



Original Article

Influence of Vegetation Type and Prescribed Fire on *Peromyscus* Abundance in a Longleaf Pine Ecosystem

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ABSTRACT Prescribed fire temporarily can alter food and cover resources for ground-dwelling wildlife, potentially leading to changes in animal abundance. Small mammals are an important ecosystem component in many terrestrial communities and depend on ground-level vegetation most commonly affected by prescribed fire. In this complex system of food and cover availability where easier access to food might compromise cover, and vice versa, it is imperative to study postfire habitat use by mice and other ground-dwelling wildlife. We evaluated effects of time since burn and vegetation type on *Peromyscus* spp. abundance in a longleaf pine (*Pinus palustris*) ecosystem in Fort Bragg Military Installation, North Carolina, USA, during 2011 and 2012. We trapped in 5 vegetation types and captured 208 individual *Peromyscus*. *Peromyscus* abundance did not differ among 1, 2, and 3 years postburn upland pine vegetation types, although we noted a trend of decreasing abundance as time since burn increased; however, abundance was greater in the lowland hardwood vegetation type than in open areas (i.e., military drop zones). The lack of an effect of time since burn could be due to the short fire–return interval at the study site, which limited the time for postburn shifts in the composition of the understory from herbaceous to woody plant species. Therefore, we suggest future research in the longleaf pine ecosystem incorporate a wider time frame to assess short- and long-term effects of fire on small mammal populations. © 2017 The Wildlife Society.

KEY WORDS capture–recapture modeling, lowland hardwood, military installation, mouse, rodent, time since burn, vegetation composition.

Prescribed fire is a critically important disturbance agent for restoration and maintenance of fire-adapted ecosystems around the world. One example is the longleaf pine–wiregrass (*Pinus palustris*–*Aristida stricta*) ecosystem, which once covered ≥ 30 million ha in the southeastern United States (Frost 1998). The highly threatened longleaf pine ecosystem represents one of the most diverse in the temperate zone and commonly targeted for ecological restoration (Drew et al. 1998, Fill et al. 2012, Lashley et al. 2015). The longleaf pine ecosystem was naturally maintained by frequent lightning-ignited fires (Brockway and Lewis 1997, Frost 1998) and Native Americans as they

used burning to clear undergrowth and improve habitat for important grazing species (Van Lear 1984, Frost 1998, Van Lear and Harlow 2000, Oswalt et al. 2012). Frequent low-intensity fires prevented encroachment of hardwoods and less fire-tolerant pines (e.g., *P. taeda*), and reduced fuel loads and increased plant diversity (Van Lear 1984, Landers et al. 1995, Brockway and Lewis 1997, Frost 1998).

Small mammals are an important component of many terrestrial ecosystems and depend on the ground-level vegetation most commonly affected by prescribed fire. Small mammals are primary consumers and an important prey source for many larger mammals, snakes, and raptors (Masters and Lochmiller 1998, Karmacharya et al. 2012). Consumption of plant material and seeds by small mammals can affect succession of plant communities and stability of plant populations (Davidson 1993, Valone and Schutzenhofer 2007). Also, many species of small mammals are important dispersers of seeds and fungal spores (Johnson 1996, Masters and Lochmiller 1998).

Received: 31 March 2016; Accepted: 13 November 2016
Published: 17 March 2017

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Prescribed fire consumes coarse woody debris and leaf litter (Bock and Bock 1983, Converse et al. 2006a, Amacher et al. 2008, Morris et al. 2011), which provide cover for small mammals (Carey and Harrington 2001, Converse et al. 2006b). Conversely, fire may increase food availability by increasing herbaceous plant production in the first few seasons after burning (Bock and Bock 1983, Outcalt 1994, Sparks et al. 1998). Moreover, consumption of the litter layer by fire can facilitate navigation and movement on the forest floor and uncover seeds previously inaccessible in deep litter (Clark et al. 1991; Reed et al. 2004, 2005; Zwolak et al. 2011). Although species abundance is regulated by numerous mechanisms, food availability and predation are the most important (Sinclair 2003, Zwolak et al. 2011). In this complex system of food and cover availability where easier access to food might compromise cover, and vice versa, studies of wildlife response in relation to time since fire are useful.

In longleaf pine ecosystems, frequent growing-season prescribed burns could substantially alter food and cover availability for mice and other small mammals, especially in upland stands that burn more homogeneously than lowland areas (Lashley et al. 2015). Growing season burns reduce woody vegetation more intensely than dormant season fire, and decrease vegetation complexity (Van Lear and Harlow 2000). Within the longleaf pine ecosystem, lowland hardwoods typically occur along streams and margins of other water bodies; the forest type is dominated by trees and tall shrubs and burns infrequently in comparison with the upland pine-dominated forest types where herbaceous species and low shrubs prevail (Sorrie et al. 2006). Wiregrass is the primary plant influencing the spread of fire in the uplands of the longleaf pine ecosystem and typically less intact in the relatively moist soils of lowland hardwood stands (Noss 1989, Lashley et al. 2015). Understory leafy biomass in upland pine forest increases with years since fire, whereas leafy biomass in lowland hardwood forest is less influenced by fire and remains more stable (Lashley et al. 2015). Additionally, wiregrass forms a dense thatch layer 2–3 years following fire, which reduces bare ground cover over time (Taillie et al. 2015).

Although habitat requirements of *Peromyscus* spp. are well-studied, effects of the frequent low-intensity prescribed fire commonly implemented in the longleaf pine ecosystem on *Peromyscus* and other small mammals are unknown. Therefore, we compared *Peromyscus* spp. abundance among vegetation types in a longleaf pine–wiregrass ecosystem managed primarily with a 3-year fire return interval. We hypothesized that *Peromyscus* abundance in the upland pine type would decline with time since fire as wiregrass thatch became increasingly dense and limited access to food and restricted movement across the forest floor.

STUDY AREA

Fort Bragg Military Installation (FBMI) encompassed approximately 65,000 ha in the Sandhills physiographic region of south-central North Carolina, USA, and contained one of the largest contiguous remnants of the longleaf

pine–wiregrass ecosystem. The average yearly rainfall was 120 cm, average yearly snowfall was 7.5 cm, and there were 175 frost-free days (Sorrie et al. 2006). The most abundant plant community type present at FBMI was the pine–scrub oak (*Quercus* spp.) sandhill, which consisted mainly of a longleaf pine canopy, oak subcanopy, and wiregrass ground layer (Sorrie et al. 2006). Other common plant communities present in this ecosystem included streamhead pocosin and ruderal areas, which were highly disturbed military training areas with no canopy (Sorrie et al. 2006). Lowland hardwood areas typically occurred along streams and margins of other water bodies and contained mature hardwoods such as oaks, blackgum (*Nyssa sylvatica*), and sweetgum (*Liquidambar styraciflua*), with a dense understory of ericaceous shrubs and hardwood midstory. Upland pine vegetation types were most commonly mature longleaf pine-dominated communities with patchy oak-dominated hardwood inclusions.

Land management at FBMI was driven by efforts to restore and maintain habitat for the federally endangered red-cockaded woodpecker (*Picoides borealis*), which requires open, mature long-leaf pine communities maintained by frequent fire (U.S. Fish and Wildlife Service 2003). Prior to 1989, prescribed burning was conducted exclusively during the dormant season. However, growing season burns comprised the majority of planned burns in forested vegetation types at FBMI since 1989 (J. Jones, Fort Bragg Wildlife Branch, personal communication). Prescribed burns were scheduled on a 3-year rotation for most forested upland areas of FBMI, whereas some nonforested areas (e.g., open military drop zones) were burned annually or biennially to remove all woody growth. Lowland areas were subjected to the same fire regime as uplands, but generally burned less frequently because of greater soil moisture levels.

METHODS

Vegetation Classification

We defined 5 major vegetation types at FBMI using a Geographic Information System incorporating existing cover type and burn history data: 1) upland pine 1 year postburning; 2) upland pine 2 years postburning; 3) upland pine 3 years postburning; 4) lowland hardwood; and 5) open. All prescribed fires in the uplands pine stands occurred during the growing season from April through July. We included the lowland hardwood and open vegetation types in addition to the fire-treated vegetation types to better assess the overall small mammal distribution at FBMI. Open areas consisted mainly of drop zones, areas used for military parachuting and supply drops, and portions of the impact areas, which were off-limits zones used for detonating explosives and firing live ammunition. Vegetation in the open areas consisted of grasses and forbs with sparse shrubs.

Small Mammal Sampling

We sampled 5 trapping grids in each of the 5 vegetation types in 2011 and 2012, for 25 total trapping grids per year. Trapping grids were placed in different locations in 2012 than in 2011. We did not sample the exact same stands, but we did sample the same cover types. We established each

trapping grid with one edge abutting a hard edge (i.e., a firebreak), so that sampling was not biased by greater edge effect in smaller stands than in larger stands. We placed 49 Sherman traps (H.B. Sherman Traps, Tallahassee, FL, USA) at each site in a square grid with 10-m spacing between traps. We baited traps with a mixture of oats and peanut butter and placed a cotton ball in each trap for bedding material. At each trap site, we cleared the ground of vegetation and sprayed with a chemical insecticide (Raid Ant & Roach Killer[®]; S.C. Johnson and Son, Inc., Racine, WI, USA) to reduce bait-stealing and predation by fire ants (*Solenopsis* sp.) without affecting small mammal trapping yield (Gettinger 1990). We sampled all 25 trapping grids in April–May of each year, trapping 5 grids at a time for 5 consecutive nights each, before moving traps and sampling the next 5 sites. We left traps open overnight and closed them during the day to reduce heat stress.

We identified, weighed, and marked all captured small mammals with individually numbered ear tags (Style 1005-1; National Band and Tag Co., Newport, KY, USA) prior to release. For recaptured individuals, we recorded the tag number and trap location and immediately released the animal at the site of capture. We identified captured individuals to species level, except white-footed mouse (*Peromyscus leucopus*) and cotton mouse (*P. gossypinus*), which were difficult to distinguish in the field and may hybridize in some areas (Barko and Feldhammer 2002); we lumped these species as *Peromyscus* spp. All field methods were consistent with the wild mammal use guidelines of the American Society of Mammalogists (Sikes et al. 2011) and approved by the North Carolina State University Institutional Animal Care and Use Committee (Protocol # 11-005-O).

Data Analysis

We used closed capture–recapture modeling in Program MARK (White and Burnham 1999) to estimate small mammal abundance for each vegetation type. We conducted a preliminary analysis where we used closed capture models M_0 (null), M_b (behavior), M_t (time), and M_h (heterogeneity) with year and vegetation type as effects on p (capture probability) and c (recapture probability; Otis et al. 1978). The closed capture model M_0 assumes that all individuals of the population are equally at risk of capture on every trapping occasion; model M_b assumes that behavior causes individual capture probabilities to vary; model M_t assumes that capture probabilities vary with time; and model M_h assumes that capture probability vary by individual animals (Rexstad and

Burnham 1991). The effect of vegetation type was modeled using the 5 major vegetation type categories previously defined. We conducted model selection using Akaike’s Information Criterion adjusted for small sample size (AIC_c; Akaike 1974), and chose the highest-ranked model (min. AIC_c) to estimate abundance parameters (Burnham and Anderson 2002). We used z -tests with a Bonferroni adjustment at $\alpha = 0.05$ to test for pairwise differences in abundance estimates between vegetation types.

On account of low capture rates, we pooled data from all 5 trapping grids within each vegetation type in each year. Additionally, we did not include the “open” vegetation type in preliminary analysis because there were not enough captures in that cover type (Appendix A in Supporting Information) to model all of the parameters in all of the 4 model types M_0 (null), M_b (behavior), M_t (time), and M_h (heterogeneity). The top 3 models from preliminary analysis were of the null (M_0) and behavior (M_b) types that had fewer parameters, which made it possible to include the open cover type in the full analysis using these selected models. The top 4 models from the preliminary analysis included a behavioral effect ($p \neq c$; Model M_b); the 2 highest-ranked models did not include an effect of year. However, the third-ranked model contained only an effect of year and no effect of vegetation type. The 3 top-ranking models were within 2 Δ AIC, so we included all 3 models in the final analysis with the full data set.

We analyzed the full data set (including the open vegetation type) using the top 3 models from the initial analysis: the null model, the model with vegetation type as an effect on p and c diff (recapture probability different), and the model with year as an effect on p and c diff. For the 2 models that did not include an effect of year, we modeled abundance with cover type only. The best model (lowest AIC) included vegetation type as an effect on p and c diff, with no year effect. Therefore, we used this model to calculate abundance estimates, \hat{N} , for each vegetation type.

RESULTS

We trapped for 12,250 trap-nights and captured 243 individuals (126 in 2011 and 117 in 2012; Table 1). Total captures, including recaptures, were similar between years, with 276 and 259 in 2011 and 2012, respectively. Three species were captured in 2011 and 5 species were captured in 2012 (Table 1). The majority of captures each year were *Peromyscus* spp. (94.6% of captures in 2011 and 84.6% of

Table 1. Small mammals (annual percent of total captures) captured at Fort Bragg Military Installation, North Carolina, USA, 2011 and 2012.

Species	2011		2012	
	Individuals	Captures	Individuals	Captures
<i>Peromyscus</i> spp.	118 (93.6)	261 (94.6)	90 (76.9)	219 (84.6)
<i>Reithrodontomys humulis</i>	7 (5.6)	12 (4.4)	5 (4.3)	5 (1.9)
<i>Microtus pinetorum</i>	1 (0.8)	3 (1.1)	0 (0)	0 (0)
<i>Sigmodon hispidus</i>	0 (0)	0 (0)	7 (6.0)	14 (5.4)
<i>Ochrotomys nuttalli</i>	0 (0)	0 (0)	2 (1.7)	3 (1.2)
<i>Mus musculus</i>	0 (0)	0 (0)	13 (11.1)	18 (7.0)
Total	126 (100)	276 (100)	117 (100)	259 (100)

Table 2. Ranking of 5 *a priori* models based on Akaike's Information Criterion (AIC) results for determining the probability of recapture model structure for closed capture models of abundance estimation of *Peromyscus* spp. captured in 2011 and 2012 at Fort Bragg Military Installation, North Carolina, USA.

Model ^a	AIC _c ^b	ΔAIC _c ^c	w _i ^d	K ^e	Deviance
p(ct)cdiff(ct)N(ct)	451.02	0.00	1.00	15	334.71
p(ct)cdiff(ct)N(ct,y)	458.66	7.63	0.022	20	331.99
p(y)cdiff(y)N(ct,y)	461.47	10.45	0.005	14	347.22
p(.)cdiff(.)N(ct,y)	470.86	19.84	0.0001	12	360.72
p(.)cdiff(.)N(ct)	470.98	19.96	0.0001	7	371.04

^a p, capture probability; cdiff, recapture probability different from capture probability; ct, effect of vegetation type but not year; N, abundance; y, effect of year but not vegetation type; ., no effect of year or vegetation type.

^b AIC_c, small-sample unbiased Akaike Information Criterion.

^c ΔAIC_c, differences in scores between each model and the best model.

^d w_i, model weight.

^e K, no. of parameters in the model.

captures in 2012). Therefore, we only analyzed capture data for *Peromyscus* spp., which consisted of capture histories from 118 individuals out of 261 captures in 2011 and 90 out of 219 captures in 2012 (Appendix A in Supporting Information).

The best model suggested recapture probability was different from capture probability and vegetation type affected *Peromyscus* spp. abundance (Table 2). Parameter estimates from the best model varied by vegetation type (25 plots each measuring 60-m × 60-m) with lowland hardwood having the greatest abundance of *Peromyscus* spp. (50) and open the lowest (12; Fig. 1). Additionally, the best model included a behavioral effect, with $c > p$ for all vegetation types, indicating a “trap-happy” response. Estimated abundance in the open vegetation type was lower than in all vegetation types except upland pine 3 years postburn (20; Appendix B in Supporting Information). Similarly, abundance in the lowland hardwood vegetation type was greater than all other vegetation types except upland pine 1 year

postburn (32; Appendix B in Supporting Information). Although abundance estimates in the upland pine vegetation types generally decreased with increasing time since burn, these differences were not statistically significant (i.e., no effect of time since burn; Fig. 1; Appendix C in Supporting Information).

DISCUSSION

Vegetation type, more so than time since burn, was an important predictor of *Peromyscus* spp. abundance in the longleaf pine ecosystem. However, we did note a trend of decreasing abundance as time since burn increased, possibly due to the increasingly dense and homogenous herbaceous layer that may interfere with nesting and foraging activities of *Peromyscus* spp. (Robinson 1981) or a decrease in seed availability, an important food source for *Peromyscus* mice (Sharp et al. 2009). Karmacharya et al. (2012) documented greater *P. gossypinus* survival soon after prescribed fire treatments, which could explain the slightly greater abundance in more recently burned forest stands. Similarly, other studies (Converse et al. 2006b, Greenberg et al. 2006) documented short-term increases in *P. maniculatus* populations after forest thinning and immediately after prescribed fire. Also, Kalies et al. (2012) documented a positive response of *P. maniculatus* to open vegetation structure characteristic of forest maintained by frequent low-intensity fire.

Long-term effects of fire, or the lack thereof, on vegetation may not have been evident within the short 3-year prescribed-fire return interval implemented on FBMI. Although ground-level vegetation biomass and complexity generally increase over time following a prescribed fire (Masters and Wilson 1996), the interval between fires may have been too short to allow substantial shifts in the composition of vegetation communities (i.e., from herbaceous dominated to woody dominated). It is possible that over longer periods of time postfire, *Peromyscus* may become increasingly rare or vegetation conditions in fire-suppressed

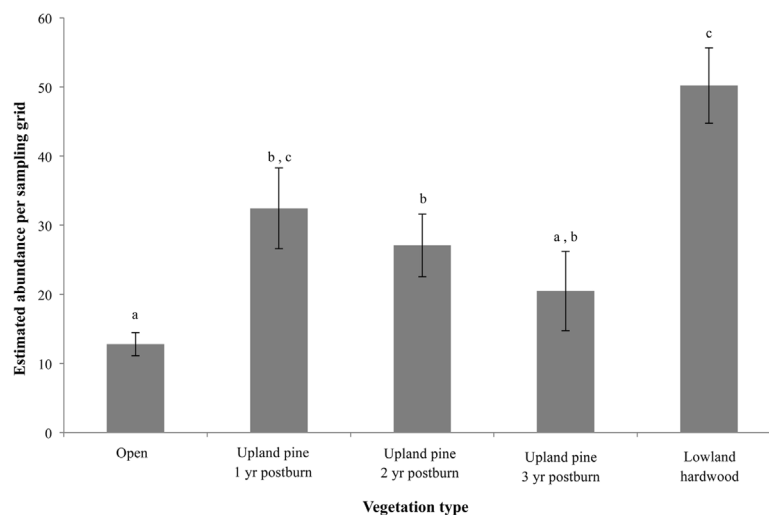


Figure 1. Abundance estimates (SE) for *Peromyscus* spp. in 60-m × 60-m plots ($N=25$) set in 5 vegetation types at Fort Bragg Military Installation, North Carolina, USA, 2011 and 2012. Small letters represent pairwise comparisons results, where values with the same letter indicate similarities between estimates ($P < 0.05$, see Appendix C in Supporting Information).

uplands may converge with the more favorable conditions in lowland areas. Therefore, we suggest future research in the longleaf pine ecosystem assess short- and long-term impacts of fire on small mammal populations as well as factors such as intensity and season of fire.

Peromyscus spp. abundance was lower in the frequently burned upland pine forests and open military training areas than in lowland hardwood, likely because of the relatively sparse and homogenous understory of the upland pine forest and military training areas. *Peromyscus* spp. select areas with dense woody understory and abundant fallen logs characteristic of the less frequently burned lowlands (Robinson 1981). Lowland hardwood communities have sparse distribution of pyrophytic fuels (i.e., wiregrass and longleaf pine needles) and greater soil moisture, resulting in less frequent and less intense burning and a more heterogeneous fire mosaic compared with the homogenous fire mosaic that typically occurs following fires in upland pine (Ellair and Platt 2013, Lashley et al. 2015). Conversely, grassy, open areas on FBMI were maintained with frequent disturbance (i.e., prescribed fire and mowing) to remove understory vegetation and allow easy and safe access for military training. Also, previous studies have shown decline in *Peromyscus* spp. reproduction associated with burning (Morris et al. 2011), which might explain the low abundance of *Peromyscus* spp. in frequently burned upland pine forest compared with less frequently burned lowland hardwoods.

Our results provide additional support for the importance of lowland hardwoods as wildlife habitat in the longleaf pine ecosystem. On FBMI, 27 of 36 wild turkey (*Meleagris gallopavo*) nests were located in either lowland hardwood or the ecotone between lowland hardwoods and adjacent uplands, where abundant low shrubs in the ecotones provided greater nest concealment than the understory vegetation in upland pine (Kilburg et al. 2014). Moreover, lowland hardwood provided seasonally important food and cover for southeastern fox squirrels (*Sciurus niger niger*) at FBMI (Prince et al. 2016). Lowland hardwoods contained greater understory leafy biomass and greater biomass of forages selected by white-tailed deer (*Odocoileus virginianus*) than all other vegetation types on FBMI (Lashley et al. 2015). With relatively low small mammal diversity and abundance in the frequently burned upland areas and across FBMI as a whole, the lowland hardwood vegetation type may be allowing *Peromyscus* populations to persist in the frequently burned longleaf pine ecosystem (Sharp et al. 2009). Thus, our results provide additional support for conserving hardwood areas within longleaf pine ecosystems (Hiers et al. 2014, Lashley et al. 2014).

MANAGEMENT IMPLICATIONS

Our results suggest low *Peromyscus* spp. abundance in the uplands of frequently burned longleaf pine ecosystems, especially in the low productivity soils characteristic of the Sandhills physiographic region of the southeastern United States. Managers of the longleaf pine ecosystem should promote heterogeneous landscape conditions that include fire-maintained uplands and less frequently burned lowland

hardwoods to provide food and cover for *Peromyscus* while conserving habitat conditions for other wildlife species associated with the ecosystem (Kilburg et al. 2014, 2015; Prince et al. 2016). Similarly, prescribed-fire return intervals should be variable, with some upland stands burned frequently (every 2–3 yr) and other stands burned less frequently (every 3–7 yr), in turn ensuring conservation of the full suite of biodiversity associated with the ecosystem (Andersen et al. 2005; Lashley et al. 2014, 2015).

ACKNOWLEDGMENTS

Funding for this project was provided by the U.S. Department of Defense through the Wildlife Branch at Fort Bragg Military Installation and Fisheries, Wildlife, and Conservation Biology Program at North Carolina State University. We thank technicians A. Schaich Borg, C. Farr, and B. Peterson for assistance with small mammal trapping efforts. Thank you to J. McAllister of the Fort Bragg Endangered Species Branch and J. Jones and A. Schultz of the Fort Bragg Wildlife Branch for technical advice and logistical support. We thank K. Pollock for statistical assistance and L. Kalies and 2 anonymous reviewers for contributions to an earlier version of the manuscript.

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Associate Editor: Kalies.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Appendix A. Trapping results for *Peromyscus* spp. at Fort Bragg Military Installation, North Carolina, 2011 and 2012.

Appendix B. *Peromyscus* spp. population parameter estimates at Fort Bragg Military Installation, North Carolina, 2011 and 2012.

Appendix C. *Peromyscus* spp. abundance estimates in 5 vegetation types at Fort Bragg Military Installation, North Carolina, 2011 and 2012.