

Pocket gopher activity across elevation gradients

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Abstract:

In ecology it is important to understand the limits of a species range and what their behaviors are within their range. *Thomomys talpoides* (Northern Pocket Gopher) and its relatives have been studied extensively at lower elevations (<2500m), but little is known about them at alpine elevations (>2700m). We asked what mechanism(s) (elevation, edaphic factors) determined their high elevational ranges. We were also interested in if there was a correlation between their burrowing and plant community composition. Our results showed a significant negative correlation between gopher disturbance and elevation on both ends of a quadratic curve which means that at lower and higher elevations gopher disturbance diminishes, and the most disturbance is in the middle. The abiotic factors of elevation cause an altitudinal pattern in pocket gopher disturbance. The edaphic and plant community composition data has not been completely analyzed at this moment.

Introduction:

Species ranges descriptions

A species range is defined as the spatial range that it inhabits, but less known is about what mechanism(s) restricts a species to that spatial area (MacArthur 1984; Owen 1990; Holt 2003; Sexton et al. 2009; Wiens 2011). The Dobzhansky-MacArthur Hypothesis suggests that abiotic factors, such as temperature and precipitation, will limit the range of a species at high latitudes/altitudes and biotic factors, such as competition and herbivory, will limit their ranges at low latitudes/altitudes (Dobzhansky 1950).

Here, I focused on the pocket gopher (*Thomomys talpoides*) to explore factors that may limit their activity and/or range. The range of *T. talpoides* extends to ~3800m, but little is known about their ecology at these high elevations because most studies have been conducted at low elevations (< 2500m) (Huntly and Inouye 1988; Case et al. 2013). What are the factors that determine their range? I considered several abiotic factors (elevation, soil depth, soil moisture, etc.) as well as vegetation composition (food supply) as a biotic factor. First, I review prior studies examining factors affecting the abundance and distribution of *T. talpoides*. Second, I consider above-belowground interactions between *T. talpoides* and the plant community as a potential biotic factor limiting both plant distribution and the distribution of *T. talpoides*.

Abiotic factors affecting *Thomomys talpoides* abundance

As elevation increases in the Rocky Mountains, climate factors such as: air temperature, atmospheric pressure, and soil nutrients decline, but precipitation increases (Becker and Bugmann 1997; Kittel et al 2002; Dunne et al 2003; Inouye and Wielgolaski 2013). Pocket gophers at alpine elevations have shown larger body sizes and higher fat contents than lower elevation gophers, but there were more individuals present (as evidenced by eskers and other signs of activity) at the lower elevations (Tryon and Cunningham 1968). This increase in population was correlated with the relative amount of grasses and forbs (Keith et al. 1959). A study analyzing the metabolism and thermoregulation of *T. talpoides* found that thermoregulation was an insignificant aspect of *T. talpoides* life history, because the tunnels they travel in keep a relatively constant temperature (Gettinger 1975). However, their metabolism was considerably higher than other fossorial rodents because pocket gophers

venture outside their burrows during critical temperatures (below 25-26 C) (Gettinger 1975). Conversely, gophers facing heat stress above 37.5 C experience absolute mortality (Gettinger 1975).

In addition to elevation, other abiotic factors could dictate pocket gopher range and activity. Soil depth preference of the pocket gopher varied with elevation: At alpine sites, shallower levels were preferred, but at sub-alpine and shrub-grasslands deeper depths were preferentially occupied (Hansen and Beck 1968). Deeper soil depths had larger gophers compared to shallow depths, and these size differences held regardless of elevation (Davis 1938). The amount and size of rocks in subalpine areas did not seem to affect gopher inhabitation, but the unoccupied areas in both alpine and shrub-grasslands had larger and more rocks compared to occupied areas (Hansen and Beck 1968). In relation to burrowing, slope has been shown to not be a major factor with *Thomomys bottae*. Their feeding tunnels were not directly associated with slope of the land, and the laterals were usually directed downhill, even on shallow slopes (Seabloom et al. 2000). Additionally, gopher burrowing increases soil erosion (Seabloom et al. 2000), and the erosion tends to limit gopher size (Davis 1938; Patton 1999).

Biotic interactions: *Thomomys talpoides* and plants

Aboveground-belowground interactions were understudied for many years (Robertson and Gross 1994; Wardle et al. 2004). It has now been realized that belowground species, both micro and macro, can influence aboveground species (Robertson and Gross 1994; Wardle et al. 2004). This has led to research on how extensively the above and belowground systems, such as fungi, mammals, and plants, interact. These studies have shown that plant communities are affected by interactions with the microbial community more than first anticipated (Wardle et al.

2004). Additionally, macro-vertebrates, such as the pocket gopher (Findley and Negus 1953; Fitzgerald et al. 1994), can exert direct and indirect effects on the above-ground vegetation (Anderson 1987).

In some ecosystems, pocket gophers can have significant effects on the composition of the plant community. Pocket gophers are considered ecosystem engineers. Their burrowing and plant manipulation can influence succession and plant composition (Reichman and Seabloom 2002). The results of past studies show that herbivory can lead to increases or decreases in plant community diversity (Harper 1969; Holt 1977; Holt 1984; Lubchenco 1978; Noy-Meir 1981). The gopher's influence can cause apparent competition, where the removal of one species by gophers indirectly affects the diversity of the remaining community (Holt 1977). When fossorial rodents burrow, they are continually consuming plant matter (Anderson 1987) and distributing nutrients to different levels of the soil thereby creating variation in the nutrients available for plant growth (Huntly and Inouye 1988; Inouye et al. 1987). The soil disturbance causes aeration providing better growing conditions for plants (Huntly and Inouye 1988; Inouye et al. 1987). A study in a short grass prairie community found that gopher soil disturbance decreased grass abundance and increased the abundance of dicot species, effectively shifting the composition of the plant community (Martinsen et al. 1990). This effect also let a competitively inferior species grow in an area that it usually did not (Martinsen et al. 1990).

Predictions of this study

The Dobzhansky-MacArthur Hypothesis suggests that abiotic factors, such as temperature, will limit the range of the gophers at high elevations (Dobzhansky 1950). We

hypothesize that gopher activity of an area will decrease with increased elevation because the lower temperatures will require an increase in metabolism and more foraging to support a higher metabolism. In turn, the decreased activity at higher elevation could affect composition of plant communities in the area. To test these ideas, we addressed the following questions. 1) Does pocket gopher activity present an altitudinal pattern? 2) Is gopher activity better correlated with site level edaphic factors (pH, soil depth, aspect, slope, soil nutrients, and moisture) than elevation? To our knowledge, prior studies addressing gopher activities along elevation gradients have not compared the relative influence of these alternative correlates. 3) Is gopher activity associated with plant community composition, and do these correlations change along elevation gradients?

Methods:

Pocket gopher biology

An understudied macro vertebrate in the Gothic-Crested Butte area is the pocket gopher, which creates disturbances (such as eskers) by burrowing underground and pushing the subsoil to the surface. The eskers loosen the soil (Turner et al. 1973) which may increase water infiltration (Hanson and Morris 1968) and lower runoff (Abaturov 1968). Pocket gophers dig an elaborate network of tunnels, potentially moving 8000-15,700 kg of soil/hectare per year (Long 2003). As a result of this large amount of soil disturbance, multiple microenvironments are created (Reichman and Smith 1985; Huntly 1991). Pocket gophers will also come to the surface to cut plants away from their tunnel openings. It has been observed that the pocket gophers will cut vegetation within a radius of 8 inches around their mounds. In general their diet

consists of bulbs, roots, tubers, and sometimes aboveground plants (Rios and Álvarez-Castañeda 2007). In a desert grassland, their diet consisted of 67% forbs, 30% grasses, and 3% shrubs and 70% of these plants were eaten aboveground (Vaughan 1967). In the high elevations of central Utah (3000-3400m), gophers primarily consumed and cut dandelion (*Taraxacum officinale*), penstemon (*Penstemon rydbergii*), sweet sage (*Artemisia discolor*), and yarrow (*Achillea lanulosa*) (Aldous 1951).

Sampling design

We assessed gopher activity over 6 replicated mountain peaks (elevation transects, Fig. 1) in the Upper Gunnison Basin, Gunnison County, CO, USA. Transects were chosen to avoid pseudo replication of the lowest sites by sampling geographically distinct watersheds/valleys that are separated by ridges. For each transect, the study sites began at ~2700m and were chosen approximately every 100m in elevation to the highest vegetated site on the peak, resulting in approximately 9-13 sites per transect.

Gopher activity measures

At each site we measured abundance of pocket gopher disturbance along three 40m (~360 rev. of a Precimeter 305 rolatape, Rولاتape Measuring Wheels 2014, Rولاتape Corporation, Spokane, WA, Fig. 2a,b) transects. Each transect was examined for gopher disturbance by running a rolatape with a 1m wide PVC pipe (2.5 cm diameter) secured perpendicular to the main axis of the rolatape to increase the area of observation (Beck and Hansen 1966; Hansen and Beck 1968). Each time a gopher disturbance was observed, it was counted as 1 with a hand-held tally counter. Gopher activity was estimated by the mean number of gopher disturbances per three 40m transects for each site.

Abiotic environment

Abiotic factors that were measured include slope, aspect, soil-depth, pH, moisture, and soil nutrients by using Plant Root Simulator probes (Plant Root Simulator (PRS™) Probes 2014, Western Ag. Innovations, Saskatoon, SK, Canada). The slope of the site was measured using an app on an iPhone to determine the angle in degrees of the hillside. Aspect (the direction the site is facing) was measured with an iPhone app in degrees and categorically (north, east, north-east, etc.). By forcing a 1.5m AMS Tile probe (AMS Tile Probes 2014, AMS, Inc., American Falls, ID into the soil as far as possible by hand, and then measuring the length the rod was plunged into the soil, we obtained a measure of soil depth (Hansen and Beck 1968). The pH was measured with a pH meter. Soil moisture (volumetric water content) was measured using a TDR probe (FieldScout 2014, Spectrum Technologies, Aurora, IL).

Vegetation surveys

Plant community composition was observed at the site level by placing three 20m parallel transects 10m apart from each other and another 20m transect through the center of the parallel transects. Every 2.5m along the transect, a 20x20cm quadrat was analyzed for percentage cover of all plant species present, resulting in a total number of 33 quadrats per site.

Statistical analysis

Regression analysis was used to determine the relationship between elevation and gopher activity (measured as average number of disturbances per three 40 m transects) to answer the question, 'does pocket gopher activity present an altitudinal pattern?' Both a linear and quadratic term was used to detect nonlinear patterns in gopher disturbance. Akaike's information

criterion (AICc) was used to determine which model (linear or quadratic) was a better fit to the data. Analysis of covariance (ANCOVA) was employed to gain insights into whether or not the elevation patterns were peak specific or general patterns across peaks. Linear mixed models (LMM) were employed to analyze the abiotic factors that influence gopher activity with peak included as the random effect. LMMs were utilized to analyze the correlations of abiotic and biotic factors, including gopher activity, on vegetation across elevation gradients. This will be measured with the Shannon diversity index (richness, evenness). All data analyses were conducted in R (R Development Core Team 2008).

Results:

Elevation/Gopher activity

The linear regression (LR, Fig. 3) showed that gopher activity significantly declined with elevation (p-value: 0.006576, slope: -0.01782). The analysis explained 9.4% (adjusted R-squared) of variance in the data.

Additionally, Gopher activity showed a humped-shaped relationship with elevation, peaking around 3200m in elevation. The quadratic linear regression (QLR, Fig. 4) had a significant correlation (p-value: 3.617e-05, equation: $y = -0.00006443x^2 + 0.4094x + -615.1$). It explained 25.1% (adjusted R-squared) of the variance in the model.

The corrected Akaike's information criterion (AICc) was used to determine whether the LR or the QLR was the better fitting model. The LR had an AICc of 581.3084 and the QLR was 569.8298, suggesting that the QLR is a better fitting model to the data because of the lower AICc value that is greater than the 2 plus the AICc value penalty for adding the quadratic term.

An ANCOVA (Fig. 5) was used to evaluate the variances in gopher disturbance between elevations, peaks, and also to see the relationship between peak identities to gopher disturbance between elevations. There was a significant variance between elevations (F-value: 11.674, p-value: 0.001199) and peak identities (F-value: 4.910, p-value: 0.000872). Also, peak identity's effect on gopher disturbance in relation to elevation was significant (F-value: 3.338, p-value: 0.010524).

Edaphic Factors & PCC

(NOTE: analysis of edaphic factors is ongoing and vegetation data collection is still in progress)

Discussion:

Does pocket gopher activity present an altitudinal pattern?

There was less gopher activity at lower elevations, the greatest activity was at middle elevations, and there was a decline near the highest elevations, describing the “mid-domain effect” (McCain 2004). Specie richness of other small mammals has been described by the “mid-domain effect” (McCain 2004). Gopher activity showed a hump-shaped altitudinal pattern which suggests that abiotic correlates of elevation may be important in predicting population distribution of *T. talpoides* (Owen 1990), and in turn can be considered part of the mechanisms that help define *T. talpoides*' spatial range (MacArthur 1984; Holt 2003; Sexton et al. 2009).

The abiotic factors that are associated with elevation (temperature, precipitation etc...) may be the main reason for the humped shaped pattern rather than the linear one (Dobzhansky 1950). Another study showed that prolonged heat exposure was fatal to pocket gophers (Gettinger 1975). The diminished activity in elevations around 2700m could be the

result of the lower elevations having warmer temperatures. The decreased amount of gopher activity in higher elevations (>3800m) can be explained through that pocket gophers can withstand cold temperatures, but their metabolism reaches a limit (Gettinger 1975). The explanations may also be coupled with pocket gophers' preference of soil depths (Hansen and Beck 1968).

Knowing species' ranges provides for a better understanding of niches and the area that they affect including the higher elevation portions (Case et al. 2013). Our study provides a firmer understanding of pocket gopher activities at high elevations compared to former studies that have focused on low elevation grasslands (~2500m) (e.g., Huntly and Inouye 1988; Case et al. 2013). As climate warming continues, there is a need to understand these ranges, so we can anticipate future shifts in the ranges (Parmesan and Yohe 2003; Root et al. 2003; Berteaux et al. 2004; Schellnhuber and Cramer 2006). The usual response of animals to an increase in temperature is to migrate towards cooler temperatures at higher elevations (Parmesan and Yohe 2003; Root et al. 2003; Berteaux et al. 2004; Schellnhuber and Cramer 2006). Increasing temperature in lower elevations has the potential to move the middle portion of the quadratic curve towards the end of the curve, making the relationship more linear (Gettinger 1975).

Altitudinal patterns of gopher disturbance were not consistent across the elevational gradients. Two of the six mountain peaks had a positive slope in comparison to the other four negative slopes. Gopher activity increased with elevation on two of the mountain peaks. The explanation for this trend, not excluding elevation, could be that the edaphic factors were more favorable as elevation increased. Pocket gophers have been shown to inhabit shallower alpine soils more than deeper soils at the same elevation, and at subalpine and grassland elevations

deeper soils are preferred to shallower ones (Hansen and Beck 1968). Avery's soil, above 3700m, was primarily comprised of scree (loose rock) making the ground continually shifting (personal observation).

Edaphic Factors & PCC

(NOTE: analysis of edaphic factors is ongoing and vegetation data collection is still in progress)

Conclusion:

Elevation/Gopher activity

Elevation can be correlated with the activity of *T. talpoides*. Their activity is described as a "mid-domain effect" having less activity near the ends and higher activity in the middle. As climate warming progresses, then the higher activity elevations may shift upwards in relation to the colder temperatures.

Edaphic Factors & PCC

(NOTE: analysis of edaphic factors is ongoing and vegetation data collection is still in progress)

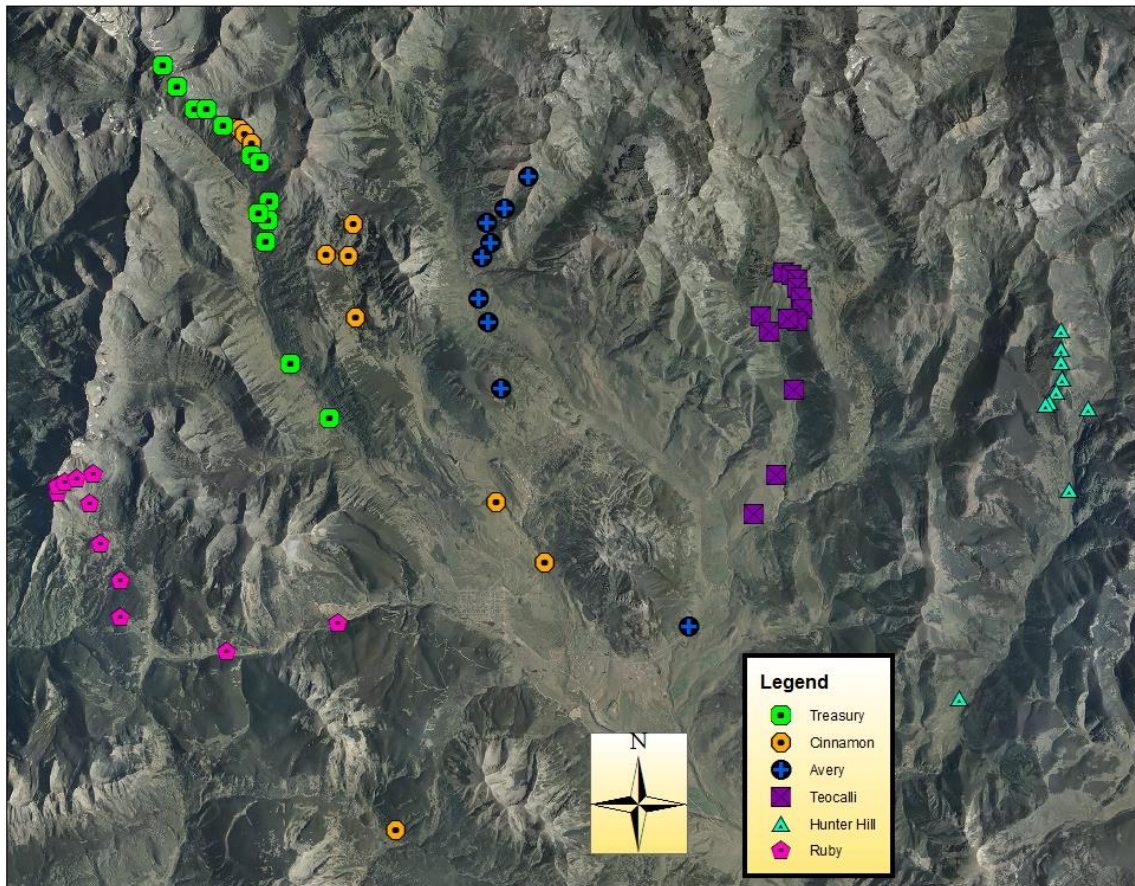


Fig. 1 – The map of the transects that were analyzed for gopher disturbance.

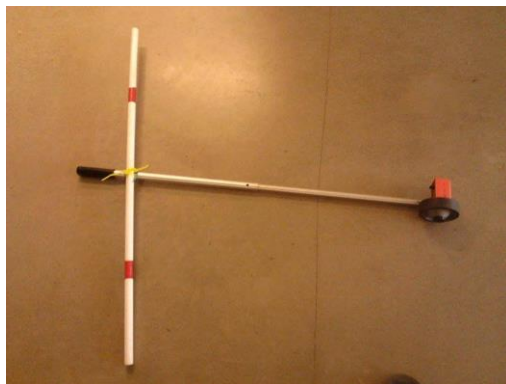


Fig. 2a,b- The rolatape that was used to measure the occurrence of pocket gopher disturbance.

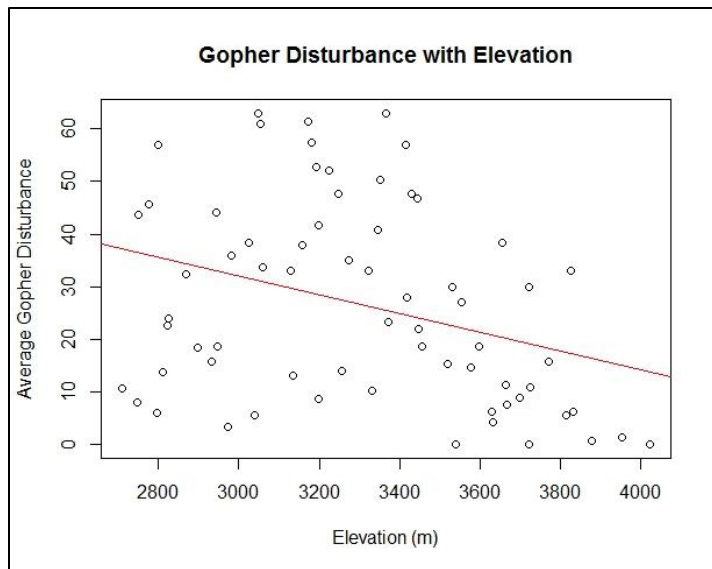


Fig. 3 – The linear regression showed that gopher activity significantly declined with elevation.

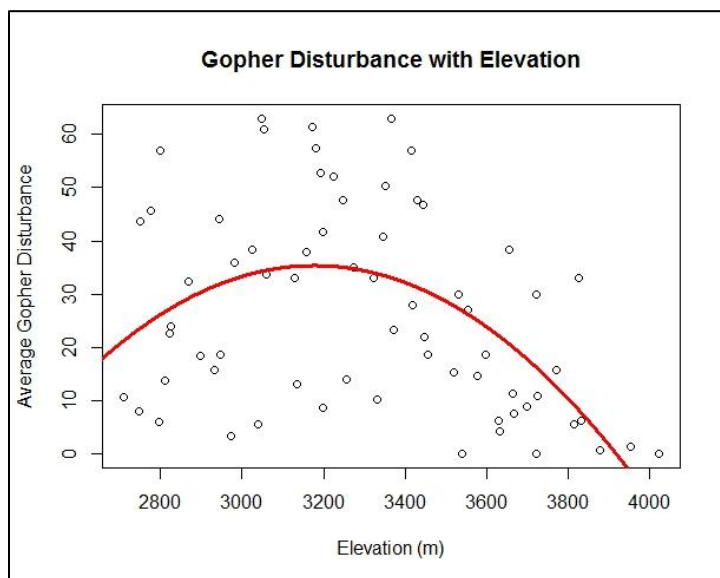


Fig. 4 – A quadratic linear regression showed a hump-shaped fit for the model where activity decreased at both high and low elevations and it peaked near 3200m.

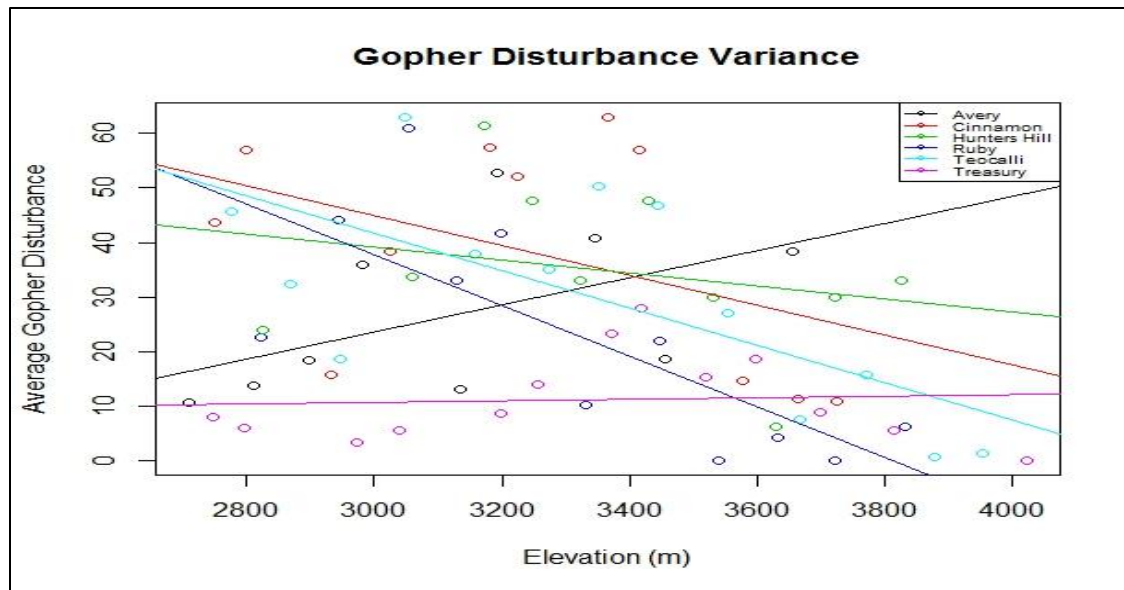


Fig. 5 – An ANCOVA showed that gopher activity varied between peaks.

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