



Critically imperiled forest fragment supports bat diversity and activity within a subtropical grassland

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Global biodiversity patterns are shaped by landscape structure and seasonality. Spatio-temporal patterns in bat assemblages are not well studied in grassland biomes but forest patches may provide important habitat for bats within these open grasslands. In the Greater Everglades Ecosystem (GEE), small fragments of diverse, critically imperiled pine rockland remain amidst a vast expanse of seasonally flooded grasslands (marl prairies). We used acoustic surveys to investigate the use of pine rocklands and marl prairies by bats across 2 distinct seasons (dry-cool and wet-warm). We detected higher mean bat activity in pine rocklands than marl prairies in the dry-cool season and higher bat species richness in pine rocklands in both seasons. Four of the 9 species of bats exhibited higher mean activity in pine rocklands than marl prairies and higher activity in the wet-warm season. The greater structural complexity of pine rocklands relative to marl prairies may be attractive to bats for roosting, foraging, and protective cover. Our finding of an interactive effect between vegetation community and season on bat activity suggests that pine rocklands may be more attractive to bats in the dry-cool season. This may be due to microclimate moderation, which likely leads to higher insect abundance for foraging bats. Pine rocklands in the GEE clearly provide ecological benefits that help support local biodiversity. These forest patches are important landscape elements for bats in grassland communities, where available roosts, prey, and protective cover may be limited.

Key words: acoustic surveys, Everglades National Park, Florida bonneted bats, grasslands, habitat use, marl prairies, pine rocklands, seasonality, subtropics

Global patterns of biodiversity are shaped spatially by landscape composition and configuration (e.g., vegetation type, heterogeneity, and connectivity; [Fahrig et al. 2011](#); [Walz 2011](#)) and temporally by seasonal variation in temperature and precipitation ([Tonkin et al. 2017](#)). Bats, accounting for 20% of all mammal diversity, serve key ecological functions ([Kunz et al. 2011](#)) and are valuable indicators of environmental change ([Jones et al. 2009](#)). Patterns in foraging, reproduction, and movement of bats are often linked to the distribution of resources (e.g., food and roosts), which can vary across the landscape and by season ([Jaberg and Guisan 2001](#); [Sperr et al. 2011](#); [McCracken et al. 2012](#)). Nonetheless, the spatio-temporal patterns in bat communities remain poorly understood in many parts of the world.

Forests provide critical habitat for many bat species for roosting, foraging, protective cover, and thermal regulation ([Lacki 2007](#)). Worldwide declines in forest cover have led to species declines due to loss and degradation of habitat ([Foley et al. 2005](#); [Donald and Evans 2006](#)). Far less is known about patterns of bat assemblages in open habitats ([Frey-Ehrenbold et al. 2013](#)),

particularly in grassland biomes where insect availability may be high ([Tschardt and Greiler 1995](#)) but roost opportunities and protective cover are very low. Two studies in South America have documented higher bat diversity or activity, respectively, within forest patches when compared with surrounding grasslands ([Aguirre 2002](#); [Barros et al. 2014](#)), suggesting that tree islands are attractive to bats in open landscapes. In subtropical ecosystems, bats are active year-round but temperature and precipitation vary seasonally. In cooler months in the subtropics, bats may be less active due to low temperatures and limited prey. Bats also may undergo local movements between habitats to track the phenology of resources as they change seasonally across the landscape (e.g., [Loayza and Loiselle 2008](#); [Stevens and Amarilla-Stevens 2011](#)). Thus, forest fragments in open habitats could vary seasonally in their importance to bats in subtropical regions.

The Greater Everglades Ecosystem (GEE) is a subtropical, seasonally flooded grassland interspersed with native tree communities that serves as a transition zone for many subtropical

and temperate species (Long 1984; Lodge 2010). Two distinct seasons are defined by changes in precipitation and temperature: dry-cool (December to April), and wet-warm (May to November; Duever et al. 1994; Lodge 2010). The GEE serves as a model system to better understand seasonal patterns of bat community dynamics in forest patches within subtropical grasslands. Historically spreading across south Florida, much of this system has been severely altered due to development, drainage, and channeling of water (Walker et al. 1997) and is threatened by sea level rise (James and Charlie 2001). Native pine forests in this region and throughout the southeastern United States have experienced sharp declines over the last half-century (Coyle et al. 2015). Pine forests in the GEE are often contained within pine rocklands, a critically imperiled vegetative community found along limestone substrates (U.S. Fish and Wildlife Service 1999b). Approximately 98.5% of the extent of pine rocklands has been lost to development (Lodge 2010; U.S. Fish and Wildlife Service 1999b) and is severely fragmented, with the largest remaining contiguous area found within Everglades National Park (ENP; U.S. Fish and Wildlife Service 1999b). Within ENP, pine rockland is surrounded by freshwater marl prairie (Fig. 1), a sparsely vegetated, graminoid-dominated community with few trees (U.S. Fish and Wildlife Service 1999a; Florida Natural Areas Inventory 2010). Bats in the GEE are understudied, have uncertain distributions and activity patterns (Lodge 2010; IUCN 2015; Florida Fish and Wildlife Conservation Commission 2016), but may be linked to forest cover (Marks and Marks 2006; Angell and Thompson 2015; Braun de Torrez et al. 2016).

The objective of our study was to investigate bat community dynamics within the GEE to test the hypothesis that forest patches support bat diversity and activity in subtropical grasslands, particularly during cooler months when prey may be limited and thermal regulation may be especially important. Specifically, we wanted to investigate how the local bat assemblage differed between imperiled pine rocklands and surrounding marl prairies, and how it changed seasonally. Using acoustic surveys, we measured bat activity (frequency of detected echolocation call sequences) and species richness (number of detected species) per night as metrics of relative habitat use (Hayes et al. 2009; Parsons and Szewczak 2009). We assumed that sites with higher bat activity and species richness received greater use by bats, and that temporal changes in activity and richness corresponded to temporal changes in use of those sites (Frick 2013). First, because the structural complexity of forest patches may provide more opportunities for roosting and foraging, protective cover, and thermal benefits relative to open grasslands, we predicted there would be higher bat activity and species richness within the pine rocklands than in the marl prairies in both seasons. Second, if bats are particularly dependent on the benefits forests provide during cooler months, we would expect bat activity and species richness to be higher in pine rocklands in the dry-cool season than in the wet-warm season.

MATERIALS AND METHODS

All research followed ASM guidelines for research on live animals (Sikes et al. 2016) and was in accordance with the

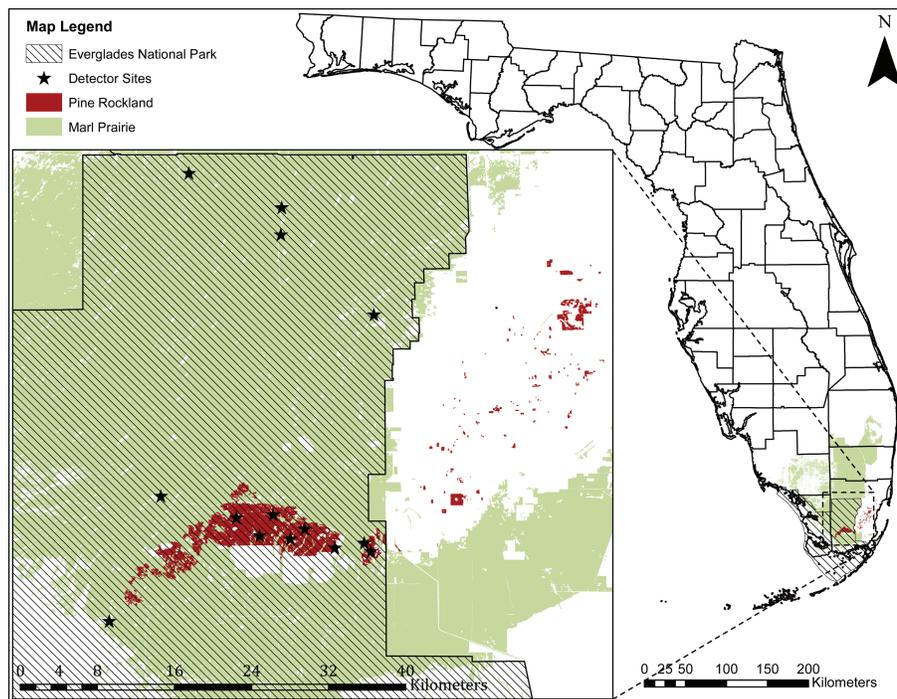


Fig. 1.—Map of Florida, USA and study area within Everglades National Park (insert) showing the extent of 2 vegetation communities (pine rocklands and marl prairies) that were sampled acoustically (stars = detector locations) for bat activity and species richness in the dry-cool and warm-wet seasons of 2015. The largest contiguous remnant block of pine rockland was sampled; small, isolated fragments exist outside the park boundary.

following approved permits: University of Florida IACUC (# 201308070), USFWS (#TE 23583B-1), and Everglades National Park (Permit No: EVER-2015-SCI-0009).

Study area.—We conducted our study in Everglades National Park (ENP), which encompasses 610,484 ha of federally protected lands and is designated an International Biosphere Reserve, a World Heritage Site, and a Wetland of International Importance in the Ramsar Convention (Maltby and Dugan 1994). The 3 dominant vegetation communities in ENP include pine rocklands, freshwater sawgrass marshes and wet marl prairies (hereafter, marl prairies), and mangrove swamps (Lodge 2010; Florida Natural Areas Inventory 2015). We investigated bats' use of vegetation communities within the remnant block of pine rockland in Long Pine Key (8,029 ha) and the surrounding marl prairies (Fig. 1). Pine rockland (characterized by an open canopy of slash pine, *Pinus elliotii* var. *densa*; 400–1,200 pines/ha) is the most diverse plant community within the GEE (439 species) and rich in endemic species (31) (U.S. Fish and Wildlife Service 1999b; Lodge 2010). Outside of ENP, fragments of pine rocklands are isolated and small (mean area only 4.9 ha; Dade County Department of Environmental Resources Management [DERM] 1995). Marl prairie is sparsely vegetated (20–40% cover) but diverse (> 100 plant species), consisting primarily of sedges (e.g., sawgrass, *Cladium jamaicense*), grasses (e.g., muhly grass, *Muhlenbergia* spp.), and scattered shrubs and dwarf Cypress trees (*Taxodium* spp.; U.S. Fish and Wildlife Service 1999a; Florida Natural Areas Inventory 2010). Within the subtropical climate of ENP, there are 2 distinct seasons: dry-cool (December to April) when average temperatures (12–25°C) and average monthly precipitation (42–47 mm) are low, and wet-warm (May to November) when average temperatures (18–32°C) and average monthly precipitation (62–200 mm) are high (Duever et al. 1994; Lodge 2010).

Acoustic surveys.—We conducted acoustic surveys to measure total bat activity, species richness, and species-specific activity levels within pine rocklands and marl prairies. Acoustic surveys are routinely used to monitor bat activity and habitat use patterns, and are particularly effective in areas (e.g., open habitats) where bats are not easily captured in mist nets (Hayes et al. 2009; Parsons and Szewczak 2009). We were specifically interested in patterns of relative habitat use by each species: we recognize that bat activity does not equate with bat abundance (Hayes et al. 2009) and acknowledge the assumptions and limitations associated with inference of acoustic data (Hayes 2000; Gannon et al. 2003). As such, we replicated our surveys to account for spatiotemporal variation, and only made comparisons of relative activity within species to account for varying detectability among species (Hayes 2000). We also recognize that detectability can change with the height at which bats fly above the microphone or the extent to which they echolocate; thus, we are unable to distinguish between spatial and altitudinal patterns of habitat use and are only able to make inferences based on echolocating individuals that fly within the range of our detectors (~20 m). While imperfect detection is possible, it would only create bias in our study if detectability differed between vegetation communities or seasons.

We sampled bat activity by conducting stationary acoustic point surveys using full spectrum Song Meter SM3BAT detectors with SM3-U1 ultrasonic microphones (Wildlife Acoustics, Inc., Maynard, Massachusetts). We connected one omnidirectional, external microphone to each detector by a 3 m cable and extended it to 3 m above ground level. Prior to deployment of equipment, we used an Ultrasonic Calibrator (Wildlife Acoustics, Inc.), to verify the sensitivity of the microphones and overall system performance. We programmed the detectors to record from 30 min before sunset to 30 min after sunrise. We collected data during 2 seasons in 2015: dry-cool (February to March) and wet-warm (June to July). We sampled 7 locations in each of the 2 major vegetation communities (pine rocklands and marl prairies) using 2 approaches. First, we located 1 detector in each vegetation community near a water source, but away from vegetative clutter and flat surfaces prone to acoustic echoes to maximize bat detections and the quality of recordings (Britzke et al. 2013; Loeb et al. 2015). We set these detectors to record for 40 nights in each season. Second, we selected 6 detector locations within each vegetation community to represent spatial heterogeneity, account for accessibility, and where the recording space above microphones was unobstructed by vegetative clutter (Fig. 1). For these 6 detector sites, we conducted two 20-night sampling sessions during each of the 2 seasons. During each 20-night sampling session, we placed 3 detectors in pine rocklands and 3 detectors in marl prairies (stratified north-south for marl prairies and east-west for pine rocklands) and then moved these detectors to 6 new locations for the second 20-night sampling session. The same 12 locations were surveyed during both the wet-warm and dry-cool seasons.

Acoustic analysis and species identification.—We used Kaleidoscope Pro 3.14B (Wildlife Acoustics, Inc.) for automated noise (non-bat ultrasound) filtering, species classifications, and to manually review the spectrograms of acoustic files. To identify calls from all possible species in the region, we used the “Bats of Florida Classifier” (beta version) and “Bats of the Neotropics” in Kaleidoscope Pro. We defined a “bat file” to be a 15-s file that contained ≥ 2 calls that satisfied the filter specifications (Fenton 1970) and used the number of bat files per night as an index of bat activity (Britzke et al. 1999; Tibbels and Kurta 2003; Davidai et al. 2015). Because Kaleidoscope Pro will classify some lower-quality bat calls as “Noise” or “NoID”, we manually reviewed all files in these categories and included any files containing ≥ 2 bat calls in analyses of total bat activity. Species with indistinguishable calls (eastern red bats, *Lasiurus borealis*, and Seminole bats, *Lasiurus seminolus*) were considered as 1 species group; however, existing distribution maps indicate that Seminole bats are much more likely to occur in this region than are eastern red bats (IUCN 2015; Florida Fish and Wildlife Conservation Commission 2016). Classifiers in Kaleidoscope Pro cannot identify Rafinesque's big-eared bats (*Corynorhinus rafinesquii*); hence, we used Townsend's big-eared bats (*Corynorhinus townsendii*) as a proxy, given the similarity in call structure between the 2 species (Szewczak 2011). To reduce species identification error and false positives

(Lemen et al. 2015), we developed a conservative protocol to identify species with infrequent detections and to filter out ambiguous or low-quality bat calls. We required that all files that were given an ultimate species classification had ≥ 5 total calls and that $\geq 75\%$ of the calls in each of these files matched the ID assigned by Kaleidoscope Pro. To confirm species identifications of files that met our criteria, we manually reviewed: 1) all unexpected species classifications based on species range maps, and 2) any species with < 10 files at a given detector location. Finally, due to the status of Florida bonneted bats as an endangered species, we manually reviewed 100% of the files classified by Kaleidoscope Pro as Florida bonneted bats, NoID, Noise, or files for which the software provided multiple species identifications including Florida bonneted bats (i.e., Florida bonneted bat was listed as an “Alternate” species). To aid in manual validation, we compiled a reference library of echolocation calls from hand-released bats captured in mist nets in south Florida and other areas in the southeastern United States, as well as from publicly available databases and journal articles (e.g., Szewczak 2011; Jung et al. 2014; Bailey et al. 2017). Two researchers independently confirmed all manually validated calls and viewed uncertain calls in a second automated call analysis software (Sonobat4). For further discussion of our protocol and assumptions, see Supplementary Data SD1. Our automated and manual validation protocols were used consistently across detectors; thus, despite some expected identification error, we were able to compare relative bat species richness and activity detected in each vegetation community.

Statistical analysis.—To evaluate habitat use and seasonal patterns in the local bat assemblage, at each detector site, we quantified: 1) total bat activity (number of “bat files” containing bat calls from any species) per night, 2) bat species richness (number of species identified) per night, and 3) species-specific bat activity (number of files with calls from each bat species) per night. Species that were acoustically indistinguishable (eastern red bats and Seminole bats) were considered as 1 species group for all subsequent analyses.

To test for differences in bat activity, species richness, and species-specific activity per night detected in each vegetation community and season, we constructed generalized linear mixed-effects models (GLMMs), with detector location as a random effect (function *glmer*; R package *lme4*; Bates et al. 2012). Based on standard diagnostic analysis of model residuals, we modeled all GLMMs with a Poisson distribution for count data. For each response variable, we constructed a suite of models with all possible combinations of the 2 fixed effects (vegetation community, season) and an interaction term between them. We used the Akaike Information Criterion (AIC) and Akaike weight (ω_i) to determine the best model (Burnham and Anderson 2002). If models were considered to be equivalent ($\leq 2 \Delta\text{AIC}$), we selected the model with the fewest parameters and calculated evidence ratios (ratios of Akaike weights [ER]), which indicate the likelihood of one model versus another (Burnham and Anderson 2002). All parameters were estimated using maximum likelihood and Laplace approximations to allow model comparisons (Bolker et al. 2009; Pinheiro et al. 2012).

For pair-wise comparisons between main effects categorical variables, we used post-hoc Tukey contrasts for multiple comparisons (function *glht*, *multcomp* package). In the case that the interaction term was included in the best model, we conducted the following post-hoc comparisons: between pine rocklands and marl prairies within each season to determine how the effect of vegetation community changed with season, and between seasons within each vegetation community. For these comparisons, we used a likelihood ratio test for nested models (function *anova*, R Stats package). All *P*-values for post-hoc comparisons were adjusted with a Bonferroni correction. We conducted all graphical and statistical analyses in the statistical software language R (v. 3.1.2) in conjunction with R studio (v. 0.98.1102). All reported errors are standard error of the mean ($\pm SE$) unless otherwise noted.

RESULTS

We recorded acoustic data from 560 detector nights (40 nights \times 14 detector sites). After removing non-bat ultrasonic or acoustic noise files (e.g., wind, insects, birds), 138,216 files containing bat sequences remained for analyses (pine rocklands = 88,674; marl prairies = 49,542). Using our conservative protocol and manual validation, we identified 39,836 files (28.8% of total files with bat calls; pine rocklands = 22,464; marl prairies = 17,372) to the level of species or species group. Across all of our sites, we detected 9 bat species (8 species and 1 species group): Brazilian free-tailed bats, *Tadarida brasiliensis* (74.95% of total bat files categorized to species); big brown bats, *Eptesicus fuscus* (18.14%); Seminole, *L. semolinus* or eastern red bats, *L. borealis* (4.06%); evening bats, *Nycticeius humeralis* (1.64%); Florida bonneted bats, *Eumops floridanus* (0.41%); velvety free-tailed bats, *Molossus molossus* (0.40%); northern yellow bats, *Lasiurus intermedius* (0.19%); tri-colored bats, *Perimyotis subflavus* (0.08%); and Rafinesque’s big-eared bats, *C. rafinesquii* (0.02%). Two of these species (velvety free-tailed and Rafinesque’s big-eared bats) were unexpected based on species distribution maps (Florida Fish and Wildlife Conservation Commission 2016). All species were detected at least once in both vegetation communities except Rafinesque’s big-eared bats, which were detected infrequently only in marl prairies (Supplementary Data SD2).

The model that received the most support in explaining total bat activity included significant effects of vegetation community, season, and an interaction between vegetation community and season (Table 1). The highest bat activity was detected in the pine rocklands during the dry-cool season (Fig. 2). As we predicted, there was significantly higher mean bat activity (bat files per site per night) detected in the pine rocklands (394.66 ± 26.05) than in the marl prairies (192.56 ± 15.75 ; 4.10 ; $\chi^2 = 4.09$, $P < 0.043$) in the dry-cool season. There was not a significant difference in bat activity between the 2 vegetation communities in the wet-warm season (pine rocklands: 190.42 ± 14.12 , marl prairies: 159.54 ± 11.18 ; $\chi^2 = 0.0008$, $P = 0.977$). Total bat activity decreased from the dry-cool to the

Table 1.—Best GLMMs (generalized linear mixed-effects models; Poisson distribution) and predictor variables explaining total bat activity and species richness per night in Everglades National Park, Florida, USA. For each dataset, the top models with $\Delta\text{AIC} < 2$ (difference between Akaike Information Criteria (AIC) score of each alternative model and model with the lowest AIC score) are listed along with their Akaike weights (ω_i). Categorical variables are “Veg” (distinguishing between pine rocklands and marl prairies) and “Season” (distinguishing between wet-warm and dry-cool). For all models, estimates were calculated using the wet-warm season as the reference season and marl prairie as the reference vegetation community.

Models	<i>K</i>	ΔAIC	ω_i	Estimate	<i>SE</i>	<i>P</i> -value
Total bat activity						
Veg + Season + Veg × Season	5	0	1			
Intercept				5.68	0.22	<0.001
Veg				−0.80	0.32	0.012
Season				−0.67	0.01	<0.001
Veg × Season				0.56	0.01	<0.001
Species richness						
Veg + Season	4	0	0.73			
Intercept				1.01	0.08	<0.001
Veg				−0.43	0.10	<0.001
Season				0.36	0.05	<0.001
Veg + Season + Veg × Season	5	2	0.27			

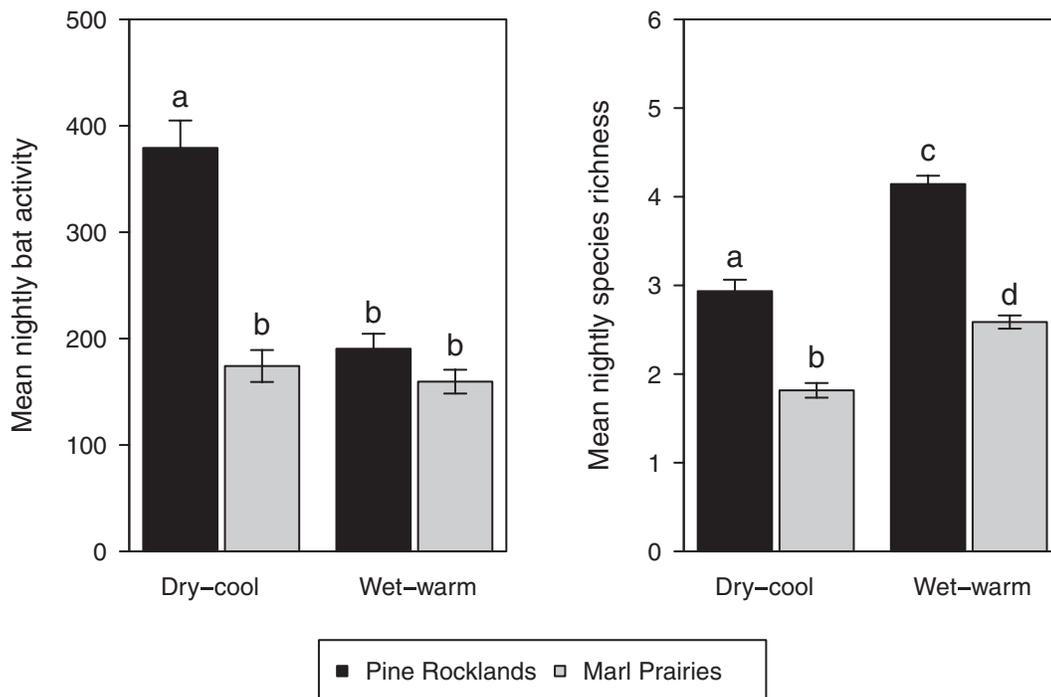


Fig. 2.—Barplots showing differences in mean bat activity (number of files per night \pm *SE*) and mean bat species richness (number of species per night \pm *SE*) per night between 2 vegetation communities and seasons sampled in Everglades National Park, Florida, USA. Letters indicate significant differences.

wet-warm seasons in the pine rocklands ($\chi^2 = 1.84$, $P = 0.351$), but did not change in the marl prairies ($\chi^2 = 6431.9$, $P < 0.001$).

The best model explaining mean nightly bat species richness included vegetation community and season (Table 1). We detected significantly higher mean bat species richness in pine rocklands (3.53 ± 0.10) than in marl prairies (2.16 ± 0.08 ; $z = 4.26$, $P < 0.001$) across both seasons (Fig. 2). Further, we detected significantly higher mean species richness in the wet-warm season (3.25 ± 0.89) than the dry-cool season (2.46 ± 0.10 ; $z = 7.41$, $P < 0.001$) across both vegetation communities. The interaction term

between vegetation and season was not included in the top model, indicating that the effect of vegetation community on species richness was consistent across both seasons (Supplementary Data SD3).

Species-specific activity patterns varied between vegetation communities and seasons (Fig. 3; Supplementary Data SD2). The best models for 3 species (Seminole bats-eastern red bats, evening bats, and velvety free-tailed bats) included significant effects of vegetation community and season (Supplementary Data SD4), with higher bat activity in pine rocklands than marl prairies (Fig. 3) and higher bat activity in the wet-warm season

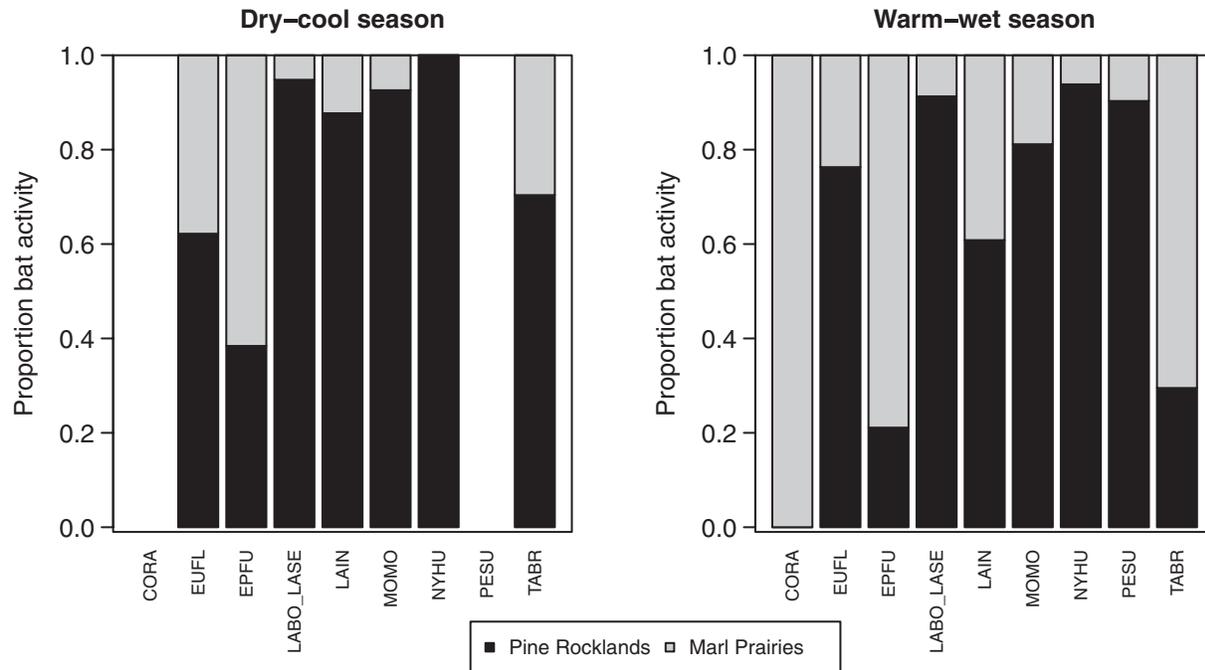


Fig. 3.—Proportion of species-specific bat activity (bat files per night) detected in each of the 2 vegetation communities (pine rocklands and marl prairies) and 2 seasons (dry-cool and wet-warm) sampled in Everglades National Park, Florida, USA. Proportion of bat activity is presented due to the difference in magnitude in activity among species and due to biases in acoustic detection and species identification that preclude direct comparisons among species. CORA = *Corynorhinus rafinesquii* (Rafinesque's big-eared bats), EUFL = *Eumops floridanus* (Florida bonneted bats), EPFU = *Eptesicus fuscus* (big brown bats), LABO_LASE = species group *Lasiurus borealis* (eastern red bats) and *L. seminolus* (Seminole bats), LAIN = *L. intermedius* (northern yellow bats), MOMO = *Molossus molossus* (velvety free-tailed bats), NYHU = *Nycticeius humeralis* (evening bats), PESU = *Perimyotis subflavus* (tri-colored bats), TABR = *Tadarida brasiliensis* (Brazilian free-tailed bats).

than the dry-cool season. A fourth species, tri-colored bats, was only detected in the wet-warm season and had significantly higher activity in pine rocklands during this season. The best models for 3 species (Brazilian free-tailed bats, big brown bats, and northern yellow bats) included significant effects of vegetation community, season, and an interaction between vegetation community and season (Supplementary Data SD4). Higher Brazilian free-tailed bat activity was detected in pine rocklands than marl prairies in the dry-cool season ($\chi^2 = 5.82$, $P = 0.031$), with the opposite observed in the wet-warm season ($\chi^2 = 8.58$, $P = 0.007$). Brazilian free-tailed bat activity decreased from the dry-cool to the wet-warm season in pine rocklands ($\chi^2 = 9254.8$, $P < 0.001$), but not in marl prairies ($\chi^2 = 2.87$, $P = 0.180$). Across both seasons, there was no significant difference in activity between vegetation communities for northern yellow bats (dry-cool: $\chi^2 = 2.68$, $P = 0.203$; wet-warm: $\chi^2 = 0.17$, $P = 1.00$) or big brown bats (dry-cool: $\chi^2 = 0.007$, $P = 1.00$, wet-warm: $\chi^2 = 2.85$, $P = 0.183$), but big brown bats decreased in activity from the dry-cool season to the wet-warm season in both vegetation communities (pine rocklands: $\chi^2 = 567.84$, $P < 0.001$, marl prairie: $\chi^2 = 51.71$, $P < 0.001$). The top model for Florida bonneted bats included a significant effect of season only, with higher activity in the dry-cool season than the wet-warm season ($\chi^2 = 43.67$, $P < 0.001$). Due to very low detections (a total of only 7 files), we did not model activity patterns for Rafinesque's big-eared bats; this species was only detected in marl prairies in the wet-warm season (Fig. 3).

DISCUSSION

We detected higher nightly bat activity and species richness in pine rocklands than in surrounding marl prairies, suggesting that forest patches are important for bats within the vast, seasonally flooded grasslands of the GEE. Similar to our study, Aguirre (2002) found bat diversity to be higher in forest islands relative to surrounding seasonally inundated grasslands in Bolivia. Four of the 9 species of bats we detected exhibited higher mean activity in pine rocklands than marl prairies during both seasons, and 1 (Brazilian free-tailed bats) exhibited higher activity in pine rocklands during the dry-cool season. The patterns we observed could be due to changes in the spatial use of habitat or vertical shifts in flight altitude (i.e., detection would increase as bats fly closer to the microphone). We suggest that the greater structural complexity of pine rocklands relative to the saw grass-dominated marl prairies is attractive to bats because it provides roosting opportunities in trees, protection from aerial predators and inclement weather, and a favorable microhabitat and microclimate for insect prey. Further, our finding of an interactive effect between vegetation community and season on total bat activity suggests that the benefits provided by pine rocklands to bats are especially pronounced during the dry-cool season when temperatures, and likely insect prey availability, are reduced.

Forest patches in grassland systems may provide benefits to bats through their physical structure. Several of the bat species that we detected in pine rocklands have been documented to

roost solitarily or communally in pine trees: Seminole-eastern red bats (Menzel et al. 1998), evening bats (Hein et al. 2009), tri-colored bats (Perry and Thill 2007), and Florida bonneted bats (Braun de Torrez et al. 2016). The slash pine-dominated pine rocklands may provide an essential source of roosts (e.g., foliage, cavities, bark) for these tree-roosting bats. In contrast, open marl prairies offer virtually no roosting opportunities apart from the foliage of shrubs and small isolated tree islands (< 4 m height). Marl prairies may also leave bats vulnerable to predation and inclement weather (e.g., storms). Aerial predation by birds can have significant impacts on bat populations, and consequently influence flight behavior and foraging decisions (Speakman 1991). While forests may also provide perching locations for predators, forests likely reduce predation risk for bats by providing night roosts in which to take cover, as well as dark corridors and obstacles that aid in predator avoidance during flight (Verboom and Huitema 1997; Lacki 2007). Further, vertical landscape features in open habitats act as wind breaks (Lewis and Dibley 1970) and may benefit bats by reducing wind speed, which is often negatively associated with flight activity (Wolcott and Vulinec 2012). Pine rocklands have been shown to withstand hurricane strength winds (Platt et al. 2000) and may provide protection for bats in this region where tropical storms are common. This may be particularly important for the smaller, slow-flying species (e.g., Seminole bats, evening bats, and tri-colored bats) that may be more vulnerable to strong winds and predation in open areas than larger species capable of fast, high flight (e.g., Florida bonneted bats, northern yellow bats, and big brown bats; Frey-Ehrenbold et al. 2013).

Forest patches may also provide benefits to bats through enhanced foraging opportunities. Bats are able to quickly shift their foraging response to changes in prey availability across the landscape (McCracken et al. 2012; Müller et al. 2012; Gonsalves et al. 2013), or even the altitude at which they forage (McCracken et al. 2008). Although we have no data on the abundance of insects during our study, a previous study sampling insect pollinators in our study region found higher species richness in pine rocklands (> 115) than in marl prairie sites (< 75), notably of Lepidoptera, Coleoptera, and Diptera (Pascarella et al. 2001), which are commonly consumed by bats (Kunz 1982). Because structural complexity of vegetation influences niche space for insects (Murdoch et al. 1972; Knops et al. 1999), diversity and abundance of insects may be higher within pine rocklands due to the greater plant diversity and biomass of this vegetation community relative to marl prairies (Gunderson 1994; Pascarella et al. 2001). Similarly, our finding of higher bat activity in pine rocklands during the dry-cool season may be a result of microclimate moderation, leading to higher prey availability. The structure and biomass of forests provide a warmer microclimate at night by retaining heat and humidity (Rambo and North 2009; Lee et al. 2011) and reducing wind velocity (Verboom and Spoelstra 1999; Platt et al. 2000) relative to the open marl prairies. Aerial insects are sensitive to small changes in temperature, humidity, and wind (Lewis and Dibley 1970). The use of warm microclimates within pine rocklands by insects during the dry-cool season may influence

selection of foraging habitat by bats at a time when prey availability is limited. In the summer, when temperatures and insect prey availability are higher overall in the GEE (Amalin et al. 2009), this warmer microclimate provided by pine rocklands may not be as critical for foraging bats.

In addition to seasonal differences in the use of pine rocklands and marl prairies, we detected overall seasonal shifts in the bat community across both vegetation communities. Although only speculative, we suggest that 3 species (Brazilian free-tailed bats, big brown bats, and Florida bonneted bats) may shift their foraging patterns seasonally to forage more within the vegetation communities in our study area during the dry-cool months (February to March) when prey availability may be limited in other areas (e.g., colder winter conditions further north or less productive systems in the region). Brazilian free-tailed bats, the most commonly detected species, are cold sensitive (Pagels 1972), do not hibernate, and migrate to warmer climates in other parts of their range (Cockrum 1969; Russell et al. 2005). In the southeastern United States, they are not thought to migrate, but local shifts in roost usage often occur seasonally (Wilkins 1989). Florida bonneted bats also have been observed to be cold sensitive (United States Fish and Wildlife Service 2013; Bailey et al. 2017) and thus may also undergo seasonal shifts in preferred foraging areas. In contrast to patterns of total bat activity driven by the most common species, nightly species richness increased in the wet-warm season due to more frequent detections of rarer species (Seminole-eastern red bats, evening bats, velvety free-tailed bats, tri-colored bats, and Rafinesque's big-eared bats) relative to the dry-cool season. Increased detections of these species may be due to an increase in individuals on the landscape (e.g., the appearance of volant juveniles entering the population during the reproductive summer months, Kunz and Fenton 2003), or local influx of bats exploiting available resources within ENP (e.g., insects, Amalin et al. 2009). The patterns we observed are likely modulated by a suite of species-specific traits (e.g., morphology, echolocation structure, foraging and roosting preferences) beyond the scope of this paper, but which warrant further investigation.

Our detection of 3 species that were rare or unexpected (Florida bonneted bats, velvety free-tailed bats, and Rafinesque's big-eared bats) likely reflects the lack of previous research on bats in our study area. These species have all been documented within 50 km of where we detected them in our study (Marks and Marks 2006; Bailey et al. 2017); thus, the occurrence of these species in ENP is very plausible. However, although we took many precautions to be conservative in our identification of bat species (Supplementary Data SD1), we recommend future efforts to validate the presence of these unexpected species in this region.

Pine rocklands have been drastically reduced from their original extent and continue to be threatened by development and climate change (U.S. Fish and Wildlife Service 1999b). In light of threats facing bats in this region and worldwide, we recommend conservation and management of the remaining pine rocklands to maintain habitat for bat species dependent on these forests. More broadly, forest patches are clearly important

to bat communities in subtropical grasslands where roosting opportunities, protective cover, and prey availability may be limited. Seasonality also can influence habitat use by bats, and thus it is important to account for these seasonal shifts when developing conservation strategies in regions where bat communities are active year-round.

ACKNOWLEDGMENTS

We especially thank M. A. Wallrichs, the primary technician responsible for data collection and processing. We also thank T. Dean and S. Snow from Everglades National Park for coordinating on project design, development and logistics, and for providing valuable input throughout the project. This study was funded by a grant from the United States Department of the Interior, National Park Service, Everglades National Park (Contract # P14AC01412). Finally, we thank the Editor in Chief, E. Heske, Associate Editor, A. Piaggio, and 2 anonymous reviewers for their helpful feedback on our manuscript.

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Assumptions, limitations and confidence in species identification of bats in Everglades National Park, Florida, USA.

Supplementary Data SD2.—Table of species-specific bat activity (mean files per night \pm SE) detected with SM3Bat recorders (Wildlife Acoustics, Inc) in Everglades National Park, Florida, USA.

Supplementary Data SD3.—Temporal patterns in bat activity and bat species richness sampled within pine rocklands and marl prairies across 2 seasons (dry-cool and wet-warm) in Everglades National Park (ENP), Florida, USA.

Supplementary Data SD4.—Table of GLMMs (generalized linear mixed-effects models; Poisson distribution) and predictor variables explaining species-specific bat activity per night sampled within Everglades National Park, Florida, USA.

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Submitted 14 June 2017. Accepted 6 November 2017.

Associate Editor was Antoinette Piaggio.