



Exposure to fire affects acorn removal by altering consumer preference

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ABSTRACT

Prescribed fire has been encouraged as a management tool to increase oak regeneration across the southeastern United States. The least utilized part of the burn window in this region is during fall, but burning in this season with the objective of oak regeneration has been discouraged because of the potential negative consequences on subsequent germination. While exposure to fire decreases acorn viability, acorns cached in recently burned areas increases their survival. By following the fate of unburned acorns added to those areas, previous studies identified post-fire habitat characteristics (e.g., altering vegetation structure, decreased leaf litter, etc.) as a cause of increased acorn establishment success. However, exposing acorns to fire may also contribute to fate of surviving acorns by changing consumer removal rates. We exposed acorns to fire and established cafeteria-style experiments in unburned forests to compare burned and unburned acorn selection and removal rate of eight oak species by caching and non-caching consumers (i.e., predator type). Exposing acorns to fire did not appear to affect selection of oak species but affected overall removal risk for acorns differently by species of consumers. For example, while one important non-caching consumer (white-tailed deer, *Odocoileus virginianus*) and caching consumer (southern flying squirrel, *Glaucomys Volans*) showed strong selection of burned acorns, other important consumers in each predator type showed little discrimination or strong selection of unburned acorns (e.g., southern fox squirrel *Sciurus niger*). Exposure to fire reduced the overall rate of removal of acorns and when an acorn was removed, fire significantly reduced the probability that it would be removed by a caching consumer. Overall, our experiment demonstrates that shifts in consumer removal for exposed acorns may play an important role in the net effects of fall burning on oak regeneration.

1. Introduction

Poor regeneration across much of the eastern U.S. is causing oaks (*Quercus* spp.) to decrease in relative dominance compared to other hardwood species (Abrams 1992, Fei et al. 2011, Alexander et al. 2021). Failure of oak regeneration has been attributed to seedlings accumulating in the understory stratum and not advancing into the midstory, causing a regeneration bottleneck (Abrams 1992, Aldrich et al. 2005, McShea et al. 2007, Moser et al. 2006, Alexander et al. 2021). There are many hypothesized explanations for observed changes in oak demographics such as the loss of American chestnut (*Castanea dentata*), climate change, changing land uses, and deer herbivory (Abrams 1992, Hanberry et al. 2020, McEwan et al. 2011, Alexander et al. 2021). The fire-oak hypothesis, however, has been the most widely accepted and

tested explanation for oak declines, positing that intentional fire exclusion is favoring fire-sensitive and fast-growing non-oak hardwoods (Abrams 1992, Albrecht and McCarthy 2006, Nowacki and Abrams 2008, Alexander et al. 2021, Arthur et al. 2021). Prescribed fire alone or in combination with canopy reductions has been promoted as a tool to improve oak regeneration (Albrecht and McCarthy 2006, Nowacki and Abrams 2008, Arthur et al. 2012, Brose et al. 2013, Brose 2014), but seasonally constrained burn windows often limit application (Chiodi et al. 2018, Haines et al. 2001, Kobziar et al. 2015).

Fall is likely a prime season to expand the prescribed burn window in the eastern US because of the high proportion of acceptable burn days in this season with relatively low utilization by managers (Chiodi et al. 2018). There are, however, concerns related to the timing of fire and the effects that mismatching prescribed burn phenology with that of

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naturally occurring fires could have on plant communities (e.g., Towne and Craine 2014, Miller et al. 2019; but see Knapp et al. 2009). One of the primary concerns with fall burning in oak forests is the reduction of acorn viability via fire damage, which has led to numerous studies measuring effects of fall fire on acorn germination and seedling establishment (e.g., Auchmoody and Smith 1993; Cain and Shelton 1998; Greenberg et al. 2012; Greenler et al. 2019; Nation et al. 2021). In fact, acorns cached in burned areas have higher germination probabilities likely because they are not directly exposed to fire (Greenler et al. 2020). However, little is known about the fate of acorns that survive direct exposure to fire.

Fire influences habitat structure and resources availability for many species of acorn predators and, in doing so, affects their behavior and abundance (Harper et al. 2016). The magnet effect of fire has been described across many systems where large herbivores respond positively to recently burned patches (Allred et al. 2011, Archibald et al. 2005, Klop et al. 2007, Pearson et al. 1995, Westlake et al. 2020). Several large herbivores, which are acorn predators (e.g., white-tailed deer *Odocoileus virginianus*, Westlake et al. 2020, Boggess et al. 2021), could be attracted to burned areas especially during periods of nutritional stress such as the fall because fire phenology (i.e., the temporal occurrence of fire) may play an important role in resource availability for those species (Nichols et al., 2021, Lashley et al., in press). An opposite effect on small mammals selecting against areas with reduced cover following fire may decrease removal of acorns from burned areas by these caching consumers (Greenler et al. 2019, Kennedy and Peter 2005, Pérez-Ramos and Marañón 2008). This magnet effect on large seed predators, who do not cache seeds, coupled with decreased removal by caching consumers during oak masting suggests that fall fires may additionally reduce oak regeneration beyond the negative effects of exposure to acorn viability. However, caching consumers may preferentially cache seeds in the riskier burned areas to reduce cache pilferage, and cached seeds fare better than acorns in unburned stands (Auchmoody and Smith 1993, Greenberg et al. 2012, Greenler et al. 2019, 2020).

A key component to understanding the net effects of fall burning on oak regeneration that, to our knowledge, has not been evaluated is how consumer preference for acorns is affected by exposure to fire. There is strong evidence that fire influences wildlife food preferences (Harper et al. 2016) so that exposure of acorns to fire may change preference for acorns by consumers. Since fire reduces the soundness of acorns (Auchmoody and Smith 1993, Cain and Shelton 1998, Greenberg et al. 2012, Greenler et al. 2020, Nation et al. 2021) and caching consumers detect acorn soundness and choose whether to cache or consume acorns based on viability (Muñoz and Bonal 2008, Steele et al. 1996), the probability of an acorn being cached may change with exposure to fire.

To date, little data exist to isolate the effects of exposure to fire on acorn removal mediated through changes in consumer type. As such, we hypothesized that exposure to fire affects acorn risk of removal by mediating the chances to be removed by different consumers. To test our hypothesis, we designed a replicated cafeteria-style experiment to monitor consumer removal of unburned and burned acorns. We used camera traps to monitor the sequential removal of acorns from eight oak species to determine whether direct exposure of acorns to fire affected acorn risk of removal, relative removal by caching and non-caching consumers, and overall removal rate while controlling for other confounding fire effects.

2. Materials and methods

2.1. Study areas

Cafeteria-style acorn selection trials were deployed at two properties: Spirit Hill Farm (SHF; 492 ha) and Strawberry Plains Audubon Sanctuary (STP; 1016 ha), located 26 km apart in NW Mississippi, USA, 7.5 km N and 25 km WSW of the city of Holly Springs, respectively.

Trials were placed in temperate mixed upland hardwood stands on both properties. The dominant overstory in both stands included white oak (*Quercus alba* L.), black oak (*Q. velutina* Lam.), scarlet oak (*Q. coccinea* Münchh.), southern red oak (*Q. falcata* Michx.), post oak (*Q. stellata* Wangenh.), sweetgum (*Liquidambar styraciflua* L.), and mockernut hickory (*Carya tomentosa* (Poir.) Nutt.). The non-oak midstory hardwood component was dominated by sweetgum, blackgum (*Nyssa sylvatica* Marshall), red maple (*Acer rubrum* L.), and winged elm (*Ulmus alata* Michx.). Understory vegetation was sparse across all plots and dominated by deerberry (*Vaccinium stamineum* L.) and seedlings of trees found in the midstory and overstory.

2.2. Acorn treatments

To test whether being exposed to fire changes risk of removal by different types of consumers, acorns from eight oak species occurring in the southeastern U.S. were selected for our study. Shumard oak (*Q. shumardii* Buckley), cherrybark oak (*Q. pagoda* Raf.), willow oak (*Q. phellos* Michx.), and Nuttall oak (*Q. texana* Buckley) acorns were collected below trees in Starkville, MS, USA during November and December 2019. Southern red oak, northern red oak (*Q. rubra* L.), black oak, and scarlet oak were purchased from Louisiana Forest Seed Company, Lecompte, LA. All acorns were visually inspected for viability (Morina et al. 2017) and non-viable acorns were discarded. Acorns were stored inside plastic bags in refrigerated storage at 4 °C for approximately 5–16 weeks (depending on species) until use. We only used species from the red oak group (sect. *Lobatae*) for our experiment because species from the white oak group (sect. *Quercus*) often germinate in refrigeration within days of collection.

Acorns from burned treatments were prepared by establishing five 1-m² plots in a bare mineral soil opening with no vegetation or other fuels present. Leaf litter consisting of post oak, white oak, and southern red oak was collected from an upland hardwood stand at SHF and dried indoors for 2 weeks prior to burns (McDaniel et al. 2021). We added 360 g/m² (air dry weight) of oak leaf litter to each plot to replicate average fine fuel loads during fall at SHF (Nation et al. 2021). Leaf litter was left to acclimate to ambient temperature and moisture in burn plots overnight. Eight 20 × 40-cm subplots were outlined within burn plots using a string grid, and acorn species were randomly assigned a subplot in every burn plot. Thirty acorns of each species were evenly distributed in their respective subplots and gently shaken into the top of the leaf litter to match acorn densities typical of excellent mast crops and location in leaf litter stratum typical during fall fire (Lashley et al. 2009, Greenberg et al. 2012, Brooke et al. 2019). All acorn species were burned in each fire plot so that heterogeneity in fire intensity would be distributed across species of acorns and reduce likelihood that one species experienced more intense fire than others.

To ensure our treatments were representative of typical prescribed fire, we related fire temperature in our experimental burns to those conducted in other studies using five pyrometers placed at the leaf litter surface of each burn. Pyrometers were constructed of aluminum tags painted with six Tempilaq® fire-sensitive paints (Tempil, South Plainfield, New Jersey, USA) that melt and change color at specific temperatures (79, 163, 246, 316, 399, and 510 °C; Arthur et al. 2015), ambient air temperature was used for pyrometers having no paint melt. Fuel consumption was estimated visually, and litter depth was measured as the difference between pyrometers and the soil surface following fires.

Burns were conducted between 1100 and 1230 in January 2020 when air temperature was 6–10 °C, relative humidity was 28–40%, and winds were out of the west at 1–2.5 m/s (Kestrel® 5500 Fire Weather Pro, Boothwyn, PA, USA). Acorns were placed on top of the leaf similar to what would be expected when burning during the fall in practice. Ring fires were lit in a leaf litter ignition zone 10 cm outside the perimeter of plots with a drip torch using a 3:1 mixture of diesel fuel and gasoline. Fire rate of spread was (61 ± 27 s), measured as time passed between when fire entered the plot to when it reached plot center.

Maximum flame height (27 ± 3 cm) was visually estimated during each burn by continually comparing flame height to a metal meter stick placed on the opposite side of the plot from the observer. Mean maximum fire temperature was 257 ± 17 °C, mean litter depth was 4.7 ± 0.4 cm, and mean fuel consumption was $94.4 \pm 0.7\%$. Our measurements of fire characteristics were comparable to those from other acorn fire experiments in upland oak systems (Greenberg et al. 2012, Nation et al. 2021, McDaniel et al. 2021). After burns, acorns were collected from their respective subplots, aggregated in plastic bags by species, and placed back in refrigeration at 4 °C until acorn removal plots were established.

2.3. Data collection

To measure acorn risk of removal of burned and unburned acorns by different predator types, 10 trial plots (≥ 500 m apart) were haphazardly selected in upland closed canopy hardwood stands with sparse understory and midstory on both properties. This forest structure is typical of upland oak forests and most of the acorn predators present on the landscape are not known, to our knowledge, to avoid this type of forest structure. On each property, five plots were randomly assigned the burned acorn treatment, and the other five were assigned the unburned acorn treatment for a total of 10 replications of each treatment on both properties. We designed our experiment to isolate the effects of acorn exposure to fire from the effects of fire on the landscape (e.g., changes in resource availability and habitat structure) by exposing acorns to fire and then placing them all in unburned stands (i.e., a common garden experimental design). Each plot consisted of nine white circular trays with diameters of 17.7 cm and depths of 2 cm. Tray bottoms were covered with 1 cm of white sand (QUIKRETE®, Atlanta, GA) and placed in a 3 X 3 grid pattern with a ≈ 15 cm gap between rows and columns of trays (Fig. 1). Each species was randomly assigned a tray and 10 acorns from the respective species were spread across the sand surface. Because we had eight acorn species and nine trays in our design, one tray in each plot did not receive acorns and served as a control to determine if animals were attracted by the tray itself out of curiosity. We monitored acorn removal using Bushnell Trophy Cam infrared camera traps set on a 1-minute delay, 30 s video, and “normal” PIR sensor mode. Cameras were placed 3.5 m above the tray monitoring the plots from above in a vertical camera trap design. Additionally, cameras were set to take a video hourly to count acorns to ensure acorns were not removed by consumers that did not trigger cameras. Acorns were deployed on Jan. 24th and 25th and trials were monitored until Feb 11th; they were visited weekly to check camera and acorn status. We assumed that conducting trials during January would not change the animal selection behavior relative to our treatment compared to another fall month. To support this assumption, we observed many of our oak species still actively dropping acorns and squirrels caching acorns during this study. Moreover, Boggess et al. (2021) observed that viable acorns that were

dropped by one of the species studied in this experiment (i.e., Shumard oak) remained in the leaf litter in a position such that acorns would have been directly exposed to fire during a January prescribed burn.

We reviewed each video and recorded metadata, acorn status (i.e., removed or present), time of removal, and consumer species removing individual acorns. Consumers were grouped by functional group with the following grouped as caching predators: southern flying squirrel (*Glaucomys volans* L.), gray squirrel (*Sciurus carolinensis* Gmelin), fox squirrel (*Sciurus niger* L.), mice (*Peromyscus* spp.), vole (*Microtus* spp.). Non-caching consumers included raccoon (*Procyon lotor* L.), white-tailed deer (*Odocoileus virginianus* Zimmerman), wild turkey (*Meleagris gallopavo* L.), and Virginia opossum (*Didelphis virginiana* Kerr). We excluded two plots due to discrepancies in data collection related to camera visibility of plots and acorn count.

2.4. Data analysis

To determine the effect of our burned treatment on acorn removal, we used a Cox proportional hazard mixed effect model (coxme package; Therneau 2020). We used acorn status (i.e., removed or in the tray) as the response variable. Number of days since the beginning of the trial to the removal were used as *time to event* variable, while for the few acorns that were not removed ($n = 36$) we recorded number of days till the end of the trial. Our predictors were treatment (i.e., burn vs unburned), property (i.e., SHF and STP), predator type (i.e., cacher or non-cacher), and the interaction between predator type and treatment, while plot, acorn species, and predator species were used as crossed random intercepts. We decided not to use property as a random effect because, with only two properties, we did not have enough levels to accurately estimate a variance parameter (Arnqvist 2020). We treated acorn and predator species as random effects because we were not specifically interested in the effects of the species *per se*, but in the overall effects of the two predator types and our experimental treatments on oaks. The analysis was performed in R (R Core Team 2019) and significance levels were set at 0.05.

3. Results

Trials ran on average 12.75 days with a range of 2–18 days before plots were terminated, determined by the length of time necessary for all acorns to be removed or when no acorns had been removed for three days. Of 1482 acorns observed across plots, 1446 were removed before the end of the study. Of these observations, we did not record any animal using control trays with no acorns.

Results from our Cox mixed regression indicated that exposing acorns to fire reduced removal risk ($\beta = 5.79$, $p < 0.001$, Fig. 2A). Removal risk of acorns did not change with property ($\beta = -0.83$, $p = 0.47$). By visually inspecting patterns of removal of oak species, we determined the decrease in risk of removal of acorns exposed to fire

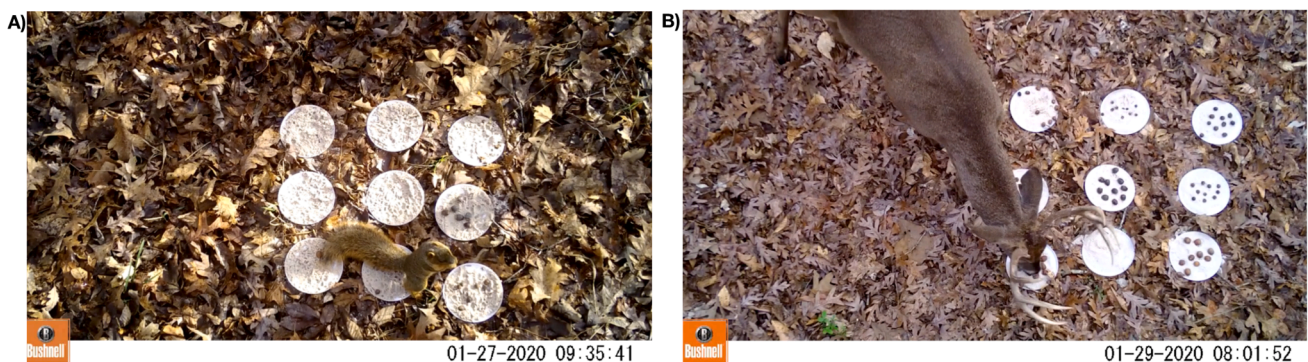


Fig. 1. Camera trap picture of one of our experimental plots visited by A) a cacher and B) a non-cacher. On each property, a total of 10 plots were deployed. Among these five plots were randomly assigned the burned acorn treatment and the other five were assigned the unburned acorn treatment.

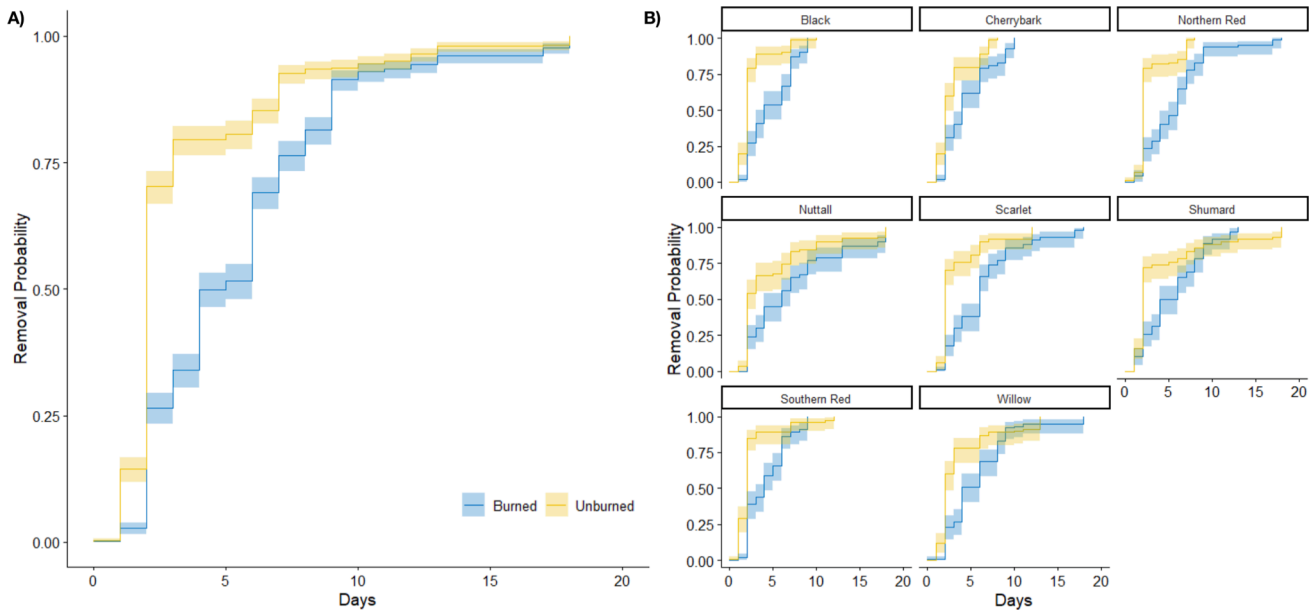


Fig. 2. A) Removal probability of acorns in treatment plots. Estimated removal probability over time for acorns tested in predator removal plots across both properties. Unburned acorns had a greater removal probability than burned acorns over our study period. B) Removal probability over time for eight acorn species. Acorn species was used as a random effect in the analysis, but visual exploration of the data showed a consistent pattern across acorn species. Across all species unburned acorns were generally removed quicker than burned acorns over our study period. Removal probability is on the y-axis, days on the x-axis, colors specify treatment (blue = burned, yellow = unburned), and shaded area represents 95% confidence intervals. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

appeared to be consistent across all 8 species of oaks represented in the study (Fig. 2B). Non-caching consumers were overall more likely to remove acorns ($\beta = 4.42, p < 0.001$, Fig. 3A), while exposing acorns to fire influenced removal risk by predator type: burned acorns were more likely to be removed by non-caching consumers, while we found no

difference in removal by predator type for unburned acorns (Table 1, Fig. 3B).

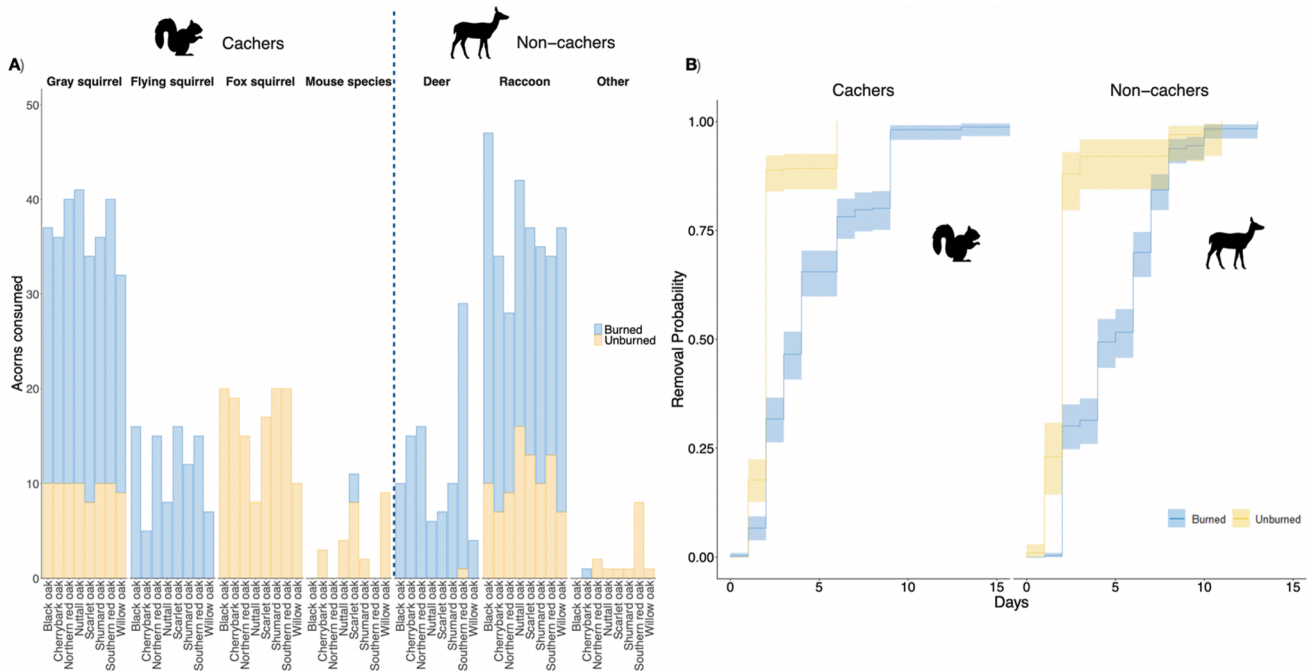


Fig. 3. A) Number of acorns removed by oak species and treatment (i.e., burned and unburned) by non-cachers (i.e., deer, raccoon, opossum [other], and turkey [other]) and cachers (gray squirrel, flying squirrel, fox squirrel and mouse species). B) Removal probability of acorns by predator type. Unburned acorns had a greater removal probability than burned acorns when removed by cachers. Note this figure does not account for autocorrelation using random effects, when accounting for these in the model the burned acorns removed by cachers had a lower hazard than burned acorns removed by non-cachers. Removal probability is on the y-axis, days on the x-axis, colors specify treatment (blue = burned, yellow = unburned), and shaded area represents 95% confidence intervals. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1

Results of the pairwise comparisons of the interaction between predator type (i.e., cacher, non-cacher) and acorn treatment (i.e., burned, unburned) of the Cox proportional hazard model. Pairwise comparisons were calculated with the emmeans package (Russell 2020). A positive estimate means that acorns in the first term of the pairwise comparison were removed quicker than the second term, while a negative coefficient indicates that that acorns in the first term of the pairwise comparison took longer to be removed. Significant results are bolded.

Contrast	Estimate	SE	Z ratio	p
Burned acorns taken by cachers – Unburned acorns taken by cachers	−5.792	1.257	−4.6	<0.0001
Burned acorns taken by cachers – Burned acorns taken by non-cachers	−4.420	0.841	−5.253	<0.0001
Burned acorns taken by cachers – Unburned acorns taken by non-cachers	−3.557	1.449	−2.454	0.0673
Unburned acorns taken by cachers – Burned acorns taken by non-cachers	1.372	1.426	0.962	0.7710
Unburned acorns taken by cachers – Unburned acorns taken by non-cachers	2.235	0.937	2.385	0.0799
Burned acorns taken by non-cachers– Unburned acorns taken by non-cachers	0.863	1.199	0.72	0.8891

4. Discussion

Our data indicate that fire delayed time to acorn removal, which is consistent with observations by Greenler et al. (2019). They reported reduced acorn removal rates by small mammals in recently burned stands in central Indiana, which they hypothesized was driven by changes in plant community structure. Interestingly, they controlled for the direct effects of fire on acorn selection by collecting acorns that were not exposed to fire and then placing them in areas already having been burned (i.e., a transplant experimental design). We designed our experiment to do the opposite by isolating the effects of fire on acorns without the associated environmental changes. These opposing designs allow us to glean that fire decreases acorn removal in at least two ways: 1) by influencing structural characteristics of the environment (i.e., Greenler et al. 2019) and 2) by directly affecting the perception of acorns by consumers (i.e., data herein). Interestingly, a reduction in removal risk could have fitness consequences to oaks. Part of the mast seeding cycle is thought to be an evolutionary strategy to satiate consumers in an effort to reduce acorn depredation to a rate that allows some acorns to germinate (Sork 1993; but see Lichti et al. 2017 for the effects of mast seeding scatter hoarders). The decrease in removal risk we observed may increase the likelihood of some acorns persisting to spring and thus increase the probability of acorns successfully germinating.

Removal of acorns by consumers often has negative effects on acorn success, but the outcome of these removals is heavily dependent on whether the consumer is a scatter hoarder or not. Scatter hoarders have positive effects on germination and seedling establishment when they cache acorns (Haas and Heske 2005, McShea and Schwede 1993, Smith and Reichman 1984, Steiner 1996, Vander Wall 1990). Scatter hoarders consume most acorns they cache (Cahalane 1942, Steele et al. 2001), but those left in caches typically have a higher survival rate and better seedling establishment success than acorns on the surface (Borchert et al. 1989, Fuchs et al. 2000, Greenler et al. 2020, Griffin 1971, Nyandiga and McPherson 1992, Vander Wall 2001). Acorns removed by non-caching seed predators are consumed and have little chance of surviving. Therefore, it is likely better for an acorn to be removed by a caching predator or not removed at all than to be removed by a non-caching predator. In our experiment, burned acorns were more likely

to be removed by non-caching predators highlighting the complex relationship between fire and plant reproduction: exposure to fire decreases germination probability (Greenler et al. 2020), but it also delays acorn removal, which could indicate that, in a landscape where burned and unburned acorns are available, burnt acorns may not be predated upon. Burning of acorns, however, also increased the chances of removal by non-caching predators ultimately decreasing the probability of the acorns that get removed growing into the seedling stage.

The results shown in our acorn selection experiment could be exacerbated by the habitat use of caching and non-caching predators. If caching predators avoid recently burned areas as a result of decreased habitat cover, they may avoid fall burned patches during mast seeding, which may expose more seeds to non-caching predators. For example, Westlake et al. (2020) observed a significant increase in use of burned patches by deer 45 days following fire, which would increase opportunity for acorn removal by this large non-caching seed predator and could greatly decrease the number of acorns persisting through winter. Indeed, deer nearly exclusive consumed burnt acorns in our study, so the magnet effect of fall burning on deer may increase their removal of acorns relative to other predators, which may also trigger cascading effects on plant communities (Boggess et al. 2021). Further, acorn removal by caching seed predators is often reduced by effects of prescribed fire on understory vegetation, affecting selection of microhabitats by small mammals (Greenler et al. 2019, Kennedy and Peter 2005, Pérez-Ramos and Marañón 2008). Any differential effects mediated by proportions removed by cacher or non-cachers is likely driven indirectly by environmental fire effects and not directly by selection differences.

The relatively controlled but unnatural setting of acorns in sand covered plastic trays could have affected the perception of acorns by seed predators in our study, but this design was essential to standardizing visibility of acorns across plots. Although animal personalities can largely affect seed predator behavior and choices (e.g., Feldman et al. 2019), our experimental design was identical between treatments so animals should have been equally attracted by our experimental trays whether they contained burned or unburned acorns. Thus, we do not believe this portion of our study design confounded our interpretations of results for this experiment. However, it is important to realize that these factors limit more broad sweeping inferences of net fire effects on oak success via this mechanism. For example, we controlled for changes in the landscape that affect acorn vulnerability following prescribed fire, but the reduction in fuel loads and charring of the soil and acorn surface could affect acorn detection by seed predators and thus may change the outcome of predator selections in the field. This study, however, was intended to be a proof of concept that fire could indirectly affect the fate of acorns by influencing interactions with predators and our controlled design allowed us to isolate that factor and demonstrate that likelihood. Thus, our experiment indicates that indirect effects of fires on species interactions should be considered in future research evaluating the net effects of fire on oak regeneration success.

Use of camera traps recording video allowed us to observe seed predators visiting plots and removing acorns, but some acorns were removed by unobserved predators because of imperfect detection. Unobserved removals were not equal between treatments and were two-fold higher in unburned acorn treatment plots at both properties. This did not influence the overarching conclusion that fire decreased removal, because all cameras were programmed to trigger automatically to provide recurring assessments of acorn persistence, regardless of wildlife detection. However, because caching seed predators tended to be smaller and thus less detectable, inferences concerning the relative role of cachers in removal could have been influenced. We explored this issue by discarding four locations with high incidence of unobserved acorn removals and reanalyzing the data, but this had little effect on the direction of inference. Thus, we are confident that our interpretation of results was robust to this issue.

Our results suggest there is an indirect effect of fire exposure to acorns that reduces the rate at which acorns are removed by seed

predators. On a forest stand scale, vegetation structure and the magnet effect may affect seed predator use of patches and further complicate the relationship of fire and removal by predators (Allred et al. 2011, Archibald et al. 2005, Greenler et al. 2019, Kennedy and Peter 2005, Klop et al. 2007, Pearson et al. 1995, Pérez-Ramos and Marañón 2008, Westlake et al. 2020). Although small mammals may temporarily avoid recently burned areas, small mammal populations are usually unaffected or slightly increase following low to moderate intensity prescribed fire, which should have a minimal effect on removal (Ford et al. 1999, Nelson 2017, Raybuck et al. 2012). Prescribed fire often varies in intensity, creating mosaics of unburned and burned patches, which will affect intensity of fire effects on acorns (Lertzman et al. 1998). These confounding effects may change the magnitude or direction of effects we observed, further adding complexity to the effects of fall fire on acorn success. Thus, future experiments could build off our work and the work of others by isolating the effects of fire on the environment, the effects of exposure of acorns on predator preference, and their interactive effects to fully understand the net effects of fall burning on oak regeneration.

5. Conclusions

Our results have important implications for oak regeneration in upland hardwood forests. Our data showing that exposure to fire reduces removal rates of acorns. Coupled with evidence from the work of others showing that caches in burned areas increase acorn success, our research indicates that fall burning does not necessarily dampen oak regeneration. It is generally accepted that fire is an essential tool to facilitate upland oak regeneration but limiting the burn window to the traditional late winter-early spring timing may constrain the amount of area that can be treated. Fall burning may be the best opportunity to expand the area treated while positive shifts in predator interactions may offset other negative effects on oak regeneration.

CRedit authorship contribution statement

C. Moriah Boggess: Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Carolina Baruzzi:** Formal analysis, Methodology, Visualization, Validation, Writing – review & editing. **Heather D. Alexander:** Conceptualization, Methodology, Validation, Writing – review & editing. **Bronson K. Strickland:** Conceptualization, Methodology, Validation, Writing – review & editing. **Marcus A. Lashley:** Conceptualization, Investigation, Methodology, Resources, Supervision, Validation, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

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

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