Patterns of Prairie Soil Preference and Occupancy for the Threatened Mazama Pocket Gopher in Washington

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Abstract

Mazama pocket gophers *Thomomys mazama* act as ecosystem engineers and are keystone species on the remnant glacial prairies of the southern Puget Sound lowlands. Three subspecies of Mazama pocket gophers are regionally endemic to Thurston County, Washington, and were federally listed as threatened in 2014. We examined patterns of occupancy and habitat, and differences among subspecies for soil type preference. In total, 1,241 Mazama pocket gopher screening surveys, comprising approximately 4,654 hectares, resulted in 165 occupancy parcels. Pocket gophers were detected more often on parcels with more preferred soils than on less preferred soils, though there were differences in occupancy rates among subspecies. Soil type and availability can act as surrogates of gopher habitat availability. Such quantification of habitat availability and potential loss is important given the absence of population estimates. Therefore, the conservation of undeveloped lands with soils identified a priori as preferred is necessary for both the recovery and continued persistence of Mazama pocket gophers.

Keywords: Mazama pocket gopher, soil preference, occupancy

Introduction

Pocket gophers (family Geomyidae) are fossorial mammals that engage in extensive underground burrowing (Sherrod et al. 2005, Jones et al. 2008, Zaitlin and Hayashi 2012, Stinson 2020). As a result, they perform important ecological roles in soil aeration as well as distribution and succession of plant species (Andersen and MacMahon 1985, Inouye et al. 1997, Reichman and Seabloom 2002). Pocket gophers can bring up to 6.5 tons of soil per acre per year to the surface (Ellison 1946, Grant et al. 1980), which can increase biodiversity at the landscape scale by altering the availability of nutrients (Litaor et al. 1996, Zaitlin and Hayashi 2012), rates of soil development, and microtopography (Huntly and Inouye 1988, Martinsen et al. 1990). This can affect the demography and abundance of plant species, thereby affecting the behavior, abundance, and diversity of local animal consumers within grassland communities (Huntly and Inouye 1988, Jones et al. 2008). In addition, abandoned gopher burrows are often used by other animal species (Kovarik et al. 2008, Stinson 2020), gopher food caches and latrines enrich soil chemistry (Witmer et al. 1996, Stinson 2020), and pocket gophers are important prey species for many predators. For these reasons, pocket gophers are considered both ecosystem engineers and keystone species (Litaor et al. 1996, Witmer et al. 1996, Verts and Carraway 2000, Reichman and Seabloom 2002, Sherrod et al. 2005, Kovarik et al. 2008). Therefore, the preservation of gopher species has disproportionately beneficial effects on biodiversity and ecosystem function.

For pocket gophers, burrowing can require 360–3,400 times as much energy as moving the same distance across the surface, depending on soil type (Vleck 1979, 1981). The high energy cost of burrowing suggests that energy conservation may be particularly important for pocket gophers. Mazama pocket gophers, *Thomomys mazama,* prefer certain soil types within the post-glacial outwash soils found within Thurston County, Washington. Soil rockiness and drainage, forage

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plant quality and availability, vegetation cover, and seasonal climate are all factors influencing Mazama pocket gopher distribution. Preferred soils are well-drained, have a deep organic layer, are nutrient rich and support the growth of the forbs Mazama pocket gophers prefer to eat, and allow for burrowing at lower energetic cost (Vleck 1979, Luna and Antinuchi 2006). In contrast, soils that are hard, wet, sticky, contain large rocks, or are high in clay or very sandy are energetically more costly to move through or do not facilitate burrow formation. Therefore, pocket gophers do not prefer them as a tunneling route for foraging (Kelt and Van Vuren 1999). In addition, areas with dense forest or woody shrub cover (e.g., Scot's broom, *Cystisus scoparius*), impervious surfaces, slopes in excess of 40%, and areas of standing water are also avoided by Mazama pocket gophers (Olson 2011, Duncan et al. 2020, Stinson 2020). Soil characteristics influence pocket gopher distribution more than grassland vegetation type and forage availability, as long as the species of plants that Mazama pocket gophers prefer are present (Stinson 2020).

Three of the subspecies of Mazama pocket gophers are regionally endemic to Thurston County, Washington, and include the Olympia pocket gopher *Thomomys mazama pugetensis*, the Tenino pocket gopher *T. m. tumuli*, and the Yelm pocket gopher *T. m. yelmensis* (Verts and Carraway 2000, Figure 1). These three subspecies were federally listed by the US Fish and Wildlife Service (USFWS) as threatened in April 2014 under the Endangered Species Act of 1973 (USFWS 1973, 2012, 2014b). The Washington Department of Fish and Wildlife listed all Mazama pocket gophers in Washington as threatened in 2006, although they stated Tacoma (*T. m. tacomensi)* and Cathlamet (*T. m. louiei)* pocket gopher subspecies appear to be extinct (Stinson 2020). While other subspecies of Mazama pocket gopher occur in Washington those other subspecies do not occur in Thurston County.

Factors leading to the federal and state listing of the three Thurston County subspecies included conversion and degradation of available habitat due to agricultural, residential, and commercial development, and woody encroachment of native

Figure 1. The Yelm subspecies of Mazama pocket gopher (*Thomomys mazama yelmensis*). (Photo by S. Nelson)

and nonnative plant species as a result of succession and fire suppression. Military training, disease, predation, and inadequate existing regulatory mechanisms to curtail habitat loss were also factors. Additional stressors include low genetic diversity, small and isolated populations, low reproductive success, and control as a pest species (Steinberg and Heller 1997; USFWS 2014b, 2022b; Warheit and Whitcomb 2016). Furthermore, pocket gophers are naturally vulnerable to local extinctions because of the small size of local breeding populations (Steinberg 1999), resulting in low effective size of local populations and relatively large genetic differences between local subpopulations, despite documented gene flow (Stinson 2020). Service Areas were established by the USFWS in 2017 (USFWS 2017) to meet conservation needs and guide mitigation actions to benefit the three listed subspecies endemic to Thurston County. Two of the subspecies (Olympia pocket gopher and Tenino pocket gopher) have one Service Area within their range, while the Yelm pocket gopher has three Service Areas within its range. Service Areas are used to direct conservation actions as well as mitigation efforts to offset impacts to Mazama pocket gophers or their habitat. Mitigation preferentially occurs within the same Service Area as the impact, although for Yelm pocket gophers, mitigation may at times be allowed in another of their Service Areas. Landscape features, occupancy patterns, habitat connectivity, barriers to movement, soil availability, and land use development were taken into consideration in the development of the Service Area boundaries.

In this analysis, we examined patterns of occupancy and habitat use for the Mazama pocket gopher using four years of field survey data (2014–2017). We postulated that soil type would be a significant predictor of Mazama pocket gopher occupancy. In addition, we examined whether there were differences in Mazama pocket gopher habitat use among different subspecies and within different Service Areas in Thurston County, Washington. These formalized relationships could then inform future management and conservation-based decisions in Thurston County, Washington, and adjacent areas.

Methods

Application for a building permit in Thurston County, Washington, initiated a process that began with determining if potential building sites contained Mazama pocket gopher soil types (Figure 2). Surveyed sites were not randomly selected, rather they represented parcels where a landowner applied for a building permit which were then evaluated for gopher soils and presence. USFWS and Thurston County reviewed and evaluated proposed projects to determine if a parcel needed surveying. A subset of building permit applications triggered a screening survey of the identified parcel to determine if there was evidence of Mazama pocket gopher occupancy based on gopher soil type and proximity to known Mazama pocket gophers.

Mazama pocket gopher occupancy was determined using a GIS layer of gopher soils and then looking for overlap with the proposed building footprint. Gopher soils were defined as soils where gophers had been found to occur, and we further categorized soils based on their preference by gophers ("more preferred" or "less preferred"). More-preferred soil types are those that Mazama pocket gophers use relatively more than those that are less-preferred, considering how many accessible acres of each gopher soil type exist on the landscape (USFWS 2018, 2022; Duncan et al. 2020; Table 1).

Figure 2. An example of the Spanaway soil series found in Thurston County, Washington, showing rock abundance and size and organic soil layer depth. Spanaway gravelly sandy loam soils (0–3% slopes or 3–15% slopes) are a more preferred soil type for the Mazama pocket gopher in Thurston County. (Photo by J. Rodriguez)

Parcels also subject to screening surveys were those located within 90 m of a preferred Mazama pocket gopher soil (Figure 3) (to account for potential soil mapping errors), or were within approximately 180 m of a previously confirmed gopher location (to account for possible tunneling distance) (USFWS 2022, Figure 4). These spatial data sets were generated using the US Department of Agriculture (USDA) soil survey geographic database (SSURGO) (USDA 2014). As a result of the distance thresholds, based on the soil data set, 41 parcels screened were not on preferred soil (Figure 4). These soil types were previously field-verified by USFWS personnel, who completed a study of soil types occupied by gophers versus soil type abundance.

Field Data Collection

Field screening for Mazama pocket gopher mounds was conducted from June 1 through October 31 of each year, for a total of four years from 2014 to 2017. Screening surveys were conducted by biologists trained specifically to identify gopher mounds as part of a two-day intensive field survey training that focused on identifying gopher mounds as compared to mounds of other burrowing animals. The USFWS assisted Thurston County with Mazama gopher field screening during this time as an interim approach to minimize the risk of unauthorized take of Mazama pocket gophers associated with their land use permit program while Thurston County worked to complete a USFWS-approved Habitat Conservation Plan.

TABLE 1. Soils that are more and less preferred for occupancy by Mazama pocket gophers in Thurston County, Washington.

Soil preference	Soil characteristics
More preferred soils	Cagey loamy soil
	Indianola loamy sand, 0–3% slopes
	Nisqually loamy fine sand, 0–3% slopes or 3–15% slopes
	Spanaway gravelly sandy loam, 0–3% slopes or 3–15% slopes
	Spanaway-Nisqually complex, 2–10% slopes
Less preferred soils	Norma fine sandy loam or silt loam
	Spana gravelly loam
	Spanaway stony sandy loam, 0–3% slopes or 3–15% slopes
	Yelm fine sandy loam, 0–3% slopes or 3–15% slopes
	Alderwood gravelly sandy loam, 0–3% slopes or 3–15% slopes
	Everett very gravelly sandy loam, 0–3% slopes or 3–15% slopes
	Indianola loamy sand, 3–15% slopes
	Kapowsin silt loam, 3–15% slopes
	McKenna gravelly silt loam, 0–5% slopes

Figure 3. A photo of a typical gopher mound for a Yelm pocket gopher found in Thurston County, Washington. The mounds are characterized by soil that is pushed in two or three directions, resulting in fan-shaped mounds, an irregular shape/perimeter, finely sifted soils, a low profile, and a tunnel entrance located at the side of the mound. (Photo by Thurston County, WA staff)

The gopher soil types identified by soil GIS data were also field-verified by USFWS personnel during screening visits (Table 1).

The number of visits per parcel varied slightly for each year; visits were up to three times and were at least 30 days apart. Once evidence of gopher occupancy was documented, no further screening surveys were needed. No gopher mounds were detected only on a third visit. Mounds with Mazama pocket gopher characteristics, as identified by a trained biologist (Figure 3), were considered a positive indication of occupancy. Screening consisted of a team of two or more biologists walking transects in parallel lines, with approximately 3–5 m between them. The team traversed the parcel and recorded mound data in a Trimble Geo7x Global Positioning System (GPS) unit (Trimble.com). Using Trimble's GPS Pathfinder Office, the GPS data were differentially corrected against nearby base stations to increase spatial accuracy. The digital data were downloaded and checked for accuracy against each parcel's field form and incorporated into a digital database.

Statistical Analysis

Survey data were pooled across years. Parcels with confirmed Mazama pocket gopher mounds were assigned a '1' indicating Mazama pocket gopher presence; parcels with no mounds were assigned '0' for no occupancy. Occupancy rates for different soil categories (i.e., more preferred, less preferred, and non-gopher soil types), subspecies, and Service Areas were calculated as the number of parcels with occupancy divided by the total number of screening surveys within each soil category. Pearson's chi-squared tests were used to determine differences in Mazama pocket gopher occupancy between soil strata. As a second measure, binomial logistic regression was used to estimate the effect of predictor variables on binary presence/absence. Logistic regression takes the exponential form:

$$p = e\beta 0 + \beta 1x1 + \ldots + \beta nxn$$

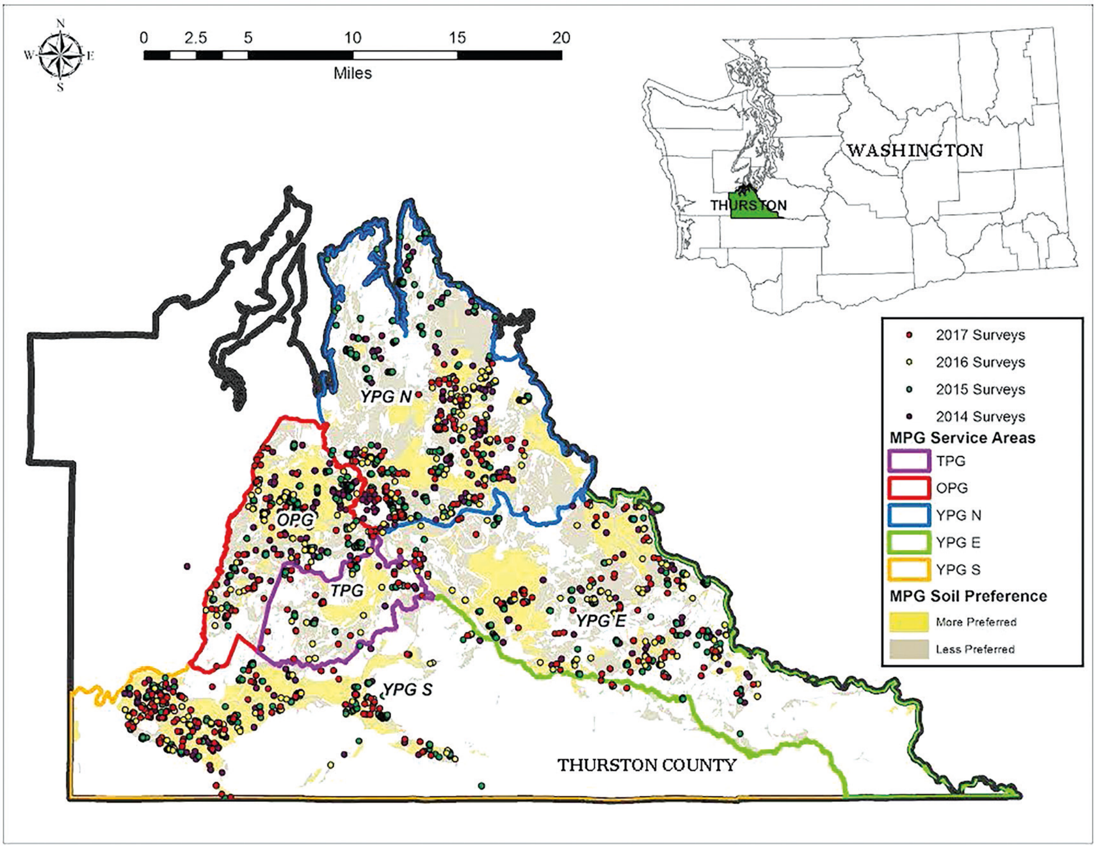

Figure 4. Map of the study area in Thurston County, Washington, and screening parcels surveyed from 2014 to 2017, showing survey parcels per year, more and less preferred soils, and Mazama pocket gopher Service Areas. OPG = Olympia pocket gopher, TPG = Tenino pocket gopher, YPG = Yelm pocket gopher North, East, and South.

where p is the probability of presence, and βn is the coefficient for each predictor variable xn. Each level (i.e., soil category, subspecies, and Service Area) was included as a predictor. All statistical analyses were performed using R Statistical Computing Language 3.4.2 (R Core Team 2017).

Results

In total, 1,241 parcels were surveyed between 2014 and 2017, comprising approximately 4,654 hectares of more and less preferred Mazama pocket gopher soils in Thurston County, Washington, and resulting in 165 parcels occupied by Mazama pocket gophers (Figure 5). Occupancy only occurred for the Olympia pocket gopher and Yelm pocket gopher. No Tenino pocket gophers were detected during our years of screening despite efforts occurring within the range of the subspecies. Therefore, there are no results for that subspecies.

In total, there were four Service Areas for the Yelm and Olympia pocket gopher subspecies. For both subspecies, gophers were found more often on parcels with soil types categorized as more preferred than those categorized as less preferred (logistic regression estimate = 2.05 ± 0.26, $P < 0.010$, Figure 4). This result was consistent across all four Service Areas. This relationship was maintained when data were stratified by subspecies, with both subspecies being found significantly

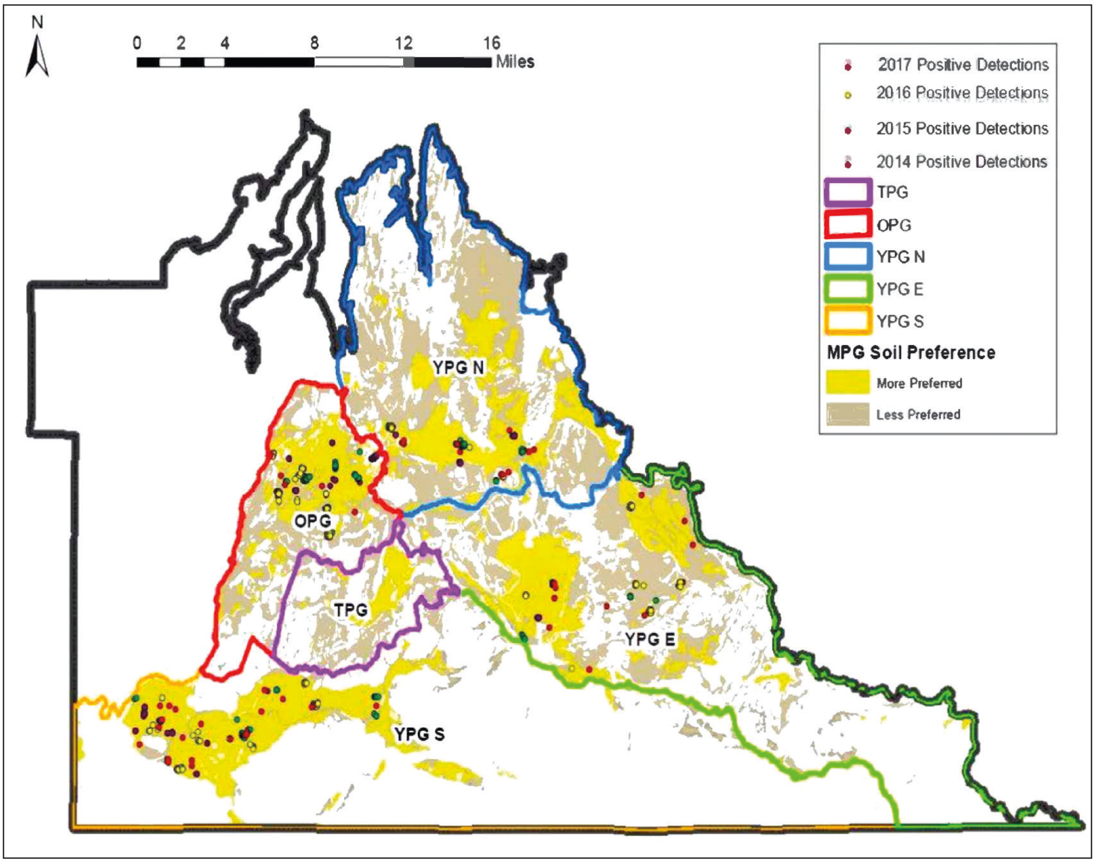

Figure 5. Map of positive detections from 2014 to 2017, showing more and less preferred soils, and Mazama pocket gopher Service Areas. OPG = Olympia pocket gopher, TPG = Tenino pocket gopher, YPG = Yelm pocket gopher North, East, and South.

more often at sites with more preferred soil types (Table 2). The results from the chi-squared test also confirmed that the relationship between more preferred and less preferred soil types was significant ($P < 0.001$). There was also a significant difference between more preferred soil and non-gopher soil ($P < 0.010$) where there was a highlighted correlation between where gophers created mounds on preferred soils more often than on non-gopher soils, largely because of the characteristics of the soil and soil type (Figure 6).

Overall occupancy rates between more preferred and less preferred soil types differed among subspecies. Olympia pocket gophers were found more often than Yelm pocket gophers (logistic regression estimate = 0.89 ± 0.19, $P < 0.001$), due to higher occupancy rates by Olympia pocket gophers than Yelm pocket gophers at parcels with more preferred soil types (40.5% compared to 17.4%, $P < 0.001$, Table 2). There was no difference in occupancy rates between Olympia pocket gophers and Yelm pocket gophers on parcels with less preferred soil types ($P = 0.660$).

Occupancy rates also differed somewhat among Yelm pocket gopher Service Areas. At parcels with more preferred soil types, Mazama pocket gophers were found more often in Yelm pocket gopher South (Yelm pocket gopher—S) than in Yelm pocket gopher North (Yelm pocket gopher—N) parcels ($P < 0.010$), while there was no difference in occupancy rates in Yelm pocket gopher—S and Yelm pocket gopher East (Yelm pocket gopher—E)

TABLE 2. Occupancy rates (number of presences/total number of screening surveys) and sample size (n) for Olympia pocket gopher and three populations of Yelm pocket gopher in Thurston County, Washington in two soil categories. The P-values are calculated from Pearson's chi-squared test for soil category comparison.

Population unit	More preferred soil	Less preferred soil	P-value
Olympia pocket gopher	40.5% (n = 116)	2.3% (n = 86)	< 0.001
Yelm pocket gopher—all	17.4% (n = 556)	4.0% (n = 398)	< 0.001
Yelm pocket gopher—North	11.1% (n = 189)	3.2% (n = 219)	0.003
Yelm pocket gopher—East	16.8% (n = 95)	5.8% (n = 156)	0.009
Yelm pocket gopher—South	22.1% (n = 272)	0% (n = 23)	0.024

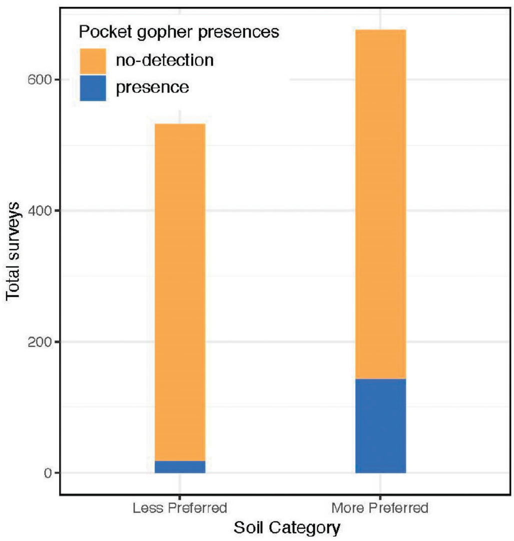

Figure 6. Histogram of total screening surveys conducted to determine presence and no-occupancy on parcels categorized by soil type preferences of Mazama pocket gophers in Thurston County, Washington.

(P = 0.350), or for Yelm pocket gopher—N and Yelm pocket gopher—E (P = 0.340) at parcels with more preferred soil types. In addition, there was no difference in occupancy rates for any of the Service Areas at parcels with less preferred soil types (P > 0.200).

Of the three subspecies, Olympia pocket gophers had access to the highest proportion of more preferred soils when compared to the total size of the Service Area, and Tenino pocket gophers had access to the lowest proportion of more preferred soils within its Service Area (Table 3). Tenino pocket gophers had access to the highest amount of less preferred soil and the lowest amount of non-gopher soils of the three subspecies. Olympia pocket gophers had access to the highest proportion of more preferred soils to less preferred soils (Table 3). The amount of gopher soils available for Yelm pocket gopher was approximately 3.5x the amount of acreage available for the two other subspecies combined. The amount of more preferred soils in the three Service Areas for Yelm pocket gopher was substantially larger than for the other two subspecies (i.e., 20,606 hectares for Yelm pocket gopher Service Areas vs 3,955 hectares and 1,163 hectares for Olympia and Tenino pocket gopher Service Areas, respectively).

Discussion

This manuscript attempted to quantify and formalize the relationship between gopher occupancy and soils preferred by gophers in Thurston County, Washington. Overall, the results improved our understanding of occupancy as it relates to gopher soil preference for Olympia and Yelm pocket gopher subspecies. This study adds to a growing body of work examining the relationship between soil type and pocket gopher habitat use on the landscape scale.

The findings in this study are very consistent with other studies examining pocket gopher soil preferences and parcel occupancy. Soil type and characteristics often predict pocket gopher presence or absence better than vegetation characteristics (Warren et al. 2017). Preferred soils tended to be sandy loam or loamy sand soils (Medine et al. 2022) rather than those containing high sand (Cormier et al. 2021) or clay content (Warren et al. 2017). As a result, soil type may be a constraint limiting potential habitat for certain gopher species (Bennett et al. 2020). A better understanding

TABLE 3. The area available of more and less preferred gopher soils for each subspecies of Mazama pocket gopher identified within Thurston County, Washington.

Mazama pocket gopher subspecies	More preferred soils (ha)	Less preferred soils (ha)
Olympia pocket gopher	3,955	4,790
Tenino pocket gopher	1,163	2,800
Yelm pocket gopher (all areas)	20,606	27,417

of this relationship between soil preference and gophers is critical, as gophers function as both keystone species and ecosystem engineers within the landscape, and can have significant impacts on soil structure in altering the soil structure, porosity, permeability, and nutrient distribution of soils where gophers reside (Reichmann and Seabloom 2002, Platt et al. 2016, Bennett et al. 2020).

This work demonstrates that soil type is a critical consideration when planning for the conservation of both the Olympia and Yelm pocket gopher. Despite the federal and state threatened status of these subspecies, current population estimates remain unknown. Mazama pocket gophers make mounds for a variety of reasons, including to find or access food, to build or rebuild tunnels, or to get rid of excess soil as they build tunnels. The type of soil a Mazama pocket gopher occupies may require that they rebuild tunnels more often or the type of vegetation on the parcel may require more mound building. If there is more disturbance on a parcel, such as vehicles or people, tunnels may collapse, which would cause more mound building. In addition, during rainy periods or after periods of no rain, more mounding is seen, so season and amount of precipitation also have an influence on mound building. Because gopher mounding is an unreliable predictor of population size (Olson 2011, 2017; Stinson 2020), the only current measure to determine the potential of an area to support gopher recovery is to use indicators of habitat suitability including occupancy and availability of preferred soil types as a surrogate for gopher population estimates.

Thus, assessment of habitat quality and soil availability serve as a method to determine where broad-scale changes to habitat status threaten the Mazama pocket gopher. Sections of Thurston County have a higher proportion of more preferred gopher soils compared to less preferred soils. These areas are important for Mazama pocket gopher conservation and present higher risk of harm to individual Mazama pocket gophers associated with future development than areas dominated by less preferred and non-gopher soils. However, less preferred soils should not be discounted for their conservation value, as these soils can be occupied, and a loss of any occupied parcel may reduce recovery potential. In addition, less preferred soils were often immediately adjacent to valuable more preferred soils on surveyed parcels. A predominant threat to the conservation of gophers is the development of lands and the associated soils that currently support them. Currently, more than 90 percent of the historic prairies and savannas in the south Puget Sound area have been lost due to a combination of agricultural conversion, encroachment by coniferous forest, and development (Crawford and Hall 1997, Dunwiddie et al. 2006). For example, the presumed extinction of the Tacoma pocket gopher is thought to be directly linked to residential and commercial development, including a large gravel pit and golf course (Stinson 2020, USFWS 2022b), As the quantity of prairie habitat has decreased through fragmentation (USFWS 2022), the quality of the prairie habitat remaining has also decreased (Herkert et al. 2003). Suitable prairie ecosystems and soil distributions are the main determinants of the subspecies' ranges.

Parcels screened for gophers are potentially representative of lands that might be developed over the next 30 years with current Thurston County zoning. The population of Thurston County is projected to increase by 75% in the next 30 years, which will add an additional 100,000 people to the area, resulting in a need for 62,000 concurrent housing units (TRPC 2018, WOFM 2018). This rate of human population increase will result in the conversion of more lands to support residential and commercial development, including those areas that contain more preferred gopher soils. This will further limit the potential for gopher recovery and the creation of high-functioning gopher conservation reserves and banks, and increase the fragmentation and genetic isolation within the gopher habitat that remains.

In total, approximately 648 hectares of Thurston County fall within the critical habitat designation for the Olympia, Tenino, and Yelm pocket gophers (USFWS 2014a). A further 1,127 hectares were excluded or exempted from critical habitat designation in Thurston County, but are still considered essential to the conservation of these three subspecies. The results of this work will provide avoidance and minimization options based on both location and soil type to guide management decisions on gopher conservation. Prior to our analysis, gopher soils and their preference by gophers were recognized by practitioners in the field but which soils are occupied at what rates was not widely available to the scientific community. These data highlight that conservation of undeveloped lands with more preferred soils is critical to the protection of the threatened subspecies of Mazama pocket gopher. These results could be extended regionally to other federally listed species with less occupancy data, including the Tenino pocket gopher in Thurston County, and the Roy Prairie pocket gopher *(T. m. glacialis)* in adjacent Pierce County, Washington. It might also be possible to extend these conservation recommendations to other Mazama pocket gopher subspecies within Washington and Oregon that have similar natural history parameters. As a prairie keystone species, all species of Mazama pocket gophers have the potential to guide larger prairie conservation efforts for sympatric species.

Efforts to define the habitat parameters required to provide functioning, high-quality habitat for Mazama pocket gophers are ongoing, and much work still remains. Because habitat use is such an important aspect to the conservation of these subspecies, additional maps, including more precise soil maps near conservation areas, greater linkage for soil maps across county boundaries, and land cover maps that show the relationship between soil and vegetation type will add additional data to the discussion. Supplemental work on the Tenino pocket gopher would further add to our understanding of their natural history and is critical if development pressure increases within their range. In sum, conserving the federally listed subspecies of Mazama pocket gopher will be further augmented by a greater understanding of soil and habitat use and additional studies that add to that body of work.

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Literature Cited

Andersen, D. C., and J. M. MacMahon. 1985. Plant succession following the Mount St. Helens volcanic eruption: facilitation by a burrowing rodent, *Thomomys talpoides*. The American Midland Naturalist 114:62-69.

Bennett, M. E., R. A. Gitzen, L. M. Conner, M. D. Smith, E. C. Soehren, and S. B. Castelberry. 2020. Interactions of soil and vegetation determine habitat for Southeastern pocket gopher (*Geomys pinetis*). The American Midland Naturalist 184:205-221.

Cormier, K., A. Medine, and J. D. Hoffman. 2021. Relationships among soil texture, burrow depth and diameter, and body mass of Baird's pocket gopher (*Geomys breviceps*). Transactions of the Kansas Academy of Science 124:109-116.

Crawford, R., and H. Hall. 1997. Changes in the south Puget prairie landscape. *In* P. Dunn and K. Ewing (editors). Ecology and Conservation of the South Puget Sound Prairie Landscape, The Nature Conservancy, Seattle, WA. Pp. 11-15.

Duncan, S., J. T. Pynne, E. I. Parsons, R. J. Fletcher Jr., J. D. Austin, S. B. Castleberry, L. M. Conner, R. A. Gitzen, M. Barbour, and R. A. McCleery. 2020. Land use and cover effects on an ecosystem engineer. Forest Ecology and Management 456:117642

Dunwiddie P., E., Alverson, A. Stanley, R. Gilbert, S. Pearson, D. Hays, J. Arnett, E. Delvin, D. Grosboll, and C. Marschner. 2006. The vascular plant flora of the south Puget Sound prairies, Washington, USA. Davidsonia 17:51-69.

Ellison, L. 1946. The pocket gopher in relation to soil erosion on mountain range. Ecology 27:1101-114.

Grant, W. E., N. R. French, and L. J. Folse, Jr. 1980. Effects of pocket gopher mounds on plant production in shortgrass prairie ecosystems. The Southwestern Naturalist 25:215-224.

Herkert J. R., D. L. Reinking, D. A. Widenfeld, M. Winter, J. L. Zimmerman, W. E. Jensen, E. J. Finck, R. R. Koford, S. K. Sherrod, M. A. Jenkins, J. Faaborg, and S. K. Robinson. 2003. Effects of prairie fragmentation on the next success of breeding birds in the Midcontinental United States. Conservation Biology 17:587-594.

Huntly, N., and R. Inouye. 1988. Pocket gophers in ecosystems: patterns and mechanisms. Bioscience 38:786-793.

Inouye, R. S., N. Huntly, and G. A. Wasley. 1997. Effects of pocket gophers (*Geomys bursarius*) on microtopographic variation. Journal of Mammalogy 78:1144-1148.

Jones, C. C., C. B. Halpern, and J. Niederer. 2008. Plant succession on gopher mounds in western Cascade Meadows: consequences for species diversity and heterogeneity. American Midland Naturalist 150:275-286.

Kelt, A., and D. Van Vuren. 1999. Energetic constraints and the relationship between body size and home range area in mammals. Ecology 80:337-340.

Kovarik, P. W., S. W. Chordas, H. Robison, P. Skelley, M. Connor, J. Fiene, and G. Heidt. 2008. Insects inhabiting the burrows of the Ozark pocket gopher in Arkansas. Journal of the Arkansas Academy of Science 62:75-78.

Litaor, M. I., R. Mancinelli, and J. C. Halfpenny. 1996. The influence of pocket gophers on the status of nutrients in alpine soils. Geoderma 70:37-48.

Luna, F., and C. D. Antinuchi. 2006. Cost of foraging in the subterranean rodent, *Ctenomys talarum*: effect of soil hardness. Canadian Journal of Zoology 84:661-667.

Martinsen, G. D., J. H. Cushman, and T. G. Whitham. 1990. Impact of pocket gopher disturbance on plant species diversity in a shortgrass prairie community. Oecologia 83:132-138.

Medine, A., J. D. Hoffman, E. K. Lyons, and F. Lemieux. 2022. Influence of vegetation and soil on relative density of Baird's pocket gopher (*Gemys breviceps*) in Louisiana. The American Midland Naturalist 187:161-172.

Olson, G. S. 2011. Mazama pocket gopher occupancy modeling. Washington Department of Fish and Wildlife. Olympia, WA.

Olson, G. S. 2017. Development of standard survey methods for Mazama pocket gophers. Washington Department of Fish and Wildlife, Olympia, WA.

Platt, B. F, K. Kolb, C. G. Kunhardt, S. P. Milo, and L. G. New. 2016. Burrowing through the literature: the impact of soil-disturbing vertebrates on physical and chemical properties of soil. Soil Science 3:175-191.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reichman, O. J., and E. W. Seabloom. 2002. The role of pocket gophers as subterranean ecosystem engineers. Trends in Ecology and Evolution 17:44-49.

Sherrod, S. K., T. R. Seastedt, and M. D. Walker. 2005. Northern pocket gopher, *Thomomys talpoides*, control of alpine plant community structure. Arctic, Antarctic, and Alpine Research 37:585-590.

Steinberg, E. K. 1999. Diversification of genes, populations, and species: evolutionary genetics of real and virtual pocket gophers *Thomomys*. Ph.D. Dissertation, University of Washington, Seattle.

Steinberg, E. K, and D. Heller. 1997. Using DNA and rocks to interpret the taxonomy and patchy distribution of pocket gophers in western Washington prairies. *In* P. Dunn and K. Ewing (editors). Ecology and Conservation of the South Puget Sound Prairie Landscape, The Nature Conservancy, Seattle, WA. Pp.43-47.

Stinson, D. W. 2020. Mazama Pocket Gopher Recovery Plan and Periodic Status Review. Washington Department of Fish and Wildlife, Olympia, WA.

[TRPC] Thurston County Regional Planning Council. 2018. Forecast work program. Employment and commute forecast. Thurston County Regional Planning Council, Thurston, WA. Available online at http://www.trpc.org/236/Population-Employment-Forecasting (accessed 20 July 2018).

[USDA] US Department of Agriculture. 2014. Official Soil Series Descriptions. United States Department of Agriculture, Soil Survey Staff, Natural Resources Conservation Service, Washington, DC. Available online at http://soils.usda.gov/technical/classification/osd/index.html (accessed July 28 2021).

USFWS. 1973. US Endangered Species Act of 1973. As amended, Public Law No. 93-205, 87 Stat. 884, Dec. 28, 1973.

USFWS. 2012. Endangered and threatened wildlife and plants; listing four subspecies of Mazama pocket gopher and designation of critical habitat; proposed rule. 77 FR 73770, December 11, 2012.

USFWS 2014a. Endangered and threatened wildlife and plants; designation of critical habitat for Mazama pocket gophers; final rule. 79 FR 19712, April 9, 2014.

USFWS. 2014b. Endangered and threatened wildlife and plants; threatened species status for the Olympia pocket gopher, Roy Prairie pocket gopher, Tenino pocket gophers, and Yelm pocket gopher, with special rule; final rule. 79 FR 19760, April 9, 2014.

USFWS. 2017. Revised Service Areas for Mazama pocket gopher mitigation, Thurston County, Washington. US Fish and Wildlife Service Technical Memorandum, Washington Fish and Wildlife Office, Lacey, WA.

USFWS. 2018. Guidance for assessing potential take of Mazama Pocket Gophers in Thurston and Pierce Counties. US Fish and Wildlife Service, Letter prepared by the Deputy Director, Lacey, WA.

USFWS. 2022a. Recovery plan for four subspecies of Mazama pocket gopher. US Fish and Wildlife Service, Technical Report, Washington Fish and Wildlife Office, Lacey, WA.

USFWS. 2022b. Species biological report for four subspecies of Mazama pocket gopher. US Fish and Wildlife Service, Technical Report, Version 1.1, Portland, OR.

Verts, B. J., and L. N. Carraway. 2000. *Thomomys mazama*. Mammalian Species 641:1-7.

Vleck, D. 1979. The energy cost of burrowing by pocket gopher *Thomomys bottae*. Physiological Zoology 52:122-136.

Vleck, D. 1981. Burrow structure and foraging costs in the fossorial rodent, *Thomomys bottae*. Oecologia 49:391-396.

Warheit, K. I., and A. Whitcomb. 2016. Geographic structure of Mazama pocket gopher (*Thomomys mazama*) populations in the south Puget Sound, Washington based on single nucleotide polymorphisms (SNPs) discovered from restriction-parcel associated DNA (RAD) sequences. Washington Department of Fish and Wildlife, Technical Report, Olympia, WA.

Warren, A. E., S. B. Castelberry, D. Markewitz, and L. M. Conner. 2017. Understory vegetation and soil characteristics of *Geomys pinetis* (Southeastern pocket gopher) habitat in Southwestern Georgia. The American Midland Naturalist 178:215-225.

[WOFM] Washington Office of Financial Management. 2018. Population forecast 2010-2045. Washington Office of Financial Management medium series forecast for Thurston County 2017-2045, Olympia, WA. Available online at https://docs.google.com/spreadsheets/d/1oyaWphxgtEgWsb0kIfs7Ssb7WzsgoKIgwkYxmqATM6s/edit#gid=0 (accessed July 2021).

Witmer, G. W., R. D. Sayler, and M. J. Pipas. 1996. Biology and habitat use of the Mazama pocket gopher *Thomomys mazama* in the Puget Sound area, Washington. Northwest Science 70:93-98.

Zaitlin, B., and M. Hayashi M. 2012. Interactions between soil biota and the effects on geomorphological features. Geomorphology 158:142-152.

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