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Intra-annual variation in oak masting affects wildlife feeding behavior

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Abstract

Oaks (*Quercus* spp.) provide an important food source for many wildlife species throughout the fall and winter. Most research evaluating oak masting patterns and the subsequent behavioral responses of wildlife focuses on the annual temporal scale. However, patterns in masting at the seasonal temporal scale may be important for wildlife behavior. We designed a study quantifying seasonal oak masting patterns of 3 oak species (water oak, *Q. nigra*; laurel oak, *Q. laurifolia*; and swamp chestnut oak, *Q. michauxii*) and linking those patterns to visitation and feeding behavior of 3 primary consumers (white-tailed deer, *Odocoileus virginianus*; gray squirrel, *Sciurus carolinensis*; and raccoon, *Procyon lotor*). We used seed traps to monitor the seasonal masting pattern of 205 trees in the fall of 2021 and 2022 and used camera traps concurrently to monitor wildlife behavior associated with a subset of 30 trees. Seasonal masting patterns differed between oak species both within a season and across years, and the timing of mast varied within oak species across years. White-tailed deer tended to visit swamp chestnut oak as the number of acorns increased and consumed their acorns. Gray squirrels and raccoons tended to visit laurel oak and consume water oak acorns with gray squirrels being more likely to consume as the number of acorns increased. Our results indicate that evaluating acorn production at multiple temporal scales may be necessary to fully understand oak masting relationships with wildlife. Furthermore, differences in wildlife behavior based on oak species may have important implications for oak regeneration.

Key words: acorns, anthropogenic subsidies, gray squirrel, *Quercus*, raccoon, white-tailed deer.

Oak (*Quercus* spp.) mast is an important food source for many wildlife species throughout the fall and winter (Korschgen 1981; Elston and Hewitt 2010; Azad et al. 2017; Barrere et al. 2020). Oaks evolved a cyclical pattern in acorn production (Koenig and Knops 2000) that influences wildlife use of acorns. For example, white-tailed deer (*Odocoileus virginianus*; hereafter deer), gray squirrels (*Sciurus carolinensis*), and raccoons (*Procyon lotor*) shift habitat use to focus on oak forests and diet switch to increase consumption of acorns during mast years (Schoonover and Marshall 1951; Harlow et al. 1975; Korschgen 1981; McShea and Schwede 1993; Massé and Côté 2013). These shifts in wildlife behavior may have important implications for acorn predation and conditional mutualism relationships with oaks leading to fitness consequences on oaks and their consumers (Janzen 1971; Steele and Yi 2020). Thus, research has primarily focused on the advantages and mechanisms of oak masting.

Numerous studies have examined annual patterns in oak masting and have presented strong evidence that acorn production is synchronized across years (Burns et al. 1954; Healy et al. 1999; Hirayama et al. 2012; Straub et al. 2016). A primary hypothesis to explain the annual synchrony of masting is the predator satiation hypothesis (PSH) which postulates that consumer populations are small during poor years and then become inundated during mast years resulting in greater

seed survival (Janzen 1971; Silvertown 1980; Kelly 1994). Masting cycles also vary between species with large acorn crops produced every 3–4 years for the red oak subgenus *Erythrobalanus* and every 2–3 years for the white oak subgenus *Leucobalanus* (Sork et al. 1993; Abrahamson and Layne 2003). However, one fundamental limitation of the PSH is that many of the vertebrate consumers are facultative, and fluctuations in their populations are relatively independent of mast cycles (Boggess et al. 2021). We propose that proximate factors (e.g., oak species and acorn production) within an annual cycle may provide important context to understand how patterns in masting affect the behavior of vertebrate consumers.

An additional factor that may influence the behavior of vertebrate consumers in response to oak masting is the availability of other resources. Anthropogenic subsidies have become prevalent in recent decades and have a consistent availability not typically found in nature (Oro et al. 2013). A common method of distributing these subsidies is through supplemental feeders which are used for management or recreational purposes to attract wildlife (Milner et al. 2014), many of which are facultative consumers of oaks. Animals change their foraging behavior or habitat selection in response to these anthropogenic subsidies (van Beest et al. 2010; Morris et al. 2011; Cherry et al. 2015; Kelleher et al. 2021) whose

availability may disrupt natural interactions between consumers and oaks. Although Ossi et al. (2020) found that roe deer (*Capreolus capreolus*) decreased their time at feeding sites when natural food resources were more readily available, it is unclear how anthropogenic subsidies influence interactions of other wildlife species with natural food resources.

To date, few studies have investigated wildlife behavioral responses to oak masting on the seasonal temporal scale. We hypothesized that oak masting patterns would affect wildlife behavior with a focus on how often animals visit oaks and their feeding behavior on acorns while there. To test this hypothesis, we used seed traps and paired camera traps to monitor seasonal oak masting patterns and wildlife behavioral responses. Also, we measured the distance of oak trees to supplemental feeders to control for the effect of anthropogenic subsidies that were available at the same time in our study area. Visitation behavior indicated the use of oak trees given there are a variety of behaviors (e.g., walking, climbing, loafing, etc.) animals may engage in near the tree. Feeding behavior indicated the consumption of acorns which has the potential to affect the regeneration of oaks. We focused on 3 consumers with 2 being facultative acorn predators (white-tailed deer and raccoon, Baker et al. 1945; Johnson et al. 1995) and one being a conditional mutualist that consumes and disperses acorns (gray squirrel, Steele and Yi 2020). We predicted that if consumers respond to fluctuations in acorn availability within the season, then they will increase their consumption of acorns as the number of acorns increases, which may depend on the specific oak species. Alternatively, if anthropogenic subsidies such as those provided by supplemental feeders are nearby, then animals will decrease their use and consumption of acorns as the distance to a feeder decreases because many wildlife species, including our focal species, are attracted to feeders and are more likely to consume anthropogenic subsidies when encountered (Reed and Bonter 2018; Candler et al. 2019).

Materials and Methods

Study sites

Our study was conducted on Four Oaks Plantation, a 6,475-ha private property in Brooks and Thomas counties, Georgia, United States. The property was split in half by the Aucilla River drainage that flows from north to south as part of the Aucilla River Basin (Torak et al. 2010). Sites were located along the east and west edges of the drainage in bottomland hardwood forests with closed canopies that were adjacent to swamps and bordered by upland longleaf pine (*Pinus palustris*) savannas (Figure 1). Forests were dominated by oaks composed primarily of water oak (*Q. nigra*), swamp chestnut oak (*Q. michauxii*), laurel oak (*Q. laurifolia*), live oak (*Q. virginiana*), and white oak (*Q. alba*). Other tree species present were hickory (*Carya* spp.), sweetgum (*Liquidambar styraciflua*), and black gum (*Nyssa sylvatica*). Understory vegetation was sparse in this closed-canopied hardwood forest.

Experimental design

Monitoring seasonal oak masting patterns

During September of 2021, we selected 205 oaks in a stratified, random design across 7 study sites. Oaks were selected if they fit the following criteria: 1) achieved dominant or codominant canopy position, 2) canopy did not overlap with other oaks, and 3) was not adjacent to another selected oak tree.

The third criterion was in place to maintain a study design for planned future experiments. The minimum distance between sites was 157 m with 20–45 trees selected per site for a total of 155 water oak, 11 laurel oak, and 39 swamp chestnut oak. The minimum distance between trees was 10 m. To monitor the seasonal masting pattern of these oak trees, we placed seed traps made of PVC pipe (1 m × 1 m × 1 m) and mesh screening (0.5 m slack in the middle) underneath the canopy of each tree to catch and prevent acorns from bouncing out (Stevenson and Vargas 2008).

Monitoring wildlife behavioral responses

To determine the placement of camera traps to monitor wildlife behavior, we conducted rapid mast surveys to get an index of probable production for each tree during the masting cycle. It was a 1-minute survey modified from Greenberg and Warburton (2007) where an observer with binoculars counted as many acorns in the canopy as possible within that time frame (Lashley et al. 2014). For our study, 2 observers conducted the survey simultaneously from different vantage points of the tree ensuring that their counts were independent of each other, and then those counts were recorded and averaged for each individual tree. Once the surveys were finished, we grouped trees by 10 based on proximity to each other using Google Earth Pro software v7.3.6. Within each group, we identified the top 3 producing trees based on survey results and randomly selected one to receive a camera trap. An additional tree from the top 2 remaining in 9 of the groups was randomly selected to place a camera trap for a total of 30 camera traps monitoring wildlife behavior in response to masting of water oaks ($n = 20$), laurel oaks ($n = 2$), and swamp chestnut oaks ($n = 8$). We standardized cameras to account for any bias in detection rate by placing them at the same height (50 cm) on the base of each tree, facing north and angled slightly down to capture gray squirrels, raccoons, and deer. If the base of a tree was too large, we placed the camera on a nearby tree ranging from 0.5 to 4.5 m away and adjusted accordingly to monitor the same area at the base of the tree. If an animal was detected and identified in any portion of the camera frame, then it was included in our detections. There were several supplemental feeders on the property near the study sites that provided animals with anthropogenic subsidies (Figure 1). To account for this additional resource that may influence behavioral responses to oak masting, we measured the minimum distance of the nearest feeder to each oak tree with a camera trap which ranged from 67 to 373 m.

Data collection

From October to December 2021 and September to December 2022, we counted the number of acorns (i.e., viable and nonviable acorns) in seed traps each week to record the weekly acorn production of each individual tree throughout the season. We included nonviable acorns in our count because consumers may be attracted to oaks based on the number of acorns produced regardless of viability. If an acorn had evidence it was handled by an animal (e.g., bite marks, partially consumed), it was excluded from the count to avoid bias from counting acorns harvested in the canopy by squirrels rather than acorns released by the tree. The camera traps on a subset of these trees were active for the same duration as seed traps in both years. We set cameras (Bushnell Trophy Cam) to capture a 10 s video on a motion trigger with a 5-min cooldown period. The 10 s video allowed us to characterize behavior
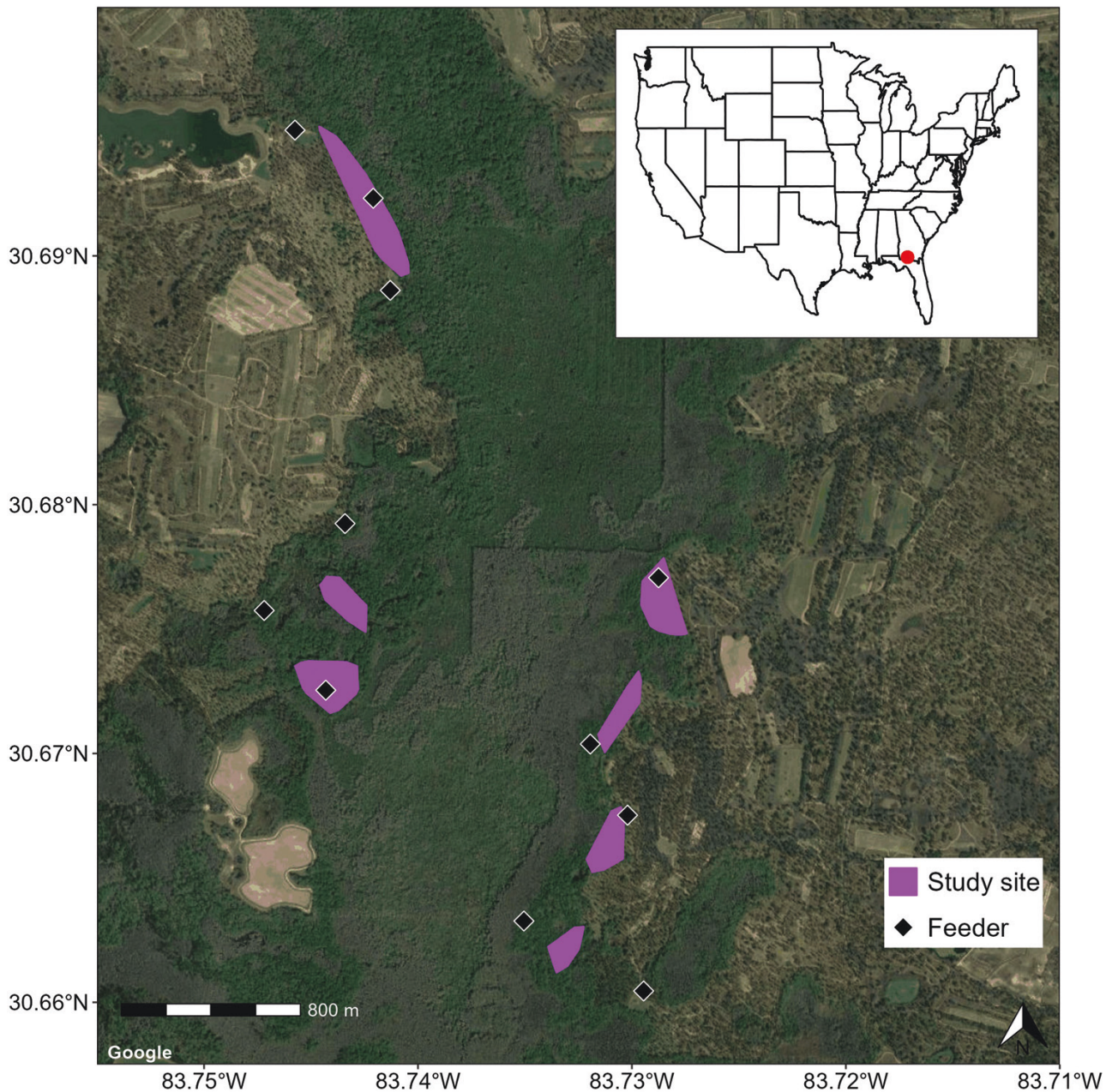
Figure 1. Map of study sites where oak trees were monitored to evaluate seasonal masting patterns and wildlife behavioral responses throughout the fall of 2021 and 2022 on Four Oaks Plantation in Georgia, United States. The distance from oak trees to supplemental feeders was measured to control for the effect of this other available resource on behavior. Map with satellite image was generated in R v4.2.2 using the package ggmap (v3.0.2, Kahle and Wickham 2013).

in each detection. For each video, we recorded species, date, time, and whether the animal was eating acorns (yes = 1, no = 0).

Data analysis

Seasonal oak masting patterns

To determine if the seasonal masting pattern differed between oak species, we used a generalized linear mixed model (GLMM) with a negative binomial distribution to account for overdispersion and the number of acorns as the response variable. Our predictor variables were oak species and time of year (week). We also included an interaction term between oak species and week of year to examine if there

were species-specific masting patterns within the season. We used water oak as our reference oak species because it was the most abundant tree across our study sites and within our dataset. To capture the variation in acorn production between weeks and across years, we transformed the week of year to a categorical variable from 1 to 26 for each sample week across the 2 years (i.e., week 1 = third week of October 2021, week 26 = third week of December 2022). We added the site as a random effect to account for potential spatial variation, but it was not a variable of interest. We conducted an analysis of variance test with adjusted *P*-values to assess significance using the car package (v3.1.1; Fox and Weisberg 2019) and the α level was set to 0.05.

Behavioral responses to masting

To test the hypothesis that oak masting patterns affect how often animals visit oak trees and their feeding behavior on acorns, we constructed a model for visitation and feeding behavior for all 3 wildlife species. We used oak species, number of acorns, and distance to a supplemental feeder (m) as predictor variables in every model. Individual tree ID nested in site and week of year were used as random effects in every model to account for spatial variation between individual trees and changes in observations over time without them being variables of interest. We transformed the variable week of the year into a categorical variable as mentioned in the previous analysis. We summarized the data as the number of observations and feeding observations at a tree per week. We added an interaction term between oak species and number of acorns to account for species-specific differences in acorn production.

We used a GLMM with a negative binomial distribution for overdispersion to model the number of observations at an oak tree for visitation behavior. We used a GLMM with a binomial distribution to model the number of feeding observations as a count-proportion (number of feeding observations/ number of observations) for feeding behavior. This proportion allowed us to account for bias in sample size given that an increase in observations may lead to an increase in feeding observations. Because the denominator in each proportion varied across weeks, we weighted the GLMM by the number of observations, which is important for binomial responses expressed as proportions (Brooks et al. 2017). For the raccoon feeding behavior model, we removed the interaction term because of issues with convergence.

All analyses were conducted in R v4.2.2 and RStudio v2023.06.0 + 421 (R Core Team 2022). We used the package glmmTMB for all GLMM analyses (v1.1.7; Brooks et al. 2017). To check the validity of each model, we used the DHARMa package to simulate residuals and then made a QQ-plot and residuals versus predicted plot (v0.4.6; Hartig 2022). If overdispersion was significant, then we conducted a zero-inflation test. We also tested multicollinearity between predictor variables using the performance package (v0.10.3; Lüdecke et al. 2021). After the models were validated, we assessed the significance with the α level set to 0.05. For data management and cleaning prior to the analyses, we used the packages dplyr (v1.0.10; Wickham et al. 2022) and lubridate (v1.8.0; Grolemund and Wickham 2011). Then, we used the package ggplot2 (v3.3.6; Wickham 2016) to visualize our results.

Results

Our seed traps were active for 10 weeks in 2021 where water oak produced, on average, 2.7 times and 5.1 times more acorns (87.2 acorns/tree) than laurel oak (32.2 acorns/tree) and swamp chestnut oak (17.2 acorns/tree), respectively. In 2022, seed traps were active for 16 weeks where water oak, on average, produced 2.1 times and 70 times more acorns (195 acorns/tree) than laurel oak (91.3 acorns/tree) and swamp chestnut oak (2.79 acorns/ tree), respectively, which was an apparent mast failure year for swamp chestnut oak. Our camera traps were active for the same weeks as seed traps each year with 2100 trap nights in 2021 and 3360 trap nights in 2022. In both years, we detected gray squirrels, on average, more often than white-tailed deer or raccoons (Table 1). Interestingly, we detected slightly less animals

Table 1. Mean (SE) number of detections per trap night from October to December 2021 (2100 trap nights) and September to December 2022 (3360 trap nights) of white-tailed deer, gray squirrels, and raccoons at oak trees on Four Oaks Plantation in Georgia, United States.

Species	Year	
	2021	2022
White-tailed deer	0.67 (0.03)	0.41 (0.02)
Gray squirrel	1.23 (0.04)	1.07 (0.03)
Raccoon	0.11 (0.01)	0.08 (0.007)

on average, regardless of species, in 2022 (1.56 detections/trap night) than in 2021 (2.02 detections/trap night).

Seasonal oak masting patterns

We found that seasonal oak masting patterns were different between oak species as indicated by a significant interaction term of oak species and week of year on acorn production ($\chi^2 = 379.97$, $P < 0.01$). Peak masting occurred in different weeks between years and in multiple weeks within a season. For example, in 2021, all 3 species peaked in the fourth week of November with laurel oak having similar acorn production the week prior (Figure 2A). Yet, in 2022, water oak and laurel oak had the highest peak 2 weeks earlier in the second week of November and swamp chestnut oak peaked 2 months earlier in the last week of September (Figure 2A). Additionally, water oak and laurel oak had another week with similar acorn production to their peaks which were the week prior and 6 weeks prior, respectively (Figure 2A). On average, water oak, laurel oak, and swamp chestnut oak produced 49%, 42%, and 59% of their acorns, respectively, during the third, fourth, and fifth weeks of November which included peak masting in 2021. During the same time period in 2022, water oak, laurel oak, and swamp chestnut oak produced, on average, 26%, 23%, and 43% of their acorns, respectively. Overall, mean annual acorn production was higher for water oak and laurel oak in 2022 and for swamp chestnut oak in 2021 (Figure 2B). Additionally, we characterized acorns based on viability following the protocol in Morina et al. (2017); although the majority of nonviable acorns were produced during September, the patterns were similar to those for total acorn production (Supplementary Figure S1A and B).

Behavioral responses to masting

None of the measured variables predicted visitation behavior for any wildlife species. However, the interaction between oak species and number of acorns tended to affect visitation behavior with marginal statistical significance ($P < 0.1$). Deer tended to increase their visitations at swamp chestnut oak by 3% with each addition of an acorn compared with water oak, whereas gray squirrels tended to decrease their visitations at swamp chestnut oak by 2% (Table 2; Figure 3A). Additionally, gray squirrels and raccoons tended to increase their visitations at laurel oak over swamp chestnut oak and water oak (Table 2; Figure 3A). The number of acorns produced and distance to a supplemental feeder, as variables not included in an interaction term, had little to no effect on any of the 3 wildlife species (Table 2).

For feeding behavior on acorns, oak species and the number of acorns were important predictors for gray squirrels. Gray squirrels had the highest mean proportion of feeding
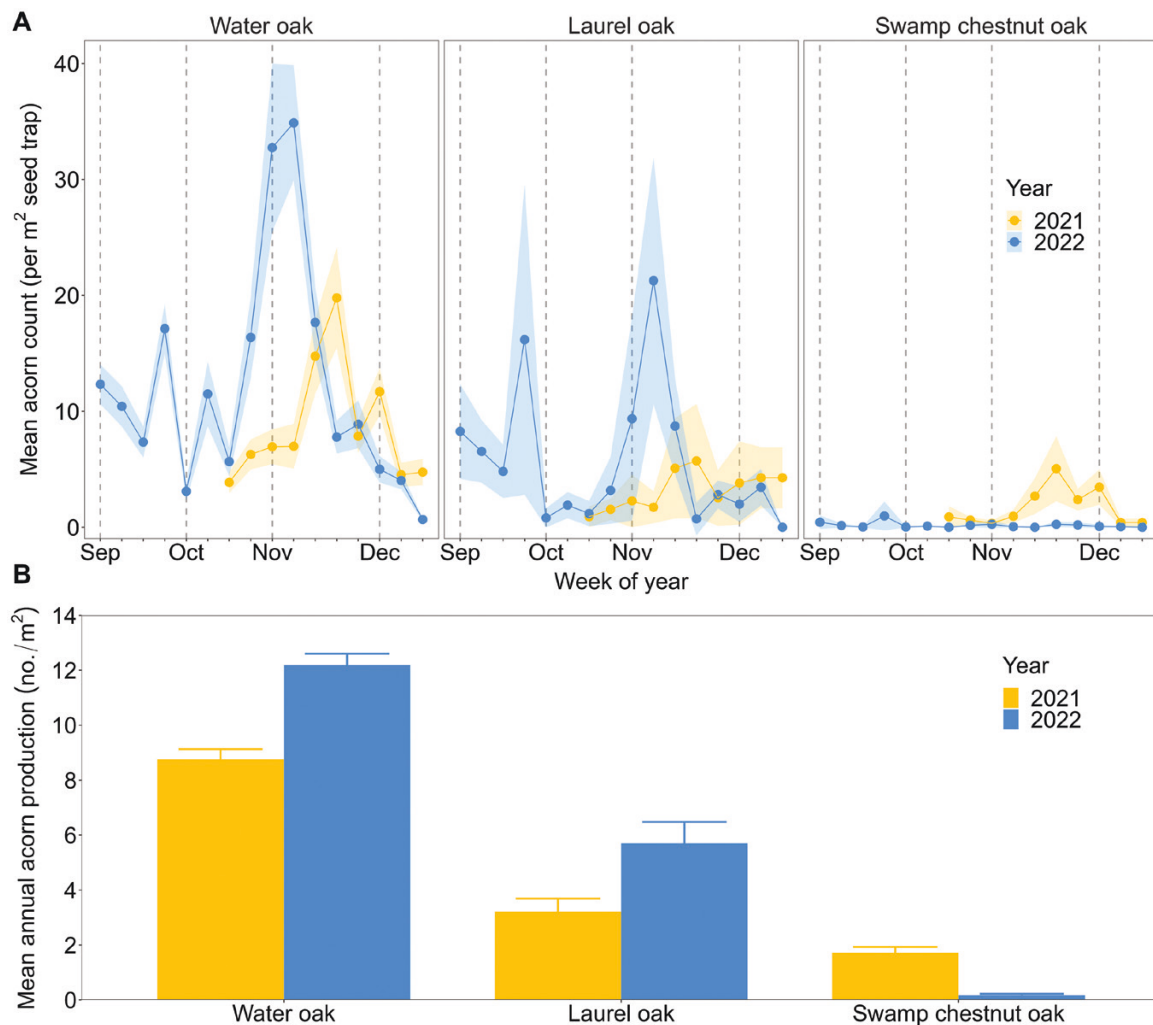
Figure 2. Mean number of acorns produced by 3 oak species per week (A) and per year (B) throughout the fall of 2021 and 2022 on Four Oaks Plantation in Georgia, United States. Dashed lines represent the first week of each month, shaded areas represent 95% confidence intervals, and vertical bars represent standard error. Acorn production varied between oak species within a season and across years, and varied in the timing of peak mast within an oak species across years. Note: our data showed a similar inference when we only considered viable acorns (Supplementary Figure S1A and B).

observations at water oak (0.11 ± 0.01 SE) and were 60% less likely to consume swamp chestnut oak acorns in comparison (Figure 3B). Furthermore, with each addition of 10 acorns, their probability of feeding increased by 2% (Table 3). Although oak species was not a significant predictor for deer or raccoon feeding behavior, there was a trend in which oak species they consumed that may have biological significance. Deer and raccoons had the highest mean proportion of feeding observations at swamp chestnut oak (0.14 ± 0.02 SE) and water oak (0.03 ± 0.01 SE), respectively (Figure 3B). Distance to a supplemental feeder had little to no effect on any of the 3 wildlife species (Table 3). There were seasonal changes in feeding behavior that fluctuated weekly, but overall, gray squirrels had a higher proportion of feeding in 2022 whereas white-tailed deer had a higher proportion in 2021 (Supplementary Figure S2). Raccoons had similar proportions of feeding each week in both years (Supplementary Figure S2). We also conducted the visitation and feeding behavior models with only viable acorns and the inferences did not change. Although many of the wildlife behavioral observations were not statistically significant, those tendencies may

have biological significance given that other unmeasured factors, such as acorn mass, nutrient quality, and juxtaposition likely play a role in the tradeoff between visitation and feeding behavior as it relates to net energy gain.

Discussion

Although synchrony in oak masting may be an important reproductive strategy to satiate consumers (Silvertown 1980; Kelly 1994) and has been demonstrated at the annual temporal scale (Burns et al. 1954; Healy et al. 1999; Hirayama et al. 2012; Straub et al. 2016), we found that oak masting between oak species was asynchronous at the seasonal temporal scale. Yet, at the annual temporal scale in our study, oak masting was similar between oak species within the same subgenus, which was consistent with other studies (Sork et al. 1993; Abrahamson and Layne 2003). Previous studies have demonstrated that consumers shift their habitat selection to oak forests and increase their consumption of acorns during annual oak mast cycles (Schoonover and Marshall 1951; Harlow et al. 1975; Korschgen 1981; McShea and Schwede 1993) and that can lead to important

Table 2. Coefficients (β) and 95% confidence intervals (CI) of variables from generalized linear mixed models of the number of observations (log-transformed) of white-tailed deer, gray squirrels, and raccoons for their visitation behavior at oak trees throughout the fall of 2021 and 2022 on Four Oaks Plantation in Georgia, United States. Animals were detected by camera traps on oak trees and observations were summarized weekly (*n* = 780). Water oak was used as the reference category for oak species because it was the most abundant across our study sites. Marginally significant relationships (*P* < 0.1) have an asterisk.

Species	Variable	β (95% CI)
White-tailed deer	Laurel oak	−0.25 (−1.39 to 0.89)
	Swamp chestnut oak	0.42 (−0.28 to 1.12)
	Number of acorns (per 100 acorns)	0.00 (−0.40 to 0.40)
	Distance to feeder (per 20 m)	−0.02 (−0.10 to 0.06)
	Laurel oak × number of acorns	−0.02 (-0.05 to 0.02)
	Swamp chestnut oak × number of acorns	0.03 (0.00 to 0.07)*
Gray squirrel	Laurel oak	0.28 (−0.35 to 0.91)
	Swamp chestnut oak	−0.01 (−0.42 to 0.40)
	Number of acorns (per 100 acorns)	−0.01 (−0.25 to 0.22)
	Distance to feeder (per 20 m)	−0.01 (−0.06 to 0.05)
	Laurel oak × number of acorns	−0.01 (−0.04 to 0.01)
	Swamp chestnut oak × number of acorns	−0.02 (−0.05 to 0.00)*
Raccoon	Laurel oak	1.02 (−0.34 to 2.38)
	Swamp chestnut oak	−0.47 (−1.39 to 0.46)
	Number of acorns (per 100 acorns)	−0.04 (−0.78 to 0.70)
	Distance to feeder (per 20 m)	−0.06 (−0.17 to 0.05)
	Laurel oak × number of acorns	0.01 (−0.04 to 0.05)
	Swamp chestnut oak × number of acorns	0.05 (−0.02 to 0.11)

fitness consequences for them and the oaks (Janzen 1971; Steele and Yi 2020). Here, we demonstrated that some of those consumers also respond to oak masting at the seasonal temporal scale as shown by the behavioral responses in our study, and although we only had 2 years of data, our findings illustrate the importance of this finer temporal scale to better understand oak masting and consumer relationships.

In addition to the asynchrony between oak species, within the same species there was asynchrony across years that may be due to year-to-year individual variation. We are unaware of any data published on asynchrony within species across years, but previous studies have reported individual variation in the number of acorns produced within species (Sork et al. 1993; Koenig et al. 1994; Greenberg 2000). For example, Lashley et al. (2009) showed high individual variation within a white oak population where a third of the trees produced more than half of the total acorns collected. Furthermore, individuals can differ in acorn production as a response to changes in resource availability such as canopy release and nutrient addition (Brooke et al. 2019). Intrinsic factors such as genetics and age (Goodrum et al. 1971; Greenberg and Parresol 2002) and extrinsic factors such as spring temperature and soil environment (Sharp and Sprague 1967; Pearse et al. 2014; Pérez-Ramos et al. 2014) can also contribute to individual variation in acorn production. These factors were outside the scope of this study, but the shift in timing of mast across years in our study has the potential to alter relationships with consumers.

Our data supported our hypothesis and indicated that oak species influenced wildlife behavior along with individual acorn production, which may be due to the perishability of acorns based on germination schedules. Acorns from the white oak group germinate soon after falling from the tree,

whereas acorns from the red oak group remain dormant for months before germination (Cecich 1994), and in our study, white-tailed deer tended to visit and consume acorns of the white oak group, whereas gray squirrels and raccoons tended to visit and consume acorns of the red oak group, which may have biological significance on oak regeneration. For gray squirrels, this behavior was inconsistent with previous studies that showed they tend to consume white oak acorns with high perishability and cache red oak acorns with low perishability (Fox 1982; Hadj-Chikh et al. 1996). Furthermore, white oak acorns have lower tannin and lipid levels than red oak acorns (Ofcarcik and Burns 1971) and studies have reported gray squirrels eat low-tannin acorns earlier in the fall, and then high-tannin acorns later in the fall when acorns are scarce (Smallwood and Peters 1986; Barthelmess 2001). The feeding behavior we observed may have been driven by feeding observations later in the fall because sampling in the first year did not start until late October. These lower tannin and lipid levels in white oak acorns (Ofcarcik and Burns 1971) along with their high perishability may have also affected the feeding behavior of deer in our study. In addition to perishability, acorn size may influence feeding behavior based on efficiency. Swamp chestnut oak has larger acorns than water oak and laurel oak (Stein et al. 2001), which may be beneficial for larger mammals, but for smaller mammals, the handling time may increase making it less efficient to consume when encountered (Jacobs 1992; Muñoz and Bonal 2008; Xiao et al. 2013). However, Hadj-Chikh et al. (1996) demonstrated that handling time did not affect squirrel feeding or caching behavior, and that perishability was more important. Although other literature has reported that white-tailed deer and raccoons consume acorns (Baker et al. 1945; McShea and Schwede 1993; Johnson et al. 1995), their preference for
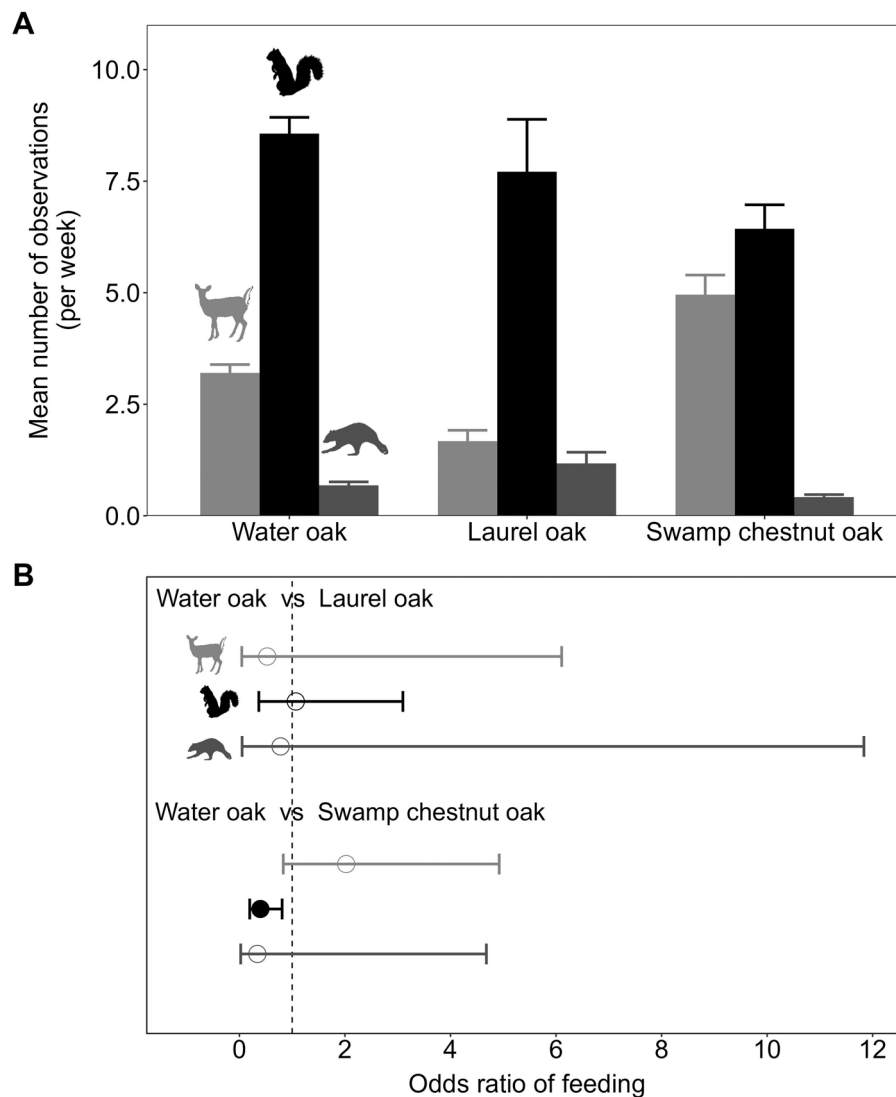
Figure 3. Mean (+ SE) number of observations per week of white-tailed deer, gray squirrels and raccoons at 3 oak species (A) and the odds ratio of feeding on laurel oak or swamp chestnut oak acorns compared with water oak acorns (baseline) (B) throughout the fall of 2021 and 2022 on Four Oaks Plantation in Georgia, United States. Horizontal bars represent 95% confidence intervals and filled-in circles represent a significant odds ratio. Deer tended to visit and consume acorns of the white oak group (swamp chestnut oak), whereas gray squirrels and raccoons tended to visit and consume acorns of the red oak group (water oak and laurel oak), which may have biological significance on oak regeneration.

acorns based on oak species is not well known, therefore the behaviors we observed provide further insight into how they respond to species-specific oak masting.

The number of acorns produced, regardless of viability, affected gray squirrel feeding behavior, but did not affect deer or raccoons, which contrasts previous studies that have reported these species select for certain areas and diet switch based on oak mast abundance (Schoonover and Marshall 1951; Harlow et al. 1975; Korschgen 1981; McShea and Schwede 1993; Massé and Côté 2013). Xiao et al. (2010) reported that acorn abundance, along with the germination schedule, led to an increase in caching and a decrease in feeding behavior by ground squirrels, which differed from the gray squirrel behavior in our study where their feeding increased with an increase in the number of acorns available. Previous oak mast abundance studies examined acorn production at the annual temporal scale, and so the different behavioral responses we observed at the seasonal temporal scale may not align simply because of the different temporal scales in our

study. For example, Boggess et al. (2021) showed that white-tailed deer did not respond to acorn additions that simulated oak masting until months after they occurred. In this case, the behavioral response can still be observed at the annual scale but may not be apparent within the season because it is delayed from the timing of mast.

For the distance to supplemental feeders, there was no effect on wildlife behavior which may be due to the availability of natural food resources as some studies suggest animals increase consumption of anthropogenic subsidies when natural food resources are scarce (Ossi et al. 2020; Pereira et al. 2021). Acorns were available in both years of our study, which may indicate the importance of natural food resources despite the consistent availability of anthropogenic subsidies in feeders. Previous studies have also demonstrated that individual variation in animal behavior affects their use of these subsidies (Newey et al. 2010; Steyaert et al. 2014), so it may be that distance to a supplemental feeder has an effect at the individual level rather than the population level. Additional

Table 3. Coefficients (β) and 95% confidence intervals (CI) of variables from generalized linear mixed models of the proportion of feeding observations (logit-transformed) of white-tailed deer, gray squirrels, and raccoons for their feeding behavior on acorns at oak trees throughout the fall of 2021 and 2022 on Four Oaks Plantation in Georgia, United States. Animals were detected by camera traps on oak trees and the proportion of feeding observations was summarized weekly for white-tailed deer ($n = 553$), gray squirrel ($n = 690$), and raccoon ($n = 236$). The interaction term between oak species and number of acorns was removed from the raccoon model because of issues with convergence. Water oak was used as the reference category for oak species because it was the most abundant across our study sites. Significant relationships ($P < 0.05$) are in bold font.

Species	Variable	β (95% CI)
White-tailed deer	Laurel oak	−0.64 (−3.09 to 1.81)
	Swamp chestnut oak	0.70 (−0.18 to 1.59)
	Number of acorns (per 10 acorns)	0.00 (−0.09 to 0.09)
	Distance to feeder (per 20 m)	−0.06 (−0.17 to 0.05)
	Laurel oak × number of acorns	−0.33 (−1.17 to 0.51)
	Swamp chestnut oak × number of acorns	0.02 (−0.01 to 0.05)
Gray squirrel	Laurel oak	0.07 (−1.00 to 1.13)
	Swamp chestnut oak	**−0.92 (−1.63 to −0.21)**
	Number of acorns (per 10 acorns)	**0.02 (0.00 to 0.05)**
	Distance to feeder (per 20 m)	0.01 (−0.06 to 0.08)
	Laurel oak × number of acorns	−0.03 (−0.08 to 0.03)
	Swamp chestnut oak × number of acorns	0.01 (−0.07 to 0.10)
Raccoon	Laurel oak	−0.25 (−2.97 to 2.47)
	Swamp chestnut oak	−1.08 (−3.70 to 1.54)
	Number of acorns (per 10 acorns)	0.07 (−0.26 to 0.40)
	Distance to feeder (per 20 m)	−0.11 (−0.38 to 0.17)

research investigating global change factors that may influence wildlife interactions with oaks may provide clarity on how these relationships could change over time.

There are likely other factors we did not measure that could influence wildlife behavior in response to oak masting. In particular, weather variables such as temperature and wind speed can influence habitat selection and foraging behavior (Aublet et al. 2009; van Beest et al. 2012). For example, Ruzicka and Conover (2011) reported that moderate wind speeds (2–4 m/s) increased raccoon foraging behavior due to an increase in movement of odor plumes that allowed them to detect food using olfaction. Predation risk can also affect wildlife behavior through environmental factors, such as vegetation type and forest structure, where animals tend to select forested areas with increased cover (Altendorf et al. 2001; Orrock et al. 2004; Verdolin 2006; Kelleher et al. 2021). Although, our study sites had similar forest structures and so we would expect that predation risk was relatively static across sites. The differences in wildlife visitation and feeding behavior based on oak species in our study have important implications for oak fitness and their relationships with consumers (Janzen 1971; Steele and Yi 2020). For example, gray squirrels support the dispersal and regeneration of oaks by being conditional mutualists, whereas white-tailed deer and raccoons hinder dispersal and regeneration by being facultative acorn predators. The responses to certain oak species could alter forest composition and structure, which may result in consequences for these wildlife populations with resource availability. How asynchrony in oak masting at the seasonal temporal scale affects these relationships warrants further investigation.

Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

Conflict of Interest statement

The authors declare that they have no known conflicts of financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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