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ARTICLE
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An omnivore's options: Altered predator behavior during periods of overlapping resource pulses

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Abstract

Resource pulses are ecologically important events that occur in most ecosystems, yet most of our previous knowledge about their effects comes from relatively simple single pulse systems. In reality, many consumers likely attempt to track multiple, sometimes overlapping, resource pulses through space and time. Indeed, pulses of food resources at lower trophic levels have been shown to decouple the response of large omnivorous predators to pulses of vertebrate prey, with implications for predator–prey interactions more broadly. However, to date, the impact of these alternative food pulses on large herbivore predation by large carnivores remains unknown. To test this alternative pulse hypothesis (APH), we tracked coyote diet and movement behavior during two overlapping resource pulses (white-tailed deer fawns followed by blackberries) over three summers in South Carolina, USA. We found that coyote diets tracked the shape of both pulses closely, and in support of APH, an eruptive pulse of blackberry availability during the period of declining fawn availability better explained fawn consumption than fawn availability alone. We estimated that the irruption of blackberries led to an 8% decrease in the weighted occurrence of fawn consumption. Movement data genetically linked to scat samples partially supported a shift in foraging, where coyotes selected habitat differently but did not move differently while consuming fawns or blackberries. Collectively, our findings provide quantitative evidence in support of how naturally occurring alternative foods can influence large carnivore behavior and potentially the consumption of large herbivores. Given many carnivores across the globe have omnivorous diets, our results open a new line of inquiry into how carnivores make decisions when resource pulses overlap, with implications for the management of apex carnivores and their herbivore prey.

KEYWORDS
carnivore, community ecology, consumer, coyote, deer, movement ecology, predator–prey, prey-switching

INTRODUCTION

Resource pulses—relatively large, yet brief, spikes in resource availability—have important ecological effects mediated by how consumers respond to them (Yang et al., 2008). These interactions occur in a variety of systems (Yang et al., 2010), from timed mast and fruit production in forests (Schmidt & Ostfeld, 2008) to the return of breeding salmon to inland waterways (Willson & Halupka, 1995). Many species have been shown to track pulses moving predictably through space (i.e., resource waves; Abrahms et al., 2021), such as how some ungulates time their migrations to follow spring green-up (Armstrong et al., 2016). Yet non-migratory species also respond to resource pulses within their home ranges by changing how or where they forage (Deacy et al., 2017; Pelech et al., 2010). The effects from resource pulses also scale up to influence communities via increased reproduction of the primary consumer, which in turn can support increases in their predators and parasites (Ostfeld & Keesing, 2000). Despite these important effects, there are still gaps in our knowledge around how consumer responses to resource pulses can have cascading effects across ecological communities.

The responsiveness of a species to resource pulses can be influenced by characteristics of both the pulse and the consumer (Holt, 2008; Yang et al., 2010). When resource pulses are predictable (e.g., annual occurrences), consumers have been shown to have stronger responses compared to pulses that are stochastic (Holt, 2008; Figure 1A). On the consumer side, the timing of the response can vary from tracking resource pulses perfectly to some amount of temporal lag (Rickbeil et al., 2019; Yang et al., 2008; Figure 1B). Ecosystems can also contain multiple, sometimes overlapping resource pulses that influence consumer behavior. For example, in Alaska, Deacy et al. (2017) showed that when the timing of red elderberry (*Sambucus racemosa*) fruiting shifted to overlap with salmon (*Oncorhynchus nerka*) spawning, brown bears (*Ursus arctos middendorffi*) reduced salmon consumption in favor of consuming elderberries. This highlights the availability of a secondary pulse as the primary driver influencing consumer behavior, as opposed to the declining availability of primary prey, as predicted by the prey switching hypothesis (Murdoch, 1969). While studies of how consumers respond to multiple, overlapping resource pulses are very limited, it is hypothesized that consumers with more generalist diets are more likely to redirect their foraging efforts, particularly as availability of the first resource pulse begins to decline (Yang et al., 2008; Figure 1C).

Understanding the response of omnivorous apex carnivores ("carnivore" in the taxonomic sense) to overlapping resource pulses is particularly important because they can exploit a variety of food sources and have important top-down effects on large herbivores within ecosystems (Ripple & Beschta, 2004). Indeed, some populations of brown bears (*Ursus arctos*) track spring green-up to optimize vegetative forage (Bowersock et al., 2023), and others aggregate at high elevations to eat moths

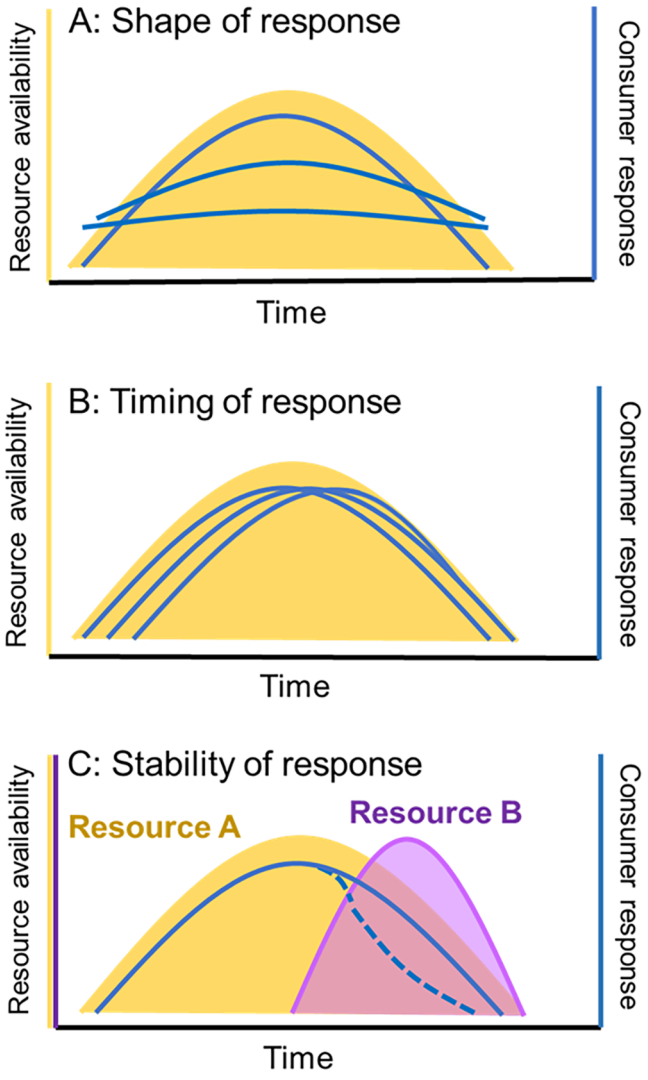

FIGURE 1 Metrics and hypotheses related to how closely consumers track resource pulses. The gold and purple mounds are resource pulse availability while the blue lines are the response to the main resource (gold mound). (A) Consumer response could vary from closely tracking the shape of the response to hardly responding at all (Yang et al., 2010). (B) A scenario in which consumers track the shape closely, but that the timing of the response could vary, as has been shown for migratory ungulates (Rickbeil et al., 2019). (C) Two potential responses to a second resource pulse. Consumers tracking the solid blue line would indicate no effect from the second resource pulse, while tracking the dotted blue line would indicate that the second resource pulse reduced the response to the first (Deacy et al., 2017).

(Mattson et al., 1991). Similarly, gray wolves (*Canis lupus*) eat insects (Barton et al., 2020) and berries during peak abundance (Gable et al., 2018). However, the influence of these alternative resource pulses from lower trophic levels on large herbivore predation have yet to be evaluated.

Following optimal foraging theory (MacArthur & Pianka, 1966), carnivores should respond to resource pulses by modifying their behavior according to food availability. Herbivore prey are typically most vulnerable to predation when newborn, making temporally synchronized births adaptive to reduce individual predation risk (i.e., predator swamping; Ims, 1990). Yet there is mixed evidence from studies tracking how carnivores respond to pulses of vulnerable prey on the landscape; in some cases, carnivores changed their behavior (i.e., habitat selection) to optimize finding ungulate neonates (Huggler et al., 2023; Rayl et al., 2018), but in other studies they did not seem to change their behavior (Ruprecht et al., 2022; Svoboda et al., 2019). While multiple factors could explain a lack of response within a given study, a decoupling of carnivores tracking the pulsatile availability of vulnerable prey could be attributed to the availability of another, alternative resource pulse, as highlighted in the elderberry and salmon example above (Deacy et al., 2017). More precisely, changes in habitat selection due to an alternative pulse could mask a signal based on primary prey availability alone. Thus, by comparing movement and habitat selection while carnivores consumed each pulse, we can better understand to what extent they are changing their behavior to optimally forage.

We studied how an apex predator—coyotes (*Canis latrans*)—responded to two resource pulses in the southeastern United States. Although considered a mesocarnivore across much of their range, coyotes are the largest terrestrial predator across a majority of the southeast, having recently colonized this region in the last 50 years after the near extirpation of larger predators (i.e., red wolves and pumas; *Canis rufus* and *Puma concolor*). Coyotes have diverse and regionally varying diets (Jensen et al., 2022) and are responsible for 40% of white-tailed deer fawn (*Odocoileus virginianus*) mortality in this region on average, which has likely contributed to deer population declines in some states (Kilgo et al., 2010, 2019; Figure 2A). Yet fawns are primarily susceptible to coyote predation for just the first three to 6 weeks of their life in early summer (Kilgo et al., 2012; Nelson et al., 2015), representing a highly nutritious, yet ephemeral, food on the landscape. Coyotes also key in on pulsatile wild fruits during these summer months, leading some to question whether abundant alternative foods could reduce consumption of white-tailed deer fawns (Cherry et al., 2016; Kelly et al., 2015; Schrecengost et al., 2008). Indeed, we have shown that these pulses (fawns and fruits) make up ~50% of summer coyote diet at the population level and nearly all (65%–81%) individuals consume them (Jensen et al., 2024). However, no previous studies have tracked the fine-scale availability of multiple food items to be able to assess the extent to which alternative foods alter predator behavior during fawning season.

Our overall goal was to test what we term the alternative pulse hypothesis (APH)—that availability of an alternative, overlapping pulse of food at a lower trophic level (i.e., blackberries) decouples the consumption of herbivore prey (i.e., fawns; Figure 1C). Our first objective was to quantify and compare how coyotes dietarily responded to each pulse of fawn and blackberry availability. Given many species do not perfectly track availability of pulsatile resources (Yang et al., 2008), we not only assessed how closely consumption tracked the shape of availability (Figure 1A), but also if there was a time lag in response (Figure 1B). In addition, for fawns, we hypothesized that availability was not just a function of abundance, but also their vulnerability, so we predicted that coyote diets would most closely match the availability of young fawns (Kilgo et al., 2012). To evaluate support for the APH, our second objective was to test our prediction that fawn consumption would be negatively associated with changes in blackberry availability (Finnegan et al., 2023). Our third objective was to use tracking data to test the hypothesis that spatial variation in the availability of fawns and blackberries on the landscape would lead to differences in coyote movement ecology during each pulse. Here we predicted that coyotes would move faster while consuming fawns and would consume blackberries in more open habitats. These tracking data help us differentiate between shifts in diet simply reflecting changes in food availability and opportunistic consumption versus changes in foraging behavior. Collectively, by tracking how predators respond to multiple resource pulses we can better understand predator–prey dynamics and inform management implications for apex predators and their large herbivore prey.

METHODS

Study area and coyote capture

We tracked coyotes and studied their diets over three years (2019–2021) on a 61-km^2 mosaic of early to late successional forested habitat in the Piedmont region of South Carolina (Appendix S1: Figure S1). Coyote density was relatively high in this portion of the state (27 coyotes/100 km^2; Youngmann, 2023) and coyotes were responsible for 60% of fawn mortality within our

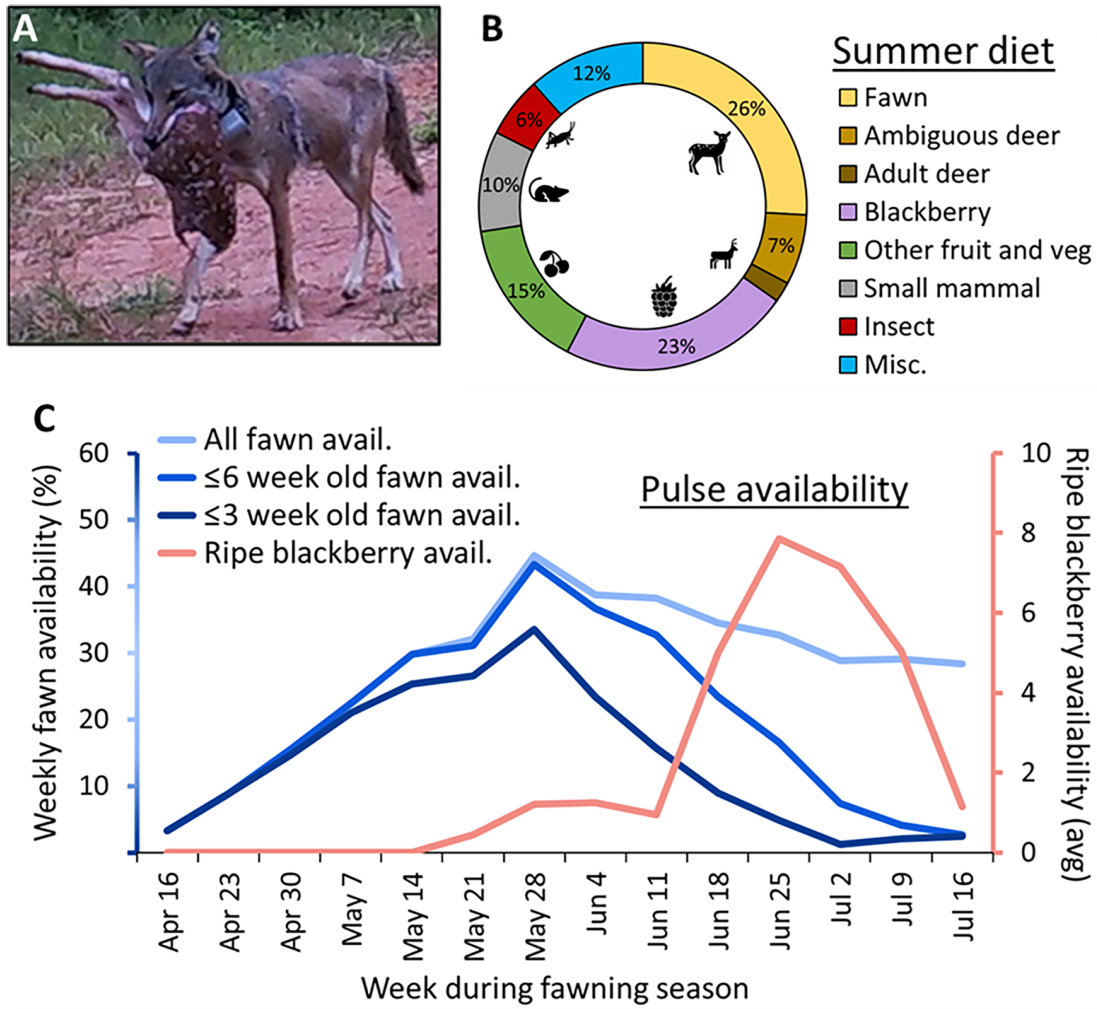

FIGURE 2 An overview of coyote diet in the summer in South Carolina, USA. (A) A photo of a (GPS-collared) coyote carrying the haunches of a dead fawn along a dirt road in our study area. Photo by the authors. (B) A summary of coyote diet in the summer, highlighting how important our focal food items are (fawns and blackberries). Ambiguous deer are deer remains in scat that we were unable to confidently age. Misc food items include birds, rabbits, and other mammals. (C) Weekly availability of fawns and blackberries, averaged across years from 2019, 2020, and 2021. We show three curves for fawns because we hypothesized that they might age out of predation risk.

study area (Muthersbaugh, 2023). We captured coyotes using Minnesota MB 550 foothold traps (Minnesota Trapline Products, Pennock, MN) set on dirt roads that had signs of coyote activity (i.e., tracks and scat) during December 2018, January–March 2020, and January 2021. We immobilized coyotes using a catchpole and electrical tape wrapped around their muzzle and ankles. We fit coyotes with a Vectronic Aerospace VERTEX Light GPS collar set to take a location fix every 30 min throughout our study period (April–July). We took a tissue sample from the ear of each captured coyote for subsequent genetic analysis. All capture and handling procedures were permitted by Clemson University IACUC permit no. AUP 2018-031 and USDA Forest Service permit no. USFS 2018-031.

Scat collection and genetic analysis

We collected scats on dirt roads in our study area every 4–7 days from early May through mid-July each year. Each week we surveyed ~16 km of dirt roads broken up into 7–15 transects distributed across our study area (Appendix S1: Figure S1). We used location data from our collared coyotes each year to inform where we established the transects to maximize collecting scats from collared individuals (Appendix S1: Section S1). We recorded the location of each scat, estimated its age in days, and preserved a pea-sized amount in dimethyl sulfoxide/ethylenediaminetetraacetic acid/tris(hydroxymethyl) aminomethane/salt buffer for genetic analysis (Stenglein et al., 2010).

We used molecular techniques to screen out scats not deposited by coyotes and matched individual scats to individuals with GPS tracking data. We conducted species and individual identification (SID and IID, respectively) on our scat samples using established DNA fragment length analyses. We first extracted any DNA present in a laboratory dedicated to low-quality DNA sources, then conducted SID polymerase chain reaction (PCR). We used a carnivore primer multiplex (De Barba et al., 2014), which is designed to amplify the mitochondrial DNA of whichever carnivore species is present. We used a capillary machine to read the PCR products, then GeneMapper 6 to analyze the lengths of the amplified DNA fragments and determine which scats were deposited by coyotes (sensu Stenglein et al., 2011). We then conducted IID PCR on the coyote samples using a multiplex of 10 loci (Seddon, 2005). We used a similar process to extract and amplify the DNA from our coyote tissue samples. We calculated that we needed matches at ≥ five loci to confidently differentiate siblings from each other, then we matched all scat and tissue samples using GenAlEx 6.5 (Peakall & Smouse, 2012).

Dietary analysis

We quantified coyote diet by isolating the solid material in each coyote scat and identifying it visually. Although genetic approaches to identify food items are becoming more common (i.e., metabarcoding; de Sousa et al., 2019), we chose to use a morphological approach for two reasons. First, we needed to be able to differentiate fawns from adult deer, and second, given our weekly temporal scale, we thought it was important to be able to estimate the amount of each food in each scat, which metabarcoding had yet to be able to do reliably (Nielsen et al., 2018). With that said, morphological approaches can be biased by overestimating the importance of foods containing solid material (e.g., hair, seeds) or certain prey items (e.g., deer; Morin et al., 2019). Digestion correction factors can partially account for these biases, but this requires feeding trial data, which we were unable to find for coyotes or with similar prey items from a closely related species (e.g., Loveridge & Macdonald, 2003).

We dried the scats in an oven at 85°C for 48 h, then washed them on a stack of five progressively fine metal sieves (6.3 mm, 2 mm, 500 μm, 63 μm, 1.25 μm), which isolated the solid material. Two observers used a combination of technical manuals on mammal hair (Moore et al., 1974; Teerink, 1991), hair reference slides, and online sources to identify the contents of each sample. We quantified the amount of deer, blackberries, small mammals, and other common foods (e.g., rabbits, birds, other fruit) in each scat sample. To differentiate fawns from adult deer, we measured the width of five hairs from three <6-week-old fawns and three adults from our field site (Calhoun et al., 2023). We determined that hairs <70 μm were likely from fawns, hairs >90 μm were likely from adults, and hairs 70–90 μm were ambiguous. Therefore, for each sample with deer hair, we measured three randomly selected deer hairs and used the average width to classify the sample as either fawn, adult, or ambiguous. In addition, if a sample from the summer was classified as ambiguous based on hair width but we found small hooves in the sample, we reclassified that sample as fawn. We then estimated the percent volume of the sample made of fawns and/or blackberries on a scale of 0–5, where 0 was not present, 1 was <2% (trace), 2 was 2%–25%, 3 was 26%–50%, 4 was 51%–75%, and 5 was 76%–100% (Prugh, 2005). We treated trace items as not present by converting scores of 1 to 0 (Prugh, 2005). To match our weekly availability data, we classified each coyote scat as representing consumption during a certain week over the summer. In order to more accurately date when the scat contents were consumed, we subtracted its estimated age from the date we collected it plus another day to account for digestion.

Fawn and blackberry availability

We used data from a concurrent study of fawn survival in our study area to estimate the availability of fawns (Muthersbaugh, 2023), where we counted the number of alive, collared fawns each day beginning in mid-April and ending in mid-July. We also estimated weekly fawn availability while accounting for fawns aging out of predation risk after they were 22 or 43 days old, based on literature which identified changes in rates of fawn survival as they aged (Kilgo et al., 2012; Nelson et al., 2015). Since there were different numbers of fawns captured each year (2019 = 37, 2020 = 27, 2021 = 20), we divided the number of available fawns each day by the total captured each year to create a daily percent. We then averaged these daily percentages each week (Figure 2C). We show fawn mortality locations attributed to coyotes in Appendix S1: Figure S1.

We also estimated weekly blackberry abundance each year by counting blackberries in the field beginning in mid-May and ending in mid-July in 2020 and 2021. We counted blackberries along dirt roads at locations where we had cameras deployed in a 1-km array (Jensen, 2023). We randomly selected four sites in 2020 and eight sites in 2021, ensuring that we sampled across successional stages in our study area to capture potential differences in fruit phenology across habitat types (Appendix S1: Figure S1). At each site, we set up four 3 m × 1 m plots where we counted blackberries each week, averaging

counts across plots and sites for each week's measure (Appendix S1: Figure S1). We did not count blackberries in 2019 but instead averaged the weekly counts across 2020 and 2021 given the timing of the peaks was the same (Appendix S1: Figure S2). Additional details on this process are in Appendix S1: Figure S1 and Section S2.

Objective one: Dietary response to fawn and blackberry availability

Our first objective was to separately quantify and compare how coyotes dietarily responded to pulses of fawn and blackberry availability. For fawns, we tested our prediction that coyotes would track younger fawns (≤3-week-old or ≤6-week-old) closer than fawns of any age by calculating the proportion of ≤3-week-old fawns, ≤6-week-old fawns, and all fawns available for each week. We also tested our prediction that coyotes would track availability with no temporal lag in response by adding a 1- or 2-week lag to availability. We thus had nine combinations of availability (including a null model; Appendix S1: Table S1), which we compared using cumulative link mixed models (CLMMs) using the ordinal package (Christensen, 2018) and corrected Akaike information criterion (AIC_c) (Burnham & Anderson, 2002). We used CLMMs because our response variable was ordinal (0–5) but the values represented by these ordinals were not all equally spaced. Our observation unit was an individual scat, and our response variable was the percent weighted occurrence of fawns in each scat. For blackberries, we tested for evidence of a temporal lag by comparing models with either ripe blackberry availability that week, the week prior, and 2 weeks prior (Appendix S1: Table S2). We included year and week as random intercepts and checked model fit using the DHARMa package (Hartig, 2022). We used delta AIC_c and model weight to identify competitive models and considered variable effects significant if 95% CIs did not overlap zero. All analyses were conducted in R version 2024.04.2.

Objective two: Does blackberry availability reduce fawn consumption?

Here we tested our hypothesis that an alternative resource pulse (i.e., blackberries) reduced consumption of the first resource pulse (i.e., fawns). To do this, we compared models containing fawn availability alone (the top model from objective one: ≤6-week-old fawns with no temporal lag), blackberry availability alone, and both fawn and blackberry availability. We would interpret support for a sole effect of fawn availability as suggesting that blackberries did not have a destabilizing effect on fawn consumption. In contrast, following our APH, support for the blackberry availability variable would be interpreted as evidence that blackberries destabilized the close tracking of fawn availability (Figure 1C). We centered and scaled our availability data and, like the previous objective, used CLMMs with year and season as random intercepts and compared models using AIC.

In order to quantify the magnitude of any effects from blackberries on fawn consumption, we estimated what fawn consumption would have been if blackberries were not consumed. To do this, we subset our data to the 8 weeks outside peak blackberry consumption (April 30–June 11 and July 16) and calculated the average difference between fawn availability (from our top model in objective one: ≤6-week-old fawns with no temporal lag) and fawn consumption. For fawn consumption, we calculated the percent occurrence of fawns in coyote scat for each week, which was the total fawn weighted occurrence divided by total weighted occurrence for all food categories. We then used this average difference to predict what fawn consumption would have been during the four peak blackberry weeks (June 18–July 9, Figure 4B) if blackberries were not available. We calculated the difference between total fawn percent occurrence using our actual data and the total using the predicted values.

Objective three: Comparing movement while consuming fawns and blackberries

We used the subset of scats that matched with tissue samples from collared coyotes to quantify movement during the period they likely consumed fawn or blackberries (Appendix S1: Figure S3). We limited our analysis to 23 scats where >50% of the scat was either fawn ($n = 14$) or blackberry ($n = 9$). We used the location of the scat and the GPS data to estimate when the scat was deposited (±30 min). We estimated that the contents of the scat were likely consumed 4–24 h prior to when it was deposited based on a coyote gut content passage study (which also found that the amount of fruit in a meal did not change gut passage time; Draper et al., 2021). Thus, for each scat containing either fawn or blackberry, we had a 20-h window of 30-min GPS data during which the coyote likely ate the contents of the scat and from which we derived speed and habitat selection estimates.

We were interested in how coyotes were moving while consuming each of these foods, so we classified each point as one of three behavior states (encamped, foraging, or traveling) using hidden Markov models and the momentuHMM package (McClintock & Michelot, 2018). The encamped state was little to no movement

(e.g., resting at a den site); foraging was moderately fast and linear movement; traveling was relatively fast directed movement. We chose to keep foraging and traveling distinct because we had evidence that coyotes often encounter fawns while traveling (Jensen, 2023) and thus this state could represent searching behavior, while traveling for blackberries would likely represent moving between foraging patches. Since there were not enough fixes from the 20-h window to accurately classify states, we classified each step in the 20 days surrounding the window. With movement states identified, we then filtered out the fixes outside of the 20-h window. We calculated the speed and turn angle at each step, then created a directedness metric by multiplying speed and turn angle. More directed steps were longer and straighter than less directed steps. We then fit separate generalized linear mixed models for foraging and traveling states with log directedness as the response variable, food type as the predictor, and individual as a random intercept. We considered variable effects significant if 95% CIs did not overlap zero.

With these same data, we used integrated Step Selection Analysis (iSSA; Avgar et al., 2016) to test our hypothesis that habitat selection would differ between coyotes consuming either fawns or blackberries. We generated 20 available steps for each used step using the amt package (Signer et al., 2019), with step lengths drawn from a gamma distribution and turn angles drawn from a von Mises distribution. We then interfaced with Dynamic World (Brown et al., 2022) using the rgee R package (Aybar et al., 2020) to extract the percent tree cover, grass cover, shrub and scrub cover, and built-up area cover at the end of each used and available step. Given Dynamic World is such high resolution (10 m), we also wanted a measure of habitat diversity near each step end. To do this, we calculated the mean percent tree, grass, shrub and scrub, and built-up cover at a 50-m resolution to capture a larger area around each step. We then calculated the average of the differences between each resolution's value for each cover type to estimate the patch diversity. We ultimately excluded grass cover and shrub and scrub cover because they were significantly negatively correlated with tree cover (−0.84, −0.83, respectively), leaving tree cover, built cover, and habitat diversity. We fit separate iSSAs for only the foraging and traveling states (four models total) and considered selection estimates to be significant if their standard errors did not overlap zero.

RESULTS

We collected 206 coyote scats during our study period, 41 in 2019, 75 in 2020, and 90 in 2021. Across years, fawns and blackberries were the largest components of the coyote diet in summer, making up 26% and 23%, respectively (Figure 2B).

Objective one: Dietary response to fawns and blackberries

We identified three competitive models for our fawn analysis (Appendix S1: Table S1). The top model with 34% weight was the ≤6-week-old fawn availability model, followed by the ≤3-week-old fawn availability model (33% weight), and the ≤3-week-old fawn availability with 1-week lag model (32% weight). All fawn availability variables in these competitive models had a positive effect on fawn consumption, with the effect from the top model being strongest (estimate [95% CIs] = 0.82 [0.52:1.12]). The only competitive model in our blackberry analysis was blackberry availability with no lag (99% of model weight; Appendix S1: Table S2), which had a positive effect on blackberry consumption (1.21 [0.88:1.55]). Thus, we found support for our predictions that fawn consumption would be positively related to younger fawn availability, and that there would be no lag in response to resource pulses (Figure 3).

Objective two: Does blackberry availability reduce fawn consumption?

In support of our APH, we found that the only competitive model predicting fawn consumption was the model that contained both fawn availability and blackberry availability (71% of model weight; Appendix S1: Table S3). Fawn availability had a slightly stronger positive effect (estimate [95% CIs] = 0.56 [0.18:0.94]) on fawn consumption compared to the negative effect from blackberry availability (−0.41 [−0.01:−0.81]; Figure 4A). We also note the fawn availability model was nearly competitive (delta AIC = 2.05; Appendix S1: Table S3) but it garnered only 25% of model weight. We calculated that the average weekly difference between fawn availability and fawn consumption (percent weighted occurrence) during nonpeak blackberry weeks was 8.9% (Figure 4B). After adding this amount to fawn consumption during peak blackberry weeks, we estimated that fawn consumption during our 12-week survey period would have been 7.8% larger (345.6 vs. 372.5 total weighted occurrence) without the blackberry peak.

Objective three: Comparing movement while consuming fawns and blackberries

We fit 76 coyotes with GPS collars during our three-year study period and were able to genetically link 23 scats to 16 of these coyotes (Appendix S1: Table S4, Figure S4). In contrast to our prediction, we found that coyotes

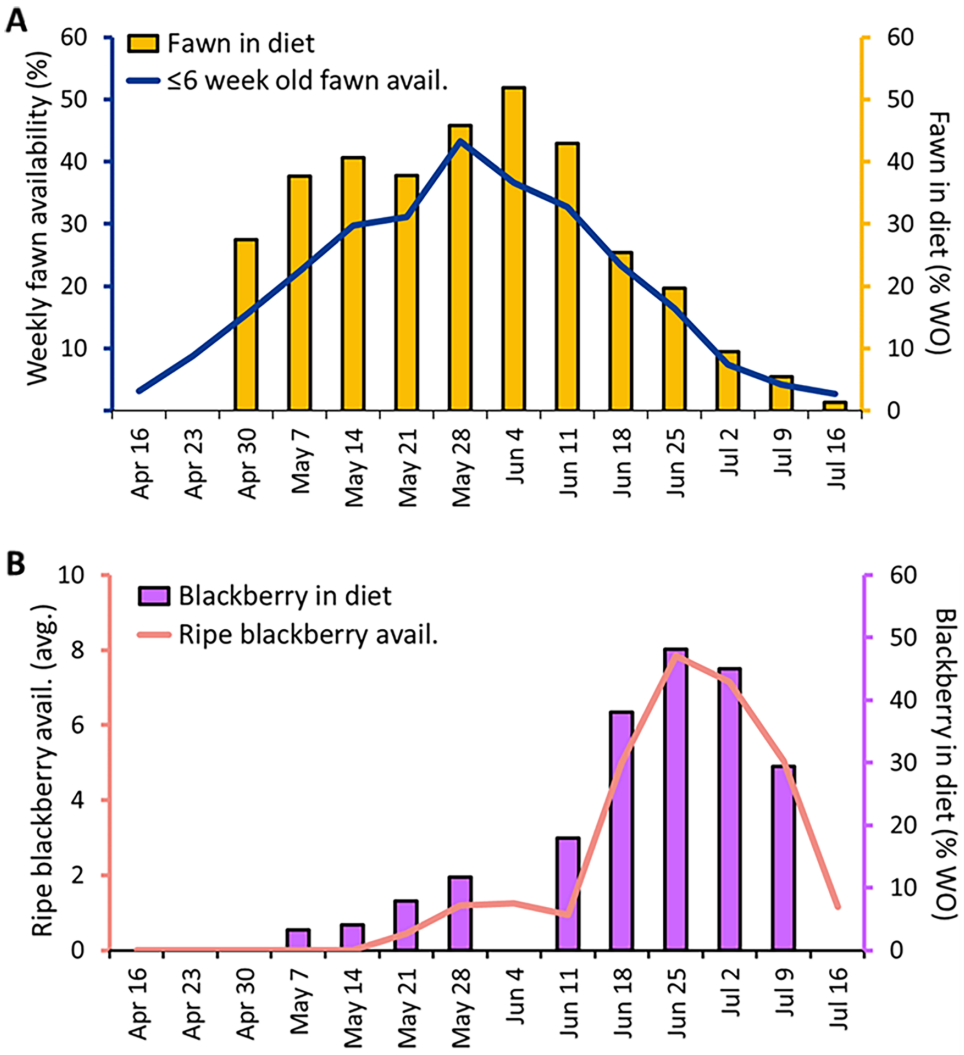

FIGURE 3 How coyotes dietarily responded to weekly changes in fawn and blackberry availability in South Carolina, USA, averaged across years from 2019, 2020, and 2021. (A) The percent weighted occurrence (% WO) of fawn consumption each week and the average ≤6-week-old fawn availability. (B) The same type of data, with only blackberries. Note that we were unable to collect dietary information during the first two weeks shown in the figure (April 16 and 23).

moved with similar directedness while foraging (estimate [95% CIs] = 0.12 [−0.42:0.66]) and traveling (−0.01 [−0.33:0.30]; Figure 5A) for fawns and blackberries. However, coyotes did select habitat differently while consuming fawns and blackberries (Figure 5B); coyotes avoided built cover while foraging (estimate ± SE = −0.174 ± 0.127) and traveling (−0.264 ± 0.160) for fawns but did not do so for blackberries. In partial support of our prediction, we found that coyotes avoided tree cover (−0.191 ± 0.090) and selected diverse patches (0.0171 ± 0.071) while traveling for fawns. Habitat diversity was the only significant predictor while consuming blackberries, where coyotes avoided diverse habitat while foraging (−0.371 ± 0.224) but selected for diverse habitat while traveling (0.115 ± 0.089).

DISCUSSION

While our results are largely correlational, they represent an important step toward quantifying how pulses of alternative foods can influence fine-scale predator behavior. Previous research on resource pulses has largely focused on a single pulse (Yang et al., 2010), but many consumers can respond to pulses of multiple different food items. In particular, apex carnivores are known to exploit resource pulses that occur at multiple trophic levels, with the potential for vegetative resource pulses to shift carnivore behavior away from vertebrate prey (Deacy et al., 2017; Jensen et al., 2024). Here we tracked coyote diets and the availability of two overlapping resource pulses at a weekly scale, showing how coyotes tracked the *shape* of

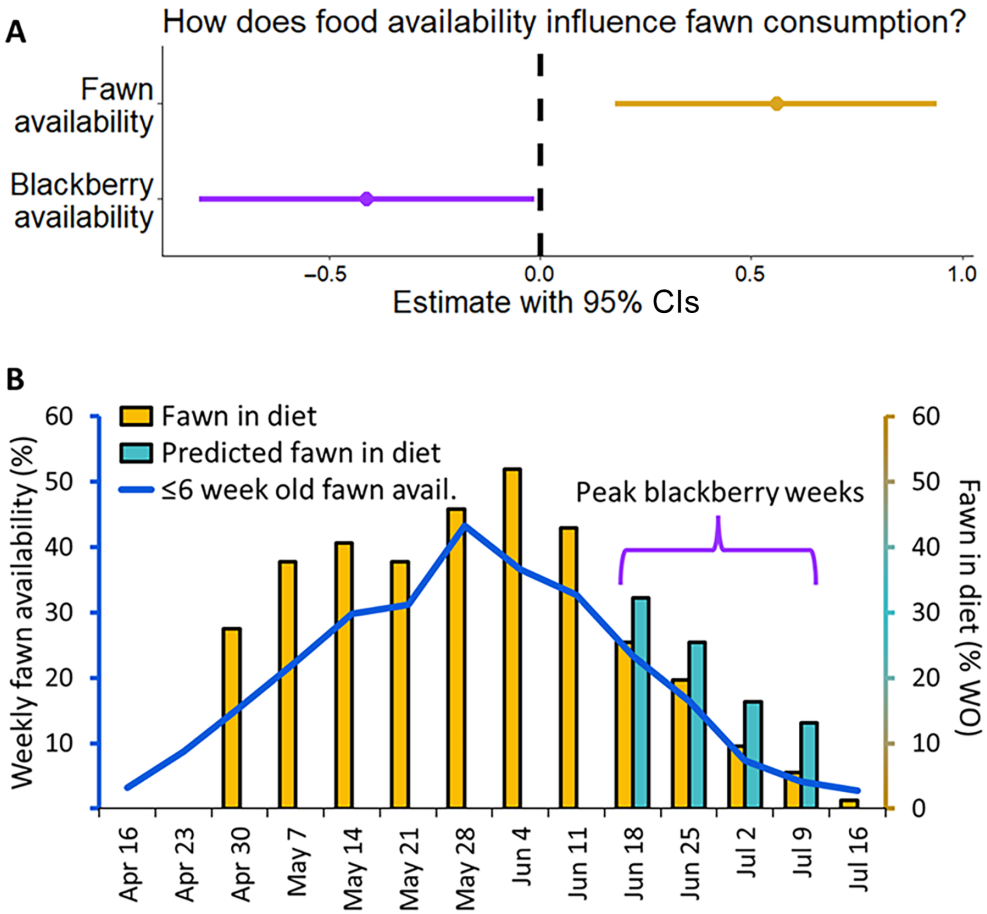

FIGURE 4 Two ways we quantified whether an alternative resource pulse (blackberries) reduced consumption of the first resource pulse (fawns) in South Carolina, USA. (A) Estimates for the effects of fawn availability and blackberry availability on fawn consumption from our top model. (B) Actual fawn consumption (percent weighted occurrence) to fawn consumption estimated using the relationship between fawn availability and consumption outside the weeks blackberries were peaking. Note that we were unable to collect dietary information during the first 2 weeks shown in the figure (April 16 and 23).

each pulse closely. When these pulses overlapped, we observed that the second pulse (blackberries) seemed to decouple the response to the first pulse (fawns). Thus, our findings provide the first quantitative support for our APH, where resource pulses of alternative food items can alter large carnivore behavior and predation on large herbivores.

One key difference between these two resource pulses was their length, where the fawn availability pulse was ~2× longer than the pulse of blackberry availability. Longer resource pulses facilitate larger consumer responses (Yang et al., 2010), and ungulates are generally known to closely time parturition across a population to shorten the window of vulnerable young availability (i.e., predator swamping). However, newborn white-tailed deer fawn availability in the southeast is relatively long (~90 days in our study area) compared to more northern regions (30–45 days; Carstensen et al., 2009; Huggler et al., 2023). This long pulse of availability combined with coyote behavioral plasticity has been speculated to be one explanation for why coyotes kill more fawns in the southeastern United States compared to other regions (Kilgo et al., 2019; Michel et al., 2020). Our findings add to this by highlighting how coyotes can change their behavior during the prolonged fawn pulse as alternative foods come available. Given that heterogeneity in predator behavior can lead to mismatches between actual and perceived risk by prey (Gaynor et al., 2019), we encourage future research to test the hypothesis that overlapping pulses of alternative food items could potentially negatively impact the adaptive potential of herbivore prey responses to predators.

We found partial support for our hypothesis that coyotes move differently while consuming fawns and blackberries. The most consistent difference we found was in selection for human development, where coyotes avoided human development while consuming fawns, but not

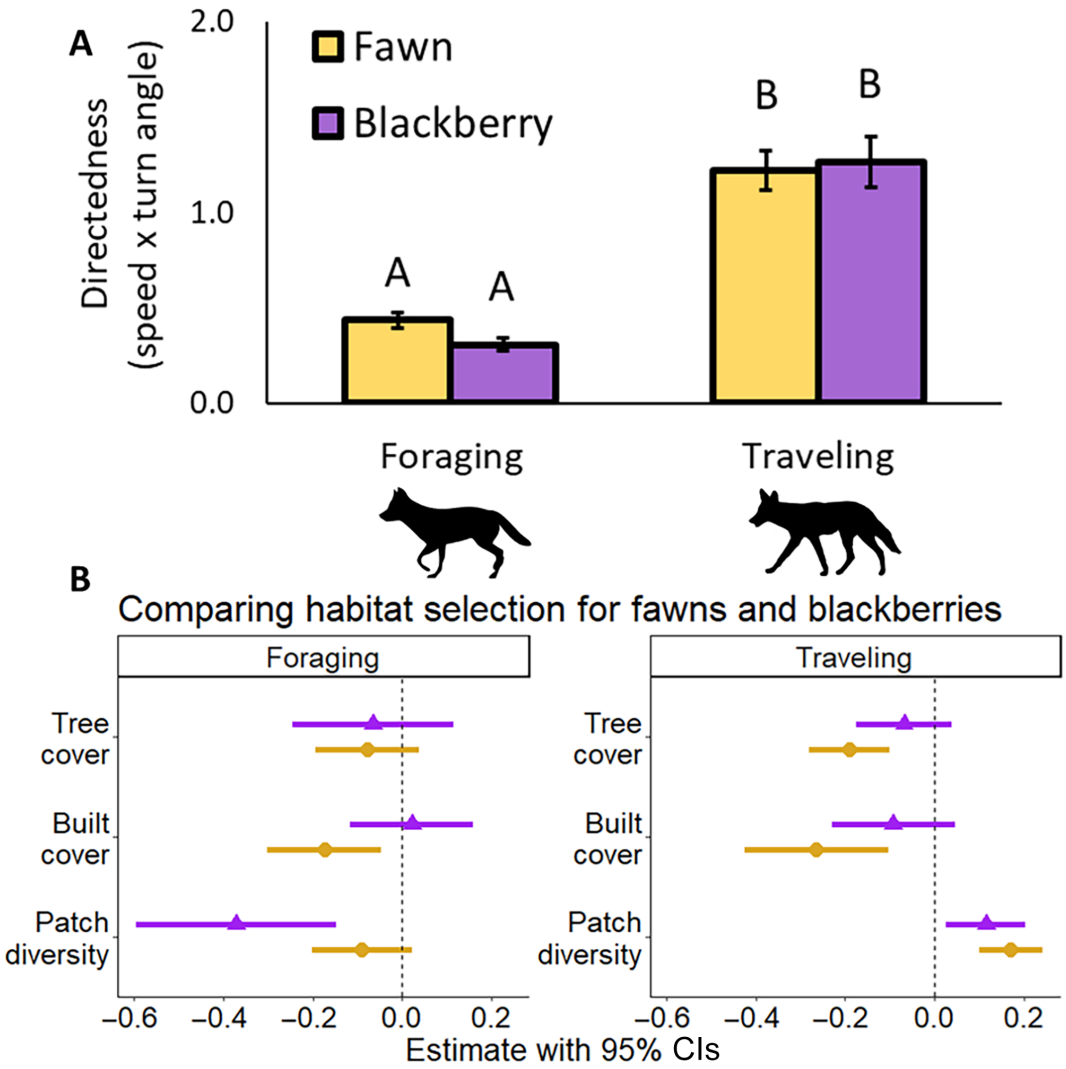

FIGURE 5 Comparing how and where coyotes moved during the period in which they likely consumed fawns or blackberries in South Carolina, USA. We linked scats to GPS-collared individuals and classified each GPS point during a 20-h window into one of three behavior states (encamped, foraging, or traveling). (A) The average directedness of movement (speed/turn angle) in the foraging and traveling states. We did not find any evidence that coyotes moved with different directedness while foraging for fawns and blackberries, as evidenced by the letters above the bars. (B) Step-selection estimates for three habitat variables, where the lines around the points represent 95% CIs.

while consuming blackberries. This could mean that coyotes perceive fawn encounter probability to be higher away from humans or that coyotes are more risk averse during the fawn pulse compared to during the blackberry pulse. However, we also found that female deer select birth sites that are closer to human development compared to what is available in their home range (Muthersbaugh, 2023). Given fawns stay relatively close to their birth sites during the first 3–6 weeks of their life (when most coyote predation occurs), this suggests that fawns are actually more available closer to humans and therefore coyotes avoiding human development while consuming fawns is incongruent with where they are most available. Collectively, these results suggest that fawns closer to humans would be safer from coyotes (i.e, support for the human shield hypothesis; Berger, 2007), though this is worth exploring further. Our other movement results were mixed—we found that there are some behavior state-dependent differences in selection but no significant differences in the directedness of movement. The behavior state-dependent differences could reflect functional differences in the utility of each state while foraging (in the general sense) for different foods; for example, our previous work suggests that coyotes are often in the traveling state when they encounter fawns (Jensen, 2023), while traveling would likely only be a means of moving between patches while searching for blackberries. Admittedly, more work is needed to tell whether these differences between fawns and blackberries represent a collective shift in behavior over time

or if coyotes can switch between foraging strategies at any given time (Lingle, 2000).

While our findings suggest predators behaviorally respond to pulsatile resources, there is a need to better understand how those behaviors scale up to influence population dynamics of both predator and prey. Specific to white-tailed deer in our study system, we predicted an 8% decline in fawn consumption associated with rising blackberry availability. Muthersbaugh et al. (unpublished manuscript) used a population projection model for white-tailed deer in our system to show that if blackberries were not available and 8% more fawns were eaten, the population of deer would decline, whereas models that include blackberry availability predict a stable or slightly declining population trend. By contrast, if managers were able to somehow increase fawn survival by a further 8% combined with modest alterations to current doe harvest quotas, the deer population could grow over time. Future field experiments are needed to explore if and by how much habitat management which promotes fruit mast (such as not spraying herbicide) reduces herbivore predation. However, given resource pulses can contribute to generalist predators maintaining high population densities (Caut et al., 2008), it is possible that increased availability of alternative food items could increase coyote density, potentially negating any potential decline in per-individual fawn consumption (Adams et al., 2010; Cherry et al., 2016). Alternatively, experiments have shown calorie-poor diets reduce coyote recruitment (Gese et al., 2016) and fruit-based canid diets are >3.75 times less calorically dense than meat-based diets (Gable et al., 2018; Ward et al., 2018). Therefore, there are competing hypotheses about how shifting diets to consuming berries could lead to growth or decline in coyote populations, and future research is needed to assess how phenological shifts in diet impact carnivore population dynamics.

Given many apex carnivores consume pulsatile non-vertebrate food resources, our findings suggest that knowledge of predator–prey dynamics in other systems could similarly benefit from tracking availability and consumption of food items at multiple trophic levels. Finding support for our APH in other systems is likely dependent on at least four factors. First, we studied an apex carnivore with an omnivorous diet that adjusted to consume a non-carrion food resource as it became available (Jensen et al., 2024). Generalist species are hypothesized to be most responsive to resource pulses (Ostfeld & Keesing, 2000), so we hypothesize that carnivores with more meat-based diets (e.g., many felids) are less likely to respond to pulses of resources at other trophic levels (Ruprecht et al., 2022). Second, the pulse of blackberry availability overlapped fawn availability, and dietary switching associated with APH is generally less likely to occur when pulses have smaller amounts of overlap (Deacy et al., 2017). Third, vegetative food resources were distributed across our entire study area and likely plentiful enough to compensate for at least some of the caloric and nutritional demands of the predator otherwise provided from vertebrate prey. Fourth, there were no bears or other larger carnivores in our system that might compete with coyotes during these resource pulses. Dominant competitors might serve to reduce resource pulse availability or restrict competitor movement, limiting the ability of subordinate carnivores to track multiple resource pulses (Ostfeld & Keesing, 2000).

We focused on two resource pulses that overlapped in space and time, yet coyotes and deer respond to other resource pulses throughout the year that could influence their ecology and the dynamics of the ecosystem. For deer, pulsatile fall and winter hard mast production has been found to be correlated with fawn recruitment the following summer (Aubin et al., 2022). In winter, coyotes often consume remains of adult deer left by hunters, and their use of this anthropogenic resource pulse likely reduces availability for other facultative scavengers that occasionally consume fawns (i.e., bobcats; *Lynx rufus*; Jensen et al., 2023). Thus, APH needs to not only be evaluated in other systems, but over entire annual cycles to account for how other pulsatile resource events could contribute to observed summer predator–prey dynamics.

We contend that both long-term phenological studies and fine-scale behavior studies will be needed to better understand how predators respond to multiple resource pulses. Long-term datasets are valuable because they can show how shifts in phenology lead to shifts in predator behavior over time (e.g., Deacy et al., 2017). Indeed, given that plant phenological responses are generally expected to outpace changes in mammal birth timing (Post & Forchhammer, 2008), there is a need to assess how global warming and extreme climatic events will differentially impact the phenological timing of multiple resource pulses and their cascading impact on predator–prey dynamics (Kharouba et al., 2018; Thackeray, 2016). Yet these longer term patterns could also be complicated to interpret—a recent study (Finnegan et al., 2023) found that salmon consumption was better predicted by salmon abundance and brown bear demographics (sex and age), rather than fruit phenology (as found by Deacy et al., 2017). By focusing on fine-scale (weekly) changes in food availability and predator behavior during a 3-year period when phenology was very similar, we provide new insight into how predators respond to overlapping resource pulses.

Collectively, our study adds additional evidence to the importance of resource pulses in the function of

ecological communities. Fluctuations in resources have long been known to influence the structure and function of ecological communities, with considerable nuance added to our understanding by studies that document the diverse ways top-down and bottom-up processes are influenced by discrete pulses of resources (Yang et al., 2008). For apex carnivores, while natural and anthropogenic alternative resource pulses have been previously shown to influence their behavior (Bautista et al., 2023; Deacy et al., 2017; Petroelje et al., 2021), we provide evidence that alternative food pulses have the potential to impact the consumption of large herbivores by large carnivores. Given that altered predation rates by large carnivores could have cascading impacts on large herbivore population dynamics and broader ecosystem processes (Owen-Smith & Mills, 2008; Ripple et al., 2014), these findings raise important future questions on how variation in the timing, magnitude, duration, and frequency of alternative food pulses influence ecosystems where large apex predators remain or are becoming established. Fortunately, with the increasing suite of methods available to researchers to simultaneously track ecosystem processes at multiple levels, ranging from predator behavior and demography to fine-scale vegetative productivity, there is potential to add important context to our understanding of predator–prey dynamics.

AUTHOR CONTRIBUTIONS

Alex J. Jensen designed the study, collected most of the data, performed the analyses, and led the drafting of the manuscript. Michael Muthersbaugh contributed fawn data and gave feedback on the manuscript. Keller Brogdon helped collect the data and gave feedback on the manuscript. Charles R. Ruth, Joseph W. Butfiloski, and John C. Kilgo helped design the study, provided guidance, and gave feedback on the manuscript. Jennifer Adams and Lisette Waits trained the lead author and helped collect some genetic data. David S. Jachowski helped design the study and helped write the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Jensen, 2025a, 2025b) are available from Figshare: https://doi.org/10.6084/m9.figshare.25757352.v1 and https://doi.org/10.6084/m9.figshare.25757400.v1, respectively.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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