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RESEARCH ARTICLE

Unintended consequences of wildlife feeders on spatiotemporal activity of white-tailed deer, coyotes, and wild pigs

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Abstract

Supplemental feeding of wild ungulates has long been and remains a common practice across Europe and North America. Yet by drawing animals together, supplemental feeding can have unintended, negative effects on individual species and broader ecological processes. These include increased risk of disease transmission, intraspecific and interspecific competition, and predation, which are of management concern for white-tailed deer (*Odocoileus virginianus*) in the southeastern United States given the arrival of nonnative wild pigs (*Sus scrofa*) and coyotes (*Canis latrans*). We conducted a field experiment between March and July of 2021 to assess the effects of supplemental feeding on spatiotemporal activity patterns of deer and wild pigs at wildlife feeders, and space use of coyotes in the Piedmont region of South Carolina, USA. We observed support for our hypothesis that interspecific competition through increased visitation by larger groups of competitor species reduces use of foraging sites by other subordinate ungulates, where feeders highly visited by wild pigs were rarely visited by deer. While adult deer and wild pigs generally did not shift their temporal activity patterns at feeders, juvenile temporal activity shifted to more frequent visits of feeders during the night, supporting our hypothesis that supplemental feed could increase risk to predator exposure, as

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coyotes tend to be active during crepuscular hours. Our findings suggest that supplemental feed put out to encourage deer activity could actually deter deer if wild pigs occupy that area, and has potential negative demographic effects if juveniles are at increased risk of predation. Collectively, based on our data, we do not recommend supplemental feeding in the southeastern United States where white-tailed deer, coyotes, and wild pigs co-occur. More broadly, given how widespread the legal use of supplemental feed remains across the United States, we encourage landowners and policymakers to consider the full suite of potential direct and indirect, short-term and long-term negative impacts supplemental feeding can have on both target and nontarget wildlife populations.

KEYWORDS

Canis latrans, competition, coyote, food subsidies, *Odocoileus virginianus*, *Sus scrofa*, white-tailed deer, wild pig

Supplemental feeding of wild ungulates by citizens, hunters, and wildlife managers alike is a common practice across Europe and North America (Putman and Staines 2004). Objectives of supplemental feeding include increasing antler or body size, increasing local population densities or sustaining populations in periods of lower food availability, diverting wild ungulates from agriculture and major vehicle corridors, and attracting individuals to specific locations for harvest, viewing, or capture for research purposes or vaccine administration (Andreassen et al. 2005, Milner et al. 2014, Sorensen et al. 2014, Goodenough et al. 2022, Muthoka et al. 2023). In the United States, supplemental feed has a long history of being used to influence the movement and abundance of ungulates (Inslerman et al. 2006, The Wildlife Society 2014). Most states allow some level of wild ungulate baiting, although many states have temporal or spatial limits to deer feeding (including limiting the ability to hunt directly over bait). For example, in Wyoming, USA, state and public land managers supplementally feed elk (*Cervus canadensis*) at multiple locations to influence their movement and enhance overwinter survival (Dean et al. 2004). Private landowners in many states provide supplemental feed for long periods of time. For example, in the Coastal Plain region of South Carolina, USA, supplemental corn feeding of white-tailed deer (*Odocoileus virginianus*; deer) is currently provided on many private properties for an average of 7.6 months each year (South Carolina Department of Natural Resources 2013).

Supplemental feeding of large herbivores has persisted despite increasing evidence that artificially drawing individuals together can have unintended, negative effects. Concentrated food sources can increase pathogen load in the environment and inflate contact rates between individuals (Murray et al. 2016), facilitating the transmission of diseases. For example, brucellosis seroprevalence levels were higher in elk populations frequenting winter feed grounds than populations in the Greater Yellowstone Ecosystem (Sorensen et al. 2014, Cotterill et al. 2018). Similarly, the effect of feeding on transmission of chronic wasting disease in wild ungulates is of high management concern across North America and Europe (Mysterud et al. 2019). Supplemental feeding also attracts nontarget species, such as mesocarnivores and wild pigs (*Sus scrofa*), with implications for interspecific interactions (Murray et al. 2016). The importance of supplemental feed to the diet of wild pigs has not been thoroughly assessed in the United States (Ballari and Barrios-García 2014), but it has been documented elsewhere as a major dietary component when mast is scarce (Dardaillon 1987, Giménez-Anaya et al. 2008, Mikulka et al. 2018). Further, supplemental corn is intentionally used in some countries to attract wild boar to hunting grounds or dissuade

agricultural crop damage (Schley and Roper 2003, Calenge et al. 2004, Ballari et al. 2015, Mikulka et al. 2018). Because concentrated food can increase species interactions and aggression (Milner et al. 2014, Theimer et al. 2015), and dominant species tend towards higher body mass than subordinate species (Morse 1974, Fisler 1977, French and Smith 2005), wild pigs might spatially or temporally displace deer from feeding sites (Crank 2016). To our knowledge, the extent to which supplemental feeding could enhance interspecific competition between wild pigs and deer has not been evaluated.

By concentrating herbivores at point sources on the landscape, supplemental feed could indirectly alter the activity of large predators. Based on optimal foraging theory, predator behavior should maximize net energetic gains, such as through increased encounter rates with prey (MacArthur and Pianka 1966). This suggests that predators might intensify their presence around anthropogenic food subsidies that aggregate target game species and nontarget small mammals (Boutin 1990, Doonan and Slade 1995). Yet even if increased predator presence does not lead to a higher predation rate, it could affect ungulate behavior and spatiotemporal activity (Say-Sallaz et al. 2019). Despite potential ramifications for prey fitness, few studies have analyzed predator movement in relation to supplemental feed. Notably, separate investigators in Georgia reported that bobcats (*Lynx rufus*) and red-tailed hawks (*Buteo jamaicensis*) were both closer than expected by random chance to northern bobwhite (*Colinus virginianus*) feeding areas (Godbois et al. 2004, Turner et al. 2008), demonstrating that supplemental feed can unintentionally induce a spatial response from predators. It remains largely unexplored if shifts in large herbivore spatial activity caused by bait induce changes in predator spatial activity (but see Woodruff and Jimenez 2019).

Our goal was to conduct a field experiment assessing the effects of supplemental feeding on spatiotemporal activity patterns of deer and wild pigs, and space use of their primary predator (coyotes [*Canis latrans*]) in the Piedmont region of South Carolina. We hypothesized that interspecific competition through increased visitation by larger groups of competitor species reduces use of foraging sites by other subordinate ungulates. We predicted that supplemental corn feeding that attracted large groups of wild pigs would negatively affect visitation by deer. We also predicted that wild pigs and deer temporally partition when they visit shared feeding sites and that subordinate competitors (i.e., deer) would adjust their temporal activity to decrease overlap with wild pigs. Our second hypothesis was that supplemental feed alters the space use of large herbivores and increases their predator exposure by providing opportunities for predators to key in on them. Given the primary protein coyotes consume during the juvenile rearing season is white-tailed deer (Schrecengost et al. 2008, Jensen 2023), we focused our experiment during the spring and summer when we predicted that coyotes shift their core area of use towards feeders to increase the probability of encountering juveniles.

STUDY AREA

We conducted our study on approximately 6,100 ha of nearly contiguous private land in the Piedmont of South Carolina. Characterized by gently rolling terrain, this physiographic region occurs between the Blue Ridge and Coastal Plain provinces. Elevation in the study area ranged from approximately 120 m to 180 m and average monthly temperature for the area ranged from 6.2°C to 27.2°C, with an annual mean of 16.9°C. The climate was subtropical, receiving an average of 119.5 cm of annual precipitation. Red clay, followed by sandy loam, were the primary soil types. Much of the study area was historically savanna that was grazed by elk, white-tailed deer, and American bison (*Bison bison*) and likely occupied by the Cherokee, Yuchi, Shawnee, Chickasaw, Apalachee, Yamasee, and Westo people. By the late 1700 s, these large herbivores and Indigenous peoples were removed from our study area by colonists as the savanna was converted to cotton and tobacco fields, which were worked by slaves (Edmonds 2001). At the time of our study, the area mainly consisted of managed loblolly pine (*Pinus taeda*) stands in various stages of ecological succession. Timber management practices included thinning, clearcutting, and prescribed burning. Pines were interspersed in areas with hardwoods, particularly hickory (*Carya* spp.), white oak (*Quercus alba*), and southern red oak (*Q. falcata*). Soft mast in the understory included persimmon (*Diospyros*

virginiana), blackberry (*Rubus alleghensis*), and muscadine (*Vitis rotundifolia*). Nonnative wild pigs were recorded near our study area by 2005, and coyotes were first recorded near our study area in 1982. In the year preceding our study (2020), Youngman (2023) estimated coyote density for our study area to be 70.62 coyotes/100 km², representing the highest density of coyotes in South Carolina.

METHODS

Experimental design

We examined the effects of supplemental feeding on the spatiotemporal activity of white-tailed deer and wild pigs during the white-tailed deer fawning season of 2021, from 30 March to 6 July, with a combination of wildlife cameras and global positioning system (GPS) collars. We expected feed use by wild pigs would affect use by other species, so we deployed wildlife feeders across a gradient of estimated wild pig use with a stratified random sampling design. We identified areas of high, medium, and low wild pig use based on results from a large array of unbaited cameras across our study area (Saldo et al. 2023; Figure 1). We then randomly identified 10 potential sampling locations per use intensity category from which to select feeder locations. In an attempt to maximize potential overlap with GPS-collared coyotes in our study area (for a full description of coyote capture and tracking methods see Jensen 2023), we selected 5 locations within each of our 3 wild pig use categories to place a feeder based on proximity to collared individuals (based on GPS points collected between 15 February and 15 March).

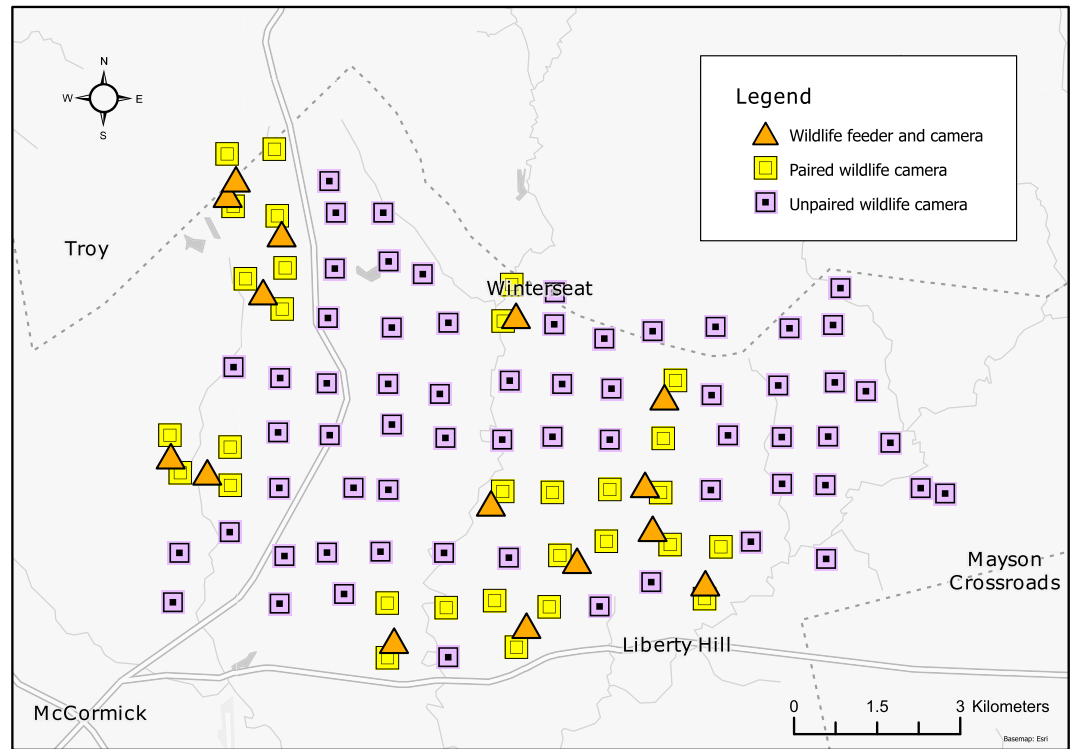


FIGURE 1 Wildlife feeder (orange triangle), paired unbaited wildlife camera (yellow square), and unpaired unbaited wildlife camera (purple square) locations near McCormick, South Carolina, USA, in spring and early summer 2021.

In late March we deployed 15 Moultrie 30-Gal Pro Hunter II Tripod self-dispensing feeders (Moultrie Feeders, Birmingham, AL, USA) 250–500 m away from an existing unbaited camera with which they were paired (Figure 1). We monitored the feeders with Bushnell CORE DS No Glow Trail Cameras (Bushnell, Overland Park, KS, USA) set to take one photograph upon detection, with a delay of one minute between triggered events. We allowed a week for wildlife acclimation to inactive feeders before monitoring them for 6 weeks (starting on 30 March), then added shelled corn immediately after wild turkey (*Meleagris gallopavo*) hunting season (1 April to 10 May). We programmed feeders to dispense approximately 3 pounds of corn at 0700 and 1800 each day to resemble amounts reported on hunting online forums. Feeders were active for 2 months (study concluded 6 July) and checked weekly to ensure adequate operation and continuous corn supply. For our temporal analysis comparing baited and unbaited sites, we included an additional 15 cameras near feeders from our larger unbaited array (Figure 1) for a total of 30 unbaited cameras to 15 feeder cameras.

Spatial overlap of deer and wild pig activity

We classified all feeder photographs to species and recorded the number of deer and wild pigs in each photograph over 14 weeks (30 March to 6 July) using Timelapse2 (Greenberg et al. 2019). We compiled weekly species detection histories at each site using the camtrapR package (Niedballa et al. 2016). We then divided the count of photographs of a species at a given camera site by the sampling effort (i.e., 7 days) to gain a photographic rate that we interpreted as the relative activity of that species at that location. We developed a set of 6 *a priori* models to investigate factors that we hypothesized could influence relative activity of deer and wild pigs at feeder sites during the unbaited and baited survey periods combined. To test for a negative effect of interspecific competition on each species, we included either deer or wild pig relative activity at each site, as calculated above. We also predicted that site-specific corn availability (unavailable or available), human relative activity (detections per week), and mean deer and wild pig group size (per week) would influence relative activity of both wild pigs and deer at feeder sites. We used generalized linear mixed models to assess support for these potential predictors of large mammal relative activity, including feeder site as a random effect. We compared models based on the Akaike's Information Criterion adjusted for small sample sizes (AIC_c; Akaike 1974, Hurvich and Tsai 1989, Burnham and Anderson 2002), where we considered models with $\Delta\text{AIC}_c < 2$ to be competitive and then determined our top performing model by assessing AIC weights of top models in that competitive set. We considered covariate effects within the top model as significant if their 95% confidence intervals did not overlap zero. We conducted these analyses in R (R Core Team 2021) with the glmmTMB (Brooks et al. 2017) and MuMIn (Bartoń 2020) packages.

Temporal overlap of deer and wild pig activity

We assessed if supplemental feeding changed the temporal activity of deer and wild pigs by comparing diel activity patterns at unbaited and baited sites. We classified all deer photographs from feeder cameras and unbaited control cameras to adult male, adult female, young of the year of unknown sex (i.e., juvenile), or a combination thereof. Because of the volume of photographs collected, we limited our survey period for this analysis to the last 2 weeks of the study (23 June through 6 July), a period in which we assumed feeder use and juvenile activity would be greatest. For this analysis, we considered photographic detections of the same species (and in the case of deer, demographic group) at a site separated by at least one minute to be independent samples of the underlying continuous activity of that group. We converted detection event times to radians and used the kernel density estimation developed by Ridout and Linkie (2009) to compare the diel activity of adult male deer, adult female deer, juveniles, and wild pigs at unbaited and baited sites. We first examined if the temporal activity of a group changed in the presence of supplemental feed and then made pairwise comparisons between groups at baited and unbaited

sites. We used the $\hat{\Delta}_4$ estimator because all groups had >50 detection events. Taking the minimum of the 2 density estimates at every time point by measuring the area under the curve yielded the coefficient of overlap (Δ), which ranges from 0 (no overlap) to 1 (complete overlap). We calculated confidence intervals for each pairing using 10,000 smoothed bootstraps (Meredith and Ridout 2018) and considered a lack of overlap between confidence intervals an indication of statistical significance. We conducted analyses in R (R Core Team 2021) with the overlap package (Ridout and Linkie 2009).

Coyote space use

In January–March of our study year, Jensen (2023) captured and fit GPS collars on 15 adult coyotes within our study area. We classified GPS data into an unbaited survey period and a baited survey period, each 6 weeks long and separated by 2 weeks to allow for corn discovery and acclimation by collared coyotes. The frequency of GPS fixes changed over time, so we tried to standardize across periods as much as possible by using fixes taken every 7 hours for the first 3 weeks of the unbaited survey period and fixes taken every 6 hours for the remainder of the study. We employed the Brownian bridge method (Bullard 1991, Horne et al. 2007) to estimate fixed kernel utilization distributions (UDs) using the adehabitatHR package (Calenge 2006) in R (R Core Team 2021). We incorporated a field-derived collar error of 22.5 m for coyotes, used a grid size of 100, and kept the extent at default. To test our prediction that coyotes with a feeder in their home range shift their core use area to be closer to a feeder when it is active, for each coyote we exported shapefiles of the 95% UD contour representing the home range and the 50% UD contour representing the core area of use during each 6-week period. We were able to estimate home ranges for 11 female coyotes and 4 male coyotes, of which 7 females and 3 males had at least one feeder in their home range during our study. We used the Near tool in ArcGIS Pro 3.0.0 (Esri, Redlands, CA, USA) to measure the shortest distance from core area edge to a feeder for each individual that had a feeder in its home range. For these individuals, we then used Wilcoxon matched-pairs signed rank tests to assess if home range size, core area size, and distance from core area edge to the nearest feeder differed between the unbaited and baited survey periods. We considered results significant if $P \leq 0.05$ and marginally significant if $P \leq 0.1$.

RESULTS

We collected 97,920 photographs over the 14 weeks that we monitored unfilled (6,185 photographs) and then active (91,735 photographs) feeders. We recorded deer in 37,663 of these photographs (unfilled = 91, active = 37,572), wild pigs in 27,881 (unfilled = 21, active = 27,860), and coyotes in 44 (unfilled = 25, active = 19). The maximum number of photographs of deer at a single site in a week was 1,797 and the maximum number of photographs of wild pigs was 1,335, with considerable variability in relative activity of deer and wild pigs across sites. Mean group size of deer at sites with deer was 1.34 individuals (SD = 0.28) and maximum group size was 7, whereas mean group size of wild pigs at sites with wild pigs was 2.23 individuals (SD = 1.27) and maximum group size was 19.

The top model predicting relative activity of both deer and wild pigs at a site contained the relative activity of the other species and the availability of corn (Tables 1 and 2). Relative activity of deer and wild pigs each increased once feeders were filled after 6 weeks; the median number of weekly photographs for the baited period was >100 times greater than the median for the unbaited period. Relative activity of wild pigs and deer were inversely related to one another (Figure 2). Averaged across the 15 feeders, baited sites without wild pigs were predicted to capture over 600 (SE = 140.29) weekly photographs of deer. Given our cameras had a delay of 1 minute between photographs, this equates to over 10 hours of feeder use by deer per week. Conversely, baited sites with approximately 10 hours of wild pig use were predicted to only have 30 ± 8.34 minutes of deer use on average per week.

TABLE 1 *A priori* candidate models, as ranked by the change in Akaike's Information Criterion for small sample sizes (AIC_c) and Akaike weight (w_i), for evaluating the effects of interspecific site use and supplemental feed availability on the relative activity of white-tailed deer near McCormick, South Carolina, USA, in spring and early summer 2021. Wildlife feeder site was included as a random effect in all models except the null.

Model ^a	K^b	AIC_c	ΔAIC_c	w_i
$\beta_0 + \beta_1(\text{pig}) + \beta_2(\text{corn})$	5	1,705.55	0.00	0.796
$\beta_0 + \beta_1(\text{human}) + \beta_2(\text{pig}) + \beta_3(\text{group}) + \beta_4(\text{corn})$	7	1,708.27	2.72	0.204
$\beta_0 + \beta_1(\text{corn})$	4	1,754.44	48.90	0.000
$\beta_0 + \beta_1(\text{human})$	4	1,948.86	243.31	0.000
Null	2	1,949.80	244.25	0.000
$\beta_0 + \beta_1(\text{pig}) \times \beta_2(\text{group})$	6	1,950.94	245.39	0.000

^aVariables included wild pig relative activity (pig), corn availability (corn), human relative activity (human), and mean wild pig group size (group).

^bNumber of parameters.

TABLE 2 *A priori* candidate models, as ranked by the change in Akaike's Information Criterion for small sample sizes (AIC_c) and Akaike weight (w_i), for evaluating the effects of interspecific site use and supplemental feed availability on the relative activity of invasive wild pigs near McCormick, South Carolina, USA, in spring and early summer 2021. Wildlife feeder site was included as a random effect in all models except the null.

Model ^a	K^b	AIC_c	ΔAIC_c	w_i
$\beta_0 + \beta_1(\text{deer}) + \beta_2(\text{corn})$	5	1,360.54	0.00	0.675
$\beta_0 + \beta_1(\text{human}) + \beta_2(\text{deer}) + \beta_3(\text{group}) + \beta_4(\text{corn})$	7	1,363.00	2.46	0.197
$\beta_0 + \beta_1(\text{corn})$	4	1,363.87	3.33	0.128
$\beta_0 + \beta_1(\text{deer}) \times \beta_2(\text{group})$	6	1,515.96	155.42	0.000
$\beta_0 + \beta_1(\text{human})$	4	1,521.83	161.29	0.000
Null	2	1,525.40	164.86	0.000

^aVariables included deer relative activity (deer), corn availability (corn), human relative activity (human), and mean deer group size (group).

^bNumber of parameters.

For our temporal overlap analysis, which focused on the last 2 weeks of the study, we found mixed evidence of shifts in temporal activity in response to baiting. Baited sites had 16.40 times as many detections of adult male deer as unbaited sites (1,903 vs. 116), 13.63 times as many detections of adult female deer (3,639 vs. 267), and 51.38 times as many detections of wild pig (7,142 vs. 139). Juveniles had very similar detection at baited sites and unbaited sites (72 vs. 67). Diel temporal activity was fairly similar at baited and unbaited sites for adult male deer ($\Delta = 0.63$, 95% CI = 0.55, 0.71; Figure 3A) and adult females ($\Delta = 0.71$, 95% CI = 0.67, 0.76; Figure 3B), but temporal activity of juveniles had low overlap between baited and unbaited sites ($\Delta = 0.37$, 95% CI = 0.27, 0.49; Figure 3C). Wild pigs had similar temporal diel activity at baited and unbaited sites ($\Delta = 0.73$, 95% CI = 0.65, 0.79; Figure 3D). Based on bootstrap confidence intervals, half of our species group pairings had lower temporal overlap in diel activity at baited sites. Male and female deer had lower temporal overlap in diel activity with each other at baited sites ($\Delta = 0.65$, 95% CI = 0.63, 0.67) than unbaited sites ($\Delta = 0.78$, 95% CI = 0.70, 0.86), female deer and wild pigs had lower temporal overlap in diel activity at baited sites ($\Delta = 0.72$, 95% CI = 0.70, 0.74) than unbaited sites

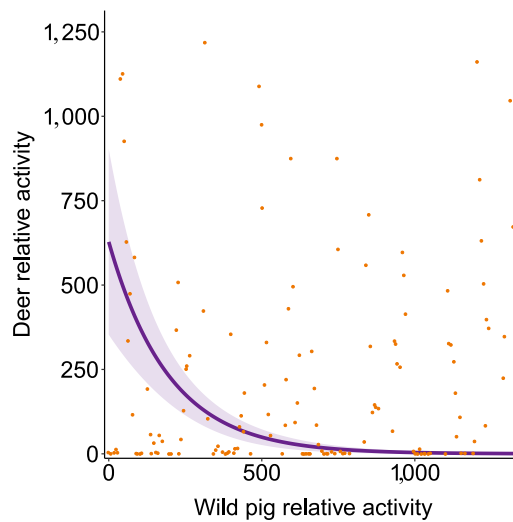


FIGURE 2 Predicted effect of the relative activity of wild pigs on the relative activity of white-tailed deer in the presence of supplemental feed near McCormick, South Carolina, USA, in spring and early summer 2021. Purple shaded area shows the 95% confidence interval and orange circles show 205 raw data points. Relative activity is presented on a weekly scale of photograph rate from wildlife cameras.

($\Delta = 0.88$, 95% CI = 0.80, 0.93), and juveniles and wild pigs had lower temporal overlap in diel activity at baited sites ($\Delta = 0.38$, 95% CI = 0.33, 0.45) than unbaited sites ($\Delta = 0.61$, 95% CI = 0.50, 0.73; Table 3).

For the 10 coyotes with at least one feeder in their home range, during the unbaited survey period, the median home range size was 4,316.91 ha ($\bar{x} = 6,282.53$, SD = 7,753.51) and the median core area size was 566.84 ha ($\bar{x} = 967.20$, SD = 990.90). Following baiting, the median home range size of these 10 coyotes was 3,596.59 ha ($\bar{x} = 5,672.39$, SD = 7,385.18) and the median core area size was 272.25 ha ($\bar{x} = 725.93$, SD = 1,098.85). We did not find evidence of a difference in home range size of coyotes ($P = 0.432$) or core area size of coyotes ($P = 0.432$) following baiting. We found marginal support ($P = 0.08$) for coyotes increasing their core area distance to the nearest feeder following the addition of corn ($\bar{x} = 112.93$, SD = 235.60 prior to addition of corn, $\bar{x} = 1,405.67$, SD = 2,933.79 following addition of corn).

DISCUSSION

Our experiment highlights how supplemental feeding increases localized relative activity of ungulates, and increases the potential for intraspecific and interspecific interactions in our system. Ungulate species tended to avoid each other in space, where deer and wild pigs had lower relative activity at feeders frequently visited by the other species. Given that wild pigs are territorial (Gabor et al. 1999, Sparklin et al. 2009, Kilgo et al. 2021) and adults usually have higher body mass than deer (Kays and Wilson 2009), they were likely the dominant species at feeders (Morse 1974, Fislser 1977, French and Smith 2005) and were spatially avoided by deer. In support of previous studies (Crank 2016), we observed lower temporal overlap in diel activity between wild pigs and both adult female deer and juveniles, suggesting deer use both spatial and temporal partitioning to avoid interspecific competition in our system. Juveniles in particular showed low temporal overlap with wild pigs, whereas adult male overlap with wild pigs did not change, suggesting that deer responses to supplemental feed can be demographic-specific and potentially influence juvenile and maternal care behaviors.

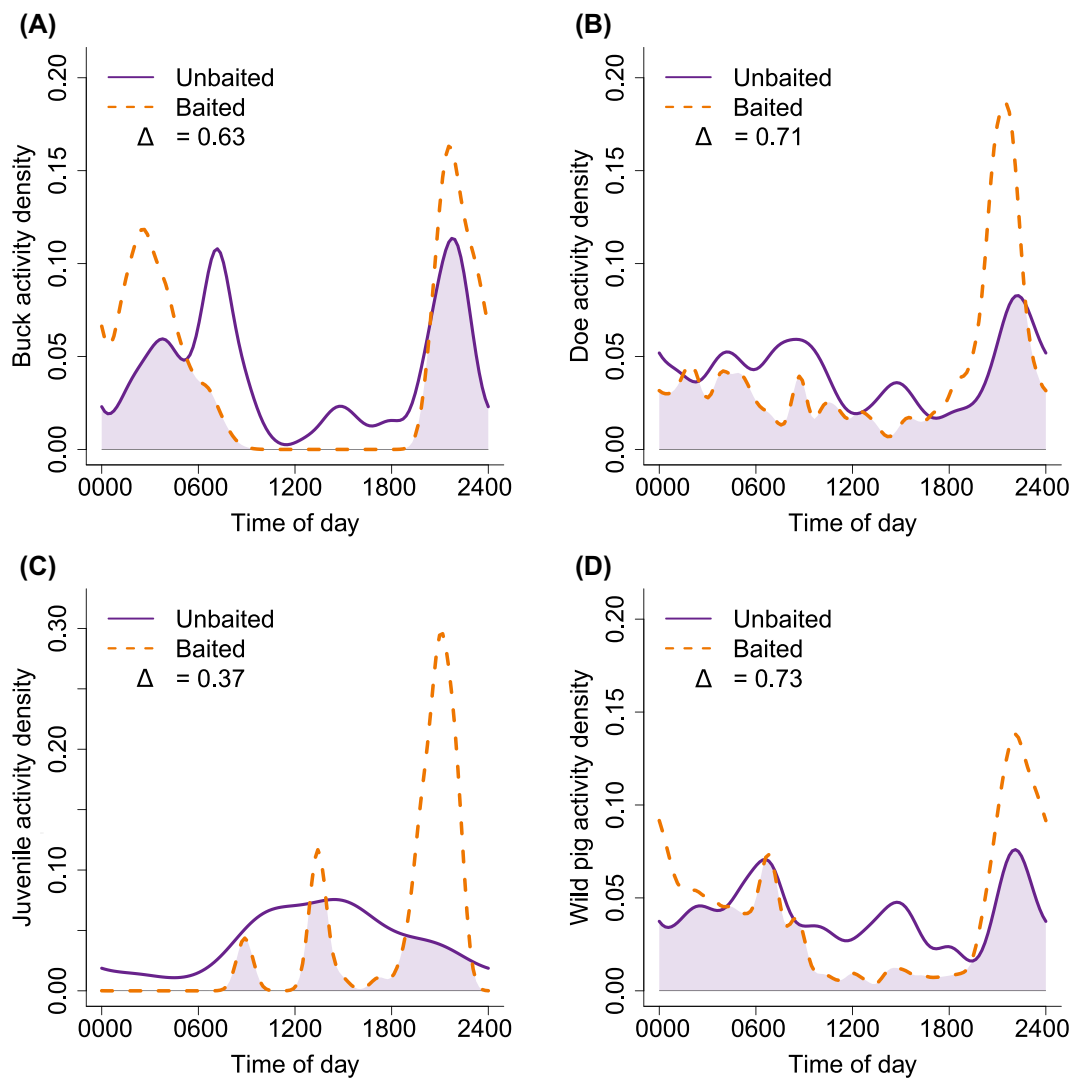


FIGURE 3 Overlap in diel activity between unbaited sites and baited sites for (A) adult male deer (buck), (B) adult female deer (doe), (C) juvenile deer, and (D) wild pigs near McCormick, South Carolina, USA, in late June and early July 2021. Shading under the curves represents the density of overlap and Δ is the coefficient of overlap, which ranges from 0 (no overlap) to 1 (complete overlap). Corn was dispensed from wildlife feeders at 0700 and 1800 each day, and sunset occurred around 2045.

We observed support for our hypothesis that interspecific competition among deer and wild pigs influences their use of feeders. In a concurrent multi-year unbaited camera study, we showed that deer were less likely to use areas occupied by wild pigs in the fall (Saldo et al. 2023), and Muthersbaugh (2023) showed that in the summer deer were more likely to use areas immediately after they were vacated by wild pigs. Similarly, at a nearby study site, Garabedian et al. (2023) suggested that white-tailed deer use fine-scale shifts in space use to minimize competition with wild pigs. Our findings add experimental evidence to these correlative studies to confirm that wild pigs directly affect deer spatial and temporal behavior through interference competition. While our study took place during the spring and summer when grasses, forbs, and browse were likely abundant, potentially limiting the detrimental impact of the lost opportunity for deer to feed on corn at our feeders, lost opportunity costs due to interspecific

TABLE 3 Coefficients of diel activity overlap between invasive wild pigs and white-tailed deer adult males, adult females, and young of the year of undetermined sex (i.e., juveniles) near McCormick, South Carolina, USA, in late June and early July 2021. The 95% confidence intervals, as calculated from 10,000 smoothed bootstrap samples, are shown in parentheses. Coefficients for unbaited sites are above the diagonal and coefficients for baited sites are below the diagonal.

Group	Male deer	Female deer	Juvenile	Wild pig
Male deer	1	0.78 (0.70–0.86)	0.44 (0.35–0.57)	0.77 (0.68–0.85)
Female deer	0.65 (0.63–0.67)	1	0.61 (0.50–0.70)	0.88 (0.80–0.93)
Juvenile	0.35 (0.30–0.39)	0.59 (0.52–0.65)	1	0.61 (0.50–0.73)
Wild pig	0.76 (0.74–0.78)	0.72 (0.70–0.74)	0.38 (0.33–0.45)	1

competition could be enhanced in fall and winter because of limited and patchy foraging resources (Yarrow 1987, Elston and Hewitt 2010) and deserve further study. In addition, given anthropogenic food subsidies can increase wild pig populations (Bieber and Ruf 2005, Geisser and Reyer 2005) and we repeatedly saw female wild pigs bring piglets to feeders, we encourage managers to consider the longer-term impacts of sustained supplemental feeding on wild pig populations.

Juveniles visited sites with supplemental feed primarily during times of peak predator activity. Juveniles were diurnal at unbaited sites, but at baited sites they showed an additional large peak in activity 2–3 hours after the timed evening feeding, suggesting female deer occasionally brought juveniles to feeders. In a concurrent study of GPS-collared juveniles, Muthersbaugh (2023) found that mothers that visited juveniles frequently at night had a higher probability of their juvenile being predated. This suggests crepuscular visits by juveniles to feeders could help predators locate and prey upon juveniles. However, we found no support for our predator attraction hypothesis as the overall number of photographs of juveniles at feeders was low and our GPS-collar data suggested that coyotes did not shift their core area of use toward feeders. We attribute this lack of predator response to our scale of investigation, limited sample size (10), and the short duration of our study. Breeding coyotes are central place foragers during the summer months when rearing pups (Jensen 2023), so foraging movements could still frequent areas near feeders without coyotes shifting their core area (which is often focused near their den or resting site). Also, we baited feeders for only 8 weeks at locations where feeders had never been placed before, and predators have been noted to learn to target predation of herbivores at feeding sites when those sites are established for longer periods of time (Woodruff and Jimenez 2019). Thus, given supplemental feeding is typically sustained over longer time periods that could facilitate learning by predators, we encourage longer-term studies of supplemental feeding on predator and prey behavior in this system. Regardless, given juvenile predation rates were relatively high in our study system and a lack of recruitment is limiting growth in this deer population (Muthersbaugh 2023), any potential negative impact of feeders shifting juvenile activity towards evening hours when coyotes are active should be of concern to managers.

Aggregation of deer and wild pigs at feeder sites such as we observed could have a number of additional consequences. Concentrating individuals together at a point source can facilitate intraspecific and interspecific disease transmission (Murray et al. 2016), and those sites can serve as reservoirs of infection for long periods of time. For example, chronic wasting disease prions excreted from infected animals can reside in the soil of a site for multiple years (Smith et al. 2011, Escobar et al. 2020). Similarly, aggregation of wild pigs can facilitate spread of several prominent diseases of concern to wildlife managers and domestic pig producers, including pseudorabies, foot-and-mouth disease, swine brucellosis, and African swine fever (Miller et al. 2017). Beyond the impact on large herbivores themselves, studies have shown that ground-nesting birds can be negatively affected by wild pigs (Oja et al. 2015, Sanders et al. 2020) drawn in by supplemental feed, and herpetofauna in the vicinity of feed are also likely vulnerable to predation and habitat destruction by wild pigs

(McDonough et al. 2022). Thus, the provision of feed can have cascading direct and indirect effects on entire ecosystems that need to be considered during local property management and wildlife policy decisions related to supplemental feeding (Milner et al. 2014).

MANAGEMENT IMPLICATIONS

Our results suggest that the benefits of supplementally feeding deer could be outweighed by the potential to increase interspecific competition with invasive wild pigs. Many hunters use feeders to attract deer to their properties or focused areas where they hunt, but our results suggest that when wild pigs are also present, they displace deer and likely lower subsequent chances of encountering deer at that site. Further, with few natural predators on the landscape, evidence suggests subsidized wild pig populations could outcompete native white-tailed deer for resources as has been observed in other systems globally. Negative impacts of supplemental feeding could also manifest in more subtle ways, where shifts in juvenile activity associated with feeders could increase the risk of juveniles being preyed upon by predators. While coyotes did not appear to key in on ungulate activity at feeders during our 8-week baited survey period, given supplemental feed is typically placed out for extended periods of time, additional research is needed to determine how longer duration feeding affects coyote behavior. Lastly, chronic wasting disease is one of the leading threats to current deer management across North America, and concentrated animal use also increases the potential for both intraspecific and interspecific disease transmission. Collectively, based on our data we do not recommend supplemental feeding in the southeastern United States where white-tailed deer, coyotes, and wild pigs co-occur. More broadly, given how widespread the legal use of supplemental feeding remains across the United States, we encourage landowners and policymakers to consider the full suite of potential direct and indirect, short-term and long-term negative effects supplemental feeding can have on both target and nontarget wildlife populations.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

All coyote capture and handling procedures were permitted by Clemson University Institutional Animal Care and Use Committee (permit AUP 2018-031) and the United States Department of Agriculture Forest Service (permit USFS 2018-031).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available because of privacy or ethical restrictions.

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