



## **Coyote diets in a longleaf pine ecosystem**

Authors: Cherry, Michael J., Turner, Kelsey L., Howze, M. Brent, Cohen, Bradley S., Conner, L. Mike, et al.

Source: Wildlife Biology, 22(2) : 64-70

Published By: Nordic Board for Wildlife Research

URL: <https://doi.org/10.2981/wlb.00144>

---

BioOne Complete ([complete.BioOne.org](https://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](https://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

## Coyote diets in a longleaf pine ecosystem

Michael J. Cherry, Kelsey L. Turner, M. Brent Howze, Bradley S. Cohen, L. Mike Conner and Robert J. Warren

M. J. Cherry (mcherry@jonesctr.org) and L. M. Conner, Joseph W. Jones Ecological Research Center, Wildlife Ecology Lab, 3988 Jones Center Drive, Newton, GA 39870, USA. – K. L. Turner, M. B. Howze, B. S. Cohen and R. J. Warren, Warnell School of Forestry and Natural Resources, Univ. of Georgia, 180 E Green Street, Athens, GA 30602-2152, USA

The ecological implications of coyote *Canis latrans* colonization of the eastern USA have drawn considerable interest from land managers and the general public. The ability to predict how these ecosystems, which have lacked larger predators for decades, would respond to the invasion of this highly adaptable species needs an understanding of coyote foraging behavior given local resource availability. Therefore, we examined the diet of coyotes in a longleaf pine *Pinus palustris* ecosystem from 2007–2012. We examined 673 coyote scats collected on the Joseph W. Jones Ecological Research Center in southwestern Georgia. We observed considerable seasonality in coyote use of rodents, white-tailed deer *Odocoileus virginianus*, rabbits and vegetation. Coyotes exploited anthropogenic food sources, particularly waste peanuts *Arachis hypogaea*, during the fall and winter when native soft mast was not available. Adult white-tailed deer were consumed during every month and was not limited to the pulse of carrion availability from hunter-harvested animals, suggesting the use of adult white-tailed deer may not be restricted to scavenging in this system. We found mesomammals, including armadillos *Dasypus novemcinctus*, raccoons *Procyon lotor*, Virginia opossums *Didelphis virginiana*, bobcats *Lynx rufus*, grey foxes *Urocyon cinereoargenteus* and striped skunks *Mephitis mephitis* in approximately 18% of coyote scats from January–August. On our site, and some adjacent properties, the use of predator trapping focused primarily on Virginia opossum, raccoon, coyote, bobcat and gray fox, to increase northern bobwhite *Colinus virginianus* production may have resulted in increased use of mesomammals through scavenging. We offer evidence that coyote colonization may alter food web dynamics in longleaf pine ecosystems through depredation of white-tailed deer and by influencing the mesomammal guild through direct predation and competition for rodents, rabbits, carrion and soft mast.

Predators can exert powerful influences on their prey via direct killing and by inducing antipredator responses (Creel and Christianson 2008). These antipredator responses have evolved through millennia. Novel predators, particularly those filling an extirpated niche, but whose behavior differs from the native predator, can have profound impacts on prey populations that do not share an evolutionary history (Salo et al. 2007, Sih et al. 2010).

The niche of the extirpated red wolf *Canis rufus* in the eastern USA has been partially filled by the coyote *Canis latrans* (Hill et al. 1987, Thurber and Peterson 1991, Gompper 2002). Unlike the more carnivorous red wolves, the omnivorous coyote shows great plasticity in foraging behavior both spatially and temporally (Chamberlain and Leopold 1999, Schrecengost et al. 2008, McVey et al. 2013). The colonization of coyotes into ecosystems of the eastern USA that have been functionally lacking non-anthropogenic, top-down regulation for decades has the potential to cause

considerable ecological change. Coyotes are an adaptable species capable of thriving in a wide array of habitats, and often interact with societal interests. For example, it has been suggested that coyotes can contribute to the emergence of Lyme disease (Levi et al. 2012), increase mammalian (Henke and Bryant 1999) and avian (Crooks and Soulé 1999) biodiversity, hinder endangered species conservation, decrease feral cat *Felis catus* populations (Crooks and Soulé 1999), increase duck nest success through exclusion of red fox *Vulpes vulpes* (Sovada et al. 1995), inflict agricultural damages (Berger 2006), attack human children (Carbyn 1989), induce trophic cascades by modifying herbivore abundance and behavior (Waser et al. 2014), and suppress white-tailed deer *Odocoileus virginianus* populations (Kilgo et al. 2012, Robinson et al. 2014, Chitwood et al. 2015). Though controversial, coyotes appear to be the largest predator native to North America compatible with the fragmented landscape of the eastern USA. Understanding their specific effects on ecosystems should thus be high priority for guiding conservation efforts.

Longleaf pine-wiregrass *Pinus palustris*–*Aristida beyrichiana* savannas of the southeastern USA are characterized by globally significant levels of biodiversity, with numerous

---

This work is licensed under a Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License (CC-BY-NC-ND) <<http://creativecommons.org/licenses/by-nc-nd/4.0/>>.

endemic flora and fauna species (Peet and Allard 1993, Mitchell et al. 2006). As many as 50 plant species can occur in a single square meter, with >1100 species on 11 000 ha (Drew et al. 1998, Kirkman et al. 2001), and many threatened and endangered species including the red-cockaded woodpecker *Picoides borealis* and gopher tortoise *Gopherus polyphemus* inhabit this ecosystem (Walters 1991, Allen et al. 2006, Mitchell et al. 2006). Since the extirpation of the red wolf and puma *Puma concolor*, the largest canid and felid species represented in the longleaf pine ecosystem have been the red fox and bobcat *Lynx rufus*, respectively. The addition of coyotes to this system likely increased the risk of predation for white-tailed deer, the largest herbivore in the system, to levels not experienced since the extirpation of large carnivores. Consequently, there has been considerable interest in the effects of coyotes on white-tailed deer populations in the southeastern USA (Kilgo et al. 2010). Because coyotes are omnivorous generalists, the availability of alternative food items may alleviate predation of white-tailed deer. In other systems alternative prey availability appears to reduce coyote use of white-tailed deer (Patterson and Messier 2000), but it is unknown if that is the case in diverse southeastern USA ecosystems. Understanding which alternative prey items may decrease the use of white-tailed deer would be of great interest to managers who aim to mitigate the effects of coyotes on ungulate populations.

Coyotes across the southeastern USA forage on an array of prey, driven by relative occurrence of food items and vegetation community succession (Andelt et al. 1987, Blanton and Hill 1989, Chamberlain and Leopold 1999, Schrecengost et al. 2008). In most southeastern USA ecosystems, this results in use of white-tailed deer, rodents, rabbits and seasonally available soft mast. Assessing the potential ecological effects of coyotes on an ecosystem as diverse as the longleaf pine-wiregrass savannas of the southeastern USA requires a thorough knowledge of their food habits; however, most coyote food habits studies have been conducted in the western USA. There have been relatively few publications on the diets of coyotes in the Southeast (Kilgo et al. 2010) and none in an ecosystem with such high biodiversity. Herein, we report the diets of coyotes in a longleaf pine-wiregrass ecosystem surrounded by center-pivot irrigated agriculture in hopes of characterizing the food habits of this generalist on an area with globally significant biodiversity.

## Study area

We conducted our study in southwestern Georgia at the Joseph W. Jones Ecological Research Center at Ichauway (Ichauway). Ichauway encompassed 11 736 ha in Baker County, Georgia, which is located in the Coastal Plain region (Boring 2001). Ichauway received an average of 137 cm of rainfall per year and experienced an average yearly maximum and minimum temperature of 25.8°C and 12.4°C, respectively. The property was bisected by Ichauwaynochaway Creek, and met its eastern bounds at the Flint River. The landscape surrounding Ichauway was dominated by agriculture. The site was actively managed with a low intensity fire on a bi-annual fire return interval resulting in a mixture of varying successional stages. Ichauway was bisected

by two state highways and included approximately 600 km of unpaved dirt roads on site. Deer vehicle collisions were extremely rare on site (i.e. <1 year<sup>-1</sup>) because of slow traveling speeds due to road conditions and a site wide speed limit of 40 km per hour. Deer vehicle collisions periodically occurred on state highways although data on the frequency are not available.

Ichauway included approximately 7250 ha of longleaf pine woodlands. Other forest types included slash *Pinus elliottii* and loblolly pine *P. taeda* forests, mixed pine and hardwood forests, lowland hardwood hammocks, oak barrens, and cypress-gum *Taxodium ascendens*-*Nyssa biflora* limesink ponds (Boring 2001). Approximately 10% (i.e. 120 ha) of the site was comprised of cultivated wildlife food plots and approximately 50% (i.e. 6000 ha) of the site was burned annually. Food plots that were planted in corn *Zea mays*, clover *Trifolium* spp., grain sorghum *Sorghum bicolor*, and wheat *Triticum aestivum* for game bird and white-tailed deer management (Joseph W. Jones Research Center 2011). Predator trapping occurred on Ichauway and some surrounding properties managed for northern bobwhite *Colinus virginianus*. The trapping program had been in place for several decades and annual removal rates were fairly consistent across years. On Ichauway, from 1998–2010 trappers removed and average of 111 Virginia opossums *Didelphis virginiana*, 111 raccoons *Procyon lotor*, 24 coyotes, 22 bobcats, 11 gray foxes *Urocyon cinereoargenteus*, two striped skunks and one red fox annually. The effect of the trapping program on local predator densities is unknown, but similar annual removal rates suggest immigration is able to keep pace with removal efforts (Conner and Morris 2015).

## Methods

We opportunistically collected coyote scats on Ichauway year round during 2007, 2008, 2011 and 2012. Scat samples were collected across the entire site, but because we were opportunistically collecting scats as we conducted other research activities, our sampling intensity likely decreased with distance from our laboratories where we started and finished our work day. We only collected scats that appeared fresh and were assumed to have been deposited within the previous week. Scat samples were stored at -20°C until processed. During preparation, the samples were dried in an oven at 60°C for 72 h (Baker et al. 1993). Upon processing, the samples were broken apart and food items were isolated. Each food item was examined macroscopically and, when necessary, through a 40× magnification light microscope. Remains were identified to lowest possible taxonomic level. Food items were separated into categories including rodent, rabbit, adult deer, fawn deer, mesomammal, invertebrate, soft mast, agricultural crops, and other. Rodents included cotton rats *Sigodon hispidus*, cotton mice *Peromyscus gossypinus*, old field mice *P. polionotus*, eastern wood rats *Neotoma floridana*, eastern gray squirrels *Sciurus carolinensis*, fox squirrels *S. niger*, southeastern pocket gophers *Geomys pinetis*, and chipmunks *Tamias striatus*. Mesomammals included armadillos *Dasypus novemcinctus*, raccoons, Virginia opossums, bobcats, grey foxes and striped skunks. Crops included corn, grain sorghum and peanuts *Arachis hypogaea*. The 'other'

category included rarely encountered items such as feral swine *Sus scrofa*, domestic cattle *Bos taurus*, domestic dogs *Canis familiaris*, domestic cats *Felis catus*, shrews *Sorex spp.*, bird eggs, reptile eggs and fishes. Hairs were identified using reference hair slides at the Univ. of Georgia's Warnell School of Forestry and Natural Resources. We calculated the percentage of scats that contained specific items to estimate the composition of the coyote diet. Of course, the percentage of occurrence of an item in various scats does not readily translate into the percentage in the diet due to differential digestibility of various foods. However, we treated all scats equally, so the temporal increases and decreases in the occurrence of specific prey items that we observed (e.g. Table 1) are likely real and our conclusions robust. To partially account for variation in digestibility we only examined the percentage of scats that contained a specific food item (i.e. presence of absence) as opposed to estimating the percentage of volume composed of each prey item in a scat. Percentage of scats was calculated per month by dividing the number of scats in which the item occurred by the number of scats collected in that month (Wagner and Hill 1993). Seasonally available food items (i.e. soft mast) can influence defecation rates of coyotes and therefore we only compare percentages calculated for discrete periods to avoid this potential source of bias on an annual diet (Andelt and Andelt 1984). We report the mean number of prey items per scat calculated for each month. We also report the percentage of scats containing specific prey remains bimonthly and seasonally.

### Modeling co-occurrence

We categorized each scat sample into biologically meaningful seasons associated with coyote reproduction (Atwood et al. 2003) – pair bonding (1 January – 15 March); gestation (16 March – 30 May); pup-rearing (1 June – 31 August); and dispersal (1 September – 31 December). To test if seasonal occurrences of alternative prey items reduced the odds of a scat containing white-tailed deer, we fit logistic regression models using maximum likelihood, with occurrence of white-tailed deer in each scat as a binary response variable. Predictor variables including the occurrence of rodents, rabbits, mesomammals, invertebrates, soft mast and crops were related to the presence of deer remains in each scat for each season. Because the pup-rearing season included the white-tailed deer fawning period, we fit separate models predicting the occurrence of fawn and adult deer. We used the occurrence of prey items in scats as opposed to percentages of vol-

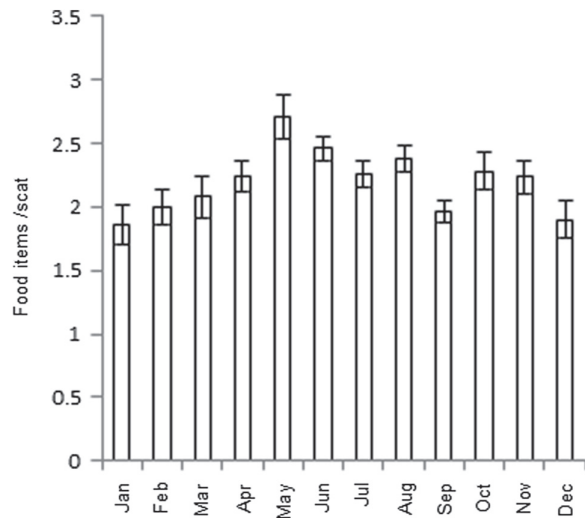


Figure 1. Monthly mean number of prey items per coyote scats ( $\pm$  SE) collected during 2007–2008 and 2011–2012 on the Joseph W. Jones Ecological Research Center in Georgia, USA.

ume to avoid the unit sum constraint (i.e. there were more than one item per scat and therefore totals did not sum to zero or lack independence). All logistic regression models were fit using package lme4 in program R (<[www.r-project.org](http://www.r-project.org)>, Bates et al. 2014). We report odds ratios for effect size and assigned significance when  $p < 0.05$ .

### Results

We collected 673 coyote scats during 2007–2012. Combining all years, the mean number of scats collected per month was 55, but ranged from 21 during January to 115 during June. The monthly diet diversity (i.e. mean number of prey items per scat) varied throughout the year and peaked in May (Fig. 1). Bimonthly diets of coyotes shifted considerably through the year, and we provide sample sizes per period and the variation in the percent of coyote scats with specific prey in Table 1. Coyotes foraged primarily on rodents, white-tailed deer and rabbit throughout the year, but a spike in white-tailed deer occurrence coinciding with the fawning period was associated with a reduction in the use of the other two prey items (Fig. 2). Adult white-tailed deer were consumed during every month and ranged in occurrence from

Table 1. Percentage of coyote scats containing specific prey items during bi-monthly periods during 2007–2008 and 2011–2012 on the Joseph W. Jones Ecological Research Center in Georgia, USA.

|              | Jan–Feb<br>(n = 52) | Mar–Apr<br>(n = 98) | May–Jun<br>(n = 161) | Jul–Aug<br>(n = 167) | Sep–Oct<br>(n = 113) | Nov–Dec<br>(n = 82) |
|--------------|---------------------|---------------------|----------------------|----------------------|----------------------|---------------------|
| Rodent       | 58                  | 76                  | 55                   | 51                   | 63                   | 62                  |
| Deer         | 35                  | 18                  | 27                   | 52                   | 22                   | 24                  |
| Rabbit       | 40                  | 33                  | 17                   | 9                    | 11                   | 24                  |
| Mesomammal   | 19                  | 17                  | 19                   | 17                   | 9                    | 15                  |
| Avian        | 13                  | 15                  | 16                   | 13                   | 10                   | 9                   |
| Invertebrate | 0                   | 12                  | 22                   | 12                   | 18                   | 13                  |
| Soft mast    | 0                   | 12                  | 78                   | 63                   | 36                   | 11                  |
| Crop         | 25                  | 24                  | 16                   | 22                   | 48                   | 46                  |



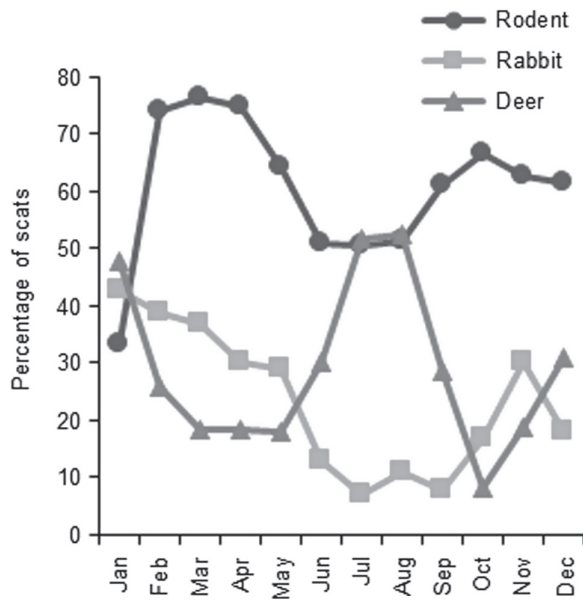


Figure 2. Percentage of coyote scats containing rodents, rabbits, and white-tailed deer during 2007–2008 and 2011–2012 on the Joseph W. Jones Ecological Research Center in Georgia, USA.

8% in October to 48% during January (Fig. 3). Fawn white-tailed deer were heavily utilized during the pup-rearing season, which included the white-tailed deer parturition season that peaks in early July, and were detected in the diet from May–September with a peak in use during August. Rabbit most commonly occurred in samples from the pair bonding season (Fig. 4). Rodent use was high during all seasons but was least during the pup-rearing season. The occurrence of avian species was relatively low during all seasons but was greatest from March–June, coinciding with the nesting and

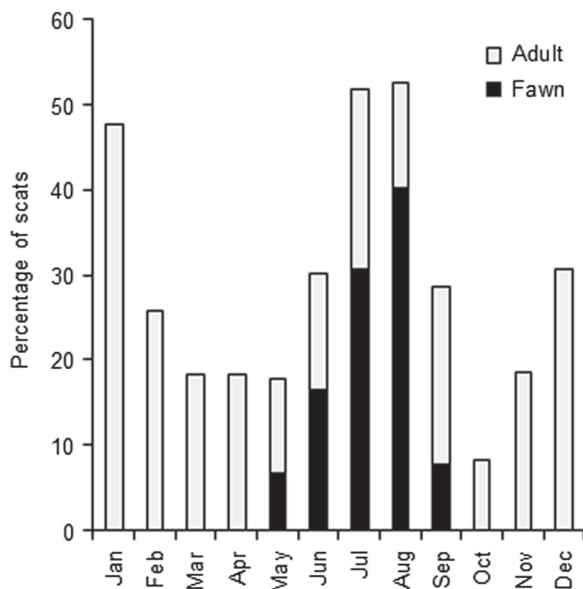


Figure 3. Monthly percentage of coyote scats containing adult and fawn white-tailed deer remains during 2007–2008 and 2011–2012 on the Joseph W. Jones Ecological Research Center in Georgia, USA.

brood-rearing periods for wild turkey *Meleagris gallopavo* and northern bobwhite (Table 1). Occurrence of mesomammals ranged from 17–19% during January–September to 9% September–October. Summed across all months and years, the mesomammal category was composed of raccoon (42%), Virginia opossum (21%), armadillo (16%), bobcat (10%), striped skunk (6%), coyote (4%) and grey fox (1%).

Utilization of vegetation was highly seasonal and consisted of a wide array of soft mast and agricultural crops (Fig. 5). Use of individual species appeared to be associated with fruiting chronology. Soft mast species observed included wild plum *Prunus* spp., blackberries *Rubus* spp., wild grape *Vitis* spp., black cherry *Prunus serotina*, American beautyberry *Callicarpa americana*, hackberry *Celtis occidentalis*, blueberry *Vaccinium* spp. and persimmon *Diospyros* spp. (Fig. 3). Vegetation occurrence was also affected by agricultural crops from offsite operations, particularly peanuts, which were used most heavily during November (Fig. 5). Crops were heavily used when fruits were seasonally unavailable.

The occurrence of certain alternative prey items reduced the probability of a scat containing white-tailed deer. During the dispersal season (1 September – 31 December) scats containing rodent ( $Z = -4.04$ ,  $p \leq 0.001$ ), rabbits ( $Z = -1.96$ ,  $p = 0.05$ ), and fruit ( $Z = -1.96$ ,  $p = 0.05$ ) were less likely to contain white-tailed deer (Table 2). During the pair-bonding season (1 January – 15 March) scats containing rodents ( $Z = -2.43$ ,  $p = 0.015$ ) were less likely to contain white-tailed deer. During coyote gestation (16 March – 30 May) no food item predicted the occurrence of white-tailed deer in coyote scat. During pup rearing (1 June – 31 August), scats containing rodents ( $Z = -2.94$ ,  $p = 0.003$ ), rabbits ( $Z = -2.88$ ,  $p = 0.004$ ), mesomammals ( $Z = -2.08$ ,  $p = 0.037$ ) and fruits ( $Z = -3.37$ ,  $p = 0.001$ ) were less likely to contain white-tailed deer remains. During the pup-rearing season, adult and fawn white-tailed deer were inversely related to different food items. Scats containing mesomammals ( $Z = -2.98$ ,  $p = 0.003$ ) and crops ( $Z = -2.01$ ,  $p = 0.044$ ) were less likely to contain adult white-tail deer remains during the pup-rearing season, whereas scats containing soft mast ( $Z = -3.13$ ,  $p = 0.002$ ) were less likely to contain fawns remains.

## Discussion

The results of this study suggest coyotes inhabiting longleaf pine-wiregrass ecosystems utilize a diverse array of animals, soft mast, and agricultural crops. Vegetation, rodent and bird consumption was greater than has been reported in other coyote diet studies in the southeastern USA (Blanton and Hill 1989, Schrecengost et al. 2008). This is likely a function of land management practices that increased abundance of these items on our site compared to the sites described in previous studies. A combination of prescribed fire promoting early successional woodlands, coupled with supplemental feeding for wildlife on our study site, results in abundant small mammal (Morris et al. 2011a, b), ground nesting birds (Sisson et al. 2000), and soft mast production. Additionally, agricultural crops found offsite were heavily used by coyotes when native soft mast was seasonally unavailable. However, domestic animals seldom occurred, with *Bos taurus* being

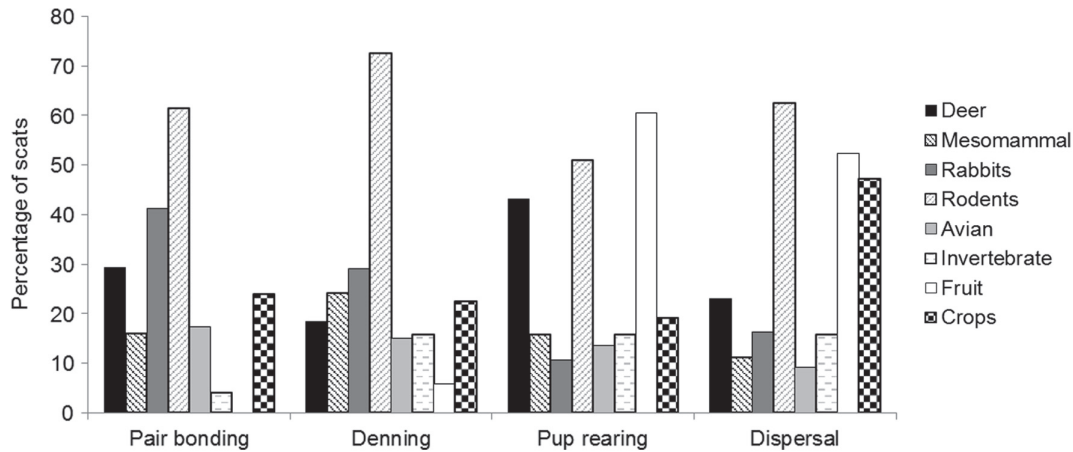


Figure 4. Seasonal percentage of coyote scats containing 8 different food item categories during 2007–2008 and 2011–2012 on the Joseph W. Jones Ecological Research Center in Georgia, USA.

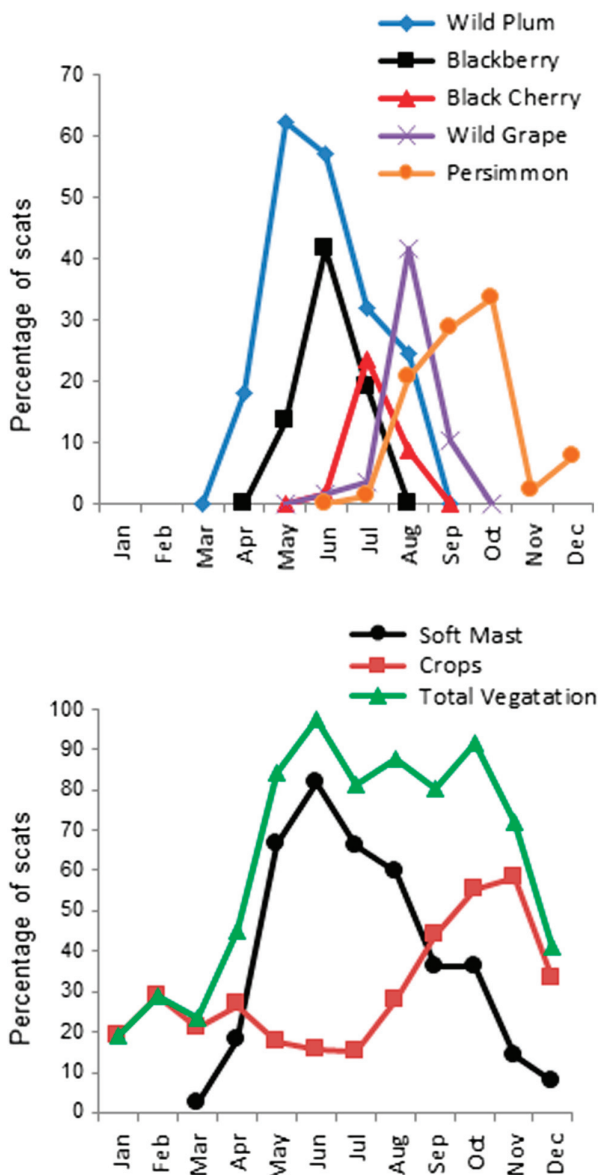


Figure 5. Percentage of coyote scats containing vegetation during 2007–2008 and 2011–2012 on the Joseph W. Jones Ecological Research Center in Georgia, USA.

the domestic animal occurring most frequently (3.0%). Our results suggest coyotes have the potential to influence the longleaf pine ecosystem through direct predation of white-tailed deer and through competition and direct predation of mesomammalian predators.

We observed a bimodal distribution of deer use throughout the year with approximately 50% of scats containing deer during fawning and post-rut (i.e. January). This pattern of high occurrence of deer in coyote diets during summer and winter with relatively lower use during spring and autumn has been observed in South Dakota (MacCracken and Uresk 1984) and South Carolina (Schrecengost et al. 2008). We also documented a constant occurrence of adult deer in coyote scats throughout the remainder of the year of > 15% in all seasons. Though other studies attribute deer use outside of the fawning seasons to scavenging (Stratman and Pelton 1997, Schrecengost et al. 2008), if use of adult deer was dependent on scavenging, then use would be expected to peak coincident with white-tailed deer firearm hunting season in Georgia (October–January). However, we observed greater use of adult deer during February–April than October–November. The occurrence of adult deer in coyote scats did not appear to be related to when carrion was most likely to be available from hunter-harvested animals. The lack of association with availability of carrion suggests the use of adult white-tailed deer is not restricted to scavenging in this system. However, this could be partially explained by longer carcass viability in the winter when decomposition rates are slower.

Herein we documented that coyotes in a longleaf pine-wiregrass dominated ecosystem rely on typically reported prey items, and that the large diversity and abundance of food items on this site was consistent with the hypothesis that this can alleviate the risk of predation on white-tailed deer fawns. Rodent and rabbit occurrence in scats was inversely related to white-tailed deer occurrence in scats during the pup-rearing and pair-bonding season. The occurrence of mesomammals in scats decreased the likelihood of adult white-tailed deer in that same scat. Larger-sized prey items may more easily satiate coyotes and decrease the likelihood of other items occurring in the same scat. We also found that the occurrence of fruits in a scat decreased the

Table 2. Parameters estimates for logistic regression models predicting the seasonal occurrence white-tailed deer in coyote scats during 2007–2008 and 2011–2012 on the Joseph W. Jones Ecological Research Center in Georgia, USA. Seasons were based on coyote reproduction (Dispersal: September–December, Pair bonding: January–15 March; Denning: 16 March–May; Pup-rearing: June–August). Standard errors (SE), Odds ratio, z-values and probabilities that a coefficient differs from 0 are also presented.

|                     | $\beta$ | SE   | Exp( $\beta$ ) | Z     | Pr(> Z )       |
|---------------------|---------|------|----------------|-------|----------------|
| <b>Dispersal</b>    |         |      |                |       |                |
| Intercept           | 0.27    | 0.38 | 1.31           | 0.71  | 0.478          |
| Rodent              | -1.59   | 0.39 | 0.20           | -4.04 | $\leq 0.001^*$ |
| Rabbit              | -1.11   | 0.57 | 0.33           | -1.96 | 0.050*         |
| Mesomammal          | -0.24   | 0.63 | 0.78           | -0.39 | 0.701          |
| Invertebrate        | -0.69   | 0.51 | 0.50           | -1.34 | 0.179          |
| Fruit               | -0.91   | 0.46 | 0.40           | -1.96 | 0.050*         |
| Crop                | -0.23   | 0.37 | 0.79           | -0.63 | 0.529          |
| <b>Pair bonding</b> |         |      |                |       |                |
| Intercept           | 0.56    | 0.62 | 1.74           | 0.90  | 0.368          |
| Rodent              | -1.55   | 0.64 | 0.21           | -2.43 | 0.015*         |
| Rabbit              | -1.23   | 0.66 | 0.29           | -1.88 | 0.060          |
| Mesomammal          | 0.24    | 0.75 | 1.27           | 0.32  | 0.750          |
| Crop                | -0.53   | 0.69 | 0.59           | -0.77 | 0.444          |
| <b>Gestation</b>    |         |      |                |       |                |
| Intercept           | -0.27   | 0.58 | 0.76           | -0.47 | 0.638          |
| Rodent              | -0.89   | 0.54 | 0.41           | -1.67 | 0.096          |
| Rabbit              | -0.85   | 0.61 | 0.43           | -1.38 | 0.167          |
| Mesomammal          | -1.39   | 0.79 | 0.25           | -1.75 | 0.080          |
| Invertebrate        | -0.09   | 0.72 | 0.91           | -0.13 | 0.898          |
| Fruit               | -0.16   | 0.55 | 0.86           | -0.29 | 0.776          |
| Crop                | -0.42   | 0.63 | 0.66           | -0.66 | 0.508          |
| <b>Pup rearing</b>  |         |      |                |       |                |
| Intercept           | 1.25    | 0.32 | 3.48           | 3.91  | 0.000          |
| Rodent              | -0.77   | 0.26 | 0.46           | -2.94 | 0.003*         |
| Rabbit              | -1.37   | 0.48 | 0.25           | -2.88 | 0.004*         |
| Meso                | -0.76   | 0.36 | 0.47           | -2.08 | 0.037*         |
| Invertebrate        | -0.59   | 0.35 | 0.55           | -1.66 | 0.097          |
| Fruit               | -0.97   | 0.29 | 0.38           | -3.37 | 0.001*         |
| Crop                | -0.64   | 0.34 | 0.53           | -1.87 | 0.062          |

Table 3. Parameter estimates for logistic regression models predicting the occurrence of adult and fawn white-tailed deer in coyote scats during the pup-rearing season (June–August) of 2007–2008 and 2011–2012 on the Joseph W. Jones Ecological Research Center in Georgia, USA. Standard errors (SE), Odds ratio, z-values and probabilities that a coefficient differs from 0 are also presented.

|              | $\beta$ | SE   | Exp( $\beta$ ) | Z     | Pr(> Z ) |
|--------------|---------|------|----------------|-------|----------|
| <b>Adult</b> |         |      |                |       |          |
| Intercept    | -0.16   | 0.24 | 0.85           | -0.68 | 0.499    |
| Rodent       | -0.55   | 0.29 | 0.58           | -1.92 | 0.055    |
| Rabbit       | -0.98   | 0.53 | 0.38           | -1.84 | 0.066    |
| Mesomammal   | -1.83   | 0.62 | 0.16           | -2.98 | 0.003*   |
| Invertebrate | -0.66   | 0.41 | 0.52           | -1.61 | 0.107    |
| Fruit        | -0.06   | 0.19 | 0.95           | -0.29 | 0.775    |
| Crop         | -0.82   | 0.41 | 0.44           | -2.01 | 0.044*   |
| <b>Fawn</b>  |         |      |                |       |          |
| Intercept    | 0.12    | 0.30 | 1.13           | 0.39  | 0.696    |
| Rodent       | -0.44   | 0.28 | 0.64           | -1.57 | 0.116    |
| Rabbit       | -0.91   | 0.52 | 0.40           | -1.74 | 0.083    |
| Mesomammal   | -0.33   | 0.39 | 0.72           | -0.85 | 0.397    |
| Invertebrate | -0.33   | 0.39 | 0.72           | -0.85 | 0.394    |
| Fruit        | -0.91   | 0.29 | 0.40           | -3.13 | 0.002*   |
| Crop         | -0.41   | 0.37 | 0.67           | -1.11 | 0.269    |

likelihood of fawn white-tailed deer in the same scat. Thus, it seems that soft mast may buffer coyote-induced mortality of white-tailed deer fawns. Across the southeastern USA, there is increasing interest in reducing coyote-induced mortality of white-tailed deer (Kilgo et al. 2010). Land management practices that provide abundant alternative prey may reduce coyote use of white-tailed deer but may also improve the habitat for coyotes. It is plausible that increasing the quality of habitat for coyotes by enhancing alternative prey may increase coyote populations and while the proportion of the diet comprised of deer may decrease the total number of deer consumed may increase. Future studies should examine the effect of increasing availability of buffer food items on coyote predation of deer.

Agricultural plantings, predominately peanuts, were heavily utilized by coyotes during the winter months when native soft mast was less abundant. Anthropogenic items (trash, pets, etc.) commonly occur in the diets of urban coyotes (MacCracken 1982, Fedriani et al. 2001, Morey et al. 2007). Furthermore, one study in the Southeast suggests anthropogenic food items are used in similar frequencies across a range of rural and urban settings (Santana 2010). Human-introduced resources, such as supplemental food, artificially inflate carrying capacity of some species and can cause increases in plant and animal species depredated in the surrounding area (Milner et al. 2014, Newsome et al. 2015). Likewise, it is reasonable to believe that agricultural plants available during late fall and winter, when native soft mast are less plentiful, may provide an increased coyote carrying capacity. This anthropogenically-induced release may result in increased abundance of coyotes during white-tailed deer fawning season and subsequently increase predation pressure on fawns (Newsome et al. 2015).

In summary, our results suggest coyotes use many typical food items in longleaf pine ecosystems, but display increased use of birds and plant material compared to other studies (Schreengost et al. 2008). Our results demonstrate that the timing of sample collection can have profound influence of implications of coyote food habits studies because of considerable temporal variation in diet. Future studies should restrict inference to the seasons samples were collected and acknowledge that the timing of sample collection will strongly influence the characterization of annual coyote diets. A greater understanding of coyote foraging behavior will allow managers to better predict the effect of coyotes in recently colonized regions of their range.

## References

- Andelt, W. F. and Andelt, S. H. 1984. Diet bias in scat deposition-rate surveys of coyote density. – *Wildl. Soc. Bull.* 12: 74–77.
- Andelt, W. F. et al. 1987. Variation in coyote diet associated with season and successional changes in vegetation. – *J. Wildl. Manage.* 51: 273–277.
- Allen, J. C. et al. 2006. Associations of breeding birds with fire-influenced and riparian-upland gradients in a longleaf pine ecosystem. – *Auk* 123: 1110–1128.
- Atwood, T. et al. 2003. Spatial home-range overlap and temporal interaction in eastern coyotes: the influence of pair types and fragmentation. – *Can. J. Zool.* 81: 1589–1597.

- Baker, L. A. et al. 1993. Bobcat prey digestibility and representation in scats. – Proc. Annu. Conf. Southeast. Ass. Fish Wildl. Agencies 47: 71–79.
- Bates D. et al. 2014. lme4: linear mixed-effects models using Eigen and S4. – R package ver. 1.1 7. <<http://CRAN.R-project.org/package=lme4>>.
- Berger, K. M. 2006. Carnivore–livestock conflicts: effects of subsidized predator control and economic correlates on the sheep industry. – Conserv. Biol. 20: 751–761.
- Blanton, K. M. and Hill, E. P. 1989. Coyote use of white-tailed deer fawns in relation to deer density. – Proc. Annu. Conf. Southeast. Ass. Fish Wildl. Agencies 43: 470–478.
- Boring, L. R. 2001. The Joseph W. Jones Research Center: Co-directed applied and basic research in the private sector. – In: Barrett, G. W. and Barrett, T. L. (eds), Holistic science: the evolution of the Georgia Institute of Ecology (1940–2000). Taylor and Francis, pp. 233–258.
- Carbyn, L. N. 1989. Coyote attacks on children in western North America. – Wildl. Soc. Bull. 17: 444–446.
- Chamberlain, M. J. and Leopold, B. D. 1999. Dietary patterns of sympatric bobcats and coyotes in central Mississippi. – Proc. Annu. Conf. Southeast. Ass. Fish Wildl. Agencies 53: 204–219.
- Chitwood, M. C. et al. 2015. White-tailed deer population dynamics and adult female survival in the presence of a novel predator. – J. Wildl. Manage. 79: 211–219.
- Conner, L. M. and Morris, G. 2015. Impacts of mesopredator control on conservation of mesopredators and their prey. – PLoS ONE 10: e0137169.
- Creel, S. and Christianson, D. 2008. Relationships between direct predation and risk effects. – Trends Ecol. Evol. 23: 194–201.
- Crooks, K. R. and Soulé, M. E. 1999. Mesopredator release and avifaunal extinctions in a fragmented landscape. – Nature 400: 563–566.
- Drew, M. B. et al. 1998. The vascular flora of Ichauway, Baker County, Georgia: a remnant longleaf pine/wiregrass ecosystem. – Castanea 63: 1–24.
- Fedriani, J. M. et al. 2001. Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. – Ecography 24: 325–331.
- Gompper, M. E. 2002. Top carnivores in the suburbs? Ecological and conservation issues raised by colonization of northeastern North America by coyotes. – BioScience 52: 185–190.
- Hill, E. P. et al. 1987. Human influences on range expansion of coyotes in the southeast. – Wildl. Soc. Bull. 15: 521–524.
- Henke, S. E. and Bryant, F. C. 1999. Effects of coyote removal on the faunal community in western Texas. – J. Wildl. Manage. 63: 1066–1081.
- Joseph W. Jones Ecological Research Center 2011. White-tailed deer management summary 1993–2011. – Joseph W. Jones Ecol. Res. Center.
- Kirkman, L. K. et al. 2001. Productivity and species richness across an environmental gradient in a fire-dependent ecosystem. – Am. J. Bot. 88: 2119–2128.
- Kilgo, J. C. et al. 2010. Can coyotes affect deer populations in southeastern North America? – J. Wildl. Manage. 74: 929–933.
- Kilgo, J. C. et al. 2012. Predation by coyotes on white-tailed deer neonates in South Carolina. – J. Wildl. Manage. 76: 1420–1430.
- Levi, T. et al. 2012. Deer, predators and the emergence of Lyme disease. – Proc. Natl Acad. Sci. USA 109: 10942–10947.
- MacCracken, J. G. 1982. Coyote foods in a southern California suburb. – Wildl. Soc. Bull. 10: 280–281.
- MacCracken, J. G. and Uresk, D. W. 1984. Coyote foods in the Black hills, South Dakota. – J. Wildl. Manage. 48: 1420–1423.
- McVey, J. M. et al. 2013. Diets of sympatric red wolves and coyotes in northeastern North Carolina. – J. Mammal. 94: 1141–1148.
- Milner, J. M. et al. 2014. To feed or not to feed? Evidence of intended and unintended effects of feeding wild ungulates. – J. Wildl. Manage. 78: 1322–1334.
- Mitchell, R. J. et al. 2006. Silviculture that sustains: the nexus between silviculture, frequent prescribed fire, and conservation of biodiversity in longleaf pine forests of the southeastern United States. – Can. J. For. Res. 36: 2724–2736.
- Morey, P. S. et al. 2007. Spatial and temporal variation in the diet of coyotes in the Chicago metropolitan area. – Am. Midl. Nat. 158: 147–161.
- Morris, G. et al. 2011a. Effects of prescribed fire, supplemental feeding, and mammalian predator exclusion on hispid cotton rat populations. – Oecologia 167: 1005–1016.
- Morris, G. et al. 2011b. Effects of predation, fire, and supplemental feeding on populations of two species of *Peromyscus* mice. – J. Mammal. 92: 934–944.
- Newsome, T. M. et al. 2015. The ecological effects of providing resource subsidies to predators. – Global Ecol. Biogeogr. 24: 1–11.
- Patterson, B. R. and Messier, F. 2000. Factors influencing killing rates of white-tailed deer by coyotes in eastern Canada. – J. Wildl. Manage. 64: 721–732.
- Peet, R. K. and Allard, D. J. 1993. Longleaf pine vegetation of the southern Atlantic and eastern Gulf Coast regions: a preliminary classification. – Proc. Tall Timbers Fire Ecol. Conf. 18: 45–81.
- Robinson, K. F. et al. 2014. Can managers compensate for coyote predation of white-tailed deer? – J. Wildl. Manage. 78: 571–579.
- Santana, E. M. 2010. Food habits and anthropogenic supplementation in the diet of coyotes *Canis latrans* along an urban–rural gradient. – Auburn Univ.
- Salo, P. et al. 2007. Alien predators are more dangerous than native predators to prey populations. – Proc. R. Soc. B 274: 1237–1243.
- Schreckengost, J. D. et al. 2008. Seasonal food habits of the coyote in the South Carolina Coastal Plain. – Southeast. Nat. 7: 135–144.
- Sih, A. et al. 2010. Predator–prey naïveté, antipredator behavior, and the ecology of predator invasions. – Oikos 119: 610–621.
- Sisson, D. C. et al. 2000. Effects of supplemental feeding on home range size and survival of northern bobwhites in south Georgia. – Proc. Natl Quail Symp. 4: 128–131.
- Sovada, M. A. et al. 1995. Differential effects of coyotes and red foxes on duck nest success. – J. Wildl. Manage. 59: 1–9.
- Stratman, M. R. and Pelton, M. R. 1997. Food habits of coyotes in Northwestern Florida. – Proc. Annu. Conf. Southeast. Ass. Fish Wildl. Agencies 51: 269–275.
- Thurber, J. M. and Peterson, R. O. 1991. Changes in body size associated with range expansion in the coyote *Canis latrans*. – J. Mammal. 72: 750–755.
- Wagner, G. D. and Hill, P. H. 1993. Evaluation of southeastern coyote diets during the wild turkey reproductive season. – Proc. Annu. Conf. Fish Wildl. Agencies 48: 173–181.
- Walters, J. R. 1991. Application of ecological principles to the management of endangered species: the case of the red-cockaded woodpecker. – Annu. Rev. Ecol. Syst. 22: 505–523.
- Waser, N. M. et al. 2014. Coyotes, deer and wildflowers: diverse evidence points to a trophic cascade. – Naturwissenschaften 101: 427–436.