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Bat Activity Following Restoration Prescribed Burning in the Central Appalachian Upland and Riparian Habitats

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ABSTRACT: After decades of fire suppression in eastern North America, land managers now are prioritizing prescribed fire as a management tool to restore or maintain fire-adapted vegetation communities. However, in long–fire-suppressed landscapes, such as the central and southern Appalachians, it is unknown how bats will respond to prescribed fire in both riparian and upland forest habitats. To address these concerns, we conducted zero-crossing acoustic surveys of bat activity in burned, unburned, riparian, and non-riparian areas in the central Appalachians, Virginia, USA. Burn and riparian variables had model support ($\Delta AICc < 4$) to explain activity of all bat species. Nonetheless, parameter estimates for these conditions were small and confidence intervals overlapped zero for all species, indicating effect sizes were marginal. Our results suggest that bats respond to fire differently between upland and riparian forest habitats, but overall, large landscape-level prescribed fire has a slightly positive to neutral impact on all bats species identified at our study site post–fire application.

Index terms: bats, central Appalachians, prescribed fire, riparian, upland

INTRODUCTION

After decades of fire suppression beginning in the early to mid-20th century in eastern North America and elsewhere, land managers now are prioritizing prescribed fire as a management tool to maintain fire-adapted vegetation communities or to impede the transitioning of fire-dependent communities to other types (i.e., mesic communities with little or no oak [*Quercus* spp.]; USDA Forest Service 2006; Nowacki and Abrams 2008; Hessl et al. 2011; Strahan et al. 2015; Block et al. 2016; Hessburg et al. 2016; Iverson et al. 2017). However, unlike other taxa, fire effects on bats in many forest ecosystems have been relatively poorly studied and many questions remain (Carter et al. 2000; Perry 2012). Moreover, with tremendous stressors such as White-nose Syndrome (Francl et al. 2012; Frick et al. 2015; Powers et al. 2015; Ingersoll et al. 2016) and wind energy development (Arnett and Baerwald 2013; Erickson et al. 2016), the need to understand fire impacts on bat assemblages, habitat use, and distribution has become even more urgent.

Fire may have different impacts in different habitats depending on forest type and landscape setting, thus strong or weak response by various bat species may depend only on the level of habitat/structural change caused by burning. For example, a single-event fire in the southern Appalachian Mountains, after 70 y of suppression, resulted in 37% tree mortality in upland forest habitat but no mortality in riparian habitat (Elliott et al. 1999), indicating perhaps little change to potential day-roost availability or change in foraging conditions therein. However,

repeated prescribed burning results in reduced regrowth and increasingly open, savanna-like conditions when compared to single-event prescribed fire or wildfire in the Appalachians (Hutchinson et al. 2005). There has been limited research on the effect of repeated, short-interval fire restoration landscapes on bat communities in the temperate deciduous forests of the Appalachians, particularly in regard to foraging habitat. Johnson et al. (2009, 2010b) found that two *Myotis* species, the northern long-eared bat (*Myotis septentrionalis* Trovessart; MYSE) and Indiana bat (*Myotis sodalis* Miller and Allen; MYSO), readily utilized fire-killed trees as roosts in habitat with reinstated prescribed fire (≤ 3 y of annual treatment) in the High Allegheny Mountains of West Virginia. In the Ozark Mountains region of Missouri, Boyles and Aubrey (2006) found a total of 63 evening bat (*Nycticeius humeralis* Rafinesque) roosts, all of which were located in habitat subjected to several years of biennial prescribed fire. Bat activity in the Chicago metropolitan area was positively associated with repeated prescribed fire (Smith and Gehrt 2010), whereas bat activity in longleaf pine (*Pinus palustris* Mill) and wiregrass (*Aristida stricta* Michaux) ecosystems of the Coastal Plain in Florida was lower in sites with longer fire-return intervals (Armitage and Ober 2012).

Riparian zones are critical habitat resources for many species, and provide important ecosystem services. For bats, riparian zones are particularly important, serving as travel corridors (Grindal et al. 1999), primary foraging areas (Ford et al. 2005; Fukui et al. 2006; Monadjem and Reside 2008),

water sources, and day-roost sites (Swystun et al. 2007). In most regions, bat activity generally is higher in riparian areas than upland areas (Grindal et al. 1999; Owen et al. 2004; Menzel et al. 2005; Rogers et al. 2006; Monadjem and Reside 2008). Riparian zone physical characteristics (i.e., water turbulence, bank steepness; Rydell et al. 1999; Lundy and Montgomery 2010; Hagen and Sabo 2014), stream order (Seidman and Zabel 2001; Ford et al. 2005; Johnson et al. 2010b; O'Keefe et al. 2013), and vegetative cover (Monadjem and Reside 2008; Ober and Hayes 2008; Akasaka et al. 2010) also may influence how bats use riparian areas.

Although fire has the potential to negatively impact bats through direct mortality, habitat loss, and disruption of group dynamics (Carter et al. 2000; Boyles and Aubrey 2006; Ford et al. 2016a), most research has shown that fire may actually benefit bats through roost enhancement/creation and forest clutter reduction (Ford et al. 2006, 2016a; Perry 2012) or have a neutral effect on bats (Johnson et al. 2010b; Buchalski et al. 2013; Lacki et al. 2017), depending on species. More broadly in the East, overall bat activity in burned upland habitat has been found to be higher than in unburned upland areas (Loeb and Waldrop 2008; Smith and Gehrt 2010; Armitage and Ober 2012; Silvis et al. 2016a), with species-specific responses linked to variation in reduction of vegetative clutter (Owen et al. 2004; Cox et al. 2016). Higher levels of bat activity in burned habitats may reflect changed insect prey abundance. Prescribed fire often benefits insect taxa that serve as bat prey species, through proliferation of nectar-producing plants (Rudolph and Ely 2000) and herbaceous growth that provides substrate on which to lay eggs (Evans et al. 2013). However, arthropod responses to fire are variable depending on species, life history stage, location, and burn season (Warren et al. 1987). In a similar hardwood system in eastern Kentucky, Lacki et al. (2009) observed that insect abundance and availability of MYSE prey increased the first few years post-fire.

To date, the majority of research on fire effects on bats has been focused either across whole landscapes or more narrowly, upland

forest habitats, despite clear importance of riparian forest habitats to bats. This is particularly true for federally protected bat species such as MYSE and MYSO (Ford et al. 2005; Carter 2006; Johnson et al. 2010b) in the central Appalachians where fire use on public land has increased greatly over the past two decades. Nonetheless, presence of these two species often causes consequential regulatory restrictions on prescribed fire use in terms of seasonality, frequency, and extent (Carter et al. 2000; Ford et al. 2016a). Accordingly, to investigate this where both species are known to be present in the central Appalachians of western Virginia, we used a paired sampling design to observe bat activity in repeatedly burned and unburned riparian and non-riparian forests. Based on previous research on bat-specific habitat correlates in the central Appalachians (Ford et al. 2005) as well as prey abundance (Rudolph and Ely 2000; Owen et al. 2004; Menzel et al. 2005; Evans et al. 2013), we predicted that responses to repeated prescribed fire in both riparian and non-riparian forests would be species-specific, with larger-bodied bats such as the hoary bat (*Lasiurus cinereus* Beauvois; LACI), the big brown bat (*Eptesicus fuscus* Beauvois; EPFU), and the silver-haired bat (*Lasionycteris noctivagans* Le Conte; LANO) displaying greater activity in burned and riparian areas than unburned and non-riparian areas due to reduced vegetative clutter and increased insect prey abundance. We predicted the relatively clutter-adapted *Myotis* species and the tricolored bat (*Perimyotis subflavus* Menu; PESU) would display a neutral response to fire and a positive response to riparian areas, due to increased insect abundance. We predicted that the eastern red bat (*Lasiurus borealis* Müller; LABO) also would display a neutral response to fire-reduced clutter and riparian forests, as seen in previous research (Ford et al. 2005; Menzel et al. 2005).

METHODS

Study Area

We conducted our study on the George Washington National Forest (GWNF) in the Warm Springs Ranger District in

Bath County, Virginia, USA (Figure 1). This portion of the GWNF lies within the Ridge and Valley subprovince of the Appalachian Mountains (Fenneman 1938). The dominant surface geology is resistant sandstone ridges and limestone valleys and there are numerous karst caves (White 2015) that serve as hibernacula for bats (Powers et al. 2015). Mountains form long, linear ridges with elevations that range from 450 to nearly 1300 m (Simon et al. 2005). An approximately 8000-ha portion of the GWNF, located adjacent to the Warm Springs Mountain Preserve, is cooperatively managed by USDA Forest Service, The Nature Conservancy (TNC), Virginia Department of Game and Inland Fisheries, and Virginia Department of Conservation and Recreation to support landscape-level prescribed fire to restore or maintain dry-mesic oak and montane pine associations (Braun 1950). In burned areas, bear oak (*Quercus ilicifolia* Wangenheim), table mountain pine (*Pinus pungens* Lambert), and pitch pine (*Pinus rigida* Miller) are present, with chestnut oak (*Quercus prinus* L.) and white oak (*Quercus alba* L.) as the dominant species. Blueberries (*Vaccinium* spp.) occur as understory vegetation in fire-dependent plant communities. Mesic, shade-tolerant white pine (*Pinus strobus* L.) and eastern hemlock (*Tsuga canadensis* L.) occur at low elevations and along riparian corridors. Fire suppression policies from the 1920s to the beginning of the 21st century have impacted forest composition and structure by increasing abundance of more mesic, fire-intolerant species such as red maple (*Acer rubrum* L.), American beech (*Fagus grandifolia* Ehrhart), blackgum (*Nyssa sylvatica* Marsh), and tulip poplar (*Liriodendron tulipifera* L.). Locally, prescribed fires typically are set via aerial ignition in March and April of each year to meet management goals that include preservation of biodiversity, control of invasive plant species, and restoration of historic fire regimes (3–9 y) in fire-dependent pine and oak forests (M. Smith, TNC, pers. comm.; USDA Forest Service 2015).

Data Collection

We recorded bat activity from 17 May through 4 August 2016 using acoustic

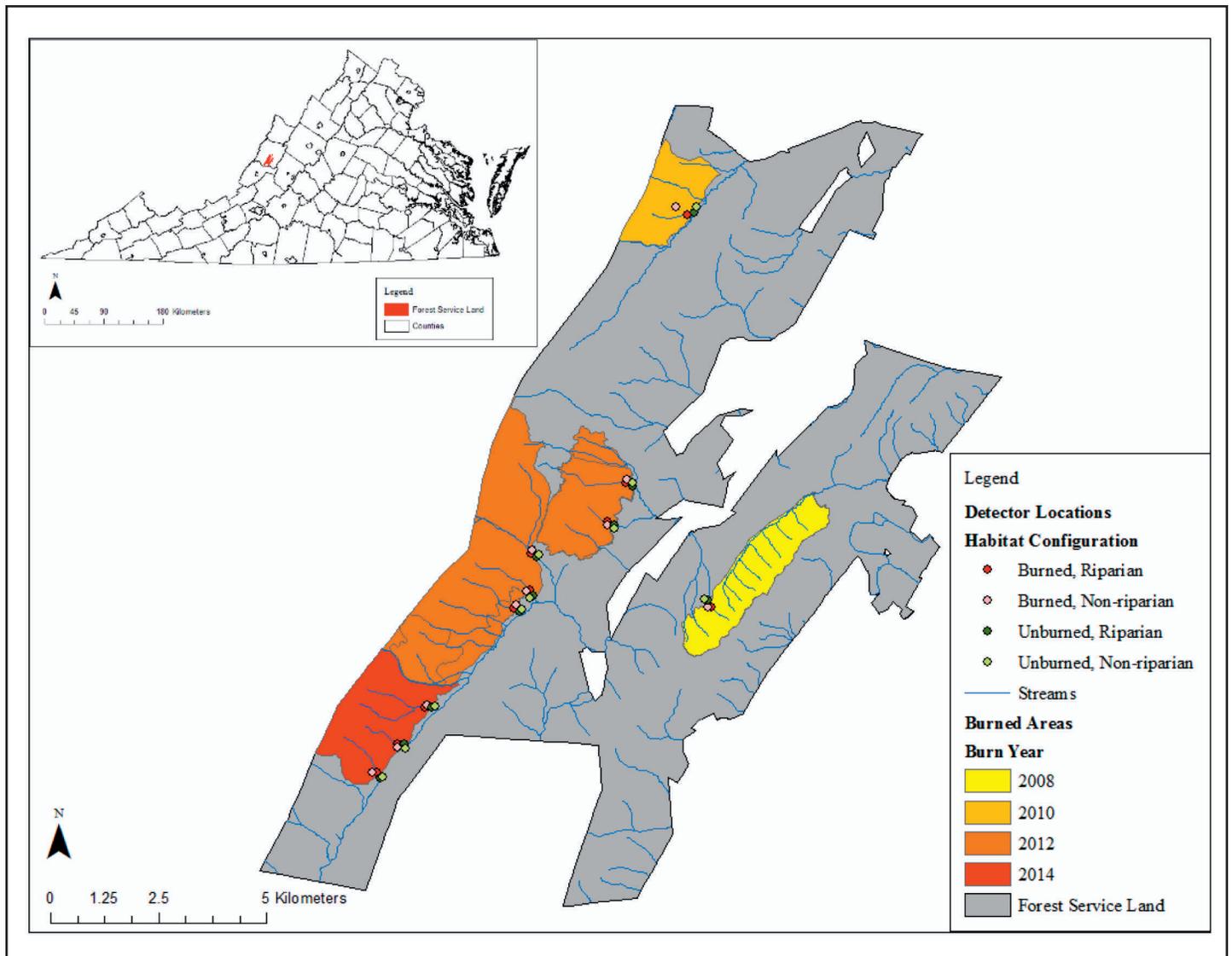


Figure 1. Map of bat detector and prescribed burn plot locations on the George Washington National Forest, Bath County, Virginia, USA, 17 May to 4 August 2016.

detectors (Songmeter ZC; Wildlife Acoustics, Maynard, Massachusetts, USA). We programmed acoustic detectors to record data from sunset to sunrise in 10 areas where a stream and corresponding riparian conditions extended from an unburned forest to a burned forest. We placed four detectors in each area—burned/riparian, burned/non-riparian, unburned/riparian, and unburned/non-riparian forest habitat—for a total of 40 detector locations surveyed over the study period (Figure 1). Our study sites consisted of nine first-order intermittent streams and one second-order stream. We blocked by each group of habitat configurations (i.e., a site with four detectors, one in each burned/riparian, burned/non-riparian, unburned/

riparian, and unburned/non-riparian forest habitat) to minimize landscape effects and enable us to attribute bat activity differences to riparian and burn variables of interest. All detectors were spaced a minimum distance of 80 m (twice the manufacturer's estimated maximum detection radius) to ensure that detectors did not record the same bat simultaneously (Agrant 2014). We selected riparian areas using 2014 TIGER/Line shapefiles for Bath County, Virginia, available through the US Census Bureau, Department of Commerce (<https://catalog.data.gov/dataset/iger-line-shapefile-2014-county-bath-county-va-linear-hydrography-county-based-shapefile>), that were USDA Forest Service owned. Burn history

was determined from records provided by the USDA Forest Service. Following the protocol of Ford et al. (2005) we collected call data, site location, and canopy closure at each survey site. We measured percent canopy cover at each detector site using the average of four hemispherical densiometer readings taken at each cardinal direction (Ford et al. 2005).

Data Analysis

Bat Call Identification

We identified bat passes using Kaleidoscope version 4.1.0, classifier version 3.1.0

at the sensitive setting (Wildlife Acoustics, Maynard, Massachusetts, USA). We used Kaleidoscope's default signal parameters (8–120 kHz frequency range, 500 maximum inter-syllable gap, a minimum number of two pulses, enhanced with advanced signal processing) and specified nine individual species that we expected to be present at our study site based upon earlier work in the central Appalachians (Ford et al. 2005; Timpone et al. 2011): EPFU, LACI, LABO, LANO, MYSE, MYSO, little brown bats (*Myotis lucifugus* Le Conte; MYLU), eastern small-footed bats (*Myotis leibii* Audubon and Bachman; MYLE), and PESU. When visually examining calls, we found a systemic error whereby large quantities of insect noise or southern flying squirrels (*Glaucomys volans* L.) were consistently being classified as either hoary bat or red bat calls (Figure 2). To account for this issue, we visually examined all calls identified to species by Kaleidoscope using AnalookW v. 3.9f (Titley Electronics, Ballina, NWS, Australia) and removed all erroneously

identified noise. After removing noise, we re-ran calls through Kaleidoscope to obtain corrected nightly counts by species.

We documented an unusually high number of LANO calls relative to other research in the region (Ford et al. 2005). In Virginia, this species typically is caught only in May as it migrates through the state (Cryan 2003), though anecdotal reports of summer captures have occurred (Timpone et al. 2011). Additionally, there is high uncertainty in automated program identification of LANO (Ford 2014), thus we grouped EPFU and LANO calls. We present results for all *Myotis* species combined to account for known program identification uncertainty/misclassification and all species combined to examine fire and riparian effects on overall bat activity.

Bat Activity

We compared mean nightly bat activity among our four habitat configurations using zero-inflated negative binomial mixed

models; we used random effects to account for time since the most recent prescribed fire (YSB – years since burn) and repeated measurements at individual sites (nights). We fit models using package glmmADMB (Fournier et al. 2012; Skaug et al. 2016) in program R version 3.2.3 (R Development Core Team 2014). We compared models of all combinations of habitat configuration, including additive and interactive effects of burn and riparian categories (Table 1), using an information theoretic approach. We ranked models using Akaike's Information Criterion corrected for small sample size (AIC_c ; Burnham and Anderson 2002). We identified a confidence set of models within $AIC_c < 4$ as competing models (Burnham and Anderson 2004). To account for uncertainty in the model selection process we used package MuMin (Barton 2016) in program R to obtain full model averaged estimates, unconditional standard errors, and 95% confidence intervals to assess individual variable effects on bat activity levels for all species and species groups of interest (Grueber et al. 2011; Symonds

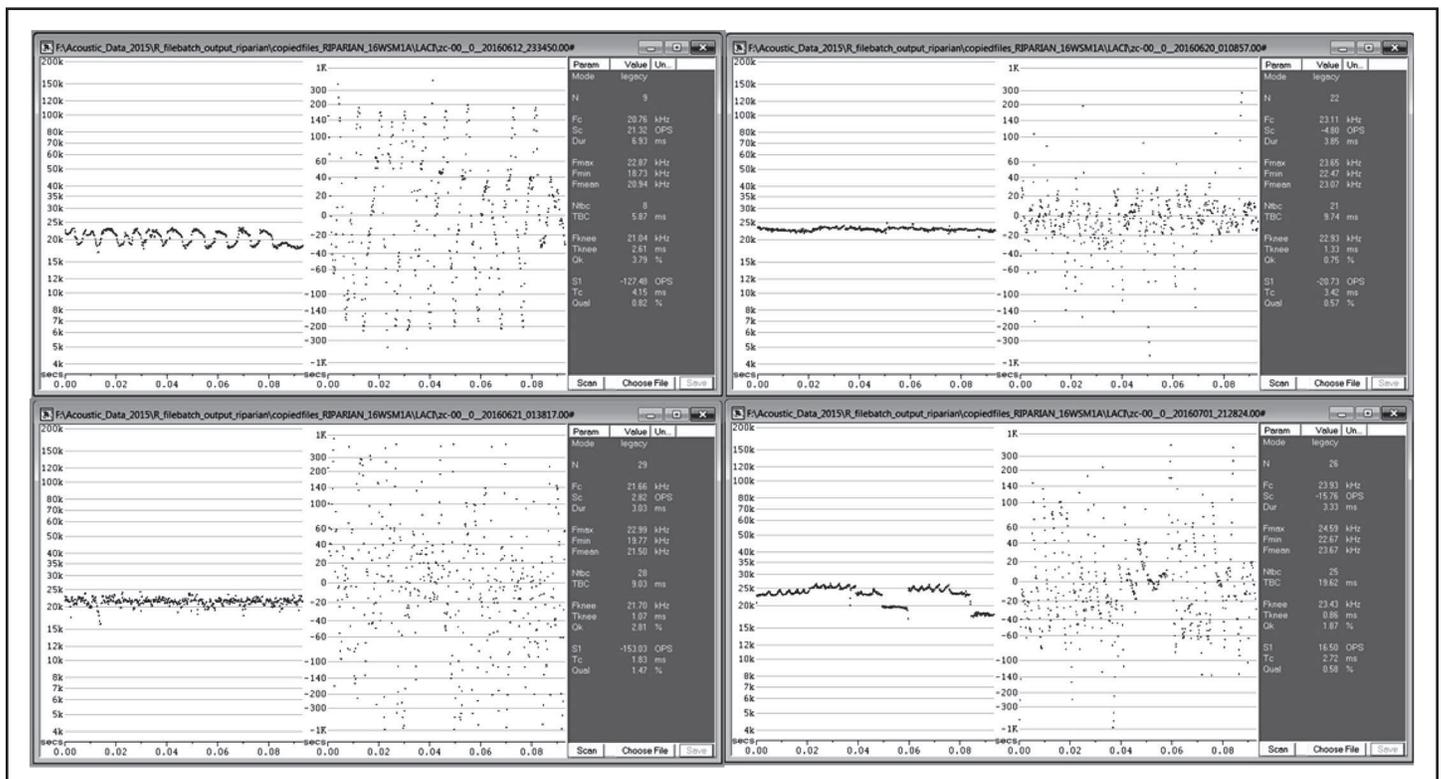


Figure 2. Graphic representation of sound files recorded on the George Washington National Forest, Bath County, Virginia, USA, 17 May to 4 August 2016, plotted by AnalookW version 3.9f for bat call analysis using ZCA. Examples of sound files identified as hoary bat (*Lasiurus cinereus*) calls by Kaleidoscope (version 4.1.0, classifier version 3.1.0). Files such as these were reidentified as insect or southern flying squirrel (*Glaucomys volans*) noise during hand verification of calls and removed from the analysis.

Table 1. A priori zero-inflated negative binomial mixed models and corresponding hypotheses that incorporate burn and riparian variables to assess effects on bat activity level, Bath County, Virginia, USA, 17 May to 4 August 2016.

A priori Models	Literature Cited
Null	Burnham and Anderson 2002
Burn	Carter et al., 2000; Loeb and Waldrop, 2008; Silvis et al., 2016a
Riparian	Ford et al. 2005; Fukui et al. 2006; Grindal et al. 1999; Monadjem and Reside 2008; Swystun et al. 2007
Burn + Riparian	Elliott et al. 1999
Burn * Riparian	Elliott et al. 1999

and Moussalli 2011).

Vegetation Configuration

We compared canopy cover among our four habitat configurations using a multiple linear mixed model; we included a random effect to account for area blocking. We determined effect sizes by comparing centered and scaled fitted estimates for canopy cover. We fit models in program R using package lme4 (Bates et al. 2015) and obtained R^2 values using package MuMIn (Barton 2016). We selected canopy cover as a measure of fire effects on vegetation because changes occur within a relatively short period of time (i.e., tree senescence or mortality with subsequent leaf fall). Comparing variations in canopy cover to the different habitat configurations enabled us to relate differences in bat activity between riparian and burn habitats to vegetative characteristics.

RESULTS

We monitored bat activity for 738, 660, 724, and 764 recording nights at our burn/riparian, burn/non-riparian, unburned/riparian, and unburned/non-riparian forest stands, respectively. Differences in sampling duration between habitat configurations arose due to periodic detector failures. After removing extraneous noise files, Kaleidoscope identified bat calls from 11,689 files, and assigned them to nine unique species: EPFU (4989), LABO (1831), LACI (355), LANO (2289), MYLE (134), MYLU (682), MYSE (348), MYSO (341), and PESU (720). We excluded YSB

as a random effect in models for LACI, LABO, EPFU/LANO, and total bat activity due to model convergence errors.

For all species and species groups, all models describing bat activity were highly competitive and consequently had model support ($\Delta AIC_c < 4$), except the riparian model for LACI (Table 2). Burn and riparian variables had slight positive effects for all species and groups. The interaction between burn and riparian variables had a slight negative effect on EPFU/LANO, LACI, and total bat activity, but a positive effect on all other species and groups. Nonetheless, coefficients were small and confidence intervals overlapped zero indicating that the effect was marginal (Table 3). The riparian condition variable had a marginally negative effect on LACI though confidence intervals overlapped zero. Overall, burn and riparian variables had a slight positive to neutral effect on the mean nightly activity of all species combined albeit with small coefficients and confidence intervals overlapping zero (Figure 3).

Percent canopy cover across habitat configuration and burn conditions were similar ($R^2 = 0.21$); however, there was greater variation in the range of canopy cover in the burned, non-riparian areas than other burn conditions (Figure 4).

DISCUSSION

We found little evidence of strong fire effects on activity of EPFU/LANO and LACI, though in absolute terms, activity was higher in recently burned (2008–2014) stands than in adjacent or nearby unburned forests. These results were counter to ex-

pectations, given that research in the South Carolina Piedmont showed higher levels of activity for EPFU in burned, thinned, and burned/thinned stands compared to control stands (Loeb and Waldrop 2008). Additionally, research in the Ohio Hills portion of the central Appalachians showed higher activity of EPFU in thinned forest and thinned/burned forest treatments compared to unburned, uncut control treatments (Silvis et al. 2016a). Given the overall similarity of canopy clutter observed across all treatment blocks in our study, we think it is likely that fires at our sites did not reduce clutter sufficiently to elicit a response from these species. Thus, our results may still be consistent with our expectation that larger-bodied and less maneuverable bats would benefit from clutter reduction resulting from prescribed fire and thinning treatments (Loeb and Waldrop 2008; Silvis et al. 2016a). Our study consisted of nine first-order streams and one second-order stream; therefore, it is possible that riparian corridors were too small to support LACI flight and/or foraging strategies (Ford et al. 2005).

We observed a negative interaction between riparian and prescribed fire conditions for LACI and EPFU/LANO. It is possible that fire affects insect prey species differently between upland and riparian habitats. For example, in most Appalachian forest systems that have been burned, the aquatic environment seems little changed post-fire (Vose et al. 2005). Lines of evidence suggest that during small controlled burns such as the ones used for this study, microsites used by insects may be drastically changed; but it remains unclear how these changes affect prey availability across habitats (Lacki et al. 2009; Dodd et al. 2012; Griffiths 2014). Land managers would benefit from

Table 2. Model selection results for zero-inflated negative binomial mixed models exploring impacts of burn and riparian conditions, with random effects for site, treatment block, and year since burn (YSB), on bat activity, by species, on the George Washington National Forest, Bath County, Virginia, USA, 17 May to 4 August 2016. We present the degrees of freedom (df), log likelihood (logLik), Akaike's Information Criteria for small sample size (AICc), delta AICc (delta), and AICc weight (weight). For each species, the null model is represented by 1 + (1|site) + (1|group).

Models by species	df	logLik	AIC _c	ΔAIC _c	weight
<i>Eptesicus fuscus</i> / <i>Lasionycteris noctivagans</i>					
Big brown bat/ Silver-haired bat					
Burn + (1 site) + (1 group)	6	- 3069.60	6151.2	0.00	0.46
Burn+Riparian + (1 site) + (1 group)	7	- 3069.30	6152.6	1.41	0.23
1 + (1 site) + (1 group)	5	- 3071.69	6153.4	2.17	0.16
Burn*Riparian + (1 site) + (1 group)	8	- 3069.28	6154.6	3.38	0.09
Riparian + (1 site) + (1 group)	6	- 3071.42	6154.9	3.64	0.07
<i>Lasiurus cinereus</i>					
Hoary bat					
Burn + (1 site) + (1 group)	6	-743.82	1499.7	0.00	0.53
Burn+Riparian + (1 site) + (1 group)	7	-743.76	1501.6	1.89	0.20
1 + (1 site) + (1 group)	5	-746.14	1502.3	2.63	0.14
Burn*Riparian + (1 site) + (1 group)	8	-743.72	1503.5	3.81	0.08
Riparian + (1 site) + (1 group)	6	-746.12	1504.3	4.60	0.05
<i>Lasiurus borealis</i>					
Eastern red bat					
Burn + (1 site) + (1 group)	6	- 1381.83	2775.7	0.00	0.28
Burn+Riparian + (1 site) + (1 group)	7	- 1380.85	2775.7	0.05	0.28
1 + (1 site) + (1 group)	5	- 1383.43	2776.9	1.19	0.16
Riparian + (1 site) + (1 group)	6	- 1382.49	2777.0	1.32	0.15
Burn*Riparian + (1 site) + (1 group)	8	- 1380.53	2777.1	1.42	0.14
<i>Myotis leibii</i>					
Eastern small-footed bat					
1 + (1 site) + (1 group) + (1 YSB)	6	-376.79	765.6	0.00	0.24
Burn*Riparian + (1 site) + (1 group) + (1 YSB)	9	-373.81	765.7	0.07	0.23
Riparian + (1 site) + (1 group) + (1 YSB)	7	-375.94	765.9	0.31	0.20
Burn + (1 site) + (1 group) + (1 YSB)	7	-376.03	766.1	0.48	0.19
Burn+Riparian + (1 site) + (1 group) + (1 YSB)	8	-375.31	766.7	1.05	0.14
<i>Myotis lucifugus</i>					
Little brown bat					
Riparian + (1 site) + (1 group) + (1 YSB)	7	- 1085.99	2186.0	0.00	0.32
Burn+Riparian + (1 site) + (1 group) + (1 YSB)	8	- 1085.10	2186.3	0.23	0.28
1 + (1 site) + (1 group) + (1 YSB)	6	- 1087.73	2187.5	1.47	0.15
Burn*Riparian + (1 site) + (1 group) + (1 YSB)	9	- 1084.89	2187.8	1.82	0.13
Burn + (1 site) + (1 group) + (1 YSB)	7	- 1086.93	2187.9	1.88	0.12
<i>Myotis septentrionalis</i>					
Northern long-eared bat					
1 + (1 site) + (1 group) + (1 YSB)	6	-685.58	1383.2	0.00	0.34
Riparian + (1 site) + (1 group) + (1 YSB)	7	-684.72	1383.5	0.27	0.30
Burn + (1 site) + (1 group) + (1 YSB)	7	-685.36	1384.7	1.55	0.16
Burn+Riparian + (1 site) + (1 group) + (1 YSB)	8	-684.50	1385.1	1.86	0.14
Burn*Riparian + (1 site) + (1 group) + (1 YSB)	9	-684.30	1386.7	3.46	0.06
<i>Myotis sodalis</i>					
Indiana bat					
Burn+Riparian + (1 site) + (1 group) + (1 YSB)	8	-668.77	1353.6	0.00	0.27
Burn + (1 site) + (1 group) + (1 YSB)	7	-669.86	1353.8	0.16	0.25
Riparian + (1 site) + (1 group) + (1 YSB)	7	-670.14	1354.3	0.72	0.19
1 + (1 site) + (1 group) + (1 YSB)	6	-671.19	1354.4	0.81	0.18
Burn*Riparian + (1 site) + (1 group) + (1 YSB)	9	-668.73	1355.5	1.92	0.10

Continued

Table 2. (Cont'd)

Models by species	df	logLik	AIC _c	ΔAIC _c	weight
<i>Perimyotis subflavus</i>					
Tricolored bat					
Riparian + (1 site) + (1 group) + (1 YSB)	7	-1007.88	2029.8	0.00	0.37
1 + (1 site) + (1 group) + (1 YSB)	6	-1009.38	2030.8	0.99	0.22
Burn+Riparian + (1 site) + (1 group) + (1 YSB)	8	-1007.51	2031.1	1.27	0.20
Burn + (1 site) + (1 group) + (1 YSB)	7	-1009.01	2032.1	2.26	0.12
Burn*Riparian + (1 site) + (1 group) + (1 YSB)	9	-1007.22	2032.5	2.70	0.10
<i>Myotis</i> spp.					
Riparian + (1 site) + (1 group) + (1 YSB)	7	-1654.71	3323.5	0.00	0.37
Burn+Riparian + (1 site) + (1 group) + (1 YSB)	8	-1654.09	3324.2	0.77	0.25
1 + (1 site) + (1 group) + (1 YSB)	6	-1656.58	3325.2	1.73	0.15
Burn*Riparian + (1 site) + (1 group) + (1 YSB)	9	-1653.71	3325.5	2.02	0.13
Burn + (1 site) + (1 group) + (1 YSB)	7	-1656.02	3326.1	2.62	0.10
Total Activity					
Burn + (1 site) + (1 group)	5	-4077.33	8164.7	0.00	0.32
1 + (1 site) + (1 group)	4	-4078.70	8165.4	0.73	0.22
Burn+Riparian + (1 site) + (1 group)	6	-4076.70	8165.4	0.75	0.22
Riparian + (1 site) + (1 group)	5	-4078.12	8166.3	1.58	0.15
Burn*Riparian + (1 site) + (1 group)	7	-4076.69	8167.4	2.74	0.08

studies that include paired insect surveys alongside bat work to determine the role of fire impacts on insect prey species. Fire may also impact the vegetative community of riparian areas differently than in upland communities. There is evidence that the mesic soil of riparian habitats promotes rapid regrowth of vegetation (Brown and Peet 2003; Dwire and Kauffman 2003) that could impede flight and foraging of larger-bodied bats (Barclay 1985).

Consistent with our predictions based on body size and habitat selection, we found little evidence of fire, riparian, or interaction effects on activity levels of *Myotis* species both jointly and individually, PESU, or LABO. Estimates of burn condition for all species, except MYSO, were smaller than those of the larger-bodied species EPFU/LANO and LACI. *Myotis* species and PESU generally are considered clutter-adapted based on morphology and call structure, with MYSE and MYLU utilizing vegetation for gleaning insects (Norberg and Rayner 1985; Aldridge and Rautenbach 1987; Ratcliffe and Dawson 2003). The best-supported model for MYSE was the null, possibly because

this species is a habitat generalist within forested conditions (Silvis et al. 2016b). Previous research has shown that LABO and PESU have similar activity in both upland and riparian forests as well as cluttered and open forests (Ford et al. 2005; Menzel et al. 2005). Throughout the East, *Myotis* activity was similar between burned and unburned upland habitat (Cox et al. 2016; Silvis et al. 2016a), whereas research in the western United States found overall activity to be higher in burned habitat than unburned upland habitat with species-specific responses to fire severity among myotids (Buchalski et al. 2013).

Regardless, overall bat activity at our sites was low, irrespective of prescribed burning and riparian status, for all *Myotis* species and PESU. This primarily can be attributed to White-nose Syndrome-related mortality in this portion of the central Appalachians (Francl et al. 2012; Powers et al. 2015; Reynolds et al. 2016), but also possibly mortality from wind energy facilities in the nearby Appalachian Plateau to the west and northwest of our study area (Erickson et al. 2016). Additionally, the small size and intermittent nature of streams at our study

site may not have provided enough contrast to surrounding upland forests. Although O'Keefe et al. (2013) documented minimal use of riparian areas associated with small streams in the southern Appalachians for MYSE and MYSO, others have found these areas to be important in the central Appalachians (Ford et al. 2005, 2016b). More generally, however, there is evidence that bat activity is positively related to stream order (Lloyd et al. 2006). Incorporation of higher-order streams may have resulted in higher bat activity; however, fire is typically excluded in the riparian zones of both the central and southern Appalachians to be consistent with current best management practices and, thus, would not have allowed for comparison of fire effects between upland and riparian habitats.

Our results suggest large landscape-level prescribed fire has a slightly positive to neutral impact on all bat species identified in at our study site post-fire suppression. This is consistent with day-roost and fire research in the region, as well (Johnson et al. 2010a; Ford et al. 2016a). Research in the western United States and Ireland has shown that a diversity of riparian

Table 3. Model-averaged coefficients, unconditional standard errors (SE), and upper and lower confidence intervals (CI) for competing ($\Delta AIC_c < 4$) zero-inflated negative binomial mixed models exploring effects of burn and riparian conditions on bat activity by species, Bath County, Virginia, USA, 17 May to 4 August 2016.

Species	Variables	Coefficient	SE	Lower CI	Upper CI
<i>Eptesicus fuscus</i> / <i>Lasionycteris noctivagans</i>					
Big brown bat/ Silver-haired bat					
	Intercept	-2.09	0.66	-3.39	-0.80
	Burn	1.18	0.92	-0.63	2.99
	Riparian	0.23	0.57	-0.90	1.35
	Burn*Riparian	-0.03	0.42	-0.86	0.80
<i>Lasiurus cinereus</i>					
Hoary bat					
	Intercept	-4.04	0.47	-4.97	-3.12
	Burn	1.02	0.67	-0.28	2.33
	Riparian	-0.04	0.34	-0.71	0.62
	Burn*Riparian	-0.02	0.31	-0.63	0.59
<i>Lasiurus borealis</i>					
Eastern red bat					
	Intercept	-3.99	0.76	-5.48	-2.50
	Burn	0.91	0.96	-0.97	2.79
	Riparian	0.52	0.83	-1.11	2.16
	Burn*Riparian	0.17	0.71	-1.22	1.56
<i>Myotis leibii</i>					
Eastern small-footed bat					
	Intercept	-5.49	0.81	-7.07	-3.91
	Burn	0.17	0.91	-1.61	1.96
	Riparian	0.22	0.92	-1.58	2.02
	Burn*Riparian	0.61	1.34	-2.01	3.23
<i>Myotis lucifugus</i>					
Little brown bat					
	Intercept	-4.51	0.85	-6.18	-2.84
	Riparian	1.05	1.00	-0.91	3.01
	Burn	0.50	0.81	-1.10	2.09
	Burn*Riparian	0.13	0.64	-1.13	1.38
<i>Myotis septentrionalis</i>					
Northern long-eared bat					
	Intercept	-4.43	0.69	-5.79	-3.08
	Riparian	0.48	0.78	-1.04	2.01
	Burn	0.15	0.57	-0.96	1.27
	Burn*Riparian	0.06	0.45	-0.83	0.95
<i>Myotis sodalis</i>					
Indiana bat					
	Intercept	-6.15	1.24	-8.58	-3.71
	Burn	1.02	1.18	-1.29	3.34
	Riparian	0.81	1.11	-1.35	2.98
	Burn*Riparian	0.06	0.66	-1.23	1.35
<i>Perimyotis subflavus</i>					
Tricolored bat					
	Intercept	-4.72	0.87	-6.42	-3.02
	Riparian	0.95	1.05	-1.10	3.00
	Burn	0.24	0.72	-1.17	1.66
	Riparian*Burn	0.12	0.65	-1.15	1.40

Continued

Table 3. (Cont'd)

Species	Variables	Coefficient	SE	Lower CI	Upper CI
<i>Myotis</i> spp.	Intercept	-3.74	0.82	-5.34	-2.13
	Riparian	1.11	1.03	-0.91	3.14
	Burn	0.33	0.76	-1.16	1.83
	Burn*Riparian	0.18	0.74	-1.27	1.64
All Species	Intercept	-1.52	0.73	-2.95	-0.09
	Burn	0.86	0.94	-0.99	2.70
	Riparian	0.41	0.74	-1.04	1.86
	Burn*Riparian	-0.02	0.46	-0.91	0.88

habitat is needed to support a diverse bat community (Ober and Hayes 2008; Lundy and Montgomery 2010). Because fire intensity and severity is affected by environmental factors within the riparian zone, it is capable of creating a mosaic of habitats (Pettit and Naiman 2007), likely

suitable for the diverse bat community found at our study site.

Prescribed fire is used to meet many land management goals: conservation of fire-dependent, oak-dominant communities, preservation of biodiversity, control

of invasive plant species, and restoration of historic fire regimes in fire-dependent pine and oak forests. However, fire faces regulatory restriction due to presence of listed bat species. Previous research examining the impacts of fire on bat foraging habitat in the central Appalachians was restricted

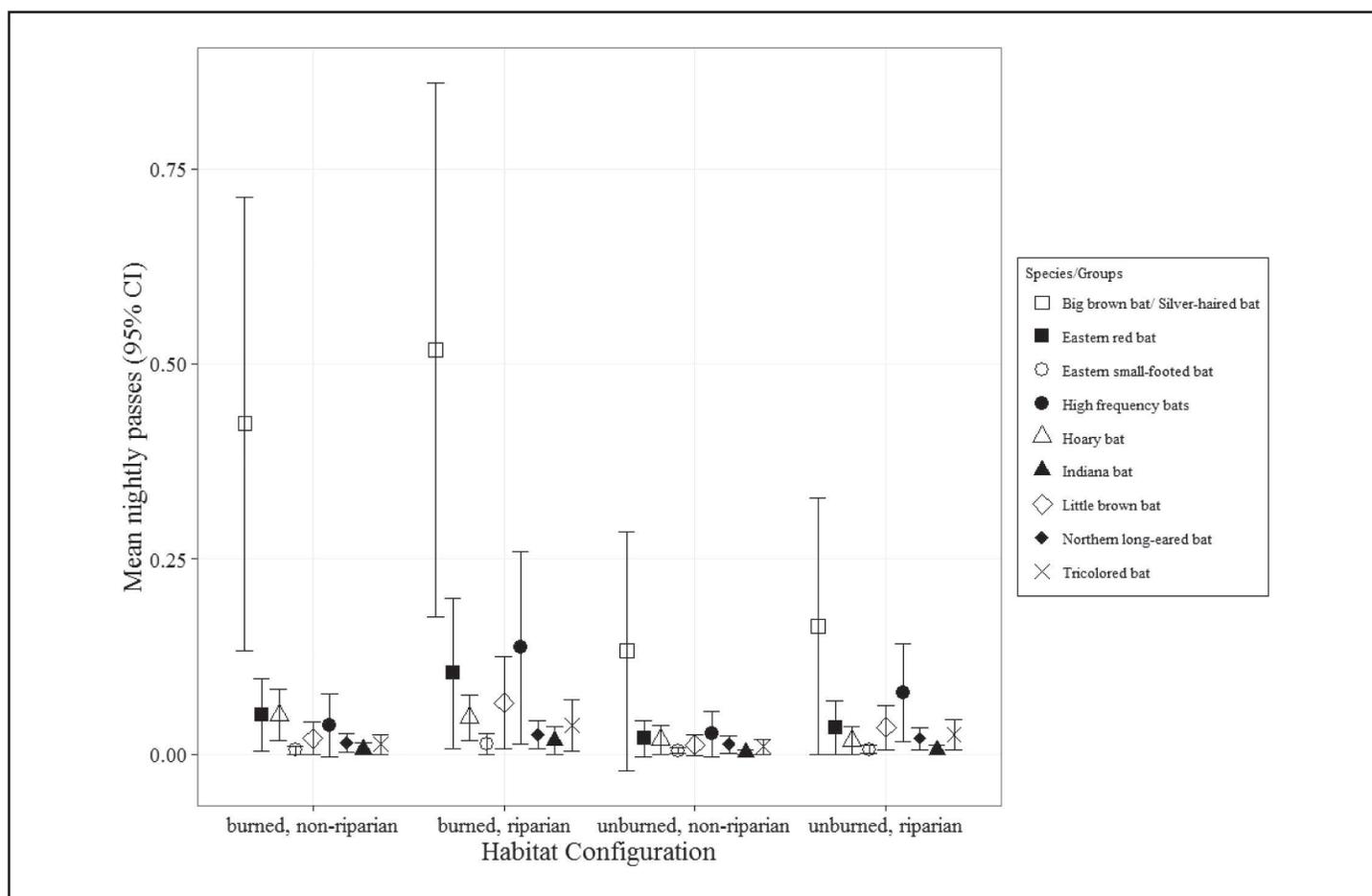


Figure 3. Mean nightly passes for bat species and species groups by habitat configuration on the George Washington National Forest, Bath County, Virginia, USA, 17 May to 4 August 2016.

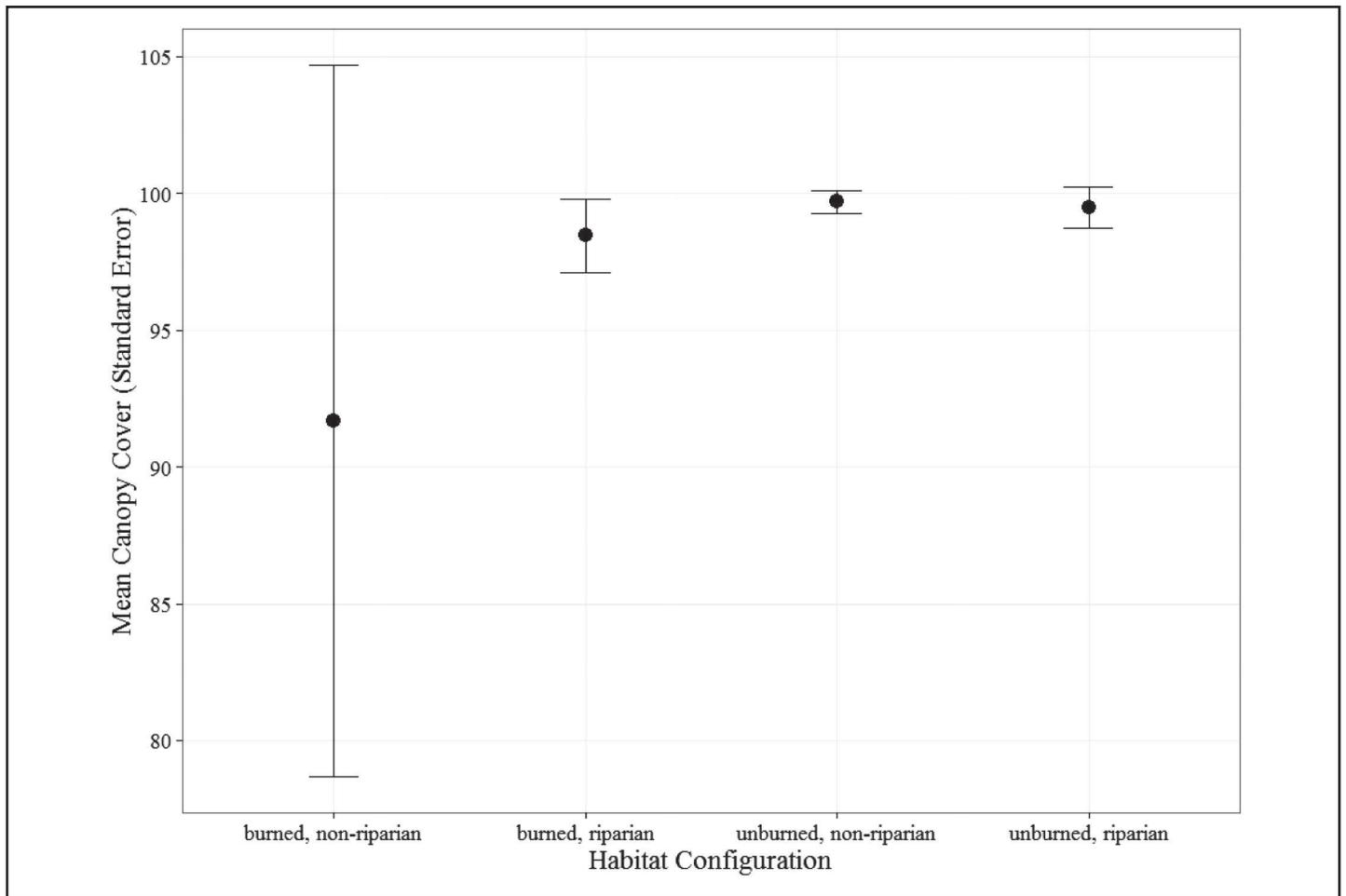


Figure 4. Estimates and corresponding standard errors for multiple linear mixed models exploring the effects of habitat configuration on percent canopy cover on the George Washington National Forest, Bath County, Virginia, USA, 17 May to 4 August 2016.

to upland habitats (Smith and Gehrt 2010; Armitage and Ober 2012; Cox et al. 2016). Our research helps to elucidate effects of prescribed fire in upland versus riparian forest on bat activity. Our results indicate that fire in both riparian and upland habitat appears to have a neutral effect on bat foraging habitat. Thus, bats should not be a strong consideration in modifying plans for use of fire on the central Appalachian landscape. Still, additional research on the impacts of prescribed fire on bat roosting habitat of a wider array of species, in riparian and upland areas, would aid land managers in decision-making processes regarding prescribed fire regimens.

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