

Fire-mediated foraging tradeoffs in white-tailed deer

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Abstract. Predation risk can induce individual prey to express behavioral, physiological, and morphological traits that can influence population-level processes. Maternal care is an intuitive link between predator-mediated traits of individuals and population-level processes because maternal investment can decrease with predation risk, and often influences processes such as neonatal growth, survival, and recruitment. During fawn-rearing, many ungulate species restrict space use to a fraction of their home range. Selection of and within these areas can influence the quality of concealment cover for fawns and forage availability during early lactation which is the peak of maternal investment. Fire influences the distribution of food resources and cover for prey and their predators. In frequently burned systems, ungulates typically move into recently burned areas to exploit increased forage quality and detection of predators that use cover to stalk their prey. We investigated the effects of time since fire on the selection of and within fawn-rearing areas and foraging behavior in white-tailed deer in a frequently burned pine savanna. White-tailed deer selected woodlands with greater time since fire and avoided recently burned areas, likely sacrificing forage quality for concealment cover during fawn-rearing. We then used camera data to test the effects of time since fire on foraging behavior and found that with increased time since fire female white-tailed deer are more likely to be feeding while foraging at concentrated resources of standardized quality and quantity. By combining these data, we revealed that the counterintuitive avoidance of high-quality forage in recently burned areas can be explained by predation risk. We documented fire effects on proactive (i.e., avoidance of recent burns) and reactive (decreased vigilance with increasing time since fire) antipredator behaviors in white-tailed deer during the fawning season. Our results suggest that fire can spatially and temporally alter a landscape causing dynamic predation risk to which prey must respond to maximize fitness.

Key words: *Canis latrans*; coyote; fawn; fire ecology; foraging behavior; longleaf pine; maternal investment; *Odocoileus virginianus*; predation risk; prescribed fire; time since fire; vigilance.

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INTRODUCTION

Fire is an organizing force that has cross-scale ecological effects, ranging from the distributions of ecosystems to the arrangement of food resources and concealment cover within a system (Bond et al. 2005). In general, herbivores are drawn to recently burned patches (Moe et al.

1990, Sensenig et al. 2010, Eby et al. 2014, Raynor et al. 2015), a phenomenon that Archibald et al. (2005) termed the “magnet effect.” This is likely because during the first growing season following fire, plant re-growth is of higher nutritional quality, more palatable, and plant species selected by herbivores are often more abundant (Christensen 1977, Batmanian and Haridasan

1985, Singh 1993, Van de Vijver et al. 1999, Eby et al. 2014, Lashley et al. 2015a). However, fire also influences vegetation structure and concealment cover for foraging herbivores and their predators (Pierce et al. 2004). An alternative, but not mutually exclusive hypothesis explaining increased use of recently burned areas by herbivores is that the reduction in vegetation height reduces predation risk by opening sight-lines and increasing detectability of predators (Wilsey 1996). This hypothesis assumes that concealment cover benefits the predator and not the prey, such as lions (*Panthera leo*), a stalking ambush predator, preferentially hunting ungulate prey in areas of thicker cover (Hopcraft et al. 2005). However, predation risk mediated by wolves (*Canis lupus*), a cursorial predator, caused moose (*Alces alces*) and elk (*Cervus canadensis*) to retreat to forested cover (Edwards 1983, Creel et al. 2005). Effects of fire and the reduction of concealment cover on predation risk are likely influenced by prey escape tactics and predator hunting mode (Morero et al. 1996, Schmitz 2008, Thaker et al. 2011).

Predation risk can induce individual prey to express behavioral, physiological, and morphological traits (Sheriff et al. 2011, Zanette et al. 2011), and predicting when individual traits influence population-level processes has been the focus of much investigation (Creel and Christianson 2008). Maternal investment is linked to predation risk and productivity (i.e., fecundity, neonate growth and survival) and therefore is among the most apparent connection between predator-mediated individual traits and population processes (Therrien et al. 2008, Love et al. 2012). Understanding the behavioral “decisions” that represent the balancing of competing demands for safety and resources during maternal care may elucidate an important linkage between individual antipredator responses to population processes.

When the energetic demands of reproduction cannot be met, ungulates decrease either current or future maternal investment (Festa-Bianchet and Jorgenson 1998, Festa-Bianchet et al. 1998, Therrien et al. 2008, Taillon et al. 2013). Resource acquisition by foraging ungulates can decline under high predation risk due to increased vigilance, or selection of safer but less productive patches (Edwards 1983, Fortin et al. 2004, Grignolio et al. 2007). Selection of parturition areas

has implications for forage availability during the most energetically demanding portion of lactation, particularly for ungulates that employ a “hiding” strategy, in which neonates stay concealed in hiding cover between feeding bouts for the first weeks of life (Carl and Robbins 1988). During parturition and early lactation, many ungulates restrict space use to a fraction of their annual home range and aggressively defend this area from conspecifics (*Odocoileus virginianus*, Ozoga et al. 1982, Schwede et al. 1993, Bertrand et al. 1996, *Dama dama*, Ciuti et al. 2006, *Capra ibex*, Grignolio et al. 2007). Selection of these areas is thought to be driven by the balancing between predation risk and the energetic demands of lactation (Bowyer et al. 1998, Kjellander et al. 2004, Bongi et al. 2008, Panzacchi et al. 2010), and therefore, it has potential to tie antipredator responses to population-level processes such as neonate growth, survival, and recruitment (Conner et al. 2015).

In the southeastern United States, coyotes (*Canis latrans*) have been linked to declines in white-tailed deer (*O. virginianus*) fawn survival (Kilgo et al. 2012), recruitment (Gulshy et al. 2015), and population growth (Kilgo et al. 2010). On our study site in Georgia, the probability of fawn survival to 20 weeks was only 29% (Nelson et al. 2015), in spite of likely overestimating survival due to capturing fawns that were already a few days old (Gilbert et al. 2014). White-tailed deer responded to this high rate of predation with a suite of antipredator behaviors including modified space use (Conner et al. 2015) and foraging behavior (Cherry et al. 2015).

In this paper, we examine the effects of fire on selection of and within fawn-rearing areas and foraging behavior of female white-tailed deer in a frequently burned longleaf pine savanna. Our study site was burned in small blocks (i.e., <100 ha units) on approximately a biannual cycle, resulting in a mosaic of patches with variable time since fire. We assumed concealment cover reduced predation risk perceived by white-tailed deer because coyotes, an opportunistic cursorial predator that is locally more abundant in open habitats (Cherry et al. 2017), were the primary predator of fawns on our site (Nelson et al. 2015), and white-tailed deer often seek refuge in thick cover (Grovenburg et al. 2012). Thus, woodlands during the first growing season

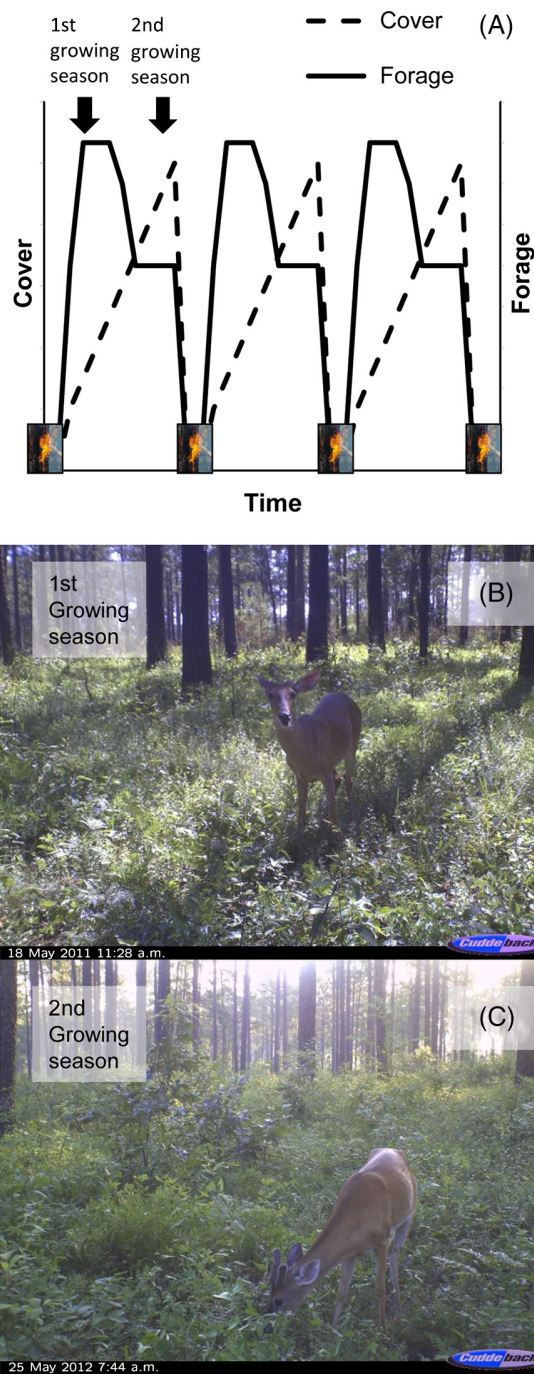


Fig. 1. (A) Illustration of a conceptual model of the effects of time since fire on cover and forage in a biannually burned landscape; (B) example of a white-tailed deer foraging at a camera trap in a pine woodland during the first growing season following fire; (C) example of a white-tailed deer foraging at the same camera

(Fig. 1. Continued)

trap in a pine woodland during the second growing season following fire. Note the difference in structure of the understory.

following fire would offer less concealment cover (Garren 1943, Bond and Keeley 2005, Smit et al. 2010), but greater forage quality (Christensen 1977, Eby et al. 2014) and abundance of leafy biomass of plant species selected by deer (Lashley et al. 2015a). During the subsequent growing season following fire, concealment cover is increased, while resource quality is decreased due to the diminishing benefits of fire (Fig. 1). When this temporal pattern is extrapolated to a spatial landscape, deer are presented with the choice between high risk–high reward patches (i.e., recently burned patches) and low risk–low reward patches (patches > 1 yr following fire). We used the spatial variation in fire history to examine the effects of time since fire on fawn-rearing site selection and foraging behavior of female white-tailed deer during lactation.

METHODS

Study site

We conducted our study at the Joseph W. Jones Ecological Research Center (JC), a 12,000-ha longleaf pine (*Pinus palustris*)-dominated research site in southwestern Georgia, USA. Longleaf pine ecosystems contain globally significant levels of biodiversity and are among the most frequently burned ecosystems in the world, with a fire return interval of 1–3 yr (Mitchell et al. 2006). The site included approximately 7250 ha of longleaf pine woodlands. Other forest types included slash pine (*Pinus elliotii*) and loblolly pine (*Pinus taeda*) forests, mixed pine and hardwood forests, lowland hardwood hammocks, oak barrens, and cypress–gum (*Taxodium ascendens*–*Nyssa biflora*) limesink ponds. Prescribed fire was the primary management tool used to maintain the longleaf pine ecosystem, and 40–50% of JC was burned annually.

Resource selection during fawning

We captured adult (≥ 2.5 yr of age) female white-tailed deer using rocket-nets and darting from tree stands from 15 January to 15 May

of 2012–2013. Deer were immobilized with 2.5 mg/kg xylazine hydrochloride and 5 mg/kg Telazol (Congaree Veterinary Pharmacy, Cayce, South Carolina, USA). We reversed the xylazine hydrochloride 80 min after initial dose with 10 mg/kg Tolazoline (Kreeger et al. 2002). Capture and chemical immobilization have the potential to negatively affect maternal investment in ungulates (Côté et al. 1998), and specifically, xylazine hydrochloride can induce anorexia in white-tailed deer (Warren et al. 1984), which could impair lactation and induce abandonment. We sought to minimize these potential effects by halting capture six weeks before estimated peak fawning (Cherry et al. 2016) and not targeting females that appeared parturient. We fit adult female deer with Global Positioning System Collars (ATS 2110 D; Advanced Telemetry Systems, Isanti, Minnesota, USA). Collars were programmed to release after approximately 14 months, at which time collars were retrieved using VHF signal and data were obtained. We captured 26 adult female white-tailed deer during 2012 ($n = 14$)–2013 ($n = 12$). We excluded six white-tailed deer from analysis because collar deployment was insufficient to calculate annual home ranges (i.e., all cases < 8 months) due to harvest ($n = 2$) or due to premature collar detachment ($n = 4$).

Our primary interest was in examining the effects of time since fire on habitat selection during fawning. Habitat selection is a hierarchical process; thus, we investigated selection of and within fawn-rearing areas. We assumed that white-tailed deer selected fawn-rearing areas from their annual home range, and therefore, we considered the annual home range as available in a use-availability framework (Manly et al. 2002). For each white-tailed deer, we used locations from all seasons to model habitats available for selection (i.e., annual home ranges) using 95% minimum convex polygons (MCP). We identified the timing of the fawn-rearing season from fawn capture records (Nelson et al. 2015) and examination of reproductive tracts for evidence of ovulation from harvested adult female white-tailed deer (Cherry et al. 2016). We used animal locations from June to August to calculate a 95% MCP for each white-tailed deer to represent a generalized fawn-rearing seasonal area of use. We also investigated selection of animal locations within the

fawn-rearing area by considering the fawn-rearing MCP available for selection and the animal locations as used in a use-availability framework.

We examined selection using systematic sampling approach for Euclidean distance analysis of habitat selection (Conner and Plowman 2001, Conner et al. 2003, and Benson 2013). We used JC Land Cover and Fire History Data in ArcMAP 10.2 (ESRI, Redlands, California, USA) to develop raster layers representing habitat features. Following Benson (2013), we created a distance raster layer with 10×10 m cells for each habitat feature using the Euclidean Distance tool in ArcMAP 10.2. For each fawn-rearing season, we developed raster layers representing pine woodlands that had been burned since the last growing season (pine–year of fire) and pine woodlands burned before the previous growing season (pine–year after fire). We also developed raster layers for hardwood forests and agricultural fields characterized by small (< 5 ha) wildlife openings. We plotted animal location on the distance raster layers and extracted the values from the raster layers to the point locations providing the distance from each animal location to each habitat feature. We used all raster cell values within each MCP (i.e., fawn-rearing areas and annual home ranges) to calculate the mean distance to each habitat feature within the annual home range and the fawn-rearing area for each deer. We then calculated a distance ratio (mean observed distance/mean expected distance) for each animal at both orders of selection. For selection of the fawn-rearing area, we used the observed mean distance within the fawn-rearing area divided by the mean distances in the home range. For selection within the fawn-rearing area, we used the mean observed distances from the animal locations divided by the mean distances within the fawn-rearing area. A habitat distance ratio < 1.0 indicated the deer was closer than expected to that habitat type (i.e., selection), whereas a distance ratio > 1.0 indicated the deer was farther than expected from a given habitat type (i.e., avoidance; Conner and Plowman 2001, Conner et al. 2003, Benson 2013).

We used a multivariate Hotelling's t test to test the hypothesis that observed distances to habitats did not differ from expected distances at both orders of selection treating the animal–year combination as the experimental unit (Conner

and Plowman 2001, Conner et al. 2003). If we observed significant results from the multivariate test, we used univariate t tests on each distance ratio for each habitat feature to identify which distance ratios differed from 1.0. We created a ranking matrix using paired t tests between each combination of habitat features at each order of selection to rank habitat types in order of preference (Conner and Plowman 2001, Conner et al. 2003, Benson 2013).

Fire and foraging behavior

To examine the effects of time since fire on foraging behavior, we established remote-sensing camera traps during September of 2011 ($n = 36$) and 2012 ($n = 45$), coincident with white-tailed deer lactation. We mounted a white-flash, remote-sensing cameras (Cuddeback Capture Trail Camera, Non Typical, Green Bay, Wisconsin, USA) with the latency time between photos set to 5 min, on the north face of a tree at each trap site. To standardize food quantity and quality at camera traps, we baited sites with 18 L of whole corn at the onset of each trial and every two days during trials as needed. Camera traps were established in frequently burned pine-dominated uplands. The two-year survey and approximately biannual fire return interval allowed time since fire to vary while standardizing camera trap locations.

Similar to Cherry et al. (2015), we categorized the behavioral state of each white-tailed deer observation as actively feeding (i.e., head down, actively consuming bait) or not. We determined sex and age (i.e., adult or juvenile) based on morphology and pelage characteristics. We assigned the group size to each observation by counting the white-tailed deer in the image and categorized the time of detection into day (8:00–20:00) and night (20:01–7:59), which was based approximately on civil twilight during the surveys. We modeled behavioral state (i.e., feeding = 1 and not feeding = 0) of adult female white-tailed deer in a generalized linear mixed model with a binomial error distribution and a logit-link function to test for difference in foraging behavior relative to time since fire (Bolker et al. 2009). We included group size, year, time of day, the presence of fawns, and the presence of adult males as covariates and treated the camera site-specific intercept as a random effect (Cherry

et al. 2015). We used Wald's statistic for inference with $\alpha = 0.05$, and report odds ratios for effects size. All analyses were conducted in program R, using package LME4 (Bates et al. 2015).

RESULTS

Fire influenced habitat selection of and within the fawn-rearing area. At both orders of selection, female deer selected concealment cover over the high-quality forage in recently burned patches. Fire also influenced the foraging behavior of female deer during the fawning season. The probability of feeding increased with time since fire.

Habitat Selection during fawning

Our analysis included 20 female white-tailed deer monitored for approximately 14 months with approximately three to four locations per day. We identified 15 fawn-rearing areas in 2012 and 17 in 2013 (Fig. 2). The average size of the annual home ranges and fawn-rearing areas was 257.3 ± 196.6 (mean \pm SD) ha and 42.4 ± 17.0 ha, respectively. Selection of the fawn-rearing area ($t = 11.61$, $P < 0.001$) and within the fawn-rearing area ($t = 5.19$, $P = 0.001$) was non-random. White-tailed deer selected fawn-rearing areas nearer than would be expected to pine-year after fire ($t = -3.04$, $df = 31$, $P = 0.005$) and agriculture ($t = -4.87$, $df = 31$, $P < 0.001$; Table 1). Within the fawn-rearing area, deer were found further than would be expected from pine-year of fire ($t = 2.83$, $df = 31$, $P = 0.008$; Table 2).

Fire and foraging behavior

We recorded 12,483 detections of female white-tailed deer at 36 and 45 camera traps during 2011 and 2012, with an average of 154.1 ± 11.5 (mean \pm SE) detections per camera per year. The probability of a white-tailed deer feeding increased with increasing time since fire ($Z = 3.30$, $P < 0.001$; Table 3). White-tailed deer were more likely to be feeding at night than during the day ($Z = 2.25$, $P = 0.024$), and with increasing group size ($Z = 8.40$, $P < 0.001$). The presence of a male did not influence foraging behavior, but the presence of a fawn ($Z = 2.34$, $P = 0.019$) resulted in an increased probability of feeding (Fig. 3).

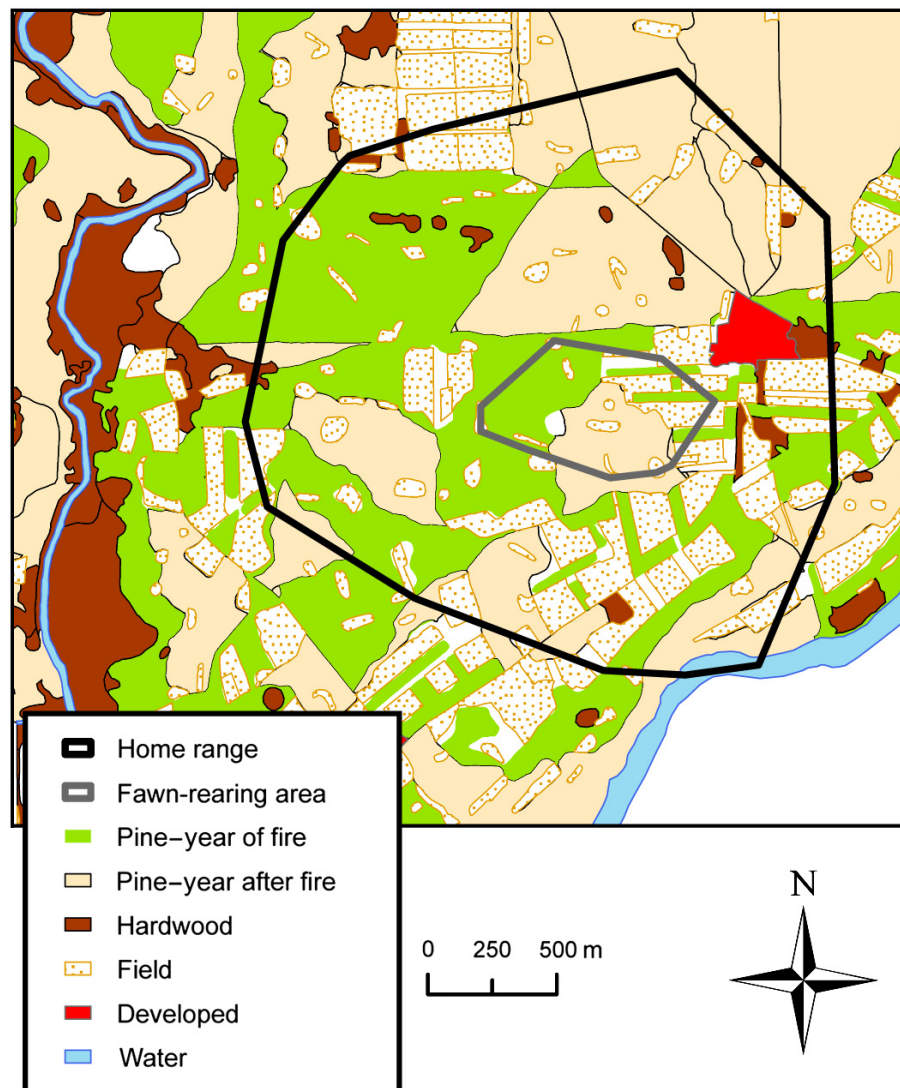


Fig. 2. Map depicting the home range, fawn-rearing area, relative to land-cover types and fire history for one adult female white-tailed deer on the Joseph W. Jones Ecological Research Center in Georgia, USA, during 2012.

Table 1. Habitat ranking matrix, mean distance ratio with lower (LCI) and upper confidence intervals (UCI), t -scores, and P -values for selection of fawn-rearing areas on the Joseph W. Jones Ecological Research Center during 2012 and 2013.

Parameter	Conclusion	DR	LCI	UCI	t -score	P -value
Agriculture	S	0.74	0.62	0.85	-4.87	<0.001 a
Pine-year after fire	S	0.76	0.61	0.92	-3.03	0.005 a
Pine-year of fire	NS	0.89	0.70	1.08	-1.17	0.295 a, b
Hardwood	NS	0.94	0.81	1.06	-0.94	0.353 b

Notes: S, selected; NS, not selected; A, avoided; DR, distance ratio. Deer selection of habitats with the same letter (i.e., a, b) did not differ based on paired t -tests ($P > 0.05$).

Table 2. Habitat ranking matrix, mean distance ratio with lower (LCI) and upper confidence intervals (UCI), *t*-scores, and *P*-values for selection within fawn-rearing areas on the Joseph W. Jones Ecological Research Center during 2012 and 2013.

Parameter	Conclusion	DR	LCI	UCI	<i>t</i> -score	<i>P</i> -value
Hardwood	NS	0.95	0.88	1.01	-1.47	0.150 a
Pine-year after fire	NS	1.10	0.82	1.38	0.72	0.470 a
Agriculture	NS	1.04	0.96	1.13	1.11	0.280 a, b
Pine-year of fire	A	1.20	1.05	1.034	2.83	0.008 b

Notes: S, selected; NS, not selected; A, avoided; DR, distance ratio. Habitats with the same letter (i.e., a, b) indicate they are not significantly different.

DISCUSSION

We documented fire effects on antipredator behaviors in female white-tailed deer during fawn-rearing in a frequently burned longleaf pine ecosystem. Contrary to the “green magnet” hypothesis, female white-tailed deer selected fawn-rearing areas with greater time since fire and avoided recent burns within their fawn-rearing areas. We assumed that resource quality was higher during the first year after fire (Christensen 1977, Eby et al. 2014) and that cover increased with time since fire (Garren 1943, Bond and Keeley 2005, Smit et al. 2010); thus, we interpret these

results as sacrificing resource quality for concealment cover during fawn-rearing. Our study is unique in that we documented avoidance of recently burned areas and used independent data to examine the effects of time since fire on the perception of predation risk. By combining these data, we revealed that the counterintuitive avoidance of high-quality forage in recently burned areas can be explained by predation risk. Similar tradeoffs of reduced forage quality for increased safety have been documented during lactation in moose (Edwards 1983), caribou (*Rangifer tarandus*; Barten et al. 2001), and mountain goats (*Oreamnos americanus*; Hamel and Côté 2007). Predator-sensitive foraging during lactation in a capital breeder, such as white-tailed deer, has potential to influence current and future reproduction, if maternal investment is compromised by antipredator defenses, or if nutritional stores lost during lactation are not replenished before the ensuing breeding season (Therrien et al. 2008, Taillon et al. 2013).

Table 3. Parameter estimates for logistic regression models predicting the behavioral state (i.e., actively feeding or vigilant) from digital images ($n = 12,483$) of adult female white-tailed deer foraging at baited stations during September of 2010–2011 on the Joseph W. Jones Ecological Research Center in Georgia, USA.

Parameter	β	SE	OR	Z value	Pr(> Z)
Intercept	-1.68	0.11	0.19	-14.98	<0.001
Time since fire†	0.15	0.05	1.17	3.12	0.002
Group size‡	0.21	0.02	1.23	9.17	<0.001
Presence of a fawn§	0.27	0.11	1.32	2.47	0.014
Presence of a male¶	-0.07	0.18	0.93	-0.41	0.684
Night#	0.11	0.05	1.12	2.23	0.026
Year	0.35	0.05	1.42	7.42	<0.001

Note: Standard errors (SE), odds ratio (OR), Z values, and probabilities a coefficient differs from 0 are also presented.

† Number of growing seasons (1–3) that have occurred since the stand was prescribed burned.

‡ Group size is the number of white-tailed deer in the image.

§ Presence of a fawn is a binary predictor describing whether a fawn white-tailed deer was present in the image.

¶ Presence of a male is a binary predictor describing whether a male white-tailed deer was present in the image.

Time of day of detection, day (8:00–20:00) is the reference class.

|| Covariate for year of study; Year 1 is the reference class.

Our results differ from numerous studies documenting attraction of ungulates to recently burned areas (Archibald et al. 2005, Eby et al. 2014, Raynor et al. 2015). In most investigations of predator–ungulate–fire interaction, ungulates experience increased quality of forage and decreased predation risk in recently burned areas because fire opened sight-lines that increased detectability of a suite of predators that prefer to hunt in thick cover (FitzGibbon 1990, Wilsey 1996, Hopcraft et al. 2005, Eby et al. 2014). In those systems, fire presents a win-win for the forager in terms of risk and resources. However, in this study, white-tailed deer were foraging and fawning in fear of a cursorial predator of open range, the coyote, and we suggest deer perceived safety with increased cover. Therefore, in our study system, risk and resources were correlated

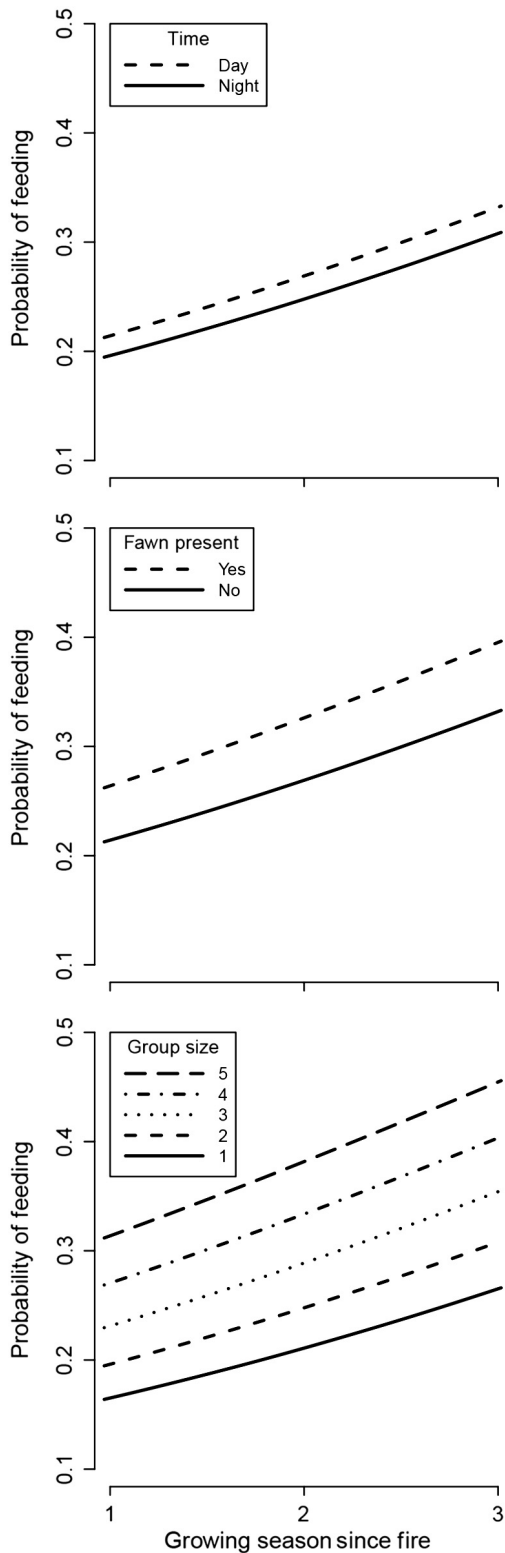


Fig. 3. Plots predicting the probability of adult

(Fig. 3. Continued)

female white-tailed deer feeding during the first, second, and third growing season following fire, while foraging at baited camera traps on the Joseph W. Jones Ecological Research Center during 2011 and 2012. Predictions were made by holding all variables except the featured variables constant (i.e., group size = 2; presence of a fawn = no; presence of male = no; year = 2011; time = night).

across space challenging lactating females to balance competing demands for safety and energy.

Studies have reported variable responses by white-tailed deer to fire. For example, Meek et al. (2008) documented avoidance of recent burns, but in their study fire was followed by extreme drought delaying vegetation recovery. Lashley et al. (2015b) reported that white-tailed deer avoided recent burns, while Main and Richardson (2002) reported that white-tailed deer increased use of recent burns. None of these studies attempted to assess the effect of fire on the perception of predation risk, but interestingly only Main and Richardson (2002) worked in a system where a stalking ambush predator, the Florida panther (*Puma concolor coryi*), was the primary predator of white-tailed deer.

Vigilance while foraging is a well-studied antipredator behavior because it can be directly related to resource acquisition and is considered a reactive behavior that should be sensitive to spatiotemporal variation in perceived risk (Brown and Kotler 2004, Fortin et al. 2004). We documented that female white-tailed deer are more likely to be feeding with increasing time since fire, while foraging at camera traps with standardized forage quality and quantity. Two important points arise from these results. First, predation risk explains the counterintuitive avoidance of high-quality foraging opportunities available in recently burned areas. Secondly, the effect of fire on predation risk across ungulates is likely driven by antipredator tactics and predator hunting mode. In contrast to numerous other studies where ungulates were preyed upon by stalking ambush predators (Main and Richardson 2002, Hopcraft et al. 2005, Eby et al. 2014), in this study, white-tailed deer experienced predation risk from a cursorial predator and increased cover resulted in decreased perceived predation risk. This is likely because

white-tailed deer often use escape cover to evade predators during fawning (Grovenburg et al. 2012). Similar to previous studies, female white-tailed deer increased feeding with increasing group size, during the night, and in the presence of juveniles (LaGory 1986, Lark and Slade 2008, Lashley et al. 2014, Cherry et al. 2015).

We examined the effects of time since fire and predation risk on space use and foraging behavior when decisions represent the balancing of competing demands of maintenance and maternal investment (Therrien et al. 2008), and therefore would have great potential to influence population-level processes. We offer evidence that fire governs the distributions of not only food resources, but also predation risk. For prey that perceive greater risk in cover than in open areas, fire increases quality of forage and decreases predation risk, making selection of burned areas an obvious choice (Archibald et al. 2005). However, our results suggest for prey that perceive cover as safer than open areas, fire increases forage quality and predation risk, presenting foraging tradeoffs that challenge prey to balance competing demands for safety and resources.

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