



Wildfire affects space use and movement of white-tailed deer in a tropical pyric landscape



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ABSTRACT

Fire influences the distributions of cover and food resources for ungulates in frequently burned systems. Fire typically improves forage quality, and as a result, herbivores are often drawn to recently burned areas—a response termed the ‘magnet effect.’ Thus, fire can be an important tool for manipulating vegetation to benefit wildlife. However, most studies of ungulate responses to fire occur at broad temporal scales (multiple years post-burn), and the immediate effects of fire on ungulates are poorly understood. While conducting a study of white-tailed deer (*Odocoileus virginianus*) in southern Florida, we were able to evaluate a natural experiment investigating the effects of wildfire on the spatial ecology of deer. In May 2015, the Mud Lake Fire Complex burned approximately 10,250 ha in Big Cypress National Preserve. This area included portions of the home ranges of 19 of 79 deer that we were monitoring via GPS-telemetry and permitted a Before-After-Control-Impact design to investigate if fire altered the area of use and movement rates of deer at 1, 2, and 3 months following fire compared to the month before the fire. Relative to the white-tailed deer in the unburned areas, white-tailed deer in the burned areas increased movement rates, potentially because fire reduced concealment cover, resulting in increased predator detection and decreased predation risk. Counter to our predictions that fire would increase forage quality and result in decreased space use, white-tailed deer exposed to the fire increased their space use following the fire when compared to deer whose home range did not include burned areas. This appeared to be the outcome of balancing competing demands for site fidelity and to increase access to improved forage in the recently burned areas. In general, deer exposed to the fire increased their use of the burned area following the fire, but also maintained portions of their home ranges that were not burned. Our results provide a behavioral confirmation that white-tailed deer are attracted to recently burned areas and that they respond rapidly to the alteration of vegetation.

1. Introduction

In frequently burned ecosystems, fire influences the distribution of food resources, concealment cover and wildlife species. Following fire, plant regrowth is typically more palatable and of higher quality (Christensen, 1977; Batmanian and Haridasan, 1985; Singh, 1993; Van de Vijver et al., 1999; Eby et al., 2014), therefore many herbivores are drawn to recently burned patches (Moe et al., 1990; Murphy and Bowman, 2007; Klop et al., 2007; Sensenig et al., 2010; Raynor et al., 2015), a phenomenon that Archibald et al. (2005) termed the ‘magnet effect’ when describing the green magnet hypothesis. Fire alters

vegetative structure, which may open sight lines and increase detection of predators that use concealment cover to stalk-and-ambush prey (Hopcraft et al., 2005). However, increased herbivore use of recently burned patches can also result in increased use of burned areas by predators (Paragi et al., 1997; Main and Richardson, 2002; McGregor et al., 2014) and the rapid removal of cover can impact predation rates if prey rely on concealment cover to avoid predators (Conner et al., 2011; Leahy et al., 2016).

Fire can have diverse effects on ungulate spatial ecology and demography. For example, Klop et al. (2007) used time since fire in resource selection functions to demonstrate that common duiker

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(*Sylvicapra grimmia*), red-flanked duiker (*Cephalophus rufilatus*), oribi (*Ourebia ourebi*), bushbuck (*Tragelaphus scriptus*), kob (*Kobus kob*), hartebeest (*Alcelaphus buselaphus*) and roan antelope (*Hippotragus equinus*) selected recently burned areas more than would be expected at random. Fire-mediated alteration in habitat selection have also been reported for North American ungulates including elk (*Cervus canadensis*), bison (*Bison bison*), moose (*Alces alces*) and deer (*Odocoileus* spp.; Irwin, 1975; Pearson et al., 1995; Raynor et al., 2015). Fire can result in increased density of moose (Peek, 1974; Hansen et al., 1973) and deer (*O. hemionus columbianus*; [Taber and Dasmann, 1957; Klinger et al., 1989]; *O. virginianus* [Vogel and Beck, 1970; Irwin, 1975]) due to immigration by yearlings, as well as increased reproductive rates and neonate survival (Taber and Dasmann, 1957; Peek, 1974). Several studies have demonstrated the long-term benefits of fire to herbivore populations (Vogl and Beck, 1970; Kruse, 1972; Peek, 1974; Irwin, 1975; Klinger et al., 1989; Pearson et al., 1995), and thus fire is an important habitat management technique in many ecosystems (Edwards, 1984).

However, for some species, such as white-tailed deer, investigations of movement and habitat selection do not universally support the green magnet hypothesis (Archibald et al., 2005). For example, Meek et al. (2008) documented avoidance of recent burns, by white-tailed deer in southern Texas; however, this avoidance may have been influenced by a post-fire drought that delayed the recovery of vegetation in the burned area. Female white-tailed deer avoid recent burns during fawn rearing perhaps because removal of cover is incompatible with the hiding strategy employed by fawns (Lashley et al., 2015a). Cherry et al. (2017) reported that during fawning, female white-tailed deer avoided areas following fire and that vigilance while foraging was inversely related to time since fire. However, they cautioned that the effects of fire on prey behavior are likely a function of attributes of the predator-prey system including the predator's hunting mode and the prey's escape tactics. No studies have reported the effect of fire on white-tailed deer movement in systems with a large stalk-and-ambush predator.

In southern Florida, white-tailed deer are the primary prey of a stalk-and-ambush predator, the endangered Florida panther (*Puma concolor coryi*). The remaining breeding populations of Florida panthers occur in an environment that is largely defined by the interactive effects of pyrogenic, hydrologic, and anthropogenic disturbance regimes. Fire improves white-tailed deer forage in southern Florida (Carlson et al., 1993) and Florida panthers increase use of burned areas during the first year following fire (Dees et al., 2001). Therefore, maintaining frequent fire may be important to sustaining populations of white-tailed deer and Florida panthers on the pyric landscape of southern Florida where historically, fires occurred every 1–3 years (Frost, 1988; Guyette et al., 2012). Lightning-initiated wildfires are relatively common in this system; however, governmental wildfire policy has limited the spatial extent of wildfires, and thus their effect on habitat conditions (Dombeck et al., 2004). Prescribed fire is now commonly used to maintain frequent fire in southern Florida. However, unlike wildfire, prescribed fire operations typically occur under conditions when fire can be controlled likely impacting fire effects on vegetation. There is a growing appreciation for the unique ecological role of wildfire and the importance of diversity of fire effects for wildlife management in frequently burned systems (Day et al., 2015; Lashley et al., 2015b; Bowman et al., 2016).

While conducting a field study on white-tailed deer in the Big Cypress Basin of southwestern Florida, lightning strikes ignited numerous fires in May 2015 across our study area. Because the fires burned across the home ranges of some of our GPS-instrumented white-tailed deer, we were able to evaluate a natural experiment examining the effects of wildfire on white-tailed deer space use and movement. We used this natural experiment to test 3 hypotheses. First, we tested the hypothesis that fire would alter resource availability and subsequently the area of space used. Given that resource availability is a primary driver of home range size (Adams, 2001), and fire improves forage conditions for white-tailed deer (Carlson et al., 1993), we predicted

deer would decrease area of space use post-burn. Alternatively, white-tailed deer have high site fidelity to their home ranges (Nelson and Mech, 1992; Aycrigg and Porter, 1997; Lesage et al., 2000) and therefore, might not alter space use in response to the fire and temporal changes in resource availability. A third possibility would be that white-tailed deer could attempt to exploit adjacent burned areas while maintaining their home ranges resulting in increased size of area of use. Secondly, we tested the hypothesis that fire influenced predation risk by decreasing concealment cover. Increased movement can increase susceptibility to predation (Yoder et al., 2004) and therefore, activity rates are often inversely related to perceived predation risk (Lima and Dill, 1990). Because the primary predator in our study area uses a stalk-and-ambush hunting mode, we assumed the fire-mediated opening of sight-lines would increase detection of predators, thereby reducing perceived predation risk. Therefore, we predicted that white-tailed deer in burned areas would have greater movement rates than white-tailed deer in unburned areas. Finally, we tested the green magnet hypotheses, which states that herbivores are attracted to resources in recently burned areas. We predicted that deer with access to the burned areas would increase use of those areas. Herein we report the results of this natural experiment investigating the behavioral response of white-tailed deer to wildfire.

2. Methods

2.1. Study area

We worked on the Big Cypress National Preserve (BCNP) and Florida Panther National Wildlife Refuge (FPNWR) in the Big Cypress Swamp physiogeographic region of southwestern Florida. The area experiences distinct wet and dry seasons and regional topography was characterized by minimal relief with slight ridges delineating relatively flat basins interspersed with depressions that can retain standing water throughout the dry season. The study site included pine forests, hardwood forests, cypress forests, prairies, and marshes.

2.2. Fire management

Numerous factors complicate fire management in BCNP including fuel loads that have increased due to historic fire suppression, invasive species, and altered hydrologic regime. Smoke management is challenging as there are nearby urban areas and major roads, including Interstate 75 (I-75) and US Highway 41 bisecting BCNP. There are approximately 2000 km² of burnable areas on BCNP, with a goal to maintain a 3–5-year return interval, which would equate to burning approximately 400–667 km² annually. Unfortunately, limited budgets, restrictions on acceptable burning conditions, and a shortage of fire management personnel often prevent the achievement of that annual goal (Fig. 1). Thus, fuel loads accumulate through time further complicating future prescribed fire and wildfire management. Historically, the response to wildfire in BCNP has been suppression through direct and indirect attack. However, the evolving fire philosophy is that wildfire is an important natural process, and that management strategies of confine and contain with natural barriers could harness wildfires to help meet fire management goals.

On 08 May 2015, lightning strikes ignited 15 fires across BCNP, collectively referred to as the Mud Lake Fire Complex (MLFC). The MLFC burned approximately 142 km² under the management of the local US Fish and Wildlife and National Park Service Interagency Type 3 Incident Management Team and transitioned to the Southern Area Type 1 (Red Team) Incident Management Team (IMT). The management strategy applied to manage the MLFC demonstrated a decision by the IMT to change wildfire response tactic in southern Florida – managers decided not to suppress the fire through direct or indirect methods. Rather, the strategy chosen for the MLFC was to confine and contain the fires using Minimum Impact Suppression Tactics (MIST) and natural

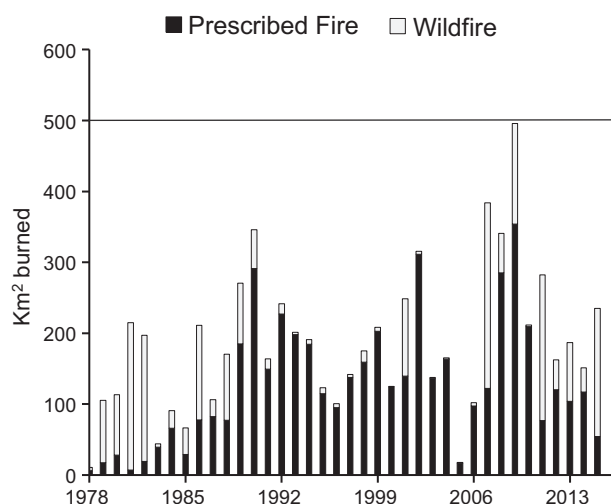


Fig. 1. Area of Big Cypress National Preserve burned with prescribed fire and wildfire from 1978–2015. There are approximately 2000 Km² of burnable area on Big Cypress National Preserve and the goal is a 3–5-year fire return interval. The horizontal line at 500 Km² represents the area goal to maintain a 4-year fire return interval.

barriers (Day et al., 2015). This approach recognized the role of wildfire in this ecosystem, was more restrained than approaches used in the past, reduced impacts from actions such as mechanical fuel manipulation and firebreaks, and targeted point protection of human structures over full fire perimeter control while prioritizing firefighter and public safety. This was a significant departure from traditional wildfire management strategies in southern Florida and across much of the USA (Dombeck et al., 2004; Dale, 2006; Calkin et al., 2015).

North of I-75, five fires combined to form the Square Fire. The primary management objective for the Square Fire was to contain the fire within the boundaries of BCNP. The fire backed southward towards I-75 with no firing on the south flank of the Square Fire. Management allowed the fire to move toward natural boundaries to the north, east, and west, and controlled fire severity by dropping water from helicopters in areas where the fuel loads likely would have resulted in canopy fires (Day et al., 2015). Fire severity varied by cover type and pre-fire fuel characteristic. For example, in areas with dense understory of saw palmetto (*Serenoa repens*) there was not complete combustion of vegetation, while in prairies there was more complete combustion of grasses (Fig. 2).

2.3. Deer capture

We used data from 79 white-tailed deer captured via net-gunning from helicopters and chemical immobilization administered via darting during January 2015 on BCNP and FPNWR. Deer captured via net-gunning were physically restrained and blindfolded during processing and were released within 20 min of capture. Deer captured by darting were administered a mixture of xylazine-hydrochloride (2.2 mg/kg body weight; Congaree Veterinary Pharmacy, Cayce, SC) and Telazol (4.4 mg/kg body weight; Congaree Veterinary Pharmacy, Cayce, SC, Kreeger et al., 2002). Once immobilized, we placed the deer in the sternal position, applied ophthalmic ointment and a blindfold. We monitored heart rate, body temperature, and respiration every 5 min until recovery. We reversed xylazine with Tolazoline (1.4 mg/kg body weight; Kreeger et al., 2002) approximately 90-min post-injection. Deer were fit with Iridium ATS (Advanced Telemetry Systems, Isante, MN) Model G2110E GPS collars programmed to record a location every 4 h on a rotating schedule such that each hour of the day was represented every 4 days. All deer were captured under University of Georgia IACUC permit A2014 07-009-Y3-A1.

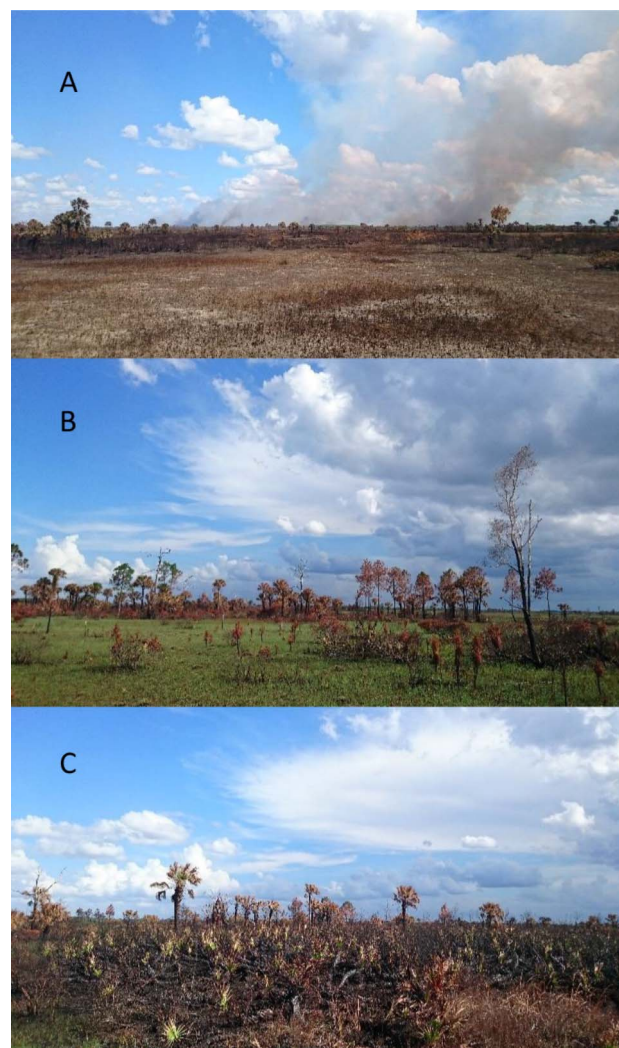


Fig. 2. Images of fire effects. Panel A is a prairie on 14 May 2015 immediately after the fire; Panel B is pine savannah on 24 May 2015; and Panel C is palmetto hammock on 24 May 2015. Note the variation in concealment between the savanna and palmetto hammock post-fire. Images by BDK.

2.4. Experimental design

The Square Fire burned across the portions of the home ranges of 19 adult deer (9M, 10 F), while the home ranges of 60 (16 M, 44 F) were not burned (Fig. 3). This allowed us to frame a natural experiment using a Before-After-Control-Impact (BACI) design, grouping deer by burn status (i.e., burned or not) and time (i.e., before vs the first, second or third month after fire; Underwood, 1992; Smokorowski and Randall, 2017). We interpreted significant interactions between burn status and time (relative to fire), as the effect of fire on the size of utilization distributions and movement rates. Spatial variation in resources is likely to result in variable space use and movement independent of the fire (Adams, 2001). This approach accommodates situations when groups are not experimentally assigned and allows for comparisons among groups that may be different before the treatment by explicitly testing whether the change through time varied by treatment group. We used this design to examine the effects of wildfire on space use and movement rate. To examine if deer selected or avoided the recently burned areas, we subset our data to include only those deer who overlapped spatially with the fire during any time of the study. We used this sample to examine if white-tailed deer exposed to the fire increased or decreased use of areas after they burned.

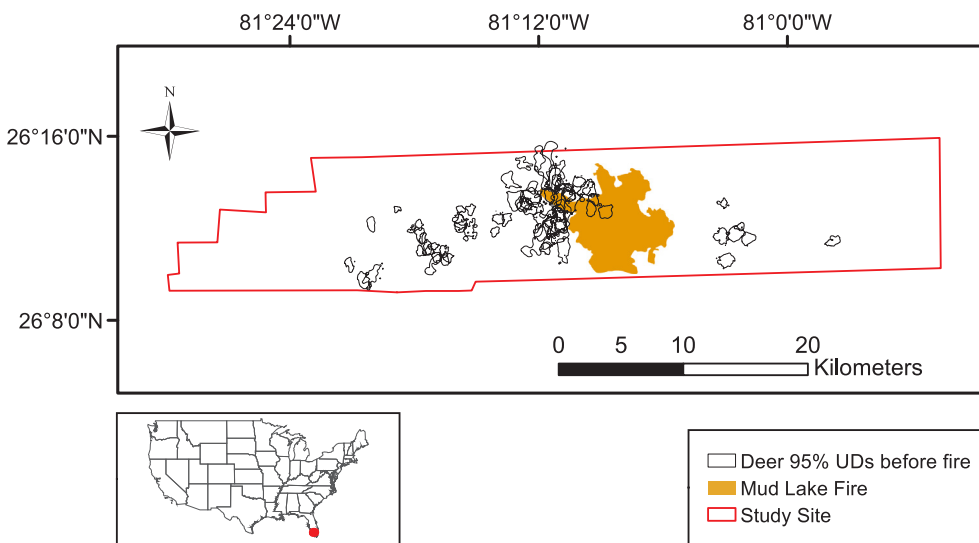


Fig. 3. Map of study area including Bear Island and North Addition Lands Units of Big Cypress National Preserve and the Florida Panther Nation Wildlife Refuge, 95% utilization distributions for GPS collared deer before the fire, and the area burned during the Mud Lake Fire.

2.5. Modeling space use

We estimated utilization distributions (UD) for each animal-period combination using Dynamic Brownian Bridge Movement Models (DBBMM; Horne et al., 2007; Kranstauber et al., 2012). This method uses the movement trajectory and behavior of an individual that is captured in the serial autocorrelation in sequential relocation data that is common in GPS collar studies, and provides a spatially explicit model describing the probability of an animal occurring in a given location during a specified period. Using DBBMM to develop UD's requires estimates of the Brownian motion variance parameter (σ_m^2). This parameter is the Brownian motion diffusion coefficient and is related to the mobility of the individual. A moving window analysis identifies changes in movement behavior and estimates σ_m^2 for each time step (Gurarie et al., 2009). The size of the moving window must include an odd number of GPS locations, because the σ_m^2 parameter is estimated using a “leave-one-out method”, and a margin of ≥ 3 locations bounding each end of the window in which no behavioral changes can occur (Horne et al., 2007; Kranstauber et al., 2012). We used a window size of 21 steps, a margin size of 5 steps, and an 18-m location error for all deer, as visual inspection indicated these settings were sufficient to identify relevant changes in behavior. We fit DBBMM to estimate the 95% UD for each animal during each period (i.e., the month before the fire, and the first, second, and third month following fire) using package *move* (Kranstauber and Smolla, 2014) in R version 3.0.0 (R Development Core Team, 2013).

2.6. Fire effects on space use

We examined the effects of fire on the area of the 95% UD using a BACI design. We assigned all deer to a burn status group based on whether any portion of their 95% UD intersected the fire polygon (burned) or not (unburned) during a given time period allowing individual animals to transition from one burn status to another between periods. This removed the possibility of interpreting the behavior of deer that moved away from the burned areas as being impacted by the fire during periods where they were not using burned areas. It also allowed us to assign the deer to the ‘burned’ group if they moved into the burned area, even if they previously had not used that area. This approach allowed us to more directly address the effect of fire on space use. We created three datasets that each included the area of the 95% UD the month prior to the fire and one of the subsequent months (i.e., first, second, and third month following fire). We used a linear mixed effects model fit with restricted maximum likelihood to compare the area of 95% UD's between burn classes during each period by including

the interaction of burn status and period. We included sex as a covariate and treated the individual-specific intercepts as random effects. We used Satterthwaite method to approximate the degrees of freedom and computed p-values for direct effects and interactions using t statistics (Bolker et al., 2009). If we observed a significant interaction between burn status and time period, we interpreted the interaction statistics as the effect of fire on UD area.

2.7. Fire effects on movement rate

We examined the effects of fire on movement rates using a BACI design by categorizing burn status and time as previously described. For each animal, we calculated the distance between sequential locations (i.e., step length) and standardized those measurements by dividing by the amount of time between sequential locations to calculate movement rate (m/h). We fit linear mixed effects models predicting movement rate as a function of sex, and a burn status by period interaction, while treating the animal-specific intercepts as random effects. Again, we used Satterthwaite method to approximate the degrees of freedom and computed p-values for direct effects and interactions using t statistics. We developed models for each combination of the first, second, and third months following fire compared to the month preceding the fire. We interpreted a significant interaction between time and burn status as the effect of fire on movement rate. We bootstrapped estimates with 200 iterations to calculate means and 95% confidence intervals for comparison of means among groups.

2.8. Fire effects on the location of activity

To examine if deer were attracted to or avoided the recent burn, we subset our data to only include animals with $\geq 1\%$ of the volume of their UD within the fire polygon during any season and survived until the end of the study. We considered this subset of deer to be those who interacted with the fire and thus had the ability to respond by either increasing or decreasing their use of burned areas after the fire. We calculated the volume of animal-specific UD within the burn polygon for each period. We then created three datasets that included the month before the fire and one of the months following the fire. We subtracted the volume of each deer's UD that intersected the burn polygon during the month before the fire from the month following the fire for each dataset. For example, if the burn polygon included 50% of the volume of a deer's UD before the fire and 75% of the deer's UD after the fire, that deer would have a value of 25 in our dataset representing a 25% increase in use of the burned area. We then used one-sample t-tests, to test the null hypothesis that the mean difference in overlap is equal to 0.

Table 1

Sample size by sex, burn status of white-tailed deer included in the study the month before (04/10/2015–05/10/2015), the first (05/23/2015–06/23/2015), second (06/24/2015–07/23/2015), and third (07/24/2015–08/23/2015) month following the Mud Lake Complex fires in Big Cypress National Preserve.

	Burned	Unburned
Before	19 (10F, 9 M)	60 (44F, 16 M)
First	20 (10F, 10 M)	55 (42F, 13 M)
Second	18 (9F, 9 M)	50 (40F, 10 M)
Third	18 (8F, 10 M)	47 (39F, 9 M)

Table 2

Beta estimates, standard errors, approximated degrees of freedom, t values, and p values generated from the linear mixed models predicting the area of utilization distributions for male and female deer during the month before and the first, second, and third, months following the Mud Lake Complex fires in Big Cypress National Preserve. The reference classes were as follows: sex = female; burn status = unburned; and period = before.

	β	SE	df	t-value	Pr(> t)
First Month					
Intercept	0.57	0.08	129.55	7.07	< 0.001
Burn	0.44	0.15	144.68	2.87	0.005
Period	0.12	0.09	75.89	1.37	0.176
Sex	0.91	0.12	77.77	7.71	< 0.001
Burn*Period	0.57	0.18	84.14	3.08	0.003
Second Month					
Intercept	0.48	0.12	127.08	4.13	< 0.001
Burn	0.30	0.22	136.49	1.38	0.170
Period	0.36	0.14	75.12	2.63	0.010
Sex	1.31	0.17	81.39	7.69	< 0.001
Burn*Period	0.61	0.27	78.02	2.23	0.029
Third Month					
Intercept	0.42	0.11	135.64	3.95	< 0.001
Burn	0.28	0.21	139.36	1.38	0.169
Period	0.50	0.14	77.42	3.47	0.001
Sex	1.50	0.15	80.80	9.94	< 0.001
Burn*Period	0.75	0.29	83.81	2.64	0.010

3. Results

3.1. Space use and movement

Our study included data from 79 deer instrumented with GPS collars but sample sizes declined slightly through the study (Table 1). The wildfire influenced multiple aspects of the spatial ecology of deer. We observed significant period-by-burn-status interactions in all three models comparing the area of use for each period to the month prior to the fire (Table 2). The significant interactive effects in our BACI design indicate that deer increased the area of their 95% UD in response to wildfire (Fig. 4). Similarly, male and female deer exposed to fire increased their movement rate during the first, second, and third month following fire relative to the white-tailed deer in the unburned area (Fig. 5). We observed significant interactions between burn status and period in all three models comparing the movement rate between the first, second, and third month following the fire compare to the month prior to the fire (Table 3). Males had larger UDs and greater movement rates than females during all periods. Regardless of burn status, males increased the area of their UDs and movement rates through the study period, which likely was an artifact of the breeding season, which peaked during the third month post fire (Table 4).

3.2. Fire and location of activity

We used the volumetric measurements of UDs estimated for each deer to examine if deer increased use of burned areas. Our dataset for this analysis included 22 deer that used the burned area during at least one period. The same deer were included in each comparison between

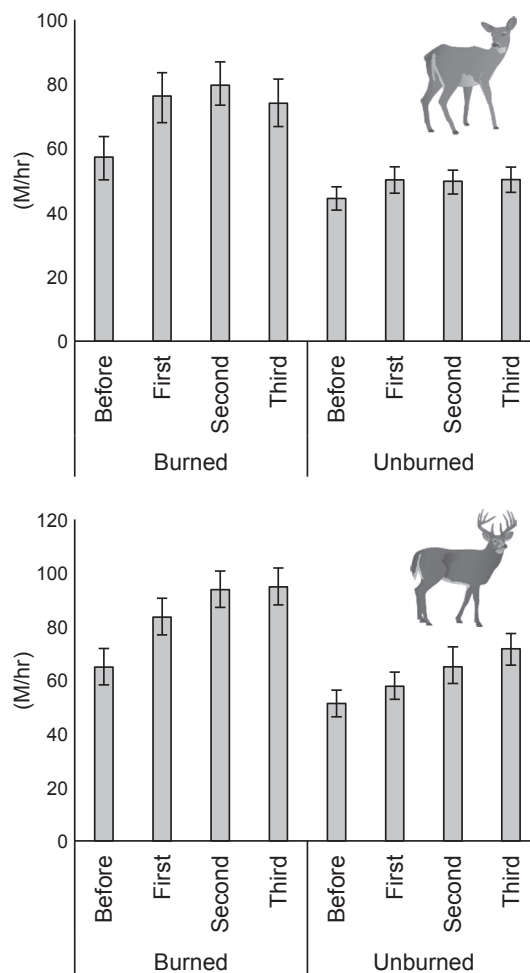


Fig. 4. Movement rate in meters/hour for female and male white-tailed deer during the month before, and the first, second, and third months following the Mud Lake Complex fires in Big Cypress National Preserve. Error bars represent the 95% confidence intervals around the means. Means and confidence intervals were estimated by bootstrapping with 200 iterations.

the month prior and each month after the fire, even if they did not use the burned area during that month. We found no evidence of sex effects during the first ($t = -1.56, P = .14$), second ($t = -1.23, P = .23$) or the third ($t = -1.32, P = .20$) month following fire and therefore we combined the sexes for subsequent analyses. Deer exposed to the fire increased their use of the burned area during all periods compared to the month before the fire (Fig. 6). During the first month following fire, deer increased the volume of the UD that included the burned area from 27% to 46% an average increase of $19.0 \pm 10.0\%$ ($x \pm 95\% \text{ CI}$; $t = 3.93, df = 21, P < .001$; Fig. 7). Relative to pre-fire, during the second month following fire, deer increased the volume of their UD that included the burned area by $19.7 \pm 13.14\%$ ($t = 3.11, df = 21, P = .005$). Relative to pre-fire, during the third month following fire deer increased the volume of their UD that included the burned area by $10.9 \pm 9.7\%$ ($t = 2.36, df = 21, P < .028$). The UDs of two deer were entirely burned and those deer did not abandon the area, but consequently did not increase or decrease their use of the burn. We conducted the analyses including (as reported above) and excluding these deer. Because they had values of 0% increase in our dataset, the models excluding these deer resulted in slightly greater increases in the use of the burn. To be conservative in our interpretations, we report the results from the models including these deer.

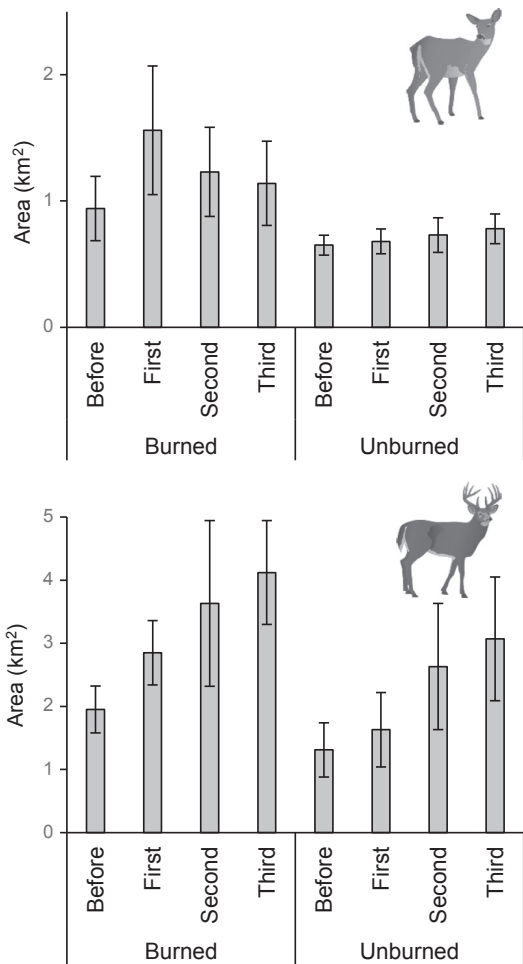


Fig. 5. Area of 95% utilization distributions for female and male white-tailed deer during the month before, and the first, second, and third months following the Mud Lake Complex fires in Big Cypress National Preserve. Error bars represent the 95% confidence intervals around the means.

Table 3

Mean area (km²) and standard error of 95% utilization distributions estimated with dynamic Brownian bridge movement models for female and male deer during the month before and the first, second, and third, months following the Mud Lake Complex fires in Big Cypress National Preserve.

		Before	First	Second	Third
Female	Burned	0.94 ± 0.13	1.56 ± 0.26	1.23 ± 0.18	1.14 ± 0.17
	Unburned	0.65 ± 0.04	0.68 ± 0.05	0.73 ± 0.07	0.78 ± 0.06
Male	Burned	1.95 ± 0.19	2.85 ± 0.26	3.63 ± 0.67	4.12 ± 0.42
	Unburned	1.31 ± 0.22	1.63 ± 0.30	2.63 ± 0.51	3.07 ± 0.50

4. Discussion

Our results suggest that wildfire can influence multiple aspects of spatial ecology of white-tailed deer in southern Florida. We found support for the green magnet hypothesis that describes the ‘magnet effect’ of recent burns for herbivores (Archibald et al., 2005). However, the magnet effect was tempered by what appears to be site fidelity to home ranges. For those deer in close proximity to the fire, their expanded area of activity provided more access to the recently burned areas, but they did not entirely abandon their pre-fire areas of use. Thus, paradoxically those animals with access to the purported improved forage conditions following the fire had larger areas of use. This may have occurred because the majority of the white-tailed deer that were exposed to fire only had a portion of their home ranges burned

Table 4

Beta estimates, standard errors, approximated degrees of freedom, t values, and p values generated from the linear mixed models predicting the movement rate for male and female deer during the month before, and the first, second, and third months following the Mud Lake Complex fires in Big Cypress National Preserve. The reference classes were as follows: sex = female; burn status = unburned; and period = before.

	β	SE	df	t-value	Pr(> t)
First Month					
Intercept	44.20	2.12	80	20.89	< 0.001
Burn	13.20	3.93	81	3.37	0.001
Period	6.03	0.68	28860	8.87	< 0.001
Sex	7.35	3.56	76	2.07	0.042
Burn*Period	12.59	1.47	28890	8.57	< 0.001
Second Month					
Intercept	42.19	2.09	80	20.17	< 0.001
Burn	11.62	3.88	81	3.00	0.004
Period	7.62	0.77	27290	9.90	< 0.001
Sex	15.08	3.52	76	4.29	< 0.001
Burn*Period	17.84	1.59	27270	11.22	< 0.001
Third Month					
Intercept	40.60	2.12	80	19.12	< 0.001
Burn	10.39	3.94	81	2.64	0.010
Period	9.49	0.82	27191	11.53	< 0.001
Sex	21.10	3.57	76	5.91	< 0.001
Burn*Period	13.20	1.66	27213	7.94	< 0.001

and the increase in space use resulted from expanding activity into the burned areas. Of the two animals whose entire home range burned, one reduced area of use and the other was largely unchanged, in spite of seasonal increases observed across the population. While limited in replication, these two observations support the idea that in the absence of site fidelity constraints, the improved foraging conditions provided by fire resulted in a reduction of space use (Adams, 2001).

We observed increased movement rates by deer with access to the burned area, potentially because fire manipulated vegetation in a manner that reduced perceived predation risk, releasing white-tailed deer to increase movement. While our data were insufficient for formal analyses of the effect of fire on survival, no animals were predated in the burned area while Florida panthers killed several deer in the unburned area; supporting our suggestion, that fire opened sight-lines and reduced perceived predation risk. Other factors such as heterogeneous distribution in improved forage or thermoregulatory cover within the burned landscape could explain increased movement rates. Additionally, while UD area and movement rates may not be directly related, increased movement could be a function of increase UD area. However, the two animals whose home ranges were entirely burned, increased movement rates in spite not increasing the area of their 95% UD.

Our results reflect other studies that have described the ‘magnet effect’ of fire on herbivores such as bison, axis deer (*Axis axis*), Thomson's gazelle (*Gazella thomsonii*), impala (*Aepyceros melampus*), Grant's gazelle (*Gazella granti*), wildebeest (*Connochaetes taurinus*), tsessebe (*Damaliscus lunatus*), Burchell's zebra (*Equus burchelli*) and roan antelope (Wilsey, 1996; Moe et al., 1990; Gureja and Owen-Smith, 2002; Raynor et al., 2015). However, they differ from other studies that report either no selection (i.e., Bohor reedbeek (*Redunca redunca*), warthog (*Phacochoerus africanus*), topi (*Damaliscus korrigum*), zebra (*Equus burchelli*); Wilsey, 1996; Klop et al., 2007) or avoidance of recent burns (i.e., caribou [*Rangifer tarandus*]; Schaefer and Pruit, 1991). Across ungulates, selection of recent burns generally decreases with increasing body size because smaller herbivores require more energy per unit of body mass, and maintain smaller home ranges than larger herbivores, and therefore attempt to maximize the quality of forage in the relatively smaller home range (Demment and Vam Soest, 1985; Senging et al., 2010). Selection of recent burns also may be greater for ruminants than hindgut fermenters because ruminants are more efficient at extracting energy from forage and are constrained by quality,

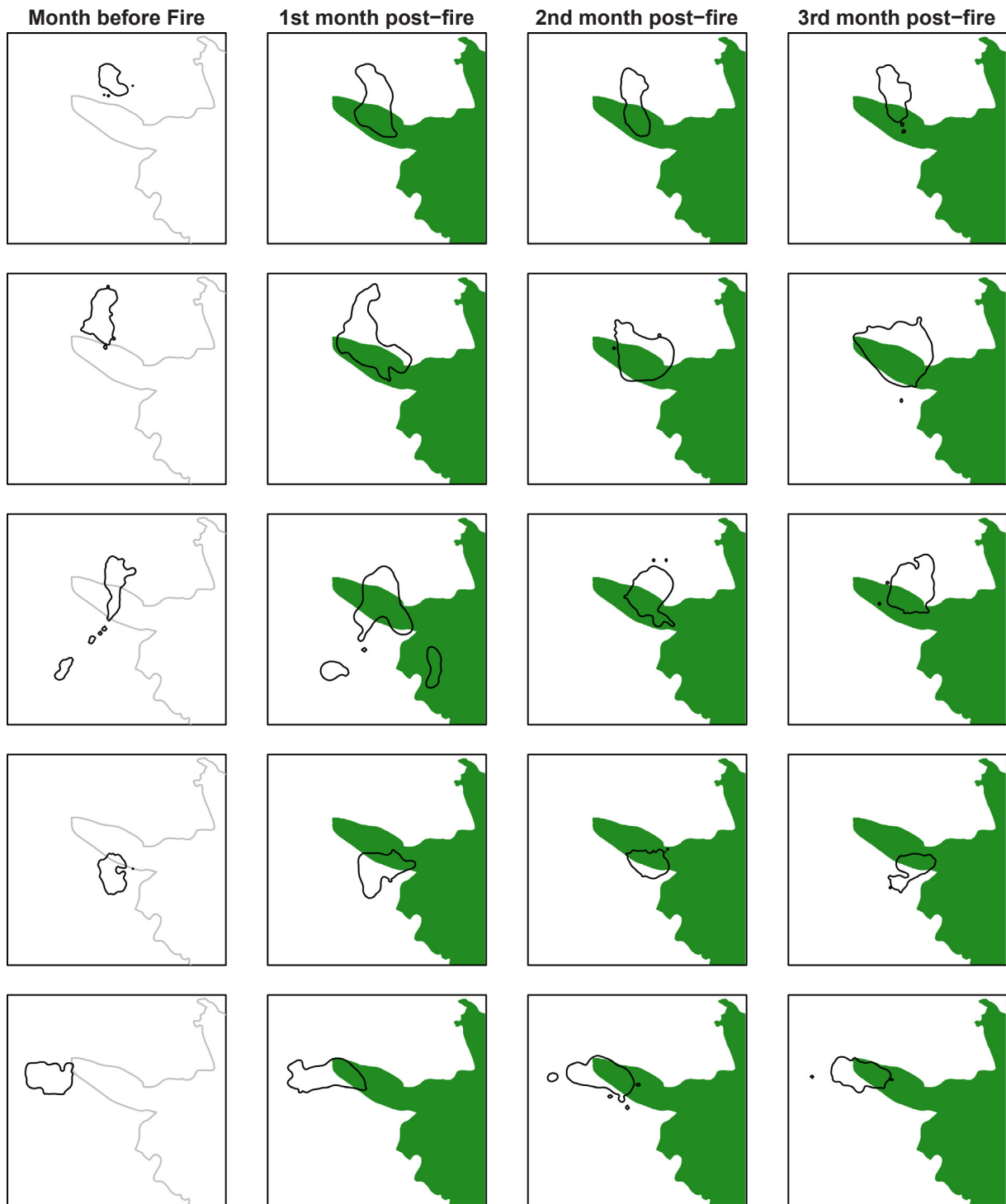


Fig. 6. Examples of shifts in location and size of areas of use represented by 95% utilization distributions estimated with dynamic Brownian bridge movement models displayed with the black-bordered polygons in relation to the Mud Lake Fire Complex, which is displayed with the gray-bordered polygons before the fire and the green polygon after the fire. Each row represents an individual deer and columns represent the month before (04/10/2015–05/10/2015), the first (05/23/2015–06/23/2015), second (06/24/2015–07/23/2015), and third (07/24/2015–08/23/2015) month following the fire.

while hindgut fermenters are constrained by quantity of forage (Illius and Gordon, 1992).

White-tailed deer are relatively small ruminants and thus should strongly select for recent burns. Our results support these predictions. However, other studies report white-tailed deer avoided recent burns during fawning in systems where significant predators of adult deer were absent and the primary predators, coyotes (*Canis latrans*) and bobcats (*Lynx rufus*), prey on fawns (Lashley et al., 2015a; Cherry et al.,

2017). During fawning, foraging adult females display greater vigilance in recent burns where cover is reduced (Cherry et al., 2017), suggesting that fire creates foraging tradeoffs by increasing forage quality and predation risk (via reduced cover). In southern Florida, the primary predator of deer is the Florida panther, an ambush predator that uses cover as concealment when stalking prey. Therefore, in this system fire may simultaneously improve forage and reduce predation risk for white-tailed deer.

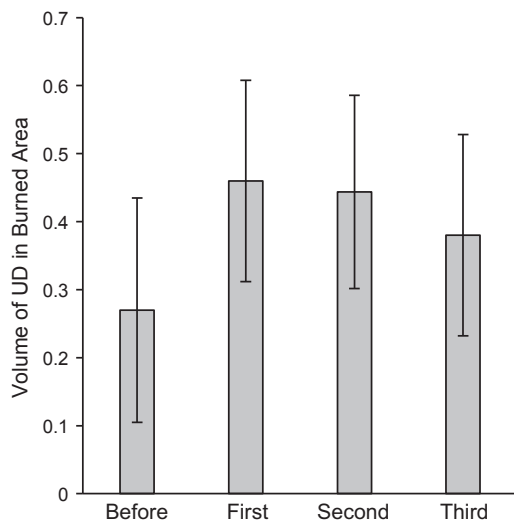


Fig. 7. Mean volume of the Utilization distributions for 22 deer that intersected the burned area during the month before and the first, second, and third months following the Mud Lake Complex fires in Big Cypress National Preserve. Error bars represent 95% confidence intervals.

Other studies have shown that fire results in increased abundance of deer due to increased productivity or immigration into burned areas (Taber and Dasmann, 1957; Vogl and Beck, 1970; Peek, 1974; Irwin, 1975; Roppe and Hein, 1978). Fire effects on white-tailed deer survival has received less attention and may be important in some predator-prey systems given that fire can influence movement rates and space use, and that moving in areas with which prey are unfamiliar can increase susceptibility to predation (Yoder et al., 2004). Understanding the effects of fire on each population process (i.e., survival, reproduction, and immigration) would facilitate predictions of fire effects on ungulate populations across systems that vary with respect to predator community and net primary production. We offer evidence of increased immigration into burned areas. Future studies should investigate fire influence on survival, and the relative importance of survival, immigration, and reproduction on population growth and abundance following fire.

Most prior studies have evaluated longer time scales and often rely on less direct methods to assess preference for burns such as camera traps (Main and Richardson, 2002), visual observations (Wisley, 1996; Tomor and Owen-Smith, 2002; Allred, 2011; Eby et al., 2014), or pellet count surveys (Archibald et al., 2005). We used GPS relocation data to compare space use and movement, which allowed us to examine fine scale spatiotemporal responses to wildfire, which have not previously been reported. A primary limitation of our study is that it was quasi-experimental, and included a modest sample size of individuals that interacted with a single fire. Therefore, future studies should investigate the effects of fire on spatial ecology of white-tailed deer under a range of fire and predator-prey conditions.

4.1. Conclusions

Resource selection decisions are thought to be the outcome of evolutionary pressures and while maladaptive decisions occur, particularly in rapidly changing environments, they are in fact rare (Van Horne, 1983; Kristin, 2003). Thus, selection decisions are thought to maximize fitness and are often used to inform wildlife management. We found that deer responded in a manner that suggests they sought to increase use of the recently burned areas. Fire managers allowed the Mud Lake Fires to burn for approximately two weeks, which was a significant departure from previous wildfire management strategies and white-tailed deer appear to respond positively to this management action. We recommend that managers continue to pursue the changing

wildfire management paradigm of allowing wildfires to provide ecological benefits where appropriate and to use wildfire in conjunction with prescribed fire to meet land area goals and heterogeneity in fire effects

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2017.11.007>.

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