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Southeastern Pocket Gopher (Geomys pinetis) Tunnels Provide Stable Thermal Refugia

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ABSTRACT.—Animals living underground deal with multiple physiological challenges, such as hypoxia and hypercarbia, but may have reduced thermoregulation demands because of the more stable underground microclimate. Southeastern pocket gophers (*Geomys pinetis* Rafinesque) occur in the fire-adapted, open-pine forests of the southeastern Atlantic Coastal Plain where prescribed fire is commonly used to manage understory vegetation. They are almost exclusively fossorial, and their tunnels provide ecological services, including shelter, for a suite of commensal vertebrates and invertebrates. To quantify potential thermoregulation benefits of southeastern pocket gopher tunnels, we compared temperatures in active tunnels (n = 31) to aboveground temperatures during winter (December 2018–February 2019), and to aboveground temperatures during prescribed fire events (n = 16) occurring in spring (March–May 2019). During winter, tunnels provided a more stable thermal environment (average range = 6.5 ± 0.8 C; mean ± SE) relative to aboveground (average range = 24.8 ± 1.8 C) temperatures. Similarly, mean tunnel temperature range (2.05 ± 0.5 C) was significantly narrower than aboveground temperature range associated with fire events (497.0 ± 101.4 C). Clearly, tunnels provide a stable thermal environment for pocket gophers and commensals that use their tunnel systems.

INTRODUCTION

Pocket gophers (family Geomyidae) are almost exclusively fossorial, except for occasional aboveground dispersal movements (Baker *et al.*, 2003; Warren *et al.*, 2017; Pynne *et al.*, 2019). They form tunnels that are used to forage, and their selective herbivory alters local plant

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communities (Huntly and Inouye, 1988; Huntly and Reichman, 1994). Pocket gopher tunnels and mounds aerate soils, facilitate nutrient turnover, and provide shelter for many invertebrates and vertebrates (Funderburg and Lee, 1968; Reichman and Smith, 1985; Skelley and Gordon, 2001; Clark *et al.*, 2018; Skelley and Kovarik, 2019). Because of their ecological services, pocket gophers are considered ecosystem engineers and indicators of ecosystem health (Reichman and Seabloom, 2002). *Geomys pinetis* Rafinesque (southeastern pocket gopher; henceforth pocket gopher) is commonly associated with *Pinus palustris* Mill (longleaf pine) and other open pine forests in the southeastern U.S., and considered an indicator of the quality of the system (McIntyre *et al.*, 2019). Longleaf pine forests require frequent fires, and prescribed fire is commonly used to manage longleaf pine and other open pine forests.

Fossorial species' subterranean existence necessitates adaptations and strategies to deal with hypoxia, hypercarbia, high humidity, and flooding (Morrison and Pearson, 1946; Ultsch and Anderson, 1986; Burda *et al.*, 2007; Marcy *et al.*, 2013; Devereaux and Pamenter, 2020). Tunneling is also energetically demanding (Vleck, 1979), despite fossorial animals having adaptations that facilitate excavation and belowground movement (McNab, 1966; Buffenstein, 2000; Marcy *et al.*, 2013; Devereaux and Pamenter, 2020). Although there are costs associated with living underground, a fossorial existence has benefits, such as shelter, access to food like roots and rhizomes during winter and after fires, decreased predation risk, and protection from environmental extremes, such as fires and severe cold (Bradley and Yousef, 1975; Pacific Northwest Research Station, 2001; Winchell *et al.*, 2016). Pocket gopher tunnels are thought to provide a buffer from temperature extremes, but little research has quantified thermal buffering characteristics within their tunnels (McNab, 1966; Bradley and Yousef, 1975). Pocket gopher tunnels may be particularly valuable as thermal refugia within areas of extreme cold and fire-maintained systems and as protection from predation post-fire.

Pocket gophers are sensitive to temperature changes and extremes (McNab, 1966; Benedix, 1994). This is particularly important given pocket gophers are known to be sensitive to hot temperatures and maximum homeostatic temperatures have been quantified (McNab, 1966; Ross, 1980). Although homeostatic minimum temperatures in pocket gophers have not been studied, behavioral studies suggest that pocket gophers also may be sensitive to cold temperatures. Pocket gophers are active year-round and do not exhibit torpor (Pembleton and Williams, 1978; Baker *et al.*, 2003), but those that occur in colder environments respond to snow cover by borrowing and backfilling through snow and by moving to drier soils in search of a more thermally stable environment (Ingles, 1949; McNab, 1966; Cox and Hunt, 1992; Marcy *et al.*, 2013). Southeastern pocket gophers are generally found in fire-maintained systems, and climate throughout their geographical range is characterized by mild winter temperatures and hot humid summers (Pembleton and Williams, 1978). Although winter temperatures are generally mild, cold snaps occur annually. Because southeastern pocket gopher tunnels are sufficiently deep as to avoid frozen soils (Baker *et al.*, 2003), it is reasonable to suggest tunnels provide thermal refugia during winter, summer, and from short-term, extreme temperatures associated with fires (Brown and Hickman, 1973; Buffenstein, 2000).

Large-bodied or highly mobile terrestrial vertebrates typically emigrate ahead of fire, but some smaller, less mobile species may seek refuge underground (Derrick *et al.*, 2010; Potash *et al.*, 2020). For example *Gopherus polyphemus* (gopher tortoise) creates burrows that provide thermal protection during fire events with stable temperatures at depths $\geq$1 m (Douglass and Layne, 1978; Ultsch and Anderson, 1986; Pike and Mitchell, 2013; Knapp *et al.*, 2018;

Potash *et al.*, 2020), and are well-documented areas of refuge from fires for many vertebrate taxa (Derrick *et al.*, 2010; Morris *et al.*, 2011b; Silva-Lugo, 2014; Dziadzio and Smith, 2016; Knapp *et al.*, 2018; Potash *et al.*, 2020). However, importance of tunnels provided by other species for mitigating thermal extremes has received little study. Pocket gophers are small-bodied rodents with poor mobility that would have difficultly emigrating ahead of fires, and instead form subterranean tunnels. To our knowledge, no studies have focused on temperature buffering qualities of pocket gopher tunnels.

Southeastern pocket gophers also occur in similar fire-adapted, hot, and humid habitats as gopher tortoises, and create tunnels that likely moderate temperature fluctuations associated with daily temperature changes and fire events. However, differences between gopher tortoise burrows and pocket gopher tunnels are conspicuous. Pocket gopher tunnels are shallower, tend to be longer ($\leq$50 m), and are irregularly shaped, with tunnel access sealed with a soil plug (Romañach *et al.*, 2005). Because pocket gopher tunnel morphology differs substantially from gopher tortoise burrows, thermal characteristics may also differ such that the value of tunnels as refugia varies from that of gopher tortoise burrows. Therefore, we quantified potential thermal refugia provided by pocket gopher tunnels. Specifically, we compared temperature ranges in tunnels to aboveground temperatures during winter and during spring prescribed fire events and hypothesized that tunnels would have more stable temperatures during the extreme cold and extreme heat from prescribed fires.

METHODS

STUDY SITE

The Jones Center at Ichauway (31.220°N, -84.478°W) is a 12,140-ha property in southwestern Georgia, U.S.A., managed for multiple uses including biodiversity and quail hunting. Most upland forested stands are dominated by longleaf pine and receive prescribed fire on a 2-y return interval. Upland understories are extremely diverse and consist largely of grasses and forbs (McIntyre *et al.*, 2019), which provide suitable habitat for southeastern pocket gophers. *Quercus* spp. (oaks) often dominate in bottomlands and riparian areas. Pocket gophers are found in the well-drained alluvial soils and are not associated with unburned hardwood drains or hammocks.

TEMPERATURE MEASUREMENT

During winter, we collected temperature data in pocket gopher tunnels using 30-gauge K-type wire thermocouples (Omega Engineering; omega.com) attached to data loggers (Hobo UX100-14M, Onset Computer Corporation, Bourne, MA) with temperature readings occurring every 30 min. We located active burrows by driving along roads and searching for mounds. Tunnels were determined to be active by observing in-tunnel soil displacement or fresh mounding activity. Because pocket gophers plug their tunnel system at the mound, we excavated mounds until the open tunnel was located. Thermocouples were placed at the approximate cross-sectional center of the tunnel. After thermocouple positioning, the tunnel was resealed such that the wire was supported by soil. We left the thermocouples in place for 3 d. We obtained matching ambient temperatures from the Jones Center at Ichauway weather station that records air temperature every 15 min and is centrally located in a 600 m^2 open field surrounded by longleaf pine stands. Mean distance from the weather station to sampled tunnel systems was 2.8 km. We used the matching ambient temperatures

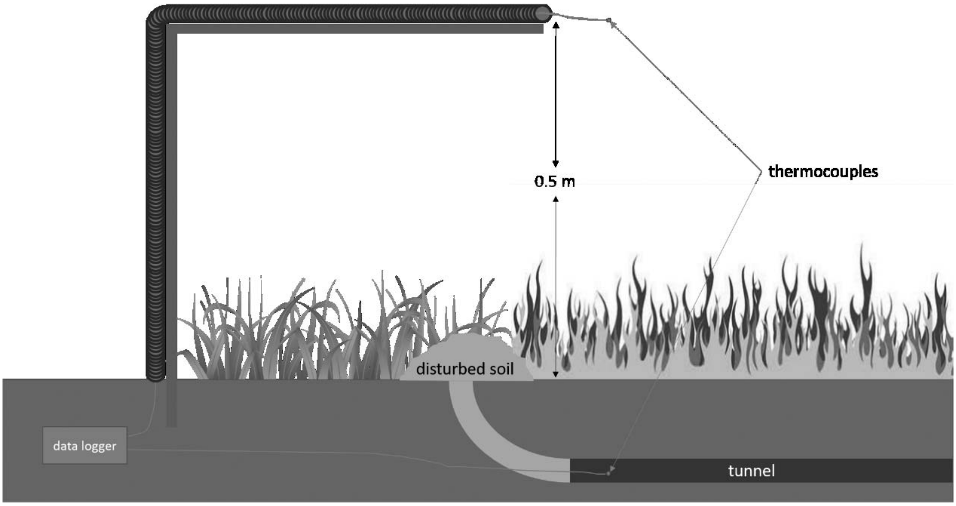

FIG. 1.—Temperatures recorded for southeastern pocket gopher tunnels (n = 16) and paired with aboveground prescribed fires at 16 locations conducted at The Jones Center at Ichauway, Newton, Georgia, U.S.A., from March 3, 2019–May 17, 2019. Temperatures were recorded using one thermocouple positioned in the tunnel and the other 0.5 m above the surface at the same location. Temperatures were recorded every 2 s below and aboveground for each fire event

from the weather station during the 3-d winter sampling periods to compare air and tunnel temperatures.

To measure aboveground temperature during prescribed fires, we placed a thermocouple 0.5 m above the ground surface directly above the thermocouple in the pocket gopher tunnel (Fig. 1). Aboveground thermocouples were supported and protected by steel fence post stands bent at right angles with flexible steel conduit attached. Data loggers were buried 10–30 cm underground inside a Nema CASE-4X-2 (Onset Computer Corporation, Bourne, MA) to protect them from fires. We placed a thermocouple belowground at the same location within an active tunnel, supported with soil to avoid contact with the walls of the tunnel. Because belowground temperatures stabilized within seconds when sealed, thermocouples were placed 30–120 min prior to fire ignition, and temperatures were logged every 2 s until sample areas had cooled enough to allow retrieval of sampling equipment. Prescribed fires occurred between March and May 2019. All fires were conducted with relative humidity between 35% and 65% and average wind speed between 0.5 and 2.0 m/s. Ignition patterns included head fires, backing fires, and strip head fires, but varied based on specific daily weather conditions. Although fires occurred in a variety of understory conditions, understories consisted mainly of longleaf pine litter and *Andropogon virginicus* L. (broomsedge) or *Aristida stricta* Michx. (wiregrass), and all sites had been burned within the past 2 y.

DATA ANALYSIS

To compare temperatures in southeastern pocket gopher tunnels to ambient winter temperature, we calculated temperature ranges (maximum temperature – minimum temperature) and compared them using an analysis of variance (ANOVA) as a function of treatment (tunnel or ambient) and sampling period (defined as the entire sampling interval at a given tunnel). To compare temperature ranges that occurred during prescribed fires, we determined maximum temperature recorded for each thermocouple treatment (above or belowground) for the period from approximately 30–60 min before to approximately 10–30 min after the fire passed the sampled tunnel. We then calculated two temperature changes for each thermocouple: maximum recorded temperature minus the first recorded temperature and maximum temperature recorded minus the last temperature recorded within the treatment time period. The early change represented aboveground warming associated with the advancing fire, whereas the late change represented aboveground cooling. We selected warming and cooling values because there is likely a time delay for thermal effects to occur underground after fires. We then modeled temperature change (response variable) associated with prescribed fire using treatment (tunnel or above ground), time (warming or cooling), and their interaction using an ANOVA in R (R Core Team, 2019).

RESULTS

Tunnel depths ranged from 15–30 cm. During the winter we observed tunnel temperatures ranging from 7–20 C, ambient air temperatures ranging from -3 – 24 C, and observed temperatures on the surface of the soil reaching temperatures >40 C. During the spring, maximum temperatures during fires reached >800 C, whereas temperatures in tunnels were consistently <16 C.

We recorded temperature data from 31 thermocouples during nine distinct 3-d periods in winter (Fig. 2; December 7, 2018–February 4, 2019). Belowground temperature stabilized <30 min after installing thermocouples in all cases. Mean temperature range associated with 3-d periods belowground (average range = 6.5 ± 0.8 C; mean ± SE) was less ($F_{1,52} = 218$, $P < 0.001$) than ambient (average range = 24.8 ± 1.8 C).

We measured temperature changes in tunnels and aboveground during prescribed fires at 16 sites from 3 March 2019–17 May 2019 (Fig. 3). During fires, average maximum temperature was 21.4 ± 1.0 C in tunnels and 303.0 ± 69.0 C aboveground. Time (warming or cooling) and treatment ($F_{1,60} = 0.001$, $P = 0.956$) did not interact to affect temperature ranges. Mean overall tunnel temperature range (2.05 ± 0.5 C) was less than ($F_{1,60} = 47.5$, $P < 0.001$) aboveground temperature range associated with fire events (497.0 ± 101.4 C).

DISCUSSION

All mammals thermoregulate, and many species have elaborate mechanisms for surviving temperature extremes. Pocket gophers can maintain homeostasis by vasodilation and vasoconstriction of blood vessels within their tail as long as temperatures are <30 C, (McNab, 1966; Baker *et al.*, 2003; Connior, 2011); however, this temperature can be exceeded during the summer and is easily exceeded during fire events. This is particularly important as pocket gophers cannot dissipate heat at temperatures >39 C (McNab, 1966; Ross, 1980). The lower temperature tolerance of pocket gophers is unknown, but winter air temperatures within their geographical range often dip to <0 C, which is likely below their tolerance. Therefore, the relatively stable temperatures within tunnels are critical to pocket gopher thermoregulation during both hot and cold aboveground temperatures.

Soil temperature changes at a slower rate than air (Parton and Logan, 1981; Kaspar and Bland, 1992), resulting in predictable temperature changes with soil depth (Parton and

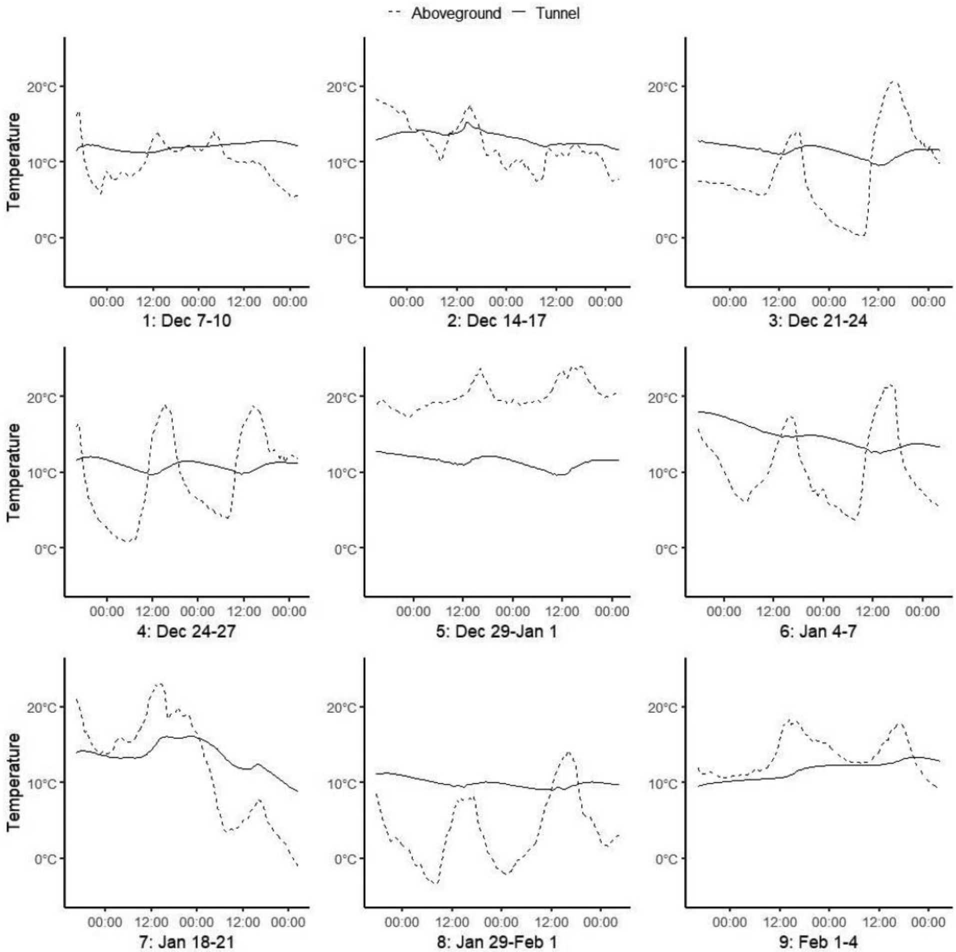

FIG. 2.—Mean temperatures recorded in southeastern pocket gopher tunnels (n = 31) and paired aboveground locations during nine sampling periods from December 7, 2018–February 4, 2019 at The Jones Center at Ichauway, Newton, Georgia, U.S.A., during winter. Temperatures represent the means of tunnels and associated aboveground locations for which sampling dates coincided (n = 2–5 sites)

Logan, 1981; Burda *et al.*, 2007). Because the microclimate of soil becomes more stable with increasing depth, subterranean animals usually maintain a depth that provides optimal temperatures, humidity, and gas exchange (Bollazzi *et al.*, 2008). For example gopher tortoise burrow temperatures decrease gradually by as much as 0.9 C/m, and gopher tortoises can select a position in the tunnel or on the apron to optimize thermoregulation (Douglass and Layne, 1978). Other fossorial mammals, like big-headed African mole-rats (*Tachyoryctes macrocephalus* Rüppell; Vlasatá *et al.*, 2017) and Mechow's mole-rats (*Fukomys mechowii* Peters; Burda *et al.*, 2007), are less active aboveground and move belowground during temperature extremes. Benedix (1994) observed predictable tunneling and activity patterns in *Geomys bursarius* Shaw (plains pocket gopher) based on

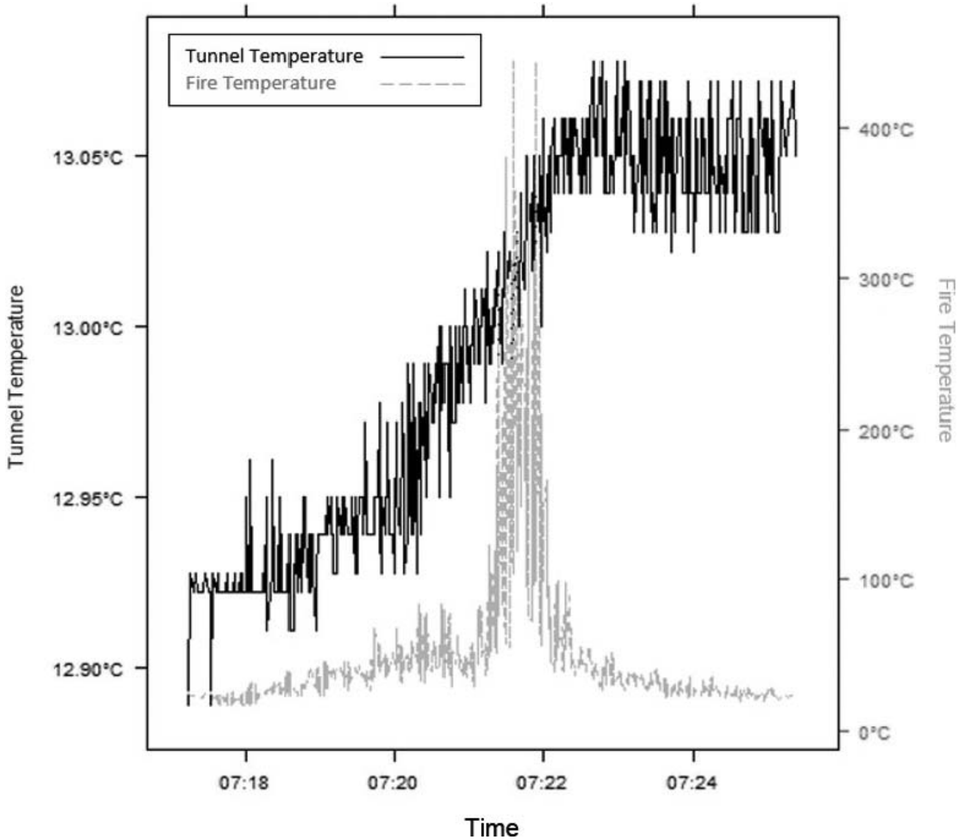

FIG. 3.—Temperatures recorded every 2 s within a southeastern pocket gopher (*Geomys pinetis*) tunnel and aboveground before, during, and after a prescribed fire event on March 21, 2019 at The Jones Center at Ichauway, Newton, Georgia, U.S.A., Similar data were collected at 16 sites. Note differing y-axis scales. Although the passing of fire affected tunnel temperatures, aboveground temperatures were greatly mitigated within the tunnel

air temperature; plains pocket gophers were less active belowground during temperatures >31 C. In this study tunnels predictably maintained more stable temperatures, giving pocket gophers an adaptive advantage when regionally extreme cold occurs or in the presence of fire.

Our data suggest even the shallow depth of pocket gopher tunnels was sufficient to insulate against the extreme temperatures caused by prescribed fires. The mean range of temperatures in tunnels during fires (2.05 $\pm$ 0.5 C) was actually smaller than the mean range we observed during winter (6.5 $\pm$ 0.8 C). The reduced range during prescribed fire events was likely due to our shorter sampling interval (only a few hours associated with fire events as opposed to 3 d during winter). However, importance of tunnels as thermal refugia during fires was great as some fires reached >700 C aboveground. Though tunnels provide thermal protection for pocket gophers during fires, as shown in Figure 3, the short time frame we had thermocouples deployed suggests that temperatures increased during the day.

However, this increase was only a few degrees and was likely from normal solar radiation warming the soil as opposed to influence of prescribed fires. This belowground response further demonstrates that tunnels are much more stable than ambient temperature fluctuations, which is especially important in fire-adapted or communities or in areas with extreme cold.

Direct mortality from fire is a severe risk for many small mammals (Quinn, 1979), and they will typically avoid fires by escaping ahead of advancing flames, finding refuge in unburned patches (McMillan *et al.*, 1995; Silva-Lugo, 2014) or moving underground (Quinn, 1979; Derrick *et al.*, 2010). These behaviors during fires generally mitigate direct mortality, but indirect effects of fire associated with reduced food resources immediately following fires (Morris *et al.*, 2011a) and increased predation risk due to lack of cover (Derrick *et al.*, 2010; Conner *et al.*, 2011; Morris *et al.*, 2011a; Morris *et al.*, 2011b) often reduce small mammal survival in the weeks following a fire. In contrast, pocket gophers rely mostly on fresh and cached belowground plant parts (*e.g.* roots, rhizomes, stolons, and tubers; Baker *et al.*, 2003) that remain largely unaffected by fires (Gates and Tanner, 1988; Parson *et al.*, 2010; Wohlgemuth *et al.*, 2018). As a result, pocket gophers tunnels provide both shelter during fires and belowground food sources that allow pocket gophers to forage without increased predation risk following fires.

The fossorial nature of southeastern pocket gophers allows them to exist in a more thermally stable environment than would be possible living aboveground, an important adaptation for living in fire-maintained communities (Means, 2006; Burda *et al.*, 2007). Southeastern pocket gophers are not exclusively found in longleaf pine, but are always associated with some sort of disturbance (e.g., prescribed fire or mowing; Duncan *et al.*, 2020). These tunnels and associated mounds are likely valuable to commensal species during aboveground temperature extremes. Many animals use pocket gopher tunnels and mounds (Vaughan, 1961; Funderburg and Lee, 1968; Skelley and Kovarik, 2001; Blihovde, 2006; Tishechkin and Cline, 2008) and several other animals retreat underground for protection from daily extremes or fires; tiger salamanders (*Ambystoma tigrinum*), six-lined racerunners (*Aspidoscelis sexlineata*), deer mice (*Peromyscus* spp.), voles (*Microtus* spp.), and Louisiana pine snakes (*Pituophis ruthveni*) use tunnels to avoid fire (Vaughan, 1961; Rudolph *et al.*, 1998). We documented several species of beetles (Coleoptera), crickets (Orthoptera), and herpetofauna in pocket gopher tunnels and mounds pre- and post-fire (J. T. Pynne, unpubl. data); therefore, benefits of pocket gophers on survival of numerous species within fire-adapted communities may be great. Future research should examine use of tunnels and mounds by commensal species during fire events to quantify pocket gopher contributions to animal communities within fire maintained systems (Hansell, 1993; Marcy *et al.*, 2013; Pike and Mitchell, 2013; Knapp *et al.*, 2018), determine how temperature fluctuates underground during summer extremes and post-fire when vegetation no longer filters solar radiation and soil heats up faster (Knapp, 1984), and investigate the relationships of thermal environments and foraging opportunities at different depths.

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