



Determining habitat requirements for the southeastern pocket gopher (*Geomys pinetis*) at multiple scales

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Pocket gophers provide vital ecosystem services; however, species like the southeastern pocket gopher (*Geomys pinetis*), endemic to the southeastern United States, are declining. Long-term conservation of this species requires greater understanding of its habitat characteristics. Our objective here was to determine habitat features associated with southeastern pocket gopher occurrence at the local (100 ha) and home-range (0.09 ha) scales. We assessed occurrence and carried out vegetation surveys at 177 sites across the species' range during the growing season (March–September) 2016–2017. At the local scale, we found a negative relationship between occurrence and groundcover height and a quadratic relationship with canopy closure. At the home-range scale, occurrence was positively related to grass groundcover and had a quadratic relationship with canopy closure. Restoration of southeastern pocket gopher habitat should focus on creating or maintaining areas with intermediate canopy (~45–55%) and an understory dominated by grasses and forbs.

Key words: canopy cover, conservation, ecosystem engineer, fossorial mammal, Geomyidae, habitat selection, herbaceous cover, multi-scale

Tunneling activities of fossorial ecosystem engineers disproportionately contribute to ecosystem structure and development (Huntly and Inouye 1988). In areas they inhabit, pocket gophers (Geomyidae) provide valuable ecological services (Jones et al. 1994; Reichman and Seabloom 2002), increasing soil aeration, water infiltration, and litter decomposition (Kalisz and Stone 1984; Forbis et al. 2004), and providing refugia for commensals (Cartwright 1939; Skelley and Gordon 2001; Blihovde 2006; Miller et al. 2012). Unfortunately, pocket gophers' low mobility and specialized nature makes them highly vulnerable to habitat fragmentation and degradation (Keinath et al. 2014; Duncan et al. 2020). Due to the suite of services they provide, maintaining and restoring populations of pocket gophers are an important part of ecosystem-level conservation and restoration.

The southeastern pocket gopher (*Geomys pinetis*) historically was associated with the longleaf pine (*Pinus palustris*) ecosystem that dominated the Coastal Plain of Alabama, Georgia, and Florida (Hickman and Brown 1973; Engstrom 1993; Van

Lear et al. 2005). Since European settlement, the longleaf pine ecosystem has experienced large-scale degradation and fragmentation, with only an estimated <3% of the original extent remaining (Landers et al. 1995; Van Lear et al. 2005; Oswalt et al. 2012). Concurrently, *G. pinetis* appears to be declining and is a species of conservation concern throughout its range (Ozier 2010; FWC 2012; ADCNR 2015). Within this region, restoration of the longleaf pine ecosystem has been a major conservation focus, including restoration of associated faunal species such as *G. pinetis*, which depend on the historical short fire return interval (1–3 years) essential for maintaining the herbaceous understories required by most of these species (FWC 2019; ADCNR 2015; GADNR 2015).

As with most species of conservation concern, understanding *G. pinetis* habitat preferences is critical for long-term restoration and management. A fundamental aspect of understanding habitat selection is the importance of assessing patterns across a range of scales (Johnson 1980; Weins 1989; McGarigal et al. 2016),

because an increasing number of multi- and broad scale studies suggest that factors driving species occurrence vary across scales (Pavlacky et al. 2012; Lipsey et al. 2017). From a conservation standpoint, a multi-scale approach is important because potential habitat management alternatives range from landscape-scale actions (e.g., maintaining connectivity among subpopulations) to fine-grain decisions (e.g., determining number and arrangement of residual trees left during forest harvest operations). Habitat selection studies also benefit from a multi-scaled approach because it may facilitate identification of limiting factors at one scale that are affecting processes at other scales (Mayor et al. 2009). Landscape-scale factors influencing *G. pinetis* occurrence were examined by Duncan et al. (2020) who determined that open canopies and areas of low urbanization were important predictors of occurrence. However, to understand drivers of larger-scale patterns and to effectively restore and maintain habitat in individual patches and properties, habitat selection needs to be understood at smaller scales as well.

The home-range scale is an important and standard focus for assessing habitat selection, as it encompasses conditions capable of supporting one or more individuals of the focal species and integrates outcomes of finer-scale foraging and security decisions (Johnson 1980). Selection at this scale has been evaluated intensively for *G. pinetis* only in two localized study areas within the range of the species (Warren et al. 2017a; Bennett et al. 2020). At finer scales, *G. pinetis* selected sandier soil and showed site-specific relationships with vegetation structure (Warren et al. 2017a; Bennett et al. 2020). However, with *G. pinetis* of conservation concern across its range, and given regional variation in factors such as climate, forest types, and land use (Duncan et al. 2020; Homer et al. 2020), a range-wide quantification of habitat at the home-range scale will strengthen understanding of habitat requirements. In addition, localized studies may encompass a relatively small portion of variation in conditions in which the species can occur, limiting our ability to detect factors that are important but relatively homogeneous within localized study areas (e.g., in a landscape dominated by suitable stand conditions in uplands; Warren et al. 2017a). Yet, management actions such as prescribed fires, timber harvest, and replanting are implemented at the scales of individual forest stands and collections of stands (Huang et al. 2018; Wheeler et al. 2020), scales much larger than the home-range size of *G. pinetis* (average 0.09 ha; Warren et al. 2017b). For taxa such as pocket gophers that have non-overlapping territories (Ford 1980; Reichman et al. 1982), maintaining a viable site-level population of a species depends on providing suitable conditions over an area larger than that of an individual home range. There is a consequent need to determine whether patterns at the home-range scale and larger landscape scales adequately guide operational management at these intermediate scales.

We assessed habitat selection by *G. pinetis* at two scales using data from the species' entire range. We examined the home range scale and a larger spatial scale that would be more suitable for land management decisions (hereafter, local scale) based on *G. pinetis* presence within a 1 km² plot. Because *G. pinetis* is

known to avoid areas with dense root systems (Ford 1980) and because other gopher species tend to choose areas of abundant herbaceous groundcover (Cox and Hunt 1992; Connior et al. 2010), we predicted that increases in structural complexity of understory (height of understory and amount of shrubs as groundcover) would decrease the likelihood of *G. pinetis* occurrence at the local scale, whereas increases in grasses and forbs and presence of suitable soils would increase the likelihood of *G. pinetis* occurrence at the home-range scale. We also examined a quadratic relationship between *G. pinetis* occupancy and canopy closure (avoidance of low or high canopy closure), because we expected *G. pinetis* occurrence to have a nonlinear relationship with canopy closure where occurrence would be highest at an intermediate range (Bennett et al. 2020).

MATERIALS AND METHODS

Study site selection.—We selected study sites within the historic range of *G. pinetis*, the Coastal Plain of Alabama, Georgia, and Florida, United States (Cassola 2016; Fig. 1); we first generated a 1-km² grid across the range using ArcMap 10.5 (ESRI 2015; Homer et al. 2015). We then randomly selected grid cells that contained ≥50% of land cover classes historically associated with *G. pinetis*, which included evergreen forests, mixed forests, shrub/scrub, grasslands/herbaceous, pasture/hay, and

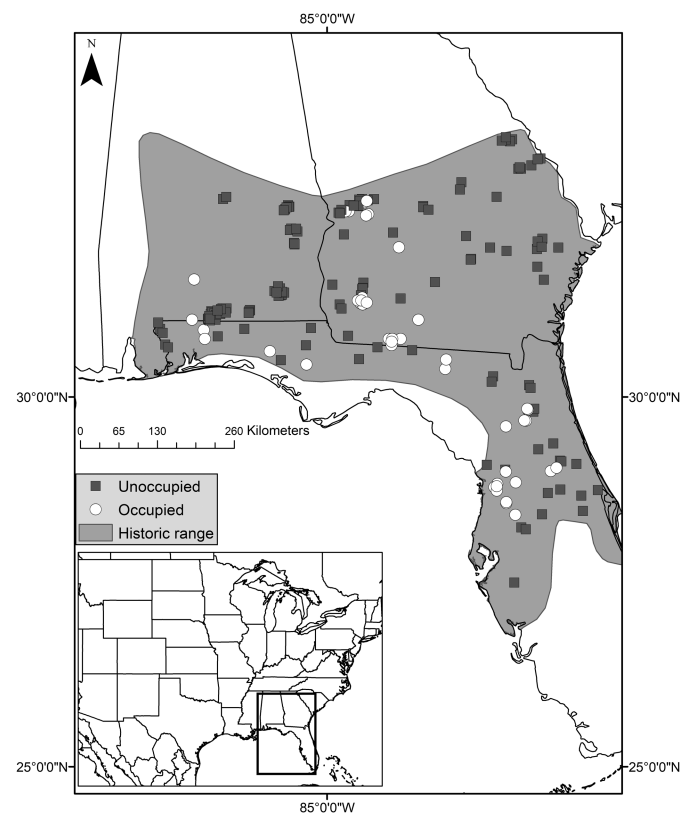


Fig. 1.—Locations of *G. pinetis* surveys in southeastern United States from 2016 to 2017 within historic range (gray). Dark gray squares indicate sites that were unoccupied at the time of survey; white circles were sites with *G. pinetis* mounds present at the time of survey.

cultivated crops (Avisé and Laerm 1982; Homer et al. 2015). In Georgia and Florida, we used the Create Random Points tool in ArcMap to place points in grid cells located on public (GADNR 2015; Florida Natural Areas Inventory 2016) and private lands. If the property could be accessed, the selected grid cells were added as a study site. In Alabama, we stratified selection of sites on public and private land. We first created the 1-km² grid and randomly selected grid cells on public lands (Conservation Biology Institute 2012). We repeated the process for sites on private land, but due to the need for landowner permission we ultimately chose sites as close as possible to the original randomly selected grid square. Following site selection, we created a 500 m square (2,000 m total length) transect inside the original 1-km² square as the survey path to avoid double sampling in case two squares were adjacent.

Transect surveys.—We carried out presence surveys of *G. pinetis* and measured habitat attributes within selected grids from March to September of 2016 and 2017. For each survey, two observers independently walked in opposite directions along the survey path searching for mounds of *G. pinetis* on either side of the transect (Harper 1912; Warren et al. 2017a, 2017b). Studies of pocket gopher occurrence generally focus on mounds as reliable indicators of presence (Connior et al. 2010; Duncan et al. 2020). Based on our experience in this region (Warren et al. 2017a, 2017b; Bennett et al. 2020; Duncan et al. 2020), mounds may be identifiable for up to several months rather than providing a snapshot of occurrence at the time of the survey. However, pocket gophers have relatively high adult survival, stable home ranges, and low dispersal capability, and occupancy status likely is static over the time scale of our study at local scales and even home-range scales (Bennett et al. 2020). Because one animal can create several mounds, we recorded the location at the center of mound clusters (Ford 1980). We defined a cluster as ≥ 3 mounds that were ≤ 5 m apart because *G. pinetis* are territorial and unlikely to have overlapping tunnel systems (Ford 1980; Reichman et al. 1982).

We recorded vegetation characteristics at each mound cluster encountered but not exceeding 10 clusters/grid. We measured canopy closure in each cardinal direction around the cluster center or plot using a spherical convex densiometer (Spherical Crown Densiometer, Forest Densiometers, Rapid City, SD; Baudry et al. 2014). We used a 1-m² frame to record percentage ground cover that was bare ground, leaf litter, woody vegetation, forbs, and grasses (Daubenmire 1959; USDA 1999). We recorded vertical vegetation cover in each cardinal direction, 4 m from the center of the mound cluster or subplot, using a 1.2-m tall Robel pole (Toledo et al. 2008). We measured basal areas of pines and hardwoods with a 10 Basal Area Factor prism (JIM-GEM Rectangular Prism, Forestry Suppliers, Jackson, MS; USDA 1999). We also measured the same vegetation characteristics every 200 m along the transects regardless of *G. pinetis* presence (hereafter, systematic plots).

Soil survey data.—We used gridded Soil Survey Geographic Database (gSSURGO) information for Alabama, Georgia, and Florida (Soil Survey Staff 2018a, 2018b, 2018c) to examine soil texture at surveyed grids. Because of the high number

of texture classes ($n = 26$), we reclassified texture classes as highly suitable, suitable, or unsuitable (Supplementary Data SD1; Warren et al. 2017a; Bennett et al. 2020). We overlaid each 1-km² survey grid on the soil polygons, and calculated area occupied by each soil texture class within each grid. Due to low spatial resolution of the gSSURGO data (30 m), we only calculated percentage of soil classes for the local scale.

Data analysis.—Before creating candidate models, we evaluated correlation among predictor variables using the *car* package in program R (Fox and Weisberg 2011; R Core Team 2018) and considered variables with a correlation coefficient $|r| \geq 0.70$ to be strongly correlated (Fox and Weisberg 2011). Canopy closure and total basal area were correlated ($r = 0.79$), we therefore omitted total basal area from subsequent modeling, because we believed that canopy closure potentially was more biologically important in that it directly influences growth of herbaceous groundcover (McGuire et al. 2001; McIntyre et al. 2019).

We carried out parallel analyses focusing first on occurrence at the local scale, then on occurrence at the home-range scale conditional on presence at the local scale. For each spatial scale, we evaluated a set of logistic models. We formed candidate models based on a priori predictions about whether occurrence was driven by food resources (measured as groundcover), understory structure, or canopy cover. The models were: CANOPY² (included percent canopy closure as a quadratic effect); FOOD (included percent groundcover of grasses and forbs); SOIL (included area of suitable soil); UNDERSTORY (included height [cm] of woody and herbaceous understory and percent shrubs as groundcover); CANOPY² + FOOD; CANOPY² + SOIL; UNDERSTORY + CANOPY²; FOOD + SOIL; FOOD + UNDERSTORY; SOIL + UNDERSTORY; and NULL (included the y-axis intercept and no additional parameters). Models did not include interactive effects.

We initially used an occupancy modeling approach to determine the number of false absences from surveys (MacKenzie et al. 2002). Due to high local-scale probability of detection (99.5%) at the local scale, we did not include a detection covariate in the models and proceeded with logistic regression. For the local scale, we averaged measured variables from the systematic plots at each site and modeled occurrence using logistic regression. We compared models using adjusted Akaike's Information Criterion for small sample sizes (AICc; Akaike 1973; Anderson and Burnham 2002). We considered models within 2 AICc units competing. We undertook all analyses in R (R Core Team 2018). We considered a variable informative if the 95% confidence interval (CI) did not cross zero. We evaluated model fit using the concordance statistic (c-statistic; Austin and Steyerberg 2012).

Following Johnson (1980), we limited home-range scale analyses to occupied sites. We used logistic regression with a random site effect to examine factors discriminating occupied clusters from unoccupied systematic plots within occupied sites using package lme4 in program R. Focusing on the same predictions as local scale analysis, we compared top models using AICc (Anderson and Burnham 2002). Following the same

procedures as the local scale analysis, we considered models within 2 AICc units competing. We considered a variable informative if the 95% CI did not cross zero.

RESULTS

We surveyed 177 sites across Alabama ($n = 56$), Georgia ($n = 70$), and Florida ($n = 51$). We detected *G. pinetis* at 38 (21.5%) sites, with Alabama having two (3.6%) sites occupied, Georgia having 17 (24.3%) sites occupied, and Florida having 19 (37.3%) sites occupied (Fig. 1).

Local scale.—The top model explaining *G. pinetis* occurrence was UNDERSTORY + CANOPY² which included effects of understory structure and quadratic effect of tree canopy (Table 1). The model indicated a negative relationship between *G. pinetis* occurrence and increasing height of vegetation in the understory ($\beta = -0.07$, $SE \pm 0.02$) (Fig. 2A) but not amount (%) of shrubs as groundcover ($\beta = 0.004$, $SE \pm 0.02$; Fig. 2B). Occupied sites occurred over a range of canopy closure (Table 2), but the greatest probability of occurrence was at ~48% closure (Fig. 2C). The concordance

Table 1.—Model selection results for variables related to *G. pinetis* occurrence at the local (100 ha) scale in Alabama, Florida, and Georgia, United States.

Model	Parameters	AICc	Δ AICc	w_i
UNDERSTORY + CANOPY ²	5	165.8	0	0.6
UNDERSTORY	3	167.6	1.8	0.2
UNDERSTORY + FOOD	5	169.6	3.9	0.1
UNDERSTORY + SOIL	4	169.7	3.9	0.1
CANOPY ²	3	178.3	12.5	1.0e ⁻³
SOIL + CANOPY ²	4	179.2	13.2	7.2e ⁻⁴
FOOD + CANOPY ²	5	181.3	15.5	2.6e ⁻⁴
NULL	1	186.1	20.4	2.3e ⁻⁵
SOIL	2	186.2	20.5	2.1e ⁻⁵
FOOD	3	187.1	21.3	1.4e ⁻⁵
FOOD + SOIL	4	188.1	22.3	8.5e ⁻⁶

statistic indicated good predictive ability of the top model ($C = 0.767$) (Austin and Steyerberg 2012).

Home-range scale.—We surveyed 675 plots within the 38 occupied sites. These plots contained both *G. pinetis* clusters and systematic plots along survey transects (occupied plots $n = 296$; unoccupied plots $n = 379$). At occupied sites, we measured an average of eight mound clusters (median = 10.0, $SD = 3.1$); 24 sites had more than 10 clusters observed (max: 96), with only the first 10 clusters being measured (Table 4).

The top model for home-range scale was FOOD + CANOPY² which included groundcover of grasses and forbs and a quadratic effect of canopy cover (AICc weight = 0.68) (Table 3; Fig. 3). There was a positive relationship between the percent of grasses and occurrence of *G. pinetis* ($\beta = 0.013$, $SE \pm 0.003$; Fig. 3A) but no conclusive relationship with amount of forbs in the groundcover ($\beta = -0.003$, $SE \pm 0.006$; Fig. 3B). As at the local scale, the highest probability of occurrence was at an intermediate level of canopy closure (~48%; Fig. 3C).

DISCUSSION

We expected that occurrence of *G. pinetis* across its range would be associated with variables related to soil texture, food resources, understory woody structure, and canopy cover. Our general expectations regarding vegetation structure were supported, because occurrence was most strongly related to canopy cover and understory structure at the local scale and to canopy cover and herbaceous groundcover at the home-range scale. Our local scale results indicated that likelihood of occurrence of *G. pinetis* decreased with increasing understory structural complexity, supporting our prediction that *G. pinetis* is associated with areas of sparse woody understory. Areas with complex woody understory may be avoided because it is energetically more expensive for *G. pinetis* to create tunnel systems through dense root systems (Hickman and Brown 1973; Ford 1980; Vleck 1981). Consistent with Bennett et al. (2020),

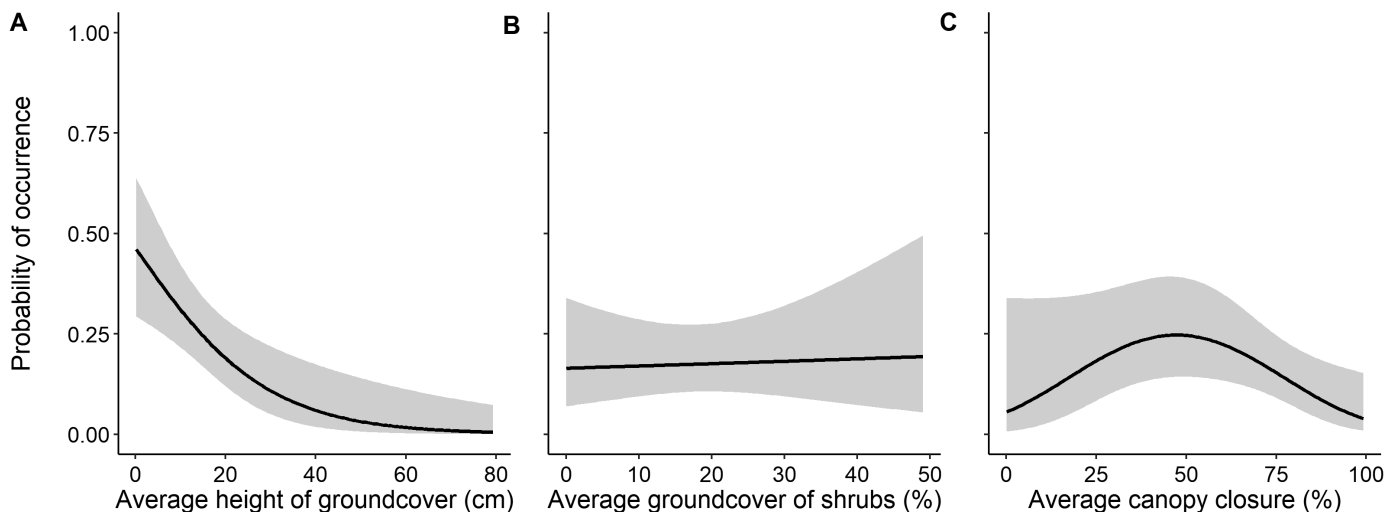


Fig. 2.—Relationship between groundcover height (cm), groundcover of shrubs (%), and average canopy closure (%) and the probability of *G. pinetis* occurrence at the local scale for sites (100 ha) surveyed in Alabama, Georgia, and Florida, United States from 2016 to 2017 (the bands represent the 95% confidence envelopes).

we observed a quadratic effect of canopy cover at both scales. Shading provided by intermediate canopy may moderate soil temperatures and slow loss of soil moisture that is necessary to maintain tunnel structure while allowing enough light for understory plant growth (Hickman and Brown 1973; Ross 1980).

Superficially, our results may suggest differential importance of woody structure at the local scale and herbaceous food resources at the home-range scale. However, these attributes

Table 2.—Mean (95% confidence limits) for local scale (100 ha) vegetation variables across all 177 sites sampled for presence of *G. pinetis* in Alabama, Georgia, and Florida, United States, 2016–2017. Occupied sites had *G. pinetis* mound clusters present; unoccupied sites had no *G. pinetis* mound clusters detected during surveys.

Variable	Occupied ($n = 38$ sites)	Unoccupied ($n = 139$ sites)
Canopy closure (%)	58.6 (52.2, 65.1)	67.0 (63.0, 70.9)
Vertical height (cm)	11.0 (7.6, 14.4)	24.6 (21.4, 27.8)
Bare/sand (%)	19.8 (14.7, 24.8)	11.7 (9.8, 13.6)
Litter (%)	32.1 (25.7, 38.4)	40.4 (37.3, 43.6)
Grasses (%)	20.1 (15.6, 24.6)	16.7 (14.8, 18.6)
Forbs (%)	8.2 (6.0, 10.5)	9.4 (8.2, 10.6)
Shrubs/woody (%)	13.0 (8.7, 17.4)	17.7 (15.9, 19.4)
Pine BA (m ² /ha)	6.8 (5.5, 8.2)	8.4 (7.5, 9.3)
Hardwood BA (m ² /ha)	3.4 (2.4, 4.3)	5.9 (5.0, 6.8)

Table 3.—Model selection results for variables related to *G. pinetis* occurrence at the home-range (0.09 ha) in Alabama, Georgia, and Florida, United States.

Model	Parameters	AICc	Δ AICc	w_i
FOOD + CANOPY ²	6	898.7	0.0	0.7
UNDERSTORY + FOOD	6	901.1	2.3	0.2
UNDERSTORY + CANOPY ²	6	902.7	4.0	0.1
FOOD	4	908.6	9.9	5.0e ⁻³
CANOPY ²	4	914.1	15.4	3.1e ⁻⁴
UNDERSTORY	4	919.1	20.3	2.6e ⁻⁵
NULL	2	929.5	30.8	1.4e ⁻⁷

are closely related; as cover of shrubs and saplings increases, cover of grasses and forbs decreases due to shading (Brockway and Lewis 1997; Outcalt and Brockway 2010). Thus, we interpret our results as indicating that occurrence at both scales is driven by the combined and interrelated requirements for open-canopied sites with well-developed herbaceous understories and low woody structural complexity. In the southeastern US, frequency and seasonality of fire are known to be the most important factors driving the restoration and maintenance of such understory conditions (Drewa et al. 2002; Glitzenstein et al. 2003; Outcalt and Brockway 2010), which also are critical for the persistence of a suite of other species of conservation concern (e.g. gopher tortoise—*Gopherus polyphemus*—Ashton et al. 2008; Red-cockaded Woodpecker—*Picoides borealis*—Stephens et al. 2019). Within our study region, open sites that are not managed consistently on a short (1–3 years) prescribed fire interval rapidly develop shrub and sapling cover, reducing the density and diversity of grasses and forbs (Drewa et al. 2002; Glitzenstein et al. 2003; Outcalt and Brockway 2010).

Our study evaluated sites across the range of *G. pinetis*, and with this and other works (Duncan et al. 2020), collectively examined a range of scales. We observed generally similar patterns of association between occupancy and vegetation structure as have been documented in past localized studies (Warren et al. 2017a; Bennett et al. 2020). The range-wide and multi-scale consistency of patterns is not surprising given that *G. pinetis* is a highly specialized mammal with low mobility (Hickman and Brown 1973). Traditional development of multi-scale selection theory and many current multi-scale studies have tended to focus on birds (Harryman et al. 2019) or highly mobile species such as large carnivores (Dellinger et al. 2020) capable of extensive movements to access different resources seasonally and over their lifespan. For such species, a top-down hierarchical framework of habitat selection can be especially relevant because different resources may be selected at different scales and times, and large-scale

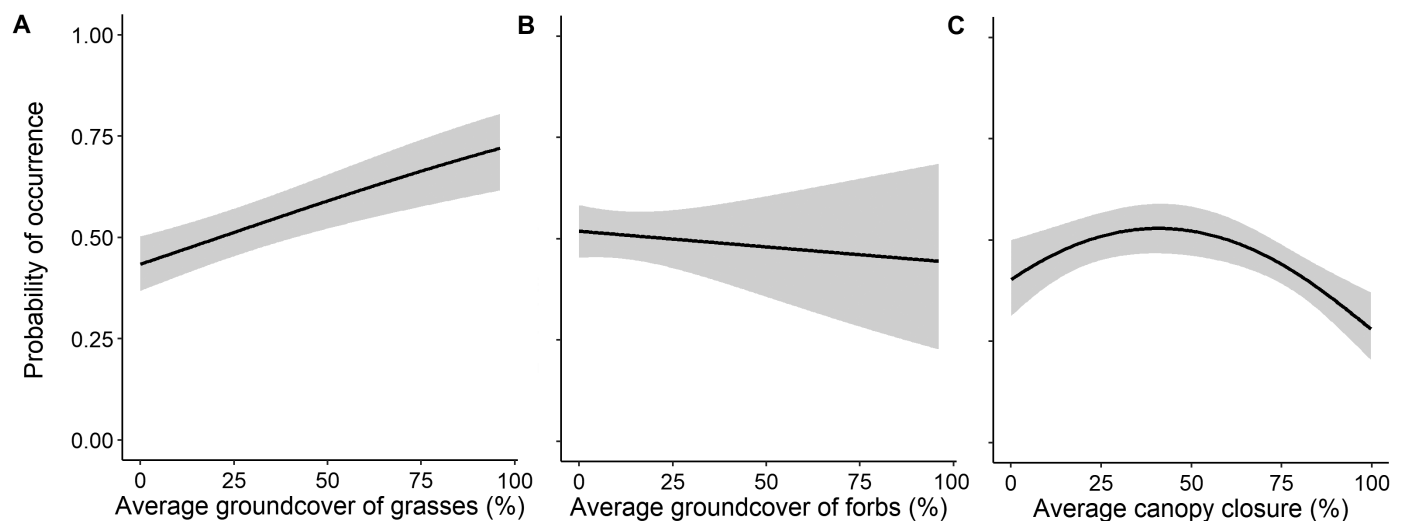


Fig. 3.—Relationship between groundcover of grasses (%), groundcover of forbs (%), and average canopy closure (%) and the probability of *G. pinetis* occurrence at the home-range scale (0.09 ha) from plots surveyed in Alabama, Georgia, and Florida, United States from 2016 to 2017 (the bands represent the 95% confidence envelopes).

Table 4.—Mean (95% confidence limits) for home-range scale vegetation variables across all 38 occupied sites sampled for presence of *G. pinetis* in Alabama, Georgia, and Florida, United States, from 2016 to 2017. Plots with mound clusters were occupied by *G. pinetis*; unoccupied plots without clusters were systematic plots along survey transects.

Variable	Occupied ($n = 296$ plots)	Unoccupied ($n = 379$ plots)
Canopy closure (%)	51.6 (48.1, 55.1)	58.7 (55.4, 62.0)
Vertical height (cm)	7.5 (6.4, 8.6)	10.9 (9.3, 12.6)
Bare/sand (%)	20.5 (17.6, 23.4)	19.6 (16.8, 22.4)
Litter (%)	23.0 (19.5, 26.4)	32.0 (28.5, 35.5)
Grasses (%)	31.0 (27.5, 34.5)	20.1 (17.5, 22.7)
Forbs (%)	8.0 (6.5, 9.6)	8.2 (6.8, 9.7)
Shrubs/woody (%)	7.9 (6.2, 9.6)	13.0 (10.6, 15.3)
Pine BA (m ² /ha)	7.4 (6.7, 8.2)	6.9 (6.1, 7.6)
Hardwood BA (m ² /ha)	1.9 (1.5, 2.3)	3.4 (2.9, 3.9)

selection may constrain habitat associates at smaller scales (Johnson 1980; Wiens 1989). However, pocket gophers have small, stable home ranges and a consistent requirement for sandy soils and herbaceous food sources (this study; Warren et al. 2017a, 2017b; Bennett et al. 2020). Movements beyond their established tunnel system are costly due to the extreme energetic expense of burrowing (Vleck 1981), and risk of predation during above-ground movements such as overland dispersal (Connior and Risch 2010; Warren et al. 2017b; Pynne et al. 2019). For pocket gophers, a “bottom-up” view of habitat selection (Mayor et al. 2009) appears more relevant, with conditions needed to support home-range establishment and development of a tunnel system also reflected in larger-scale patterns of occurrence (Duncan et al. 2020).

Although our results generally are consistent with those from localized studies, our results included several noteworthy findings. Counter to our prediction, we did not detect an association at the home-range scale between forbs and presence of *G. pinetis*. For other gopher species, forbs are the preferred food resource even when abundance of grasses is high (Connior et al. 2010; Rezsutek and Cameron 2011). Moreover, we frequently observed forbs cached in tunnel systems during livetrapping efforts on a subset of our sites. We therefore, suggest that a fuller evaluation of the potential importance of forbs may require finer-scale samples of forage-species preferences and diet. In addition, as claw-diggers, *Geomys* are tied to sandy or sandy loam soils (Lessa and Thaler 1989), and studies that incorporated intensive soil sampling found that soil characteristics are strong predictors of *G. pinetis* occurrence (Warren et al. 2017a; Bennett 2020). However, we found a lack of association at local- and range-wide scales that may be indicative of low variation in the 30-m resolution SSURGO data (Duncan et al. 2020).

Our results, in combination with those of Duncan et al. (2020), suggest a complementary hierarchy of management and restoration priorities for *G. pinetis*. At the broadest scales, management activities should concentrate on measures to prevent fragmentation and slow the process of urbanization into open-canopy forests throughout the region (Duncan et al.

2020). At finer spatial scales and within areas of suitable soil, we should ensure forest stands are managed to provide suitable understories, generally requiring measures to stop woody encroachment such as short burn rotations (1–3 years) that facilitate a diversity of herbaceous understory vegetation.

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CONFLICT OF INTEREST

None declared.

SUPPLEMENTARY DATA

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

Supplementary Data SD1.—Reclassified soil suitability categories based on gSSURGO texture classes for *G. pinetis* occurrence in Alabama, Georgia, and Florida.

Supplementary Data SD2.—Variable names and description of parameters examined to determine *G. pinetis* occurrence for local and home-range scale models in Alabama, Georgia, and Florida, 2016 and 2017.

LITERATURE CITED

- Akaike H. 1973. Information theory and an extension of the maximum likelihood principle. In: Petrov BN, Csaki F, editors. 2nd International symposium on information theory. Akadémiai Kiadó, Budapest, Hungary; p. 267–281.
- Alabama Department of Conservation and Natural Resources [ADCNR]. 2015. Alabama’s wildlife action plan. Alabama Department of Conservation and Natural Resources Division of Wildlife and Freshwater Fisheries, Montgomery, AL.
- Anderson D.R., Burnham K.P. 2002. Avoiding pitfalls when using information-theoretic methods. *Journal of Wildlife Management* 66:912–918.
- Ashton K.G., Engelhardt B.M., Branciforte B.S. 2008. Gopher tortoise (*Gopherus polyphemus*) abundance and distribution after prescribed fire reintroduction to Florida scrub and sandhill at Archbold Biological Station. *Journal of Herpetology* 3:523–529.
- Austin P.C., Steyerberg E.W. 2012. Interpreting the concordance statistic of a logistic regression model: relation to the variance and

- odds ratio of a continuous explanatory variable. *BMC Medical Research Methodology* 12:82.
- Awise J.C., Laerm J. 1982. Gophers of the southeastern United States. *Florida Naturalist* 55:7–10.
- Baudry O., Charmetant C., Collet C., Ponette Q. 2014. Estimating light climate in forest with the convex densiometer: operator effect, geometry and relation to diffuse light. *European Journal of Forest Research* 133:101–110.
- Bennett M.E., Gitzen R.A., Conner L.M., Smith M.D., Soehren E.C., Castleberry S.B. 2020. Interactions of soil and vegetation determine habitat for southeastern pocket gopher (*Geomys pinetis*). *American Midland Naturalist* 184:205–221.
- Blihovde W.B. 2006. Terrestrial movements and upland habitat use of gopher frogs in central Florida. *Southeastern Naturalist* 5:265–276.
- Brockway D.G., Lewis C.E. 1997. Long-term effects of dormant-season prescribed fire on plant community, structure and productivity in a longleaf pine wiregrass ecosystem. *Forest Ecology and Management* 96:167–183.
- Cartwright O.L. 1939. Eleven new American Coleoptera (Scarabaeidae, Cicindelidae). *Annals of the Entomological Society of America*. 32:353–364.
- Cassola F. 2016. *Geomys pinetis*. The IUCN Red List of Threatened Species. Version 2018-1. <https://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T42589A22218215.en>. Accessed 2016 May 20.
- Connior M.B., Kershen A.A., Medlin R.E., Elrod D.A., Sasse D.B., Risch T.S. 2010. Distribution and habitat attributes of an endemic subspecies of pocket gopher. *American Midland Naturalist* 164:217–229.
- Connior M.B., Risch T.S. 2010. Home range and survival of the Ozark pocket gopher (*Geomys bursarius ozarkensis*) in Arkansas. *American Midland Naturalist*. 164:80–90.
- Conservation Biology Institute. 2012. Protected areas Alabama. <https://databasin.org/datasets/d56650767b6d48ca82cfc5f6c7006f89>. Accessed 2016 Jan 10.
- Cox G.W., Hunt J. 1992. Relation of seasonal activity patterns of valley pocket gophers to temperature, rainfall, and food availability. *Journal of Mammalogy* 73:123–134.
- Daubenmire R.A. 1959. Canopy coverage method of vegetation analysis. *Northwest Science* 33:43–64.
- Dellinger J.A., Cristescu B., Ewanyk J., Gammons, D.J., Garcelon D., Johnston P., Martins Q., Thompson C., Vickers T.W., Wilmers C.C., et al. 2020. Using mountain lion habitat selection in management. *The Journal of Wildlife Management* 84:359–371.
- Drewa P.B., Platt W.J., Moser E.B. 2002. Fire effects on resprouting of shrubs in headwaters of southeastern longleaf pine savannas. *Ecology* 83:755–767.
- Duncan S.I., Pynne J.T., Parsons E.I., Fletcher R.J., Austin J.D., Castleberry S.B., Conner L.M., Gitzen R.A., Barbour M., McCleery R.A. 2020. Land use and cover effects on an ecosystem engineer. *Forest Ecology and Management* 456:117642.
- Engstrom R.T. 1993. Characteristic mammals and birds of longleaf pine forests. *Proceedings of the Tall Timbers Fire Ecology Conference* 18:127–138.
- ESRI. 2015. ArcMap GIS. Version 10.3.1. Environmental System Research Institute, Redlands, CA.
- Florida Natural Areas Inventory. 2016. Florida conservation lands. <http://fnai.org/gisdata.cfm>. Accessed 2016 Jan 15.
- Forbis T.A., Larmore J., Addis E. 2004. Temporal patterns in seedling establishment on pocket gopher disturbances. *Oecologia* 138:112–121.
- Ford C.R. 1980. The status and preservation of the colonial pocket gopher. Master's thesis, University of Georgia, Athens, Georgia.
- Fox J., Weisberg S. 2011. An R companion to applied regression. 2nd ed. Sage Publications, Thousand Oaks, CA.
- Florida Fish and Wildlife Conservation Commission [FWC]. 2012. Pocket gopher: *Geomys pinetis*. <https://myfwc.com/wildlifehabitats/profiles/mammals/land/pocket-gopher/>. Accessed 2016 November 6.
- Florida Fish and Wildlife Conservation Commission [FWC]. 2019. Florida's Wildlife Legacy Initiative: Florida's State Wildlife Action Plan. Florida Fish and Wildlife Commission, Tallahassee, Florida.
- Georgia Department of Natural Resources [GADNR]. 2015. Georgia state wildlife action plan. Georgia Department of Natural Resources. https://georgiawildlife.com/sites/default/files/wrd/pdf/swap/SWAP2015MainReport_92015.pdf. Accessed 2016 Nov 6.
- Glitzenstein J.S., Streg D.R., Wade D.D. 2003. Fire frequency effects on longleaf pine (*Pinus palustris* P. Miller) vegetation in South Carolina and northeast Florida, USA. *Natural Areas Journal* 23:22–37.
- Harper R.M. 1912. NOTES on the distribution of the Southeastern Salamanders (*Geomys tuza* and Allies). *Science* (New York, NY) 35:115–119.
- Harryman S.W.H., Grishman B.A., Boal C.W., Kahl S.S., Martin R.L., Hagen C.A. 2019. Multiscale habitat selection of lesser prairie-chickens in a row-crop and conservation reserve program land matrix. *Journal of Fish and Wildlife Management* 10:126–136.
- Hickman G.C., Brown L.N. 1973. Mound-building behavior of the southeastern pocket gopher (*Geomys pinetis*). *Journal of Mammalogy* 54:786–790.
- Homer C., Dewitz J., Jin S., Xian G., Costello C., Danielson P., Gass L., Funk M., Wickman J., Stehman S., et al. 2020. Conterminous United States land cover change patterns 2001–2016 from the 2016 National Land Cover Database. *ISPRS Journal of Photogrammetry and Remote Sensing* 162:184–199.
- Homer C., Dewitz J., Yang L., Jin S., Danielson P., Xian G., Coulston J., Herold N., Wickman J., Megown K. 2015. Completion of the 2011 national land cover database for the conterminous United States – representing a decade of land cover change information. *ISPRS Journal of Photogrammetric Engineering and Remote Sensing* 81:345–354.
- Huang R., Zhang X., Chan D., Kondragunta S., Russell A.G., Odman M.T. 2018. Burned area comparisons between prescribed burning permits in southeastern United States and two satellite-derived products. *Journal of Geophysical Research: Atmospheres* 123:4746–4757.
- Huntly N., Inouye R. 1988. Pocket gophers in ecosystems: patterns and mechanisms. *BioScience* 38:786–793.
- Johnson D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- Jones C.G., Lawton J.H., Shachak M. 1994. Organisms as ecosystem engineers. *Oikos* 63:373–386.
- Kalisz P.J., Stone E.L. 1984. Soil mixing by scarab beetles and pocket gophers in north-central Florida. *Soil Science Society of America Journal* 48:169–172.
- Keinath D.A., Griscom H.R., Andersen M.D. 2014. Habitat and distribution of the Wyoming pocket gopher (*Thomomys clusius*). *Journal of Mammalogy* 95:803–813.
- Landers J.L., Van Lear D.H., Boyer W.D. 1995. The longleaf pine forests of the southeast: requiem or renaissance? *Journal of Forestry* 93:39–44.

- Lessa E.P., Thaler Jr. C.S. 1989. A reassessment of morphological specializations for digging in pocket gophers. *Journal of Mammalogy* 70:689–700.
- Lipsey M.K., Naugle D.E., Nowak J., Lukacs P.M. 2017. Extending utility of hierarchical models to multi-scale habitat selection. *Diversity and Distributions* 23:783–793.
- MacKenzie D.I., Nichols J.D., Lachman G.B., Droege S., Royle J.A., Langtimm C.A. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83:2248–2255.
- Mayor S.J., Schneider D.C., Schaefer J.A., Mahoney S.P. 2009. Habitat selection at multiple scales. *Ecoscience*. 16:238–247.
- McGarigal K., Zeller K.A., Cushman S.A. 2016. Multi-scale habitat selection modeling: introduction to the special issue. *Landscape Ecology* 31:1157–1160.
- McGuire J.P., Mitchell R.J., Moser E.B., Pecot S.D., Gjerstad D.H., Hedman G.W. 2001. Gaps in a gappy forest: plant resources, longleaf pine regeneration, and understory response to tree removal in longleaf pine savannahs. *Canadian Journal of Forest Research* 31:765–778.
- McIntyre K., Conner L.M., Jack S., Schlimm E., Smith L. 2019. Wildlife habitat condition in open pine woodlands: field data to refine management targets. *Forest Ecology and Management* 437:282–294.
- Miller G.J., Smith L.L., Johnson S.A., Franz R. 2012. Home range size and habitat selection in the Florida pine snake (*Pituophis melanoleucus mugitus*). *Copeia* 4:706–713.
- Oswalt C.M., Cooper J.A., Brockway D.G., Brooks H.W., Walker J.L., Connor K.F., Oswalt S.N., Conner R.C. 2012. History and current condition of longleaf pine in the Southeastern United States. General Technical Report SRS–166:1–51. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, North Carolina.
- Outcalt K.W., Brockway D.G. 2010. Structure and composition changes following restoration treatments of longleaf pine forests on the Gulf Coastal Plain of Alabama. *Forest Ecology and Management* 259:1615–1623.
- Ozier J. 2010. Species account: southeastern pocket gophers. https://gakrakov.github.io/profiles/geomys_pinetis.pdf. Accessed 2016 Dec 4.
- Pavlack Jr. D.C., Blakesley J.A., White G.C., Hanni D.J., Lukacs P.M. 2012. Hierarchical multi-scale occupancy estimation for monitoring wildlife populations. *The Journal of Wildlife Management* 76:154–162.
- Pyne J.T., Castleberry S.B., Conner L.M., Parsons E.I., Gitzen R.A., Austin J.D., Duncan S.L., McCleery R.A. 2019. Timber rattlesnake (*Crotalus horridus*) predation on a southeastern pocket gopher (*Geomys pinetis*). *Southeastern Naturalist* 18:34–36.
- R Development Core Team. 2018. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. www.R-project.org/.
- Reichman O.J., Seabloom E.W. 2002. The role of pocket gophers as subterranean ecosystem engineers. *Trends in Ecology & Evolution* 17:44–49.
- Reichman O.J., Whitman T.G., Ruffner G.A. 1982. Adaptive geometry of burrow spacing in two pocket gopher populations. *Ecology* 63:687–695.
- Rezsutek M.J., Cameron G.N. 2011. Diet selection and plant nutritional quality in Attwater's pocket gopher (*Geomys attwateri*). *Mammalian Biology* 76:428–435.
- Ross J.P. 1980. Seasonal variation of thermoregulations in the Florida pocket gopher, *Geomys pinetis*. *Comparative Biochemistry and Physiology* 66A:119–125.
- Skelley P.E., Gordon R.D. 2001. Scarab beetles from pocket gopher burrows in the southeastern United States (Coleoptera: Scarabaeidae). *Insecta Mundi* 15:77–93.
- Soil Survey Staff. 2018a. Gridded Soil Survey Geographic (gSSURGO) Database for Alabama. United States Department of Agriculture, Natural Resource Conservation Service. https://www.nrcs.usda.gov/wps/portal/nrcs/detail/soils/survey/geo/?cid=nrcs142p2_053628. Accessed 2018 Aug 9.
- Soil Survey Staff. 2018b. Gridded Soil Survey Geographic (gSSURGO) Database for Georgia. United States Department of Agriculture, Natural Resource Conservation Service. https://www.nrcs.usda.gov/wps/portal/nrcs/detail/ga/soils/?cid=nrcs142p2_053628. Accessed 2018 Aug 9.
- Soil Survey Staff. 2018c. Gridded Soil Survey Geographic (gSSURGO) Database for Florida. United States Department of Agriculture, Natural Resource Conservation Service. https://www.nrcs.usda.gov/wps/portal/nrcs/detail/soils/survey/geo/?cid=nrcs142p2_053628. Accessed 2018 Aug 9.
- Stephens S.L., Kobziar L.N., Collins B.M., Davis R., Fulé P.Z., Gaines W., Ganey J., Guldin J.M., Hessburg P.F., Hiers K., et al. 2019. Is fire “for the birds”? How two rare species influence fire management across the US. *Frontiers in Ecology and the Environment*. 17:391–399.
- Toledo D., Abbott L.B., Herrick J.E. 2008. Cover pole design for easy transport, assembly, and field use. *Journal of Wildlife Management*. 72:564–567.
- United States Department of Agriculture [USDA]. 1999. Sampling vegetation attributes: interagency technical reference. https://www.nrcs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb1044175.pdf. Accessed 2016 Dec 4.
- Van Lear D.H., Carroll W.D., Kapeluck P.R., Johnson R. 2005. History and restoration of the longleaf pine-grassland ecosystem: implications for species at risk. *Forest Ecology and Management* 211:150–165.
- Vleck D. 1981. Burrow structure and foraging costs in the fossorial rodent, *Thomomys bottae*. *Oecologia* 49:391–396.
- Warren A.E., Castleberry S.B., Markewitz D., Conner L.M. 2017a. Understory vegetation structure and soil characteristics of *Geomys pinetis* (southeastern pocket gopher) habitat in southwestern Georgia. *The American Midland Naturalist* 178:215–225.
- Warren A.E., Conner L.M., Castleberry S.B., Markewitz D. 2017b. Home range, survival, and activity patterns of the southeastern pocket gopher: implications for translocation. *Journal of Fish and Wildlife Management* 8:544–557.
- Wheeler E.A., Gulsby W.D., Kush J.S., Gitzen R.A. 2020. Effects of longleaf pine planting density and other factors on stand structure and associated wildlife habitat. *Restoration Ecology* 28:594–602.
- Wiens J.A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385–397.

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