's 50% contour, visibility within the subplot, habitat type, or any other interaction term tested by the model ( $F < 1.04$ ,  $P > 0.39$  for each). While the model did not indicate any statistically significant differences based on treatment type, there was an apparent, although non-significant, decrease in the proportion of locations for urine impacted and active control plots, with no apparent difference between passive control plots (Fig. 2.2).

## **DISCUSSION**

Anti-predator responses (APRs) represent tradeoffs between the likelihood of being attacked by a predator versus the potential energy gained by choosing to stay and forage in a particular area (Lima 1998). In our study, we assumed that locations inside a raccoon's core area should represent areas with some critical resource, such as foraging locations, that an individual would be giving up after treatment with coyote urine. However, raccoons in this study were no more likely to stop using what we presumed to be more important areas than areas outside of the 50% contour. Prey are also more likely to change their space use in areas where habitat structure makes capture by a predator more likely (e.g. Wirsing et al. 2010), but raccoons in our study were no more likely to

change their space use based on habitat structure within plots. The lack of response of raccoons to the coyote urine treatment in this study suggests either: 1) coyotes do not present a threat to raccoons in this area; 2) coyotes present a threat to raccoons, but the urine treatment was not a strong enough indicator of increased threat levels; or, 3) coyotes present a threat to raccoons, but raccoons do not change their space use based on that threat.

One predator species may pose a threat to another by either direct predation, where one species kills and consumes another, or by interspecific killing, where one species kills another to alleviate interspecific competition but does not consume the carcass (Palomares and Caro 1999). A 2-yr study of coyote diet on the TYWCHP conducted concurrently with this study found raccoon remains in only one percent of scats (see Chapter 1, this document). Other studies of coyote food habits in the southeastern US have also failed to document raccoons as a significant food source (Crimmins et al. 2012, Grigione et al. 2011, Schrecengost et al. 2008, Chamberlain and Leopold 1999). Even so, coyote ecology can be extremely variable from region to region and coyote food habits change based on differences in body size (Gompper 2002), group size (Bowen 1981), habitat composition (Gese et al. 1988), and prey availability (Bartel and Knowlton 2005, Blanton and Hill 1989). Coyotes in the northeastern US in particular have larger body sizes than other populations (Gompper 2002), and O'Connell et al. (1992) documented the largest percentage of raccoons in coyote diet at a site in Maine (47.5% of autumn scats). While many studies do not report non-anthropogenic causes as a major mortality source of raccoons (Rosatte et al. 2010, Nixon et al. 2009,

Urbanek et al. 2009, Henner et al. 2000, Chamberlain et al. 1999), some authors have documented low levels of both coyote predation (Gehrt and Fritzell 1999, Hasbrouck et al. 1992) and interspecific killing (Kamler and Gipson 2004) of raccoons. Gehrt and Prange (2007) attributed a lack of raccoon mortality caused by coyotes and varying degrees of spatial overlap between coyotes and raccoons to a lack of significant interspecific competition between the species. The lack APR shown in our study may indicate that coyotes do not present a threat to raccoons on the TYWCHP, potentially due to a lack of significant interspecific competition. However, although both species are considered generalist omnivores, no study to date has attempted to quantify competition between coyotes and raccoons by investigating niche or dietary overlap.

Coyotes could present a threat to raccoons on the TYWCHP, but the urine treatment in our study may not have been a strong enough indicator of increased threat levels to influence a change in raccoon behavior. Scent-based cues only definitively imply that a predator was once at a particular location, without providing any information on the current position of that individual. Scat or urine may be especially inadequate in providing information on the current location of comparatively active species with large home ranges, such as coyotes. In a meta-analysis of 194 papers published on the nonconsumptive effects of predation, Pressier et al. (2007) found that cues from stationary, sit-and-wait predators were more likely to evoke a behavioral response in prey than cues from predators with more active hunting methods. Several studies have also only documented APRs when prey individuals were presented with the predator itself, as opposed to a urine or scat treatment (Vanak et al. 2009, Scheinin et al. 2006). Urine or



scat can also serve as an attractant for mesopredators in some cases, such as with coprophagy in Virginia opossums, *Didelphus virginiana* (Livingston et al. 2005). Gehrt and Prange (2007) found that raccoons were attracted to scent stations baited with coyote urine at a site with no documented raccoon mortality related to non-human predation. Conversely, Gipson et al. (2003) found that raccoons and opossums were attracted to coyote scat, despite the fact that coyotes were the largest mortality source for both species during the study period. Further, many prey species show differences in APRs based on predator diet (Cox et al. 2010, Nolte et al. 1994, Berton et al. 1998, Wilson and Lefcort 1993). Urine used in this study was commercially available and collected from animals fed a furbearer diet blend not representative of wild coyote diet. This could diminish the ecological relevance of the urine treatment if raccoons can detect differences in coyote diet. Moreover, the persistence of urine in the environment over time is unknown; raccoon responses to a urine treatment may be more evident in the first few days following urine application. The total proportion of locations within plots was also relatively low for every treatment, suggesting that raccoons spent the majority of their time away from test plots, no matter the treatment. This low rate of visitation to test plots in general might have made any behavioral response by raccoons harder to detect given our study design.

Coyotes in this system could present a threat which is either unrecognized by raccoons or not sufficient enough to affect raccoon space use. Prey species may be more likely to recognize threats from native rather than exotic predators. Cox et al. (2010) found repellents manufactured from tiger (*Panthera tigris*) scat were more likely to repel

goats, a historically sympatric species, than those manufactured with scat from Tasmanian devils (*Sarcophilus harrissi*). Western grey kangaroos (*Macropus fuliginosus*) also fed less and exhibited more flight behaviors in the presence of urine from dingos (*Canis dingo*) than when presented with coyote urine (Parsons et al. 2007). However, when prey lack of recognition of exotic predators, they become more susceptible to predation by recently sympatric species, as is the case with many extinctions of endemic bird species on oceanic islands (Blackburn et al. 2004). Even though coyotes and raccoons are recently sympatric in this area, the two species were historically sympatric in the coyote's historic range in the western US. While it is possible that raccoons on the TYWCHP have not yet learned to recognize the threat coyotes pose, the strength of the historic competition between coyotes and raccoons is difficult to evaluate and was not addressed in our study. Raccoons may also respond to the coyote urine treatment without changing the proportion of time they spend inside study plots. Our study only addressed changes in the actual locations of raccoons, but not in their specific behaviors. Raccoons inside treatment plots could still have been aware of a potential predator in the area and exhibited other APRs such as increased vigilance, decreased foraging, or decreased activity overall. Further, female raccoons with vulnerable young may also be more likely to avoid areas of high coyote activity, while we were only able to capture and collar male animals.

The lack of raccoon response seen in our study may also be explained if raccoons are adequately able to defend themselves against coyote predation. For example, Hunter (2008) showed that larger predators are more likely to avoid the aposematic coloration of

skunks in areas where there is a higher skunk population, suggesting that predators may learn the hard way that skunks are capable of defending themselves by spraying a foul odor. In a study similar to ours, Prange and Gehrt (2007) used a simulated increase in coyote activity to show skunks do not avoid areas with coyote urine treatments, and suggested that skunks may be able to adequately defend themselves against coyote attack. Raccoons are known to be aggressive when cornered and are periodically accused of killing domestic hunting dogs, although such events are rarely reported in the literature. Coyotes approaching raccoons may quickly learn that raccoons are able to defend themselves. If so, there should be less incentive for coyotes to attack raccoons, making it less likely for raccoons to stop using areas with increased coyote activity.

Raccoons in our study did not significantly change their use of plots for any treatment type. However, there was a similar, but non-significant, decrease in raccoon use of impact and active control plots as compared to passive control plots. The similarity in raccoon response to urine treated areas and active controls, where transects were walked but no urine was applied, might suggest that, if anything, raccoons were more likely to respond to human activity than the coyote urine. Taken together with a lack of coyote predation of raccoons on the TYWCHP, the lack of raccoon response to a simulated increase in coyote activity in our study supports increasing skepticism over applications of the MRH outside of the Candiae (Cove et al. 2012, Gehrt and Prange 2007, Prange and Gehrt 2007, Gehrt and Clark 2003). However, future studies should examine other APRs, such as changes in vigilance, foraging, and activity levels, to investigate other non-consumptive effects such as might be predicted by the MRH.

## **MANAGEMENT IMPLICATONS**

As recent invaders of many southeastern ecosystems, coyotes represent an unknown conservation challenge for many wildlife managers. The MRH predicts coyotes suppress populations of smaller-bodied predators, such as raccoons, and that this suppression should result in raccoons adopting various APRs to avoid coyotes in space and time. However, raccoons in our study did not avoid areas with an artificial increase in local coyote activity, suggesting coyotes do not represent a large enough threat for raccoons to change their space use. This, coupled with a lack of raccoons in coyote diet (Chapter 1, this document) makes it unlikely coyotes are suppressing raccoons in this system. Our study adds to the growing evidence that the MRH may have limited applications involving coyotes and other predators outside of the Canidae (Cove et al. 2012, Gehrt and Prange 2007, Prange and Gehrt 2007, Gehrt and Clark 2003). However, future studies should examine the potential that raccoons may be utilizing other APRs than spatial avoidance.

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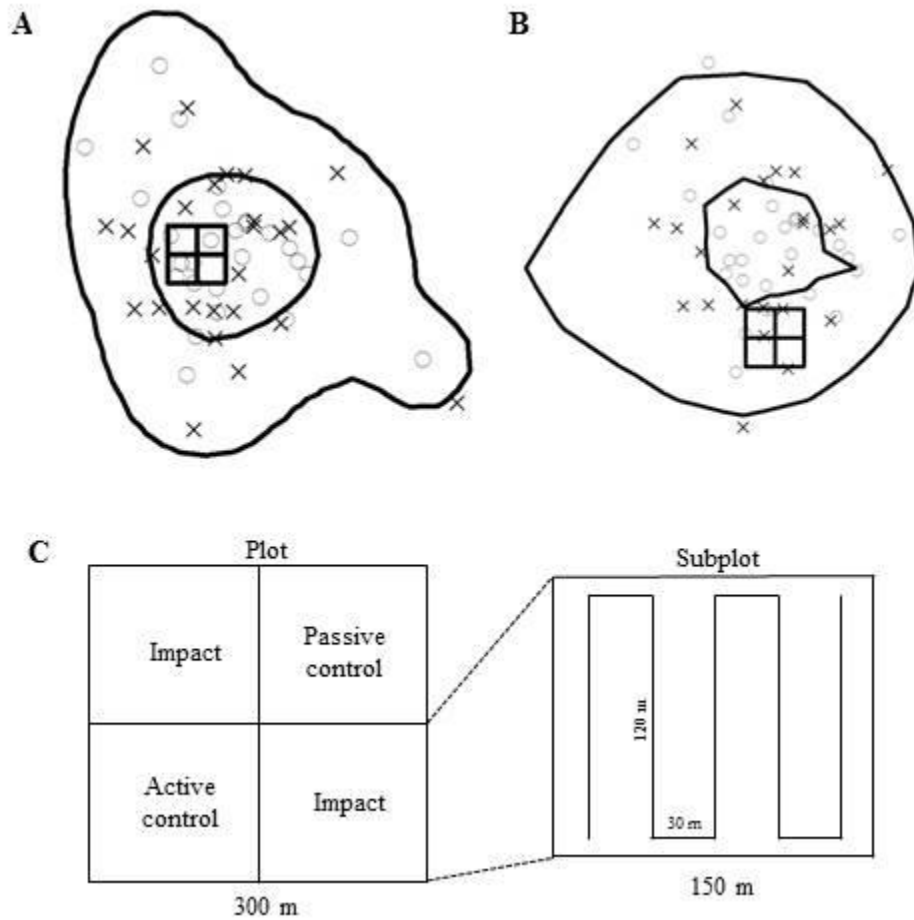
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**Table 2.1.** Name and description of independent variables used in a mixed effects model to estimate raccoon spatial avoidance of 2.25-ha plots treated with coyote urine on the Tom Yawkey Wildlife Center and Heritage Preserve, South Carolina, USA, 2011.

Effect	Effect	Description
treatment	Fixed	Treatment type (impact, active control, passive control)
use	Fixed	Plot use (high, low)
visibility	Fixed	Visibility mean inside the subplot (covariate)
treatment*use	Fixed	Interaction between treatment and use
treat*visibility	Fixed	Interaction between treatment and visibility mean
plot	Random	Specific plot ID
raccoon	Random	Focal animal identity
period	Random	Treatment period
subplot	Random	Specific subplot ID

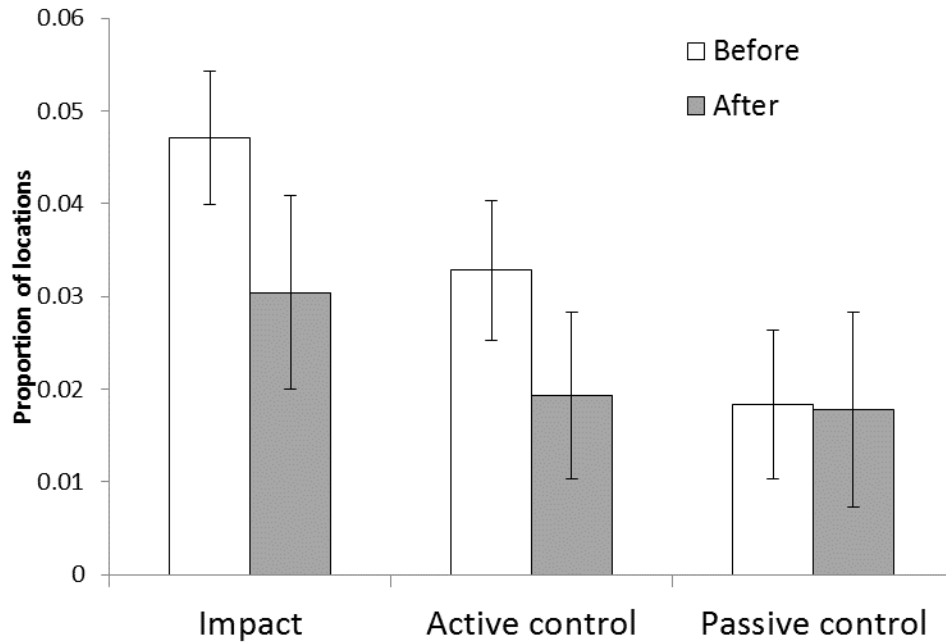
**Table 2.2.** Treatment periods and focal raccoons used to test raccoon spatial avoidance of subplots treated with coyote urine on the Tom Yawkey Wildlife Center and Heritage Preserve, South Carolina, USA, 2011. “High use” indicates individual raccoons used on specific plots placed inside a focal animal’s 50% fixed kernel contour during the week before treatment. “Low use” indicates individual raccoons used on plots placed outside a focal animal’s 50% contour, but within its 95% contour. Similar letters represent the same individual focal animal.

Period	Date	Plot ID	High use	Low use
1	Mar 27 – Apr 11	1	BOJ	
		2	LOA	
		3	MAX	
		4	TAM	
2	May 1 – May 16	5	TAM	
		6		TAM
		7		BOJ
		8	BOJ	
3	Jun 5 – Jun 20	9		BOJ
		10	CAS	
		11		BOJ, SAM, CLI
		12	CLI, SAM	TAM



**Figure 2.1.** Example of the application of coyote urine to simulate a local increase in coyote activity on impacted subplots at the Tom Yawkey Wildlife Center and Heritage Preserve, South Carolina, USA, 2011. Xs represent raccoon locations before urine application and circles represent locations after urine application. A) High-use plot inside focal raccoon core area. B) Low-use plot outside focal raccoon core area. C) Example of subplot designations within a plot and the transect pattern for urine application inside impacted subplots. Transects were walked inside active control plots without spraying urine, while no transects were walked and no urine sprayed in passive control plots.





**Figure 2.2.** Proportion of focal raccoon locations ( $\pm$  SE) inside impact, active control, and passive control subplots before and after treatment on the Tom Yawkey Wildlife Center and Heritage Preserve, South Carolina, USA, 2011. Impact plots contained coyote urine applied along transects. In active controls, transects were walked but no urine was applied. No transects were walked or urine applied in passive controls.

## CHAPTER THREE

### THE RELIABILITY OF BEHAVIOR TO INFORM UPON THE STRENGTH OF INTER-SPECIES RELATIONSHIPS

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#### **ABSTRACT**

Studies attempting to discern the nature of the relationship between potential interference competitor species often rely on the behavioral response of a “defender” species to an “aggressor” species odor. However, interpreting the results of these studies can be difficult when no behavioral response is found. In particular, studies utilizing commercially available predator urine or scat may not adequately represent wild predator semiochemicals which could obfuscate results. Here, we evaluate whether experimental investigations of interference competition produce ecologically relevant results by using behavior to indicate the strength of the competitive relationship between coyotes (*Canis latrans*) and raccoons (*Procyon lotor*). We monitored wild raccoon behavior in artificially constructed arenas and at supplemental feeding sites with 1) high threat trials with scat from coyotes eating a diet high in raccoon meat, 2) intermediate threat trials with scat from coyotes eating no raccoon meat, and 3) low threat trials with no coyote scat. Scat treatment in arena trials significantly affected raccoon grooming and traveling, with raccoons in high threat trials spending less time grooming and more time travelling than those in low threat trials. However, treatment had no effect on raccoon vigilance,

feeding, location inside arenas, or time spent in arena dens. Treatment moderately affected raccoon attendance at feeding sites, but did not affect vigilance or food consumption. Our study highlights the extreme caution that should be used when interpreting experimental behavioral studies to inform on the nature of inter-species relationships. *Key words:* interference competition; *Procyon lotor*; *Canis latrans*; predator diet; semiochemicals

## **INTRODUCTION**

An anti-predation response (APR) is any behavior which decreases the probability of prey encountering a predator or increases the probability of prey survival after a predator encounter has occurred. APRs commonly reported in the literature include increased vigilance, decreased activity, decreased time spent in non-defensive behaviors (e.g., foraging, grooming), and avoidance of habitats where predators frequent (reviews by Lima and Dill 1990; Stankowich and Blumstein 2005; Apfelbach et al. 2005). Because each of these responses relate directly to a prey's perceived probability of injury or death, stronger APRs often result from higher degrees of perceived threat (Lima and Dill 1990; Stankowich and Blumstein 2005; Preisser et al. 2007). Porcupines (*Erethizon dorsatum*), for example, are more likely to reduce foraging when presented with urine from a specialist predator (fishers, *Martes pennanti*) than that from a generalist predator (coyotes, *Canis latrans*) (Osburn and Cramer 2013). Tawny owls (*Strix aluco*) employ different APRs when their intraguild predator (eagle owls, *Bubo bubo*) occurs at different densities, such that tawny owls are more likely to avoid risky habitat when eagle owls are present at higher densities (Sergio et al. 2007). APRs may also include behaviors outside

of traditional predator-prey relationships, such as those aimed at alleviating interference competition between a larger “aggressor” and smaller “defender” species within the same guild (Palomares and Caro 1999; Linnell and Strand 2000). For instance, coyotes do not regularly prey on red fox (*Vulpes vulpes*), but will regularly kill foxes without consuming the carcass in a process called interspecific killing (Palomares and Caro 1999). Foxes use APRs to reduce the chance of encountering a coyote by limiting overlap in fox and coyote space use (Harrison et al. 1989; Sargeant et al. 1987; Gosselink et al. 2003).

Prey may use semiochemicals to accurately assess the degree of potential threat posed by individual predators. Rodents forage less and are less active when presented with urine or scat from predators fed meat as opposed to urine or scat from the same predator species maintained on a vegetarian diet (Nolte et al. 1994; Berton et al. 1998). Many prey species exhibit greater APRs in the presence of semiochemicals from predators that have recently fed on conspecifics (Wilson and Lefcort 1993; Chivers et al. 1996; Pillay et al. 2003; Cox et al. 2010). Tadpoles of common frogs (*Rana temporaria*), for example, were less active when in the presence of dragonfly (*Aeshna juncea*) larvae fed tadpoles than in the presence of dragonfly larvae fed insects (Laurila et al. 1997). However, literature describing APRs in the context of a predator diet that is experimentally manipulated most often utilizes invertebrate or aquatic vertebrate models which are easier to maintain in a laboratory setting (review by Chivers and Mirza 2001). A minority of authors utilize terrestrial vertebrates: Pillay et al. (2003) found increased APRs in striped mice (*Rhabdomys pumilio*) presented with feces from ring-necked spitting cobras (*Hemachatus haemachatus*) fed conspecifics compared to feces from

snakes fed house mice (*Mus musculus*). Cox et al. (2010) documented increased APRs in both goats (*Capra hircus*) and eastern grey kangaroos (*Macropus giganteus*) when tested with scat from tigers (*Panthera tigris*) fed conspecifics compared to control tiger scat. However, in the same study, Cox et al. (2010) failed to find any significant APRs with goats and kangaroos presented with scat from Tasmanian devils (*Sarcophilus harrisii*) regardless of predator diet.

The vast majority of APR studies examine systems where the competitive relationship between species is either known beforehand (e.g. Gosselink et al. 2003; Sergio et al. 2007; Osburn and Cramer 2013), or experimentally manipulated (e.g. controlling predator diet, Wilson and Lefcort 1993; Chivers et al. 1996; Pillay et al. 2003; Cox et al. 2010). In contrast, an increasing number of studies utilize experimental tests of APRs to inform on the nature of unknown competitive relationships (Table 1). In these studies, hypothesized prey species are exposed to semiochemicals from a potential predator and APRs (e.g., increased vigilance or avoidance) are taken as evidence of interference competition between the species tested. Using APRs to infer the nature of ecological relationships may be especially appealing because this type of evidence better lends itself to experimentation and shorter time scales than population-level studies, which often rely on correlative evidence or expensive and difficult removal studies. When behavioral studies testing hypothesized competitive relationships yield significant results, APRs can be relatively easy to interpret as evidence in the investigation of the nature of the inter-species relationship. However, when no behavioral effect is detected, results can be much more difficult to understand. For example, in a test of potential

interference competition between mammalian mesopredators, Gipson et al. (2003) compared visitation of raccoons (*Procyon lotor*) and opossums (*Didelphis virginiana*) to scent stations with scat from bobcats (*Felis rufus*), coyotes, and a control scent. Both raccoons and opossums were attracted to bobcat and coyote scat, despite the fact that coyotes were a major cause of death for both opossums and raccoons during the study period. Gipson et al. (2003) suggested that opossum attraction to coyote and bobcat scat could be due to coprophagy, where opossums were seeking scat out as a food source, compromising the use of scat to test APRs in this case.

The degree of interference competition between coyotes and raccoons has recently received attention as biologists become increasingly interested in the effects of mesopredator release (Rogers and Caro 1998; Gehrt and Clark 2003; Gehrt and Prange 2007). Both species are widespread across North America, are considered members of the same guild, are important generalist predators of a wide variety of domestic and threatened species, and are often the subjects of extensive predator removal programs. While few studies have measured the degree of niche overlap between coyotes and raccoons (Azevedo et al. 2006), a number of authors have suggested that interspecific competition may exist between the two and that this competition results in the suppression of raccoons by coyotes (Rogers and Caro 1998; Crooks and Soule 1999). While some interspecific killing and predation by coyotes of raccoons has been documented (O'Connell et al. 1992; Kamler and Gipson 2004), correlative evidence supporting interference competition between these predators is sparse and may be misinterpreted (Cove et al. 2012). Even so, the experimental evidence against

interference competition between coyotes and raccoons remains mainly indirect and behavioral (Gehrt and Prange 2007; Chapter 2, this document).

In this paper, we use the disputed competitive relationship between coyotes and raccoons as a model to test the ecological relevancy of studies which utilize APRs as a response variable in tests of unknown relationships between predator species. By experimentally controlling coyote diet, we are able to compare APRs of raccoons across three levels of potential threat: high threat, with scent from coyotes fed a high raccoon diet; low threat, with scent from coyotes fed a low raccoon diet; and no threat, with a control scent. Our purpose is to 1) determine if raccoon APRs vary in response to increasing threat levels, and 2) determine if chemosensory cues from a known predator result in behavioral changes as might be predicted by an experimental study investigating interference competition between carnivores.

## **MATERIALS AND METHODS**

### **Scat collection and processing**

To test raccoon behavioral responses to chemosensory cues, we introduced wild raccoons to scent produced from coyote scat representing three potential threats: a high, intermediate, and low threat level produced from coyotes fed a high-raccoon diet, coyotes fed a no-raccoon diet, and a no-scat “blank” treatment, respectively. We collected all scat from captive animals at the USDA-WS-National Wildlife Research Center Predator Research Facility in Logan, UT, from June 2011 to July 2011. Two weeks prior to scat collection, we started 6 high-threat coyotes (4 adult males, 2 adult females) on a raccoon diet with 25% of their normal diet consisting of raccoon meat (162 g raccoon meat

coupled with 488 g furbearer diet blend provided six days a week) to allow their digestive systems to acclimate to the new diet. One week prior to scat collection, we increased the ratio of raccoon meat to a 50% raccoon diet (325 g raccoon and 325 g diet blend). To help prevent the introduction of raccoon roundworm (*Baylisascaris procyonis*) into the coyote colony, we fed coyotes only raccoon skeletal muscle with all bones and hairs removed. Raccoon meat was also frozen for three days post-harvest at -78°C to further prevent the spread of unknown parasites or diseases. All raccoon meat used in this study was harvested from animals collected by USDA-Wildlife Services in and around Salt Lake City, UT.

We maintained control coyotes (4 adult males, 4 adult females) on their regular diet (650 g diet blend) throughout scat collection. This diet blend was composed of a mixture of agricultural animal byproducts, cheese, grains and vegetable pulp and contains no wild foods (Fur Breeder Agricultural Cooperative, Logan, UT). We collected scat once daily for three weeks and froze samples immediately after collection. To minimize the potential for disease transfer between scat collection and behavior trial locations, we extracted aromatic compounds from scat one day before testing following protocols detailed by Cox et al. (2010). High and intermediate treatments refer to the product of these aromatic extractions for the different types of coyote scat. Low threat treatments refer to “blank” extractions, where protocols are followed without scat present. We conducted all extractions with pooled scat samples, so each treatment should represent a composite sample of all coyote individuals used for that threat level.



## **Arena trials**

We used arena trials to investigate the effects of scat treatments on the behavior of wild raccoons. We captured raccoons with box traps baited with sardines or cat food at 4 secluded riparian sites on and around the campus of Clemson University, Clemson, South Carolina (34°39' N, 82°49' W) from November 2011 to February 2013. To minimize behavioral effects related to relocating animals, we constructed arenas in the field within 0.1 km of all traps. We used a 3.05 x 3.05 m design, constructed of metal conduit pipe with 1 x 1 cm hardware cloth around the sides, hexagonal chicken wire on the top, and a 1-m skirt of hardware cloth along the bottom to prevent raccoons from digging under the enclosure. Each arena contained two den boxes in opposite corners and two open cans of sardines to provide cover and foraging opportunities within the enclosure (Fig. 3.1). We deconstructed and thoroughly cleaned arenas with 10% bleach after each trial to minimize odor contamination between trials. Because odor cannot be easily removed from soil, we also used spray paint to mark the ground beneath arenas to ensure trials were not conducted on the same piece of ground twice.

After capture, we transferred raccoons to a squeeze box (RM24, Tomahawk Livetraps, LLC., Hazelhurst, WI) and ear-tagged them with colored washers (tag 1005-1, washer 3/8" 1842; National Band and Tag Co., Newport, KY) so that only new individuals were used in trials. In order to avoid the possible behavioral effects of anesthetic drugs, we kept raccoons alert and minimized handling time as much as possible. We immediately released raccoons into the arena after ear-tagging by attaching the squeeze box to the side of the arena and opening the door (Fig. 3.1). Trials lasted 1 hr

starting immediately after opening the box door. We constructed time budgets for arena trials (JWatcher 1.0) using mutually exclusive behaviors and mutually exclusive locations defined in Table 3.2 to test the following hypotheses regarding high threat trials compared to intermediate or low threat trials:

- (1) Raccoons in high threat trials are more vigilant and spend more time in den boxes,
- (2) Raccoons in high threat trials forage less, groom less, and rest less in the open,
- (3) Raccoons in high threat trials spend less time close to the treatment, and
- (4) Raccoons in high threat trials spend less time on the ground and more time hanging from the enclosure.

Because raccoons could become habituated to either treatments or the arenas themselves over time, we constructed time budgets for 4 consecutive 15-min periods (bins). We used general linear mixed models ( $\alpha = 0.05$ ; SAS proc mixed, SAS Institute, Cary, NC) to test the effect of treatment on the proportion of time spent in each behavior by holding treatment and bin as fixed effects and season and site as random effects. We defined seasons as follows: winter (Dec-Feb), spring (Mar-May), summer (Jun-Aug), and fall (Sep-Nov). Only trials that lasted a full 1 hr were included in analyses.

### **Feeding trials**

In order to test the effect of treatment on wild raccoon behavior in a more natural setting, we used infrared game cameras with an 18-m range and no lights or flash (HC600; RECONYX, Inc., Holmen, WI) to monitor raccoon use of supplemental feeding sites.

We established a total of nine sites from November 2011 to February 2013 in riparian areas on the Issaqueena Area of Clemson Experimental Forest in Clemson, South Carolina (34°44' N, 82°09' W) that is closed to hunting. All sites were < 50 m away from secondary forest roads and were determined to be equally likely to be disturbed by recreational forest users (horseback riders, mountain bikers) based on location. The Issaqueena Area is closed from dusk to dawn which limits anthropogenic disturbances to raccoons when they are more active at night. To encourage consistent use of feeding sites, we added 2.5 kg whole kernel corn to sites once a week for the duration of the study and did not use sites for trials until corn was being consistently removed from an area.

On the evening prior to a feeding trial, we added 2.5 kg corn to a site and used a 7.5-cm grid to visually estimate the amount of corn on the pile by counting the number of vertices with corn directly underneath them. We placed a randomly selected scat treatment within 20 cm of the corn pile and also added a pre-weighed open can of sardines at the site to encourage raccoon visitation. We set cameras 1 m above the ground and 10 m away from the corn pile. Cameras were set to take three pictures per trigger with 1 s between pictures and no delay between triggers. We randomly selected sites for trials without replacement until all sites had been used before starting another round of site selection, keeping at least 7 days between same-site trials. We scored photographs to test the following hypotheses regarding high threat trials compared to intermediate or low threat trials:

- (5) Raccoons in high threat trials stay for shorter periods of time,
- (6) Raccoons in high threat trials are more vigilant, and

(7) Raccoons in high threat trials consume less corn and sardines.

Because of the difficulty in identifying individual raccoons, we made no effort to test for differences in the number of raccoons attending trials. In order to test the hypothesis that raccoons stay for shorter periods of time, we calculated raccoon attendance as total raccoon-min for each trial (1 raccoon-min = 1 raccoon present for 1 min). Raccoons were arbitrarily considered to have left the site if > 10 min separated photos. We also scored each raccoon photo for vigilance, where each raccoon in a head-up and alert posture was considered to be vigilant. We then divided the total number of vigilant raccoon photos by the total number of raccoon photos to calculate an average vigilance score for each trial. The morning after trials we reweighed the sardine can and visually estimated the amount of corn left in the pile with the same grid placed in the same position as the previous evening. We calculated the percent of corn and sardines consumed as a simple difference between pre- and post-trial measurements divided by the pre-trial measurements. We used general linear mixed models ( $\alpha = 0.05$ ; SAS proc mixed, SAS Institute, Cary, NC) to test the effect of treatment on raccoon-min, vigilance and the amount of corn and sardines consumed by holding treatment as a fixed effect and season and site as random effects. We defined seasons in the same manner as for arena trials. Only feeding trials with  $\geq 1$  raccoon present were used in the analysis of food consumption.

All procedures were approved by the Clemson University Institutional Animal Care and Use Committee (AUP2011-016) and the USDA-WS-National Wildlife

Research Center (QA1864). Work in South Carolina was conducted under a South Carolina Department of Natural Resources Scientific Collecting Permit (permit G-11-08).

## **RESULTS**

### **Arena trials**

Arena trials were conducted from Nov 2011 to Feb 2013. Three raccoons escaped low threat level treatments, leaving a total of 3 high threat, 7 intermediate threat, and 5 low threat arena trials for analysis. Raccoons groomed less ( $F_{2,43} = 7.75$ ,  $p = 0.0013$ ) in high and intermediate threat trials compared to low threat trials and travelled more in high threat trials than intermediate or low threat trials ( $F_{2,43} = 4.51$ ,  $p = 0.0167$ ; Fig. 3.2).

Raccoons did not change the amount of time spent exploring the arena, being vigilant, hiding in den boxes, resting in the open, or foraging based on threat level (Table 3.3).

Regardless of threat level, raccoons spent more time on average travelling at the beginning of trials than later in trials ( $F_{3,43} = 3.43$ ,  $p = 0.0027$ ), but did not change time spent in any other behavior as each trial progressed. There were no differences in raccoon location inside the arena, either with respect to the treatment itself or between time spent on the ground or hanging on the arena (Table 3.2, Fig. 3.3).

### **Feeding trials**

A total of 44 feeding trials were conducted from Nov 2011 to Mar 2013 (Table 3.4).

Treatment had a weak effect on raccoon attendance ( $F_{2,30} = 3.25$ ,  $p = 0.053$ ) with intermediate treatments having moderately higher attendance rates than low or high treatments (Table 3.4). Treatment had no effect on raccoon vigilance ( $F_{2,17} = 1.82$ ,  $p =$

0.19), percent corn consumed ( $F_{2,13} = 0.31$ ,  $p = 0.74$ ), or percent sardines consumed ( $F_{2,13} = 0.37$ ,  $p = 0.69$ ).

## **DISCUSSION**

Taken on their own, results from arena trials might indicate weak evidence of increasing APRs in raccoons exposed to increasing levels of threat. Arena trials supported only one of our initial hypotheses: raccoons in high and intermediate threat treatments groomed less often than those in low threat trials. Decreased time spent in non-defensive behaviors such as grooming constitutes a typical mammalian response to predator odors (Apfelbach et al. 2005). However, if raccoons were decreasing non-defensive behaviors in the arena during intermediate or high threat trials, it follows that there would also be differences in vigilance or the amount of time spent in dens, which did not occur. Although we did not specifically hypothesize about treatment effects on raccoon travelling inside arenas, raccoons in high threat trials did travel more than raccoons in other trials. Increased travelling is not a typical response to predator odor, as prey are typically less likely to move in predator odor experiments (Apfelbach et al. 2005). However, increased travelling inside high threat arenas could still indicate additional stress (e.g., stereotyped pacing behaviors, Mason 1991), or could simply result from raccoon attempts to leave the treatment area. Stress responses of raccoons in the unnatural environments of arena trials may also have obscured other differences in behaviors. Raccoons travelled more often at the beginning of the trials than at the end, potentially indicating some degree of acclimation to the arena setting, the scat treatment, or both.

Treatment had a weak effect on raccoon attendance in the more natural setting of feeding trials, but not in the way we predicted: raccoon attendance was moderately higher in intermediate threat treatments compared to low threat or high threat treatments. Because sites were used multiple times, it is possible that raccoons became habituated to treatments over time (Apfelbach et al. 2005), although this was not specifically addressed in our study. Coyotes are present on the Clemson Experimental Forest, which could mean that raccoons are already habituated to coyote scent and simply cannot detect conspecifics in coyote diet.

Many different prey species alter their behavior in the presence of different types of odors, including decreases in foraging (e.g., Boag and Mlotkiewicz 1994; Nolte et al. 1994; Grostal and Dicke 1999; Cox et al. 2010), decreases in attendance (Boag and Mlotkiewicz 1994), increases in flight behaviors (Parsons et al. 2007; King et al. 2008), lower activity levels (Wilson and Lefcort 1993; Pillay et al. 2003), and differences in site selection for foraging or nesting (Grostal and Dicke 1999; Parsons et al. 2007; Eichholz et al. 2012). Further, a wide variety of taxa are able to detect conspecifics in predator diet (e.g., Wilson and Lefcort 1993; Chivers et al. 1996; Pillay et al. 2003; Cox et al. 2010). It is unclear whether raccoons in this study are able to detect conspecifics in coyote diet and simply do not conform to our hypothesized APRs, or if raccoons cannot distinguish well between treatments. Olfaction may not be highly developed in raccoons, which heavily utilize their tactile senses when foraging (Gehrt 2003). Even if raccoons do recognize the scat treatments as coming from a potential predator, odors from scat may still only represent locations where a predator has once been, without necessarily giving

information on the current location of that predator (Pillay et al. 2003; Preisser et al. 2007). Raccoons may recognize the odor as coming from a potential predator, but may not choose to employ an APR unless the coyote is physically present at the time. Behavioral syndromes also could play a large role in individual raccoon responses to treatment (Sih et al. 2010). Larger sample sizes for arena trials might average out some of the effects of syndromes and make differences between treatments easier to detect. Further, prey responses to predator presence can vary widely between prey species (Wirsing et al. 2010) and between habitats with different likelihoods of detection or capture (Lima and Dill 1990), some of which would not be predicted as typical vigilance or space use responses in behavioral experiments (e.g., predator mobbing).

Experimental tests of interference competition between predator species often make the assumption that competitors within a single guild will exhibit the same kinds of APRs as are commonly reported for predator-prey relationships. Prange and Gehrt (2007), for example, assume that if there is significant interference competition between coyotes and skunks (*Mephitis mephitis*), then skunks should avoid areas with high coyote activity (simulated by a coyote urine treatment). Skunks in their study did not avoid the coyote urine treatments, and this lack of response was taken as a line of evidence against strong interference competition between the two predators. Similarly, Scheinin et al. (2006) and Vanak et al. (2009) both used a urine treatment to investigate potential interference competition between canid species. Both authors found a lack of APR when the hypothesized defender species was exposed to the aggressor species urine, which they could have used as evidence against strong competition between the species. However,



both authors found decreased foraging of the defender species in the presence of a live aggressor in a kennel, and both authors concluded there was strong evidence for interference competition in those cases.

In our study, a comparison of APRs between just the low and intermediate threat treatments would be comparable to most experimental tests of interference competition (Table 3.1). We found some evidence for APRs in arena trials, which taken alone could indicate some degree of competition between coyotes and raccoons. However, by manipulating coyote diet, we also compared APRs to a known relationship, where coyotes should represent a high degree of threat to raccoons. In both trial types, APRs did not increase in a predictable fashion across threat levels, which complicates our presumed interpretation of interspecific competition between the species. Raccoons in arena trials were not more vigilant when presented with semiochemicals from a known predator, nor did they hide more, were less active, or avoid the source of the odor. Any of these APRs alone could have been used as the basis for a behavioral test of interference competition. In feeding trials, raccoons actually increased attendance at intermediate threat treatments, which taken alone would suggest that raccoons are attracted to coyote scent.

The degree of interference competition between coyotes and other mesopredators such as raccoons remains highly speculated (e.g. Gehrt and Clark 2003; Gehrt and Prange 2007; Prange and Gehrt 2007), and intraguild competition can often be difficult to demonstrate without the use of supporting behavioral data. More direct studies showing how species respond to one another on the population level can be difficult to fund,

logistically difficult, or in the case of population correlation studies, can produce results that are easily misinterpreted (Cove et al. 2012). While behavioral studies often produce results that do indicate interference competition when one species affects the behavior of another, this study makes it clear that the absence of a behavioral response should not be automatically taken for a lack of competition between the two.

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**Table 3.1**  
**Examples of experimental studies using behavioral responses to infer interference competition**

Citation	Defender species	Aggressor species	Avoidance stimulus	Competition hypotheses supported?
Gipson et al. 2003	Raccoon ( <i>Procyon lotor</i> ) Virginia opossum ( <i>Didelphis virginianus</i> )	Bobcat ( <i>Felis rufus</i> ) Coyote ( <i>Canis latrans</i> )	Feces	No
Scheinin et al. 2006	Red fox ( <i>Vulpes vulpes</i> )	Golden jackal ( <i>Canis aureus</i> )	Urine Mount Live animal	No No Yes
Prange and Gehrt 2007	Striped skunk ( <i>Mephitis mephitis</i> )	Coyote ( <i>Canis latrans</i> )	Urine	No
Hunter 2008	Mammalian mesopredators	Striped skunk ( <i>Mephitis mephitis</i> )	Mount	Conditional on skunk density
Harrington et al. 2009	American mink ( <i>Mustela vison</i> )	European otter ( <i>Lutra lutra</i> ) Polecat ( <i>Mustela putorius</i> )	Anal gland secretions	Unclear
Vanak et al. 2009	Indian fox ( <i>Vulpes bengalensis</i> )	Domestic dog ( <i>Canis familiaris</i> )	Urine Live animal	No Yes
Etheredge 2013 (Ch2)	Raccoon ( <i>Procyon lotor</i> )	Coyote ( <i>Canis latrans</i> )	Urine	No



**Table 3.2**  
**Mutually exclusive behaviors and mutually exclusive locations used in arena trials**

Category	Definition
<b>Behavior</b>	
Exploration	Pawing or mouthing arena, dens, or squeeze box, either while stationary or moving; digging
Foraging	Stationary and eating sardines or handling sardine dish
Grooming	Stationary and licking or pawing self
In den	> 1/2 body inside either den box
Resting	Stationary and not alert, either lying on ground outside of den boxes or hanging and not vigilant on enclosure
Travel	Moving around arena without investigating enclosure components
Vigilant	Stationary and alert with head up for >3 s
<b>Location</b>	
Near	Head located in the half of the arena with treatments
Far	Head located in the half of the arena without treatment
Hang	At least three paws on arena walls; hanging arena top
Ground	At least two feet on ground or den box

**Table 3.3****Type III tests of fixed effects for coyote scat treatments and raccoon time budgets in arena trials**

Effect	Explore		Travel		Vigilance		Groom		Den		Rest		Forage	
	F	p	F	p	F	p	F	p	F	p	F	p	F	p
treat	0.08	0.9271	4.51	0.0167	2.46	0.0976	7.75	0.0013	1.38	0.2617	1.01	0.3741	0.49	0.6171
bin	0.39	0.7577	5.52	0.0027	1.76	0.1688	0.28	0.8382	0.16	0.9227	0.94	0.4273	0.34	0.7938
treat*bin	0.88	0.5184	0.29	0.9361	1.35	0.2558	0.28	0.942	0.64	0.6981	0.38	0.8893	1.49	0.2043

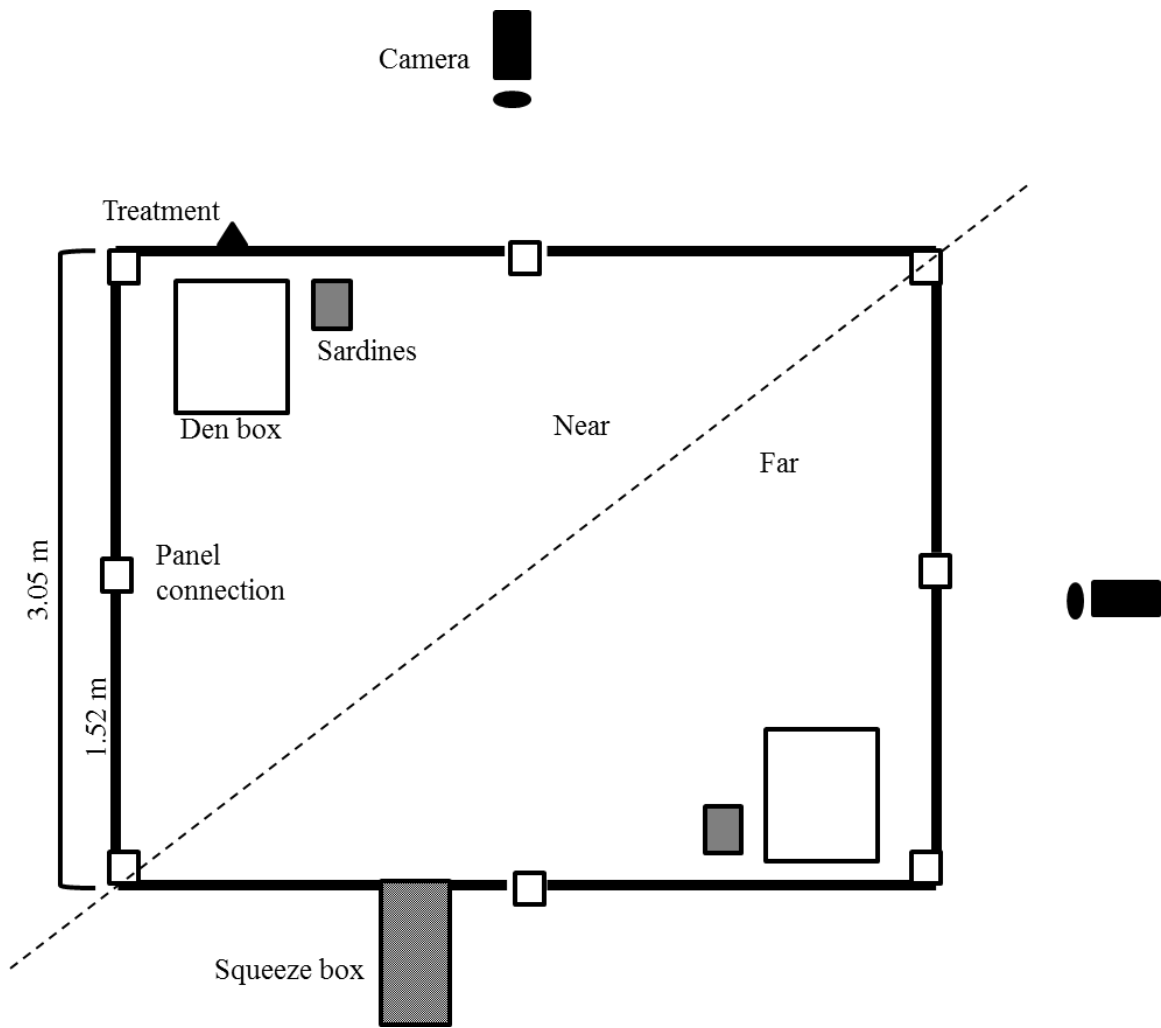
Effect	Near		Far		Ground		Hang	
	F	p	F	p	F	p	F	p
treat	0.05	0.9526	0.05	0.9526	0.9	0.4167	0.9	0.4167
bin	0.9	0.4488	0.9	0.4488	1.04	0.3864	1.04	0.3864
treat*bin	0.45	0.8428	0.45	0.8428	1.51	0.2007	1.51	0.2007

Arena trials lasted 60 min. Treat refers to coyote scat treatment (high, intermediate, or low threat). Near and far indicate raccoon location with relation to the treatment. Ground indicates time spent on the arena ground while hanging indicates time spent hanging on arena walls. Bin refers to 1 of 4 consecutive 15-min periods.

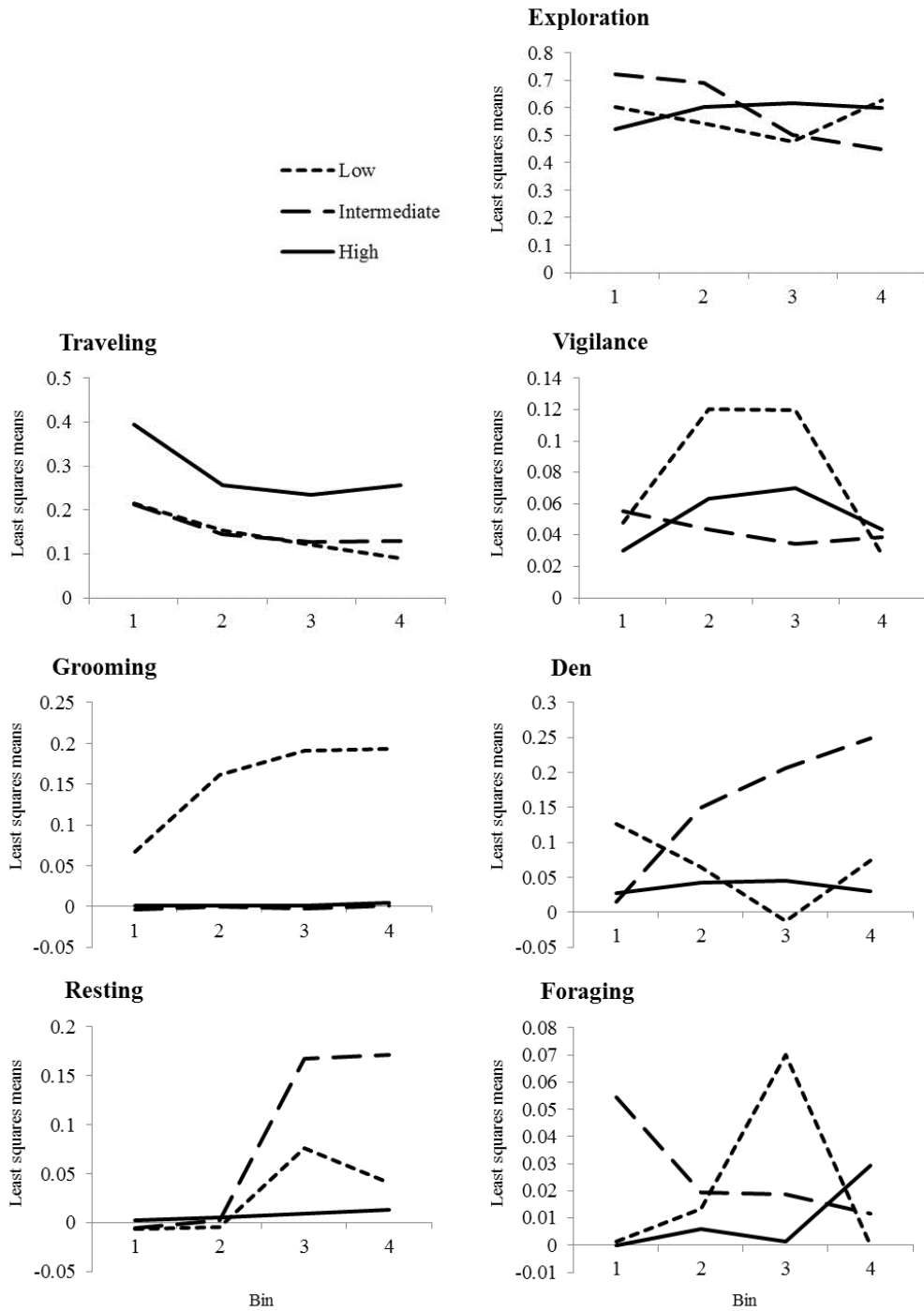
**Table 3.4****Attendance, vigilance and food consumption of raccoons under different degrees of threat**

Treatment	Total trials	Raccoon trials	Attendance min	Vigilance % photos	Corn consumed % difference	Sardines consumed % difference
Blank	14	10	17.73 ± 7.81	53.07 ± 3.73	24.10 ± 11.03	90.00 ± 3.29
Low	15	8	46.64 ± 22.17	47.69 ± 7.25	18.46 ± 8.96	88.88 ± 3.69
High	15	10	36.60 ± 12.51	61.26 ± 4.63	25.17 ± 9.21	84.63 ± 8.83

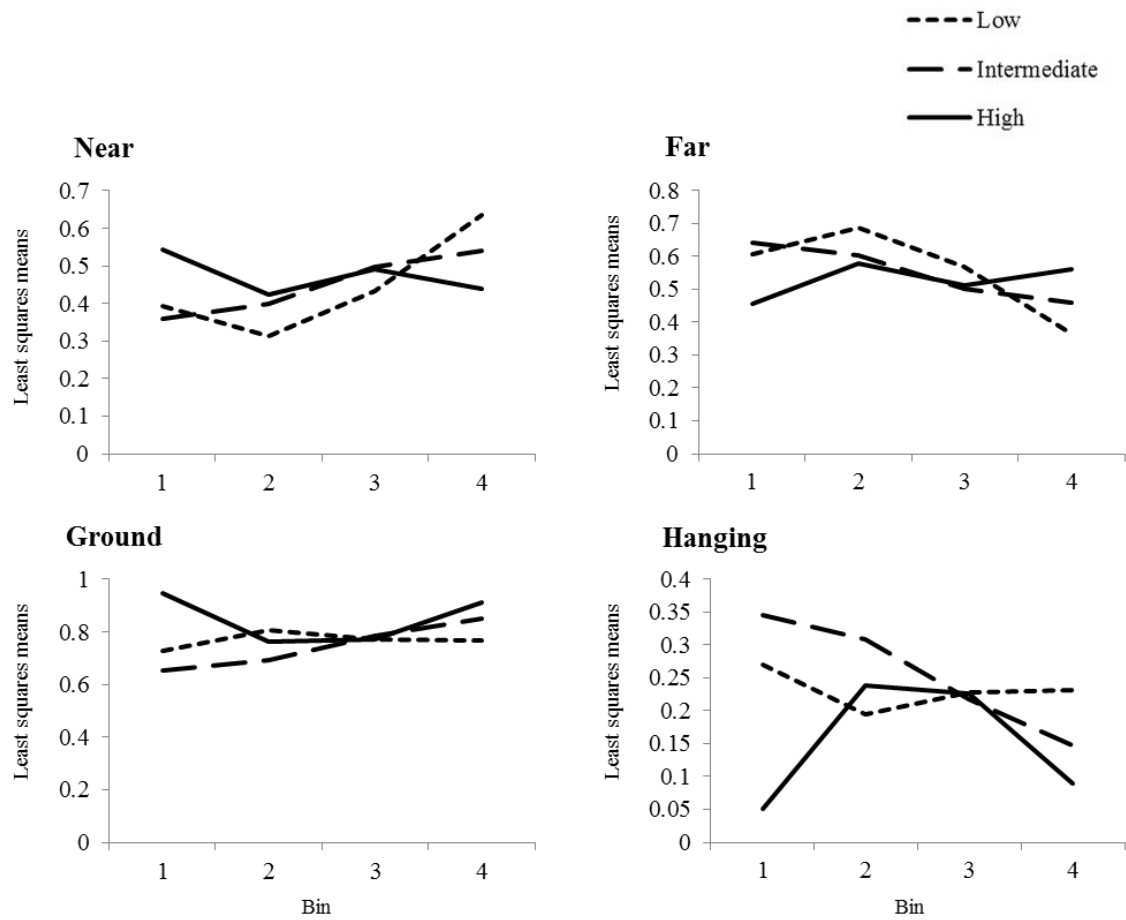
Treatments represent coyote scat treatments where high and low indicates scat from coyotes fed a high and low raccoon diet respectively and blank indicates a no scat treatment. Raccoon trials gives the number of trials where raccoons were present in photos. Attendance is calculated as total raccoon minutes/raccoon trials and vigilance is calculated as the # of head up raccoon photos/total # of raccoon photos. Corn consumed and sardines consumed represented the % difference in the amount of either food left after trials/raccoon trials.



**Figure 3.1**  
 Arena configuration for testing raccoon response to coyote scat treatments.



**Figure 3.2**  
Least squares means estimates for treatment\*bin effects on raccoon behavior in arena trials. Bin refers to 1 of 4 consecutive 15-min periods.



**Figure 3.3**

Least squares means estimates for treatment\*bin effects on raccoon location inside arenas during arena trials. Near and far indicate raccoon location with relation to the treatment. Ground indicates time spent on the arena ground while hanging indicates time spent hanging on arena walls. Bin refers to 1 of 4 consecutive 15-min periods.

## CHAPTER FOUR

### SAVE A DEER, KILL A COYOTE? SEMANTICS, ECOLOGY AND MANAGEMENT IN THE SOUTHEASTERN UNITED STATES

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**ABSTRACT** Coyotes may well represent the single largest challenge to wildlife managers throughout the southeastern United States. Southeastern coyotes are larger than their western cousins, and may have a variety of different impacts on the systems in which they reside. In this paper we review what is currently known about the ecology of coyotes in the Southeast, as well as explore the potential impacts of semantics involving coyote management. We also attempt to dispel rumors related to the reasons for coyote range expansion and suggest 19 different lines of inquiry to focus future research on the ecology and impacts of coyotes throughout the region.

#### INTRODUCTION

Coyotes (*Canis latrans*) are easily one of the best studied animals in North America, due in large part to rapidly expanding populations and increasingly common cases of human-coyote conflict. While more and more studies have focused on coyote ecology east of the Mississippi River, there is still a paucity of research on southeastern coyotes. In a recent review of literature, Mastro et al. (2012) identified over 360 documents relating to eastern

coyote ecology. Only 88 of those studies related research conducted in the southeastern United States, while 55 of those southeastern studies are only available as theses, dissertations, conference proceedings, or other grey literature. Here, we present a synopsis of what is currently known about southeastern coyotes and suggest areas to better focus future research efforts. For the purposes of simplicity, we follow Hill et al.'s (1987) definition of the Southeast, including Louisiana and Arkansas eastward and Kentucky, West Virginia and Maryland southward.

### **RANGE EXPANSION**

As our knowledge of coyotes outside of their native range expands, differences between eastern and western coyotes are increasingly documented. Eastern coyotes are larger than their western cousins (Way 2007a, Kennedy et al. 1986) due to interbreeding with eastern wolves (*Canis lycaon*) and a diverse and abundant food supply (Chambers 2010, Way et al. 2010, Larivière and Crête 1993, Thurber and Peterson 1991, Schmitz and Lavigne 1987, Schmitz and Kolenosky 1985). Northeastern coyotes have benefited the most from hybridization with wolves and are the largest extant coyote (Way 2007a). As northern coyotes expanded their range southward into Indiana, Ohio, Pennsylvania and New Jersey, western coyotes pushed eastward into Louisiana, Arkansas and Missouri and on from there all the way to the Atlantic Coast (Parker 1995). Southeastern coyotes today are the result of multiple lines of range expansion, and represent a genetic mixing of smaller coyotes from the west with larger animals from the north (Dennis 2010, Peppers 1994, Lydeard and Kennedy 1988). Eastern coyotes are also considered slightly



less opportunistic than western animals and are more likely to form social groups comprising non-family members (Hilton 1978).

### **By the Hand of Man?**

Attempts to understand the root causes of coyote range expansion into the Southeast has led to the prevalence of three basic theories: 1) coyotes exist in the Southeast due to specific introduction events; 2) coyotes moved into the Southeast after the extirpation of red wolves (*Canis rufus*), which formally prevented coyote advances; and 3) coyote range expansion was due almost entirely to anthropogenic habitat conversion from a primarily forested to a primarily agrarian landscape. Whether intentional releases to establish huntable populations or accidental escapes from fox pen operations, there have been 20 documented releases of coyotes across the Southeast since 1925 (Hill et al. 1987). This version of coyote range expansion is so well known by the public in some areas that it presents a common problem for some state agencies which are battling rumors that coyotes were stocked by agency biologists to control white-tailed deer (*Odocoileus virginianus*) populations (see Georgia and South Carolina in Table 4.1).

While it makes intuitive sense that so many coyote introductions across the region would be responsible for establishing permanent coyote populations, the majority of these introductions were likely not large enough to establish viable populations in the long term (Parker 1995). The idea that red wolves may have been preventing coyote expansion east of the Mississippi river is also appealing, given the fact that wolves kill coyotes on a regular basis and that coyotes are often excluded from wolf home ranges (Levi and Wilmers 2012). However, coyotes in their native range existed with both grey wolves

(*Canis lupus*) and Mexican wolves (*Canis lupus baileyi*; Parker 1995). Coyotes have also successfully invaded other areas with healthy grey wolf populations (Parker 1995).

Coyote colonization of the Southeast, similar to their range expansion into the Northeast, is strongly correlated with habitat conversion (Fener et al. 2005, Parker 1995). Prior to European colonization, eastern North America was covered with dense hardwood forests. As Europeans moved eastward, forests were cleared and converted to family farms. Some of these farms were subsequently abandoned, providing primary successional habitat, further fragmenting the landscape and providing optimal habitat for coyotes (Fener et al. 2005, Parker 1995).

## **IMPACTS ON NATIVE SYSTEMS**

### **Game Species**

Potential impacts of coyotes on white-tailed deer and other game species are arguably one of the most politically contentious issues facing wildlife managers throughout the region. While impacts of coyote on turkey (*Meleagris gallopavo*), bobwhite quail (*Colinus virginianus*) and other game birds appear to be minimal (Staller et al. 2005, Wagner and Hill 1994, Grogan 1996, Gabor 1993, Hoerath 1990), potential impacts reported for white-tailed deer vary widely from study to study. Northeastern coyotes are larger-bodied than those in southern populations and are significant predators of adult and neonate white-tailed deer (Lavigne 1992, Messier et al. 1986). Northeastern coyotes take advantage of harsh winters, targeting healthy adult deer outside winter yarding areas (Patterson and Messier 2003, 2000; Messier and Barrette 1985) and potentially contributing to additive mortality in areas with lower deer densities (Patterson and

Messier 2000). While southeastern coyotes are more likely scavengers of adult deer carcasses (Crimmins et al. 2012, Bixel 1995), coyote predation on neonates is commonly reported (Albers 2012, Kilgo et al. 2012, Schrecengost et al. 2008, Hoerath 1990, Blanton and Hill 1989). Predation of neonates can be at high enough levels to limit deer populations in some areas (Kilgo et al. 2012) and has been implicated in the state-wide decline of white-tailed deer populations in South Carolina (Kilgo et al. 2010). Blanton and Hill (1989) documented higher rates of predation in areas with higher deer densities than in areas with fewer deer at wildlife management areas across the Southeast, which could serve to control overabundant deer populations. This suppression of deer populations in exurban or agricultural areas could be viewed as a welcome benefit by some managers (Morey 2004), and might contribute to overall deer herd health by reducing deer density (Maehr et al. 2005, Hoerath 1990). More often, however, stakeholder groups identify coyotes as a nonnative predator that is adversely affecting native wildlife populations (Main et al. 2002, Jones 1987). Like most large predator species, coyotes are often viewed as competing with humans for hunting opportunities (Howze 2009, VanGlider et al. 2009). Kilgo et al. (2012, 2010) linked coyote predation of white-tailed deer neonates to lower hunter harvest of deer and emphasized the need for wildlife managers throughout the Southeast to begin seriously considering coyotes as an additional source of mortality for white-tailed deer populations.

Southeastern coyotes also have the potential to impact native furbearer species such as bobcats (*Lynx rufus*), red fox (*Vulpes vulpes*), and grey fox (*Urocyon cinereoargenteus*). A handful of studies have investigated the effects of interference

competition between coyotes and other mammalian predators, although no real consensus has been reached on how coyotes may be impacting the mammalian predator community. Coyote visitation at scent stations in Florida did not impact visitations by red fox or bobcats (Main et al. 1999); however, coyote density may not have been large enough to influence competitor space use in that system. Chamberlain and Leopold (2001) found that grey foxes in Mississippi avoided core areas of use within coyote and bobcat home ranges. They also reported extensive overlap between home ranges and core areas of bobcats and coyotes, as opposed to Thornton et al. (2004) who reported non-overlapping core areas and only a small amount of dietary overlap between bobcats and coyotes in Florida. Crossett and Elliot (1991) likewise reported only a small degree of dietary overlap between coyotes and red foxes, but did not include information about coyote and fox space use. These low levels of dietary overlap and lack of extreme spatial avoidance could be due to the diversity in the prey base of most Southeastern systems (Litvaitis 1992). Grey fox also use more wooded areas than coyotes and may be able to avoid direct predation by climbing trees (Wooding 1984). Even though a multitude of western and northern studies have indicated negative correlations between populations of coyotes and other furbearers (e.g. Gosselink et al. 2004, Henke and Bryant 1999, Litvaitis and Harrison 1989, Robinson 1961), we were unable to find any publications reporting population level effects between coyotes and bobcats, grey fox, or red fox in the Southeast.

To further our understanding of coyote impacts on game species we suggest researchers concentrate their efforts on the following questions:

- 1) What, if any, are the best predictors of heavy coyote utilization of white-tailed deer fawns in different habitat types across the region?
- 2) What is the potential cost:benefit ratio for coyote control to increase white-tailed deer recruitment in areas managed for hunting opportunities?
- 3) How do coyote population increases relate to other furbearer population trends on a region wide basis?

### **Nongame Species**

Published impacts of coyotes on threatened and endangered species are particularly lacking for the southeast region, with the notable exception of coyote hybridization with red wolves being the largest single threat to red wolf restoration (e.g. Roth et al. 2008, Fredrickson and Hedrick 2006). Coyote impacts on loggerhead sea turtle (*Caretta caretta*) nesting success are a significant conservation challenge in areas where coyotes have colonized beaches along the Atlantic Ocean and Gulf of Mexico. For instance, coyotes first colonized an island off the coast of South Carolina in 2006 and destroyed 30% of loggerhead turtle nests in the same year (Eskew 2012). Coyote depredation on that site was particularly devastating because most depredation occurred the same night the nest was laid, before traditional nest monitoring and protection efforts took place the next morning. Depredation rates continued to increase in the following years until an effective management strategy was developed in 2010 which combined targeted control of coyotes on beaches with a shift from morning monitoring to overnight patrols to protect nests before coyotes located them (Eskew 2012). This shift in management reduced coyote depredation of turtle nests from 52% of nests to 2.7% in 2011. Coyote

depredation of sea turtle nests along Cape San Blas, Florida was also fairly common from 1994-1997 (20% - 40% of nests depredated each year) until an aggressive predator control program at Eglin Air Force Base virtually eliminated coyote depredation in 1998 (Lamont et al. 2012).

Other potential impacts on nongame species are less well documented and sometimes completely speculative. For example, one coyote scat in northwestern Florida contained remains of a 2-3 yr old gopher tortoise (*Gopherus polyphemus*; Moore et al. 2006). Coyotes in Mexico were reported to hunt adult terrapins in ponds (Minckley 1966), which could also occur in the southeastern United States. Some authors have reported low occurrences of songbird remains in coyote scat (Hoerath 1990, Hall 1979, Michaelson 1975, Gipson 1974), although most studies report these occurrences only as unidentified passiformes. Hall (1979) did identify ten different songbird species in coyote scat in Louisiana, none of which were considered a high priority species for conservation and all of which occurred in less than 1% of scats. Etheredge (chapter 1, this document) reported 42-60% of coyote scat samples containing bird remains on two islands off the coast of South Carolina. While none of those samples contained flight feathers which might have allowed for identification of species, the lack of flight feathers along with a high abundance of wading birds in the study area might indicate the potential for coyote impacts on wading birds in that system.

To further our understanding of coyote impacts on nongame species we suggest researchers concentrate their efforts on the following questions:

- 4) What are the best predictors of coyote depredation of loggerhead turtle nests?  
Are there beaches with coyotes but no coyote depredation of nests? Are problem coyotes typically related, or is any coyote on the beach likely to become a problem?
- 5) Are coyote impacts on sea turtle nests larger in magnitude than coyote impacts on terrapin or tortoise nests?
- 6) What are the potential impacts of coyotes on wading bird populations and space use?

### **Community Dynamics and Indirect Effects**

Understanding how coyotes might be changing community dynamics in southeastern systems is one of the most complicated questions facing wildlife biologists; it is also the one question on which the fewest southeastern studies have been directed. No published studies to date have specifically addressed how coyotes in the Southeast might be indirectly affecting ground-nesting prey populations by suppressing smaller mesopredators such as red fox, raccoons (*Procyon lotor*), striped skunks (*Mephitis mephitis*), Virginia opossums (*Didelphis virginiana*), nine-banded armadillos (*Dasypus novemcinctus*), and feral cats (*Felias catus*). Studies in other parts of the United States indicate the ability of coyotes to act as a “strongly interacting species” in plant and animal community organization (Soulé et al. 2005). In particular, Henke and Bryant (1999) demonstrated a lower diversity of rodent species in areas of intense coyote removal compared to areas without removal. Similarly, Crooks and Soulé (1999) reported increased song bird diversity and abundance in areas where coyotes are present

as opposed to areas without coyotes. Even so, the coyote potential to control mesopredator populations is likely site specific and is a contentious subject among wildlife biologists (Cove et al. 2012, Gehrt and Clark 2003).

To further our understanding of coyote impacts on community dynamics we suggest researchers concentrate their efforts on the following questions:

- 7) What are the potential ecosystem services coyotes may provide?
- 8) What is the potential for coyotes to indirectly benefit ground nesting prey?
- 9) Are coyotes able to influence plant community composition by controlling white-tailed deer and other herbivores like lagomorphs?
- 10) Do coyotes increase the diversity of small mammal communities in the Southeast?

## **MANAGEMENT**

### **State Agencies**

On their websites, southeastern state wildlife agencies present information related to coyote range expansion and associated impacts on native wildlife in vastly different ways (Table 4.1). Coyotes are no longer considered a new invader of states bordering the native range of coyotes such as Louisiana and Arkansas, which have had established coyote populations since the 1930's (Parker 1995). These states tend not to present any information on range expansion. Most states avoid calling coyotes either native or nonnative, although Florida and Tennessee list "natural range expansion" as the reason for coyote presence in their state, while Alabama lists coyotes under a native mammals heading. Most states provide some amount of information relating to basic elements of



coyote ecology and natural history, such as diet, body size and coloration and track identification, although the focus and interpretation of this information varies widely from state to state. For example, Kentucky and Maryland emphasize coyote depredation of livestock, with Louisiana going on to label coyotes “outlaw quadrupeds,” along with feral hogs (*Sus scrofa*). Similarly, South Carolina is specifically enlisting the help of hunters to remove coyotes to help save deer populations (Fig. 4.1). This is contrasted with Georgia and North Carolina, which emphasize the coyote’s misunderstood nature and the importance of coyotes in ecosystems. West Virginia also specifically advises that there is no need to control coyotes to benefit other wildlife populations.

To further our understanding of how state agencies may influence region-wide coyote management we suggest researchers concentrate their efforts on the following questions:

- 11) How does biological information provided by state agencies shape public opinion in their states? Or, to what extent is the information provided by agencies a reflection of current public opinion in that state?

### **Managing for Native Systems**

An implicit goal of many wildlife agencies is to promote healthy populations of native wildlife in accordance with both the ecological and cultural carrying capacities of the systems where they are found. While promoting native wildlife makes for good agency mission statements, using such broad language rarely makes for easy interpretation with on-the-ground management strategies. After economic considerations, a species’ status as native or nonnative can determine whether that species will be managed for or against

in accordance with the goals of a particular property (Byers et al. 2002). But which species qualify as native? A variety of definitions for the basic vocabulary of the field of invasion biology make interpreting agency policy difficult at best (Shrader-Frechette 2001).

While it is certainly possible that a lack of red wolves and remnants of introduced coyote populations may have aided the range expansion of coyotes into the Southeast, the real implications of the root causes of colonization may be more important politically than biologically. It is much easier to call a species “introduced” when they exist in a new area solely due to the physical translocation of individuals, whereas considering coyote range expansion a natural process caused entirely by habitat conversion could lead to an acceptance of coyotes as a native species. In this respect, range expansions present special challenges for wildlife biologists attempting to manage native wildlife populations. Classifying an expansion as “natural” when so many systems are affected by anthropogenic landscape fragmentation and climate change seems a nearly impossible task. It is likewise tempting to explain southeastern coyote ecology in terms of “natural” red wolf impacts on southern systems previous to the extirpation of wolves around the turn of the twentieth century. Several authors invoke red wolf impacts on white-tailed deer populations when explaining coyote control of deer (e.g. Ballard et al. 1999), suggesting that coyotes may be able to fill the niche left by wolves. Understanding the previous impacts of red wolves or colonizing coyote populations on deer are both also complicated by the compounding effects of land-use changes, as the same agricultural conversion which favored coyotes likely also favored deer (Kilgo et al. 2010).

To further our understanding of how coyotes might fill the niche of red wolves we suggest researchers concentrate their efforts on the following questions:

12) How similar are coyote and red wolf diets in areas where their ranges overlap?

13) Do white-tailed deer respond differently to the presence of coyotes and the presence of wolves?

14) What were the historic impacts of wolves on southeastern ecosystems?

### **Coyotes and Livestock**

Just as coyotes in their native range, southeastern coyotes can be significant predators of cattle, sheep, goats, domestic swine, poultry, and agricultural crops such as watermelon (Houben 2004, Lowney et al. 1997, Jones 1987, Gipson 1975). As coyotes have grown more common throughout the region, producers have expressed growing concerns about coyote depredation (Armstrong and Walters 1995, Philipp and Armstrong 1994, Philipp and Armstrong 1993), and have increasingly called for bounties (Jones 1987) as well as more research on coyote-livestock depredation (Main et al. 2002). While bounty systems are not recognized as effective tools for the prevention of livestock depredation (Gélinas 1980), model programs for the control of coyote damage in the Southeast emphasize a combination of lethal and nonlethal methods (Houben et al. 2004, Lowney et al. 1997). In Virginia, state agencies cooperating with the United States Department of Agriculture-Animal and Plant Health Inspection Service-Wildlife Services (USDA-APHIS-WS) and local producer groups to increase education about coyote damage and increase the popularity of guard dogs (Lowney et al. 1997). These efforts, in combination with the legal use of select toxicants such as M-44's and Livestock Protection Collars decreased

coyote depredation of sheep in Virginia by 74% in the first 5 years of the program (Lowney et al. 1997). A similar program in West Virginia also utilizes select toxicants by USDA-APHIS-WS personnel and also includes a cost-sharing program for the purchase of guard dogs (Houben et al. 2004). In both of these state programs, preventative lethal control is used only in areas with a history of livestock depredation, along with corrective control which attempts to remove problem animals once depredation has occurred (Houben et al. 2004, Lowney et al. 1997).

To further our understanding of coyote impacts on livestock and agricultural production we suggest researchers concentrate their efforts on the following questions:

- 15) What, if any, are the predictors of coyote depredation of livestock and crops in the Southeast?
- 16) What are the most effective methods for mitigating current damage in the Southeast, and what, if any, are the current social or legal barriers to the use of those methods?
- 17) What are the most effective methods for preventing damage in the Southeast, and what, if any, are the current social or legal barriers to the use of those methods?

### **Coyotes and People**

Human-coyote conflicts are increasingly becoming a serious concern in urban areas (Curtis et al. 2007). While a variety of studies throughout the United States and Canada have reported extensively on the ecology of urban coyote populations, relatively few studies have focused on the urban or suburban populations in the Southeast. For

example, in a recent review of coyote attacks on humans, White and Gehrt (2009) report less than five coyote attacks on humans in southeastern states. Of all reported attacks, 37% were deemed to be predatory in nature (mostly targeting children), 22% were investigatory, while rabid animals, human protection of pets, or defensive action on the part of the coyote were implicated only in a minority of attacks (<10% each; White and Gehrt, 2009). The majority of these attacks most likely result from coyotes becoming habituated to humans in areas where they are fed (Gehrt 2009). Often urban residents are completely unaware of coyotes in their communities (Billodeaux 2007), as coyotes in most cases avoid areas of heavy human use (Page 2010, Gehrt 2007) and become strictly nocturnal in landscapes dominated by human activity (Jantz 2011, Page 2010, Morey 2004, Dumond et al. 2001). However, old or ill individuals have been documented using human structures such as overturned boats or docks in suburban areas for cover (Way 2009).

Public education may be the most important tool for mitigating human-coyote conflict in the Southeast (Way 2007b). Even so, it is important for state agencies and education campaigns to realize the effect that language may have on human acceptance of coyotes, as the public is likely to adopt the tone of the education programs provided to them (Draheim et al. 2011, Draheim 2007). While control options for coyotes vary widely from state to state based on local legislation, extreme intolerance for coyote damage (Philipp and Armstrong 1994) and a public disapproval of coyotes in general (Billodeaux 2007) seem to translate to more control options available in southern states as opposed to northern ones. For example, leg-hold traps are not legal in Massachusetts,

leaving only inefficient box traps as a tool for animal control officers (Way et al. 2002). In New York, public disapproval prevented the passage of legislation that would have allowed year-round hunting of coyotes in 1990 (Inslerman 1991).

To further our understanding of the ecology of urban coyote and the mitigation of human-coyote conflict we suggest researchers concentrate their efforts on the following questions:

18) What, if any, are the predictors of human-coyote conflict in the Southeast?

19) How effective are educational programs at changing human behavior and preventing conflict? Similarly, how effective are educational programs at preventing the need for lethal coyote control?

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**Table 4.1.** Information gathered from southeastern state wildlife agency websites concerning coyote ecology and management. All websites were accessed from 5 May 2013 to 20 May 2013.

<b>State</b>	<b>Agency</b>	<b>Range expansion information</b>	<b>Other information</b>
Alabama	Department of Conservation and Natural Resources	Range expansion from the west; includes coyotes as a native species	Very little additional information
Arkansas	Game and Fish Commission	No information	Only life history information
Florida	Fish and Wildlife Service Commission	Introduced and natural range expansion	Coyotes are not a threat to human safety; Main emphasis on coyote biology
Georgia	Department of Natural Resources	Coyotes were not stocked by the agency	Coyotes are largely misunderstood; Main emphasis on coyote biology
Kentucky	Department of Fish and Wildlife Resources	Range expansion from the north and southwest	Limited information on biology; Emphasizes depredation on deer and livestock
Louisiana	Department of Wildlife and Fisheries	No information	No biology information; coyotes labeled as "outlaw quadrupeds"
Maryland	Department of Natural Resources	Due to extirpation of competitive predators	Extensive biology information provided; Focuses on negative impacts on native species, pets and livestock
Mississippi	Department of Wildlife, Fisheries, and Parks	No information	Trapping and hunting regulations only

**Table 4.1.** continued

<b>State</b>	<b>Agency</b>	<b>Range expansion information</b>	<b>Other information</b>
North Carolina	Wildlife Resources Commission	Primarily due to landscape change and wolf removal, but also releases	Coyotes are important parts of the ecosystem; Stresses coexistence
South Carolina	Department of Natural Resources	Releases and landscape change; coyotes were not stocked by the agency	Some biology but heavy emphasis on control; Save a Deer campaign
Tennessee	Wildlife Resources Agency	Decline of wolves, changes in habitat availability, natural range expansion	Comprehensive information on preventing conflicts with urban coyotes; Well-rounded biology and control information
Virginia	Department of Game and Inland Fisheries	Due to eastward migration and extirpation of larger predators	Some biology and emphasis on coyotes as a nuisance species
West Virginia	Division of Natural Resources	Due to migration, lack of predators, hybridization with dogs and wolves and large deer herds	Comprehensive biology information and details about coyote effects on deer and other wildlife; coyote control to alleviate predation on wildlife is unwarranted



**Figure 4.1.** Website promotion of a coyote control campaign initiated by the South Carolina Department of Natural Resources.