Sediment, Gophers, and Time: A Model for the Origin and Persistence of Mima Mound—Vernal Pool Topography in the Great Central Valley

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ABSTRACT. Vernal pools are seasonal wetlands that harbor rare and endemic plants and animals. In California, vernal pools are often associated with Mima mounds, roughly circular soil mounds, found in grassland landscapes. The processes that form and maintain the mound-pool complexes have not yet been conclusively identified, even though such information is necessary to understand the effects that land use and climate change may have on the resilience and longevity of these important landscapes. One hypothesis for the origin and persistence of Mima mound—vernal pool systems proposes that pocket gophers (Rodentia: Geomyidae) maintain and possibly create the mounds by preferentially translocating soils towards mound centers as an adaptive response to perched water tables. The topographic characteristics and above-ground gopher activity of one of the largest remaining Mima mound—vernal pool systems in California were studied in order to investigate the gopher hypothesis. A detailed topographic survey of a 3,507 m^2 region was conducted near the city of Merced, CA. Downslope erosion rates off Mima mounds were estimated using a mass balance model that incorporates a diffusive sediment transport law. The median calculated net erosion rate was 15 cm of soil per 1,000 years, while the measured rate of above-ground gopher sediment movement was approximately 57 cm of soil per 1,000 years. Assuming that some portion of the gopher sediment movement is in an upslope direction, these results suggest that gopher soil transport may be large enough to compensate for erosion, and this activity may play a dominant role in maintaining Mima mound—vernal pool systems. The results of this study were used to guide the development of a quantitative model of gopher-driven sediment transport on Mima mound—vernal pool landscapes. This model will be used to infer the origin of the landscapes and the rates of processes critical to their continued functioning and will also help to determine, quantitatively, the role of burrowing animals as "keystone" species on these landscapes.

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INTRODUCTION

Mima mounds are dome-shaped soil mounds (up to 2 m high and 10-50 m in diameter) which were first identified on the Mima Prairie in the Puget Sound lowlands of Washington State and which are found in many locations on the western coast of North America (Cox, 1984; Dalquest and Scheffer, 1942). In addition, Mima-type mounds have been observed in nearly all states west of the Mississippi (Washburn, 1988), as well as in East (Cox and Gakahu, 1983) and South (Lovegrove and Siegfried, 1986) Africa and in Argentina (Cox and Roig, 1986). Mima mounds are often associated with adjacent, internally drained depressions called vernal pools, especially in the Great Central Valley of California. The mound-pool complex creates a unique seasonal set of wetlands that harbor endemic and endangered plants and aquatic species. As a result of agricultural development throughout much of the 20th century, these landscapes have been largely destroyed and now are the focus of an intensive biodiversity conservation effort. It should be noted that although Mima mound and vernal pool systems have been found to exist exclusively of each other, this study focuses on systems in which the two are colocated.

The origin of the Mima mound—vernal pool systems has long been controversial, with a range of theories proposed, including those that point to erosional (e.g., Cain, 1974), depositional (e.g., Collins, 1975), clay swelling (e.g., Hallsworth et al., 1955), animal (e.g., Dalquest and Scheffer, 1942), periglacial (e.g., Malde, 1964), or seismic (e.g., Berg, 1990) sources. The Fossorial Rodent Hypothesis (Dalquest and Scheffer, 1942), which is gaining widespread acceptance but has yet to be conclusively verified, posits a biologic mechanism for the mounds. Briefly, it is suspected that fossorial rodents, such as pocket gophers (Rodentia: Geomyiae), move soil directionally and build the mounds on more well drained areas of the landscape in order to protect themselves from shallow groundwater tables caused by impermeable underlying soil layers.

In this study, we conducted a preliminary investigation of rates of sediment movement in Mima mound landscapes in order to better understand their origin and maintenance, and, ultimately, to predict the effects of land use change and climate change on vernal pool ecosystems. Specifically, we aimed to quantify the role of soil movement by gophers and to test the hypothesis that the rate of upslope soil movement by these organisms is large enough to compensate for the rate of downslope soil movement driven largely by gravitational forces.

Background and Environmental Significance

Soil formation processes and hydrology are integral components of the Fossorial Rodent Hypothesis of Mima mound formation. As soils age, impermeable subsurface layers can develop (via processes such as ferrolysis, clay formation and translocation, and calcium carbonate accumulation, Hobson and Dahlgren, 1998) causing a seasonal perched water table to form near the land surface. According to the Fossorial Rodent Hypothesis, this near-surface water table prompts gophers to move sediment in order to construct (or maintain) soil mounds, which can be utilized as burrowing habitat, above the level of saturation.

Mima mounds are consistently correlated with geomorphic surfaces that are either old enough for such impermeable horizons to form or are underlain by bedrock. Smith and Verrill (1998) showed that vernal pool systems within California's Great Central Valley were correlated with specific soil, geologic formation, and landform types, and were predominantly found on the oldest mid to early Pleistocene to late Pliocene landforms—landforms which have had ample time to undergo pedogenesis and form underlying hardpans.

Several other key characteristics found in many Mima mound—vernal pool systems also support the Fossorial Rodent Hypothesis. A gopher-driven redistribution of soil should result in particle size sorting, and one notable feature of many Mima mound—vernal pool landscapes is a conspicuous gravel layer that underlies mounds, and which crops out or serves as the surface of the interlying vernal pools (Cox, 1984). These observations are consistent with the fact that gophers are limited in their transport of larger gravels and cobbles, which then tend to settle to the base of the biologically mixed surface zone. In addition, the mound—pool complexes generally occur only in regions that are inhabited by burrowing animals (Cox, 1984) or that have been inhabited in the recent past (e.g., Horwath and Johnson, 2006). Generally, a well-mixed A horizon is observed on the surface of the mounds and pools, indicating significant biological mixing.

The Fossorial Rodent Hypothesis of Mima mounds, if verified, would support the designation of gophers as keystone species in these mound—pool systems. If gophers are responsible for creating and/or maintaining the mound—pool topography, then their activities significantly impact the physical structure of their environment, influencing both the habitat of other species and a range of ecosystem processes, such as hydrology and nutrient cycling. As such, gophers could be classified as keystone species—specifically keystone habitat modifiers—in these systems. Any change in gopher populations could have a marked affect on the other species in the habitat.

Vernal pools are vital natural resources in California: they provide habitat to a wide range of species and are essential to maintaining California's biodiversity. Naturalists have identified more than one hundred species in California that live only in and around vernal pools (Wong, 2006). In California's Great Central Valley, approximately half of the crustacean species appear to be vernal pool endemics (King, 1996). Furthermore, the vernal pools in California are part of the Pacific flyway, and are important for the migration of several species of waterfowl (San Joaquin County Resource Conservation District, 2002).

Climate change could have a significant negative impact on Mima mound—vernal pool ecosystems, and this has been the focus of several studies (Bauder, 2005; Brooks, 2004; Pyke, 2004, 2005; Rice and Emery, 2003). For example, Pyke (2005) evaluated the hydrologic sensitivity of the vernal pools in California's Great Central Valley using both global and regional climate models and found that, at the local scale, the modeled climate changes could negatively impact branchiopod abundance by increasing the suitability of vernal pools for branchiopod predators.

However, to our knowledge, none of the vernal pool climate change studies has considered the effect of climate on the origin or maintenance of the pools themselves. A mechanistic understanding of how the mound—pool complexes form could provide valuable insight on the potential effects of climate change – especially if gopher populations change or relocate due to climate change. A recent study revealed a 50% decline in the population of pocket gophers during the Medieval Warm Period when compared with other, cooler periods (Hadly, 1997). If pocket gophers are the active agents that form and/or maintain the mound—pool systems, then it is imperative that we study the role of gophers in more detail and integrate the resulting information into vernal pool climate change studies.

In the past decade, more than 30 million dollars have been spent by the State of California and non-governmental organizations (NGOs) to set aside these landscapes in Merced County (UC Merced and The Nature Conservancy, 2002), yet no funds have been allocated to understand the processes which form and maintain the vernal pool—Mima mound landscapes. Additionally, one of the chief strategies for mitigating development is the construction of artificial vernal pools (King, 1998). For example, the Del Sol Vernal Pool Enhancement Plan was implemented in 1986. Under this plan, several governmental and non-governmental agencies collaborated to enhance, restore, and create a 4 ha area of vernal pool habitat near Santa Barbara, California (Ferren, 2006). Although endeavors such as these have achieved some degree of success, the long-term management and reconstruction of vernal pools—and their rare plants and animals—can only effectively proceed if we understand the processes which produce them in nature.

METHODS

Study Site

The study was conducted on one of the largest remaining tracts of Mima mound—vernal pool systems in California, in the vicinity of the University of California at Merced (UC Merced, 2005; Vollmar, 2002) (Figure 1). The site is located on a nearly level remnant of the China Hat member of the Laguna Formation, a Plio-Pleistocene terrace that is part of a regional chronosequence, a series of river terraces that span nearly 4 million years of time. The Laguna Formation, of which the China Hat member is the highest exposure, is composed of gravelly, granitic alluvium (Marchand, 1976), and is possibly the oldest level landscape in California. The soils on the Laguna formation are classified as Palexeralfs and Durixeralfs of the Corning and Redding series, respectively (Arkley, 1962). These soils are highly weathered, with large quantities of clay and cementing agents. The climate is Mediterranean, characterized by cool, wet winters and hot, dry summers, with an average annual rainfall of 31 cm and average temperature of 16^{o}C (Hoare, 2005). Annual grasslands, dominated by non-native grasses, cover the landscape, which has been grazed for over a century (Vollmar, 2002). The specific site examined here was chosen because of its robust distribution of Mima mounds and vernal pools, generally level topography, relatively minor observable impact due to human activities, and active gopher burrowing.

Field Methods

A comprehensive topographic survey of the site was conducted using a Trimble® differential Global Positioning System (GPS). Positions were continuously recorded every 3 seconds, and the area was surveyed using a grid-based approach such that each mound and inter-mound area was sufficiently represented. The small mounds generated by gopher activity (herein referred to as gopher mounds—as opposed to Mima mounds) were identified, flagged, and their locations were recorded using GPS. Gopher mounds were identified as loose piles of soil on the ground surface, with no vegetation growing on them. If any uncertainty existed about whether a mound was caused by gopher activity (or by activity during an earlier season), it was not flagged. We note that there is a relatively clear distinction between "fresh" mounds and older mounds (mounds that had been subject to a rain event or events) based on the degree of hardening of soil on the gopher mound surface. Thus, we believe that the number of mounds reported is a minimum, although it is possible that older mounds are misidentified as younger ones.

Measurements of gopher activity were made in both November 2005 and May 2006. At both times, approximately 25 mounds were randomly selected and

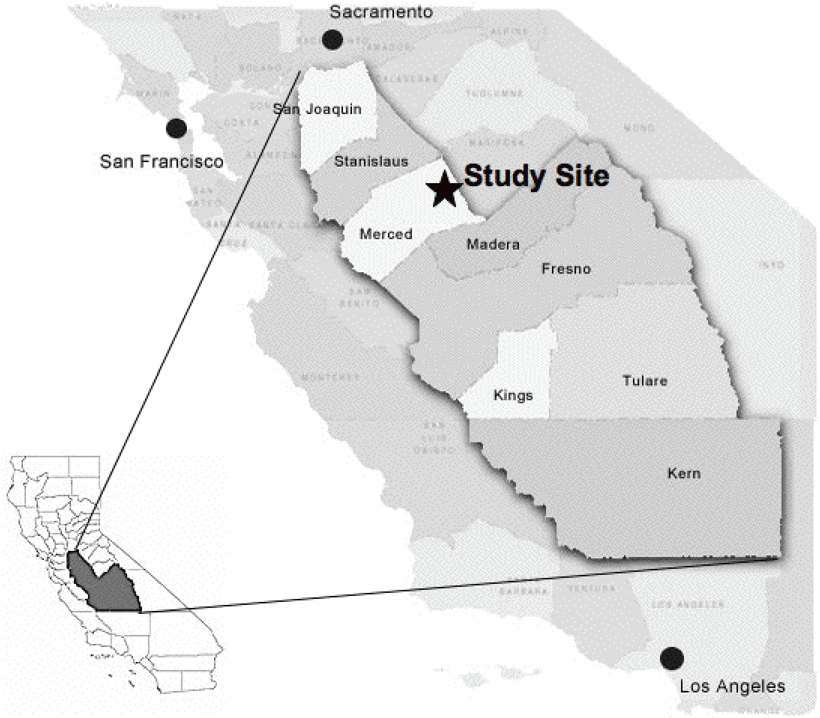

FIGURE 1. Location map showing the study site in central California. Map after CCVEDC (2006). The site is centered near 37°23'53"N and 120°23'28"W, in the northwest quarter of Section 24 of the Yosemite Lake USGS Quadrangle. It is located on a portion of the Laguna formation and bears soils primarily of the Corning series.

weighed with a field spring balance in order to obtain estimates of mass movement associated with burrowing.

Mapping Procedures

All curvature and erosion calculations were performed, using data gridded from survey points by Kriging using SURFER® software. Topographic, curvature, and erosion maps were created and subsequent calculations were performed using grid sizes of 0.5 m, 3 m, and 3 m, respectively. The specified grid sizes were chosen because they minimized local data variations.

Mound concentrations were based on the abundance of mounds in the survey area. We note that not all of the survey area had the gopher mound distribution mapped due to time constraints, and these uncharacterized areas are not used to calculate gopher densities.

Theoretical Framework

In order to quantitatively examine the landscape, we begin with the observation that Mima mounds are essentially miniature, gentle, soil-mantled hillslopes. Gentle hillslopes in California, which have been the subject of much geomorphic research, are characterized by convex upslope regions that grade downward towards concave footslopes. Mima mounds in this study have a range of (convex) curvature values (0-0.16 m^{-1}, average = 0.04 m^{-1}) similar to, but generally greater than those of larger hillslopes, such as Tennessee Valley, northern California (0-0.04 m^{-1}) (Heimsath et al., 1997) and such as those found in the Atacama Desert, Chile (0-0.05 m^{-1}) (J. Owen, Soil Scientist, UC Berkeley, personal communication, 2006). These topographic similarities support the application of geomorphological principles to Mima mound—vernal pool systems.

Sediment transport on convex hillslopes such as those discussed above is commonly characterized as a slope-dependent process, driven, in this setting, by biological movement of soil material which is slowly transported in a net downslope direction by gravity. (In other environments the slope-dependent transport can be driven by shrink-swell cycles.) The following diffusive transport law, originally introduced by Davis (1892) and Gilbert (1909) has been used by several researchers, (e.g., Dietrich et al., 1995; Heimsath et al., 1997) to represent biogenic transport on hillslopes:

$$q_s = -K \nabla z \qquad (1)$$

where the sediment flux q_s ((length)^2(time)$^{-1}$) is proportional to the hillslope gradient ∇z, and K is equivalent to a diffusion coefficient with dimensions (length)^2(time)$^{-1}$. Several methods have been developed to estimate K, including those that use hillslope curvature data or morphological dating techniques, (Fernandes and Dietrich, 1997). Here, using values derived for systems similar to our field area, we assume that K is both spatially and temporally constant and apply K values ranging from 25-75 cm^{2}yr^{-1} in order to calculate a range of likely erosion rates. This range of values is representative of those (mean = 49 ± 37 cm^{2}yr^{-1}) that have been determined for grassland sites in northern California where gopher activity is the main transporter of sediment (Dietrich et al., 1995; Heimsath et al., 1997; McKean et al., 1993; Reneau, 1988).

The mass conservation equation for soil thickness used by Heimsath et al. (1997) to derive a soil production function for hillslopes was used in this study as an initial framework for describing the development and maintenance of the mounds. The conservation equation is expressed as:

$$\rho_s \frac{\partial h}{\partial t} = -\rho_r \frac{\partial e}{\partial t} - \rho_s \nabla \cdot q_s \qquad (2)$$

where ρ_s and ρ_r represent densities of soil and rock, respectively, h is the soil thickness, e is the elevation of the bedrock-soil interface, and q_s is the sediment transport vector. Here, $\rho_r \frac{\partial e}{\partial t}$ represents the production of soil from bedrock and $\rho_s \nabla \cdot q_s$ represents soil removal from the column.

We consider this expression in terms of the Mima mound—vernal pool systems. If Mima mounds are enduring features, then they exist in an approximately steady state environment and the soil thickness, h, remains constant. In Mima mound landscapes, the “soil” implied by this concept is the actively cycling soil layer—the A horizon(s), which are those most subject to biological mixing in California grasslands (Johnson et al., 2005). Thus, at steady state, $\partial h/\partial t \approx 0$, and erosion (E) and soil production (P) are balanced. Solving for $\partial e/\partial t$ and combining equations (1) and (2), we find that the soil production rate (P) must thus be equal to $-(\rho_s/\rho_r) K \nabla^2 z$ under steady state conditions. The term $-(\rho_s/\rho_r) K \nabla^2 z$ describes the mass of soil removed from a given slope area per unit time, which is equivalent to the more general term for erosion (E):

$$E = -(\rho_s/\rho_r) K \nabla^2 z \qquad (3)$$

Our measurements allow us to calculate the spatial distribution of erosion rates across mound—pool landscapes. As mentioned, K values were chosen from nearby ecosystems. The ratio of soil bulk density to rock bulk density (ρ_s/ρ_r) was assumed to be equal to 0.75, a ratio close to the median value of a compilation of values reported by Reichman and Seabloom (2002), who stated that the density of material in gopher mounds is generally 10-40% lower than the underlying consolidated soil. Finally, curvature values were calculated using data from GPS measurements, and average erosion rates for the entire survey area were calculated using a site-wide average mound curvature value of 0.04 m^{-1}. This average curvature value was calculated using the range in values obtained during the topographic portion of the survey and did not include the curvatures at the locations of individual gopher mounds so as to avoid a bias towards areas of burrowing.

The rate of gopher sediment movement, assumed to at least partially represent soil production on the slopes, was estimated using measurements of gopher activity and several key assumptions. The total volume of gopher mounds across the site was calculated using the average individual gopher mound mass, the average concentration of gopher mounds on the active areas (active areas were designated by identifying clusters of gopher activity), and the average of twenty-four soil bulk densities measured for the Laguna Formation (Harden, 1987). The gopher mound masses were not corrected for soil moisture content. The average rate of above-ground gopher sediment movement was estimated using the assumption that the measured gopher mound material had been produced within the past six months. We make this assumption based on meteorological data collected at nearby weather stations (NOAA, 2007), which show that substantial rain events occurred within the six months previous to each of the surveys. As mentioned above, we maintain that it is possible to distinguish between "fresh" mounds and older mounds based on the degree of hardening of soil (due to drying after a rain event) and re-establishment of plants on the gopher mounds. All reported gopher mound volume, mass, and concentration approximations are the average of the two annual measurements.

RESULTS

A 3,507 m^2 area was surveyed and mapped. The topographic map of the survey area (which included twelve full Mima mounds) is shown in Figure 2. Calculations of total Mima mound surface area and volume yielded 537 m^2 and 220 m^3, respectively (assuming a common baseline at the bottom of the mounds). Because the landform remnant was small and bounded by nearby escarpments, the intermound areas were generally not closed. Intermound areas were frequently mantled with varying concentrations of cobbles, similar to many other vernal pools on the Laguna Formation. In addition, a coring into the intermound area revealed a dense, clay-rich material, immediately near the surface, which is also common to vernal pools in the region.

A key focus of the work was to quantify the abundance and distribution of gopher mounds. An average of 255 gopher mounds was calculated between the two survey periods. Average gopher mound mass was 1.64 kg (Figure 3) and average gopher mound concentrations ranged from 0.089 mounds m^{-2} over the entire site to 0.297 mounds m^{-2} over areas of active gopher burrowing. Average individual gopher mound volume was estimated to be 963 cm^3, while the total volume of gopher mounds on the surveyed area was approximately 0.25 m^3. In general, the gopher mounds were found on convex rather than concave portions of the landscape (Figure 4). Based on a November/May average, approximately 55% of the gopher mounds were found on convex areas, 42% were found on concave areas, and 3% were found on planar surfaces. Note that only 215 of the 241 November burrows and only 212 of the 268 May burrows were positively assigned to a curvature class due to edge effects of the gridding process. On the convex portions, the gopher mounds were predominantly on the side slopes of the Mima mounds, rather than on the summits. Mounds were observed up to 90 cm above local, intermound depressions (a conservative estimate). In the concave depressions, the gopher mound concentration was near zero close to the absolute bottom of the intermound areas and most burrows in the concave areas were found roughly 30 cm above the basin bottoms. Gopher mound concentrations and masses did not differ significantly between November 2005 and May 2006. The locations of the gopher mounds between November 2005 and May 2006 generally occurred in the same region, with small shifts (Figure 2). There was, however, a difference between the mound curvature distributions in the two time periods. In November 2005, several more mounds were found in the extreme convex and concave portions of the site (> 0.06 m^{-1}). In May 2006, the mounds were not found on these highly convex and concave areas, but instead were concentrated on the planar slopes.

The average curvature of the Mima mounds was 0.04 m^{-1}. Using this average value, erosion rates (off of the Mima mounds) ($E = -(\rho_s/\rho_r)\, K\, \nabla^2 z$) ranged from 8-23 cm/1,000 yr (based on the previously mentioned range of K values). This range of erosion rates represents erosion rates off of the mounds and not erosion rates across the entire site. The estimated rate of above-ground sediment gopher sediment movement was 49 cm/1,000 yr in November 2005; 66 cm/1,000 yr in May 2006; and 57 cm/1,000 yr for the two-season average.

The results of field measurements and numerical calculations are summarized in Table 1.

DISCUSSION

While a gopher-derived origin for Mima mounds in California has long enjoyed some support, this project – while preliminary in nature – provides the first estimates of rates of processes relevant to both downwearing and regeneration of mounds on geological time scales. Experimental work by Cox and Allen (1987) showed that gophers directionally move soil, providing some of the first substantial evidence that they engage in constructional processes. However, gopher sediment movement can only be a viable process for the presence of Mima mounds if its rate is reasonably close to the rates of downslope sediment transport that affect any soil-mantled slope on earth. Thus, here we are able to quantify both these fluxes with varying degrees of certainty, and we find that, as a first approximation, gopher sediment movement can indeed be comparable to erosion. Below, we discuss our data in relation to other California environments, discuss uncertainties, and pose questions and challenges for further work.

The novel contribution of this project is the estimation of soil erosion rates off the Mima mounds. Mounds cannot be static features. They are inhabited by ground squirrels, ants, and other burrowing or soil-disturbing organisms and subject to gravity which drives the disturbed sediment downslope.

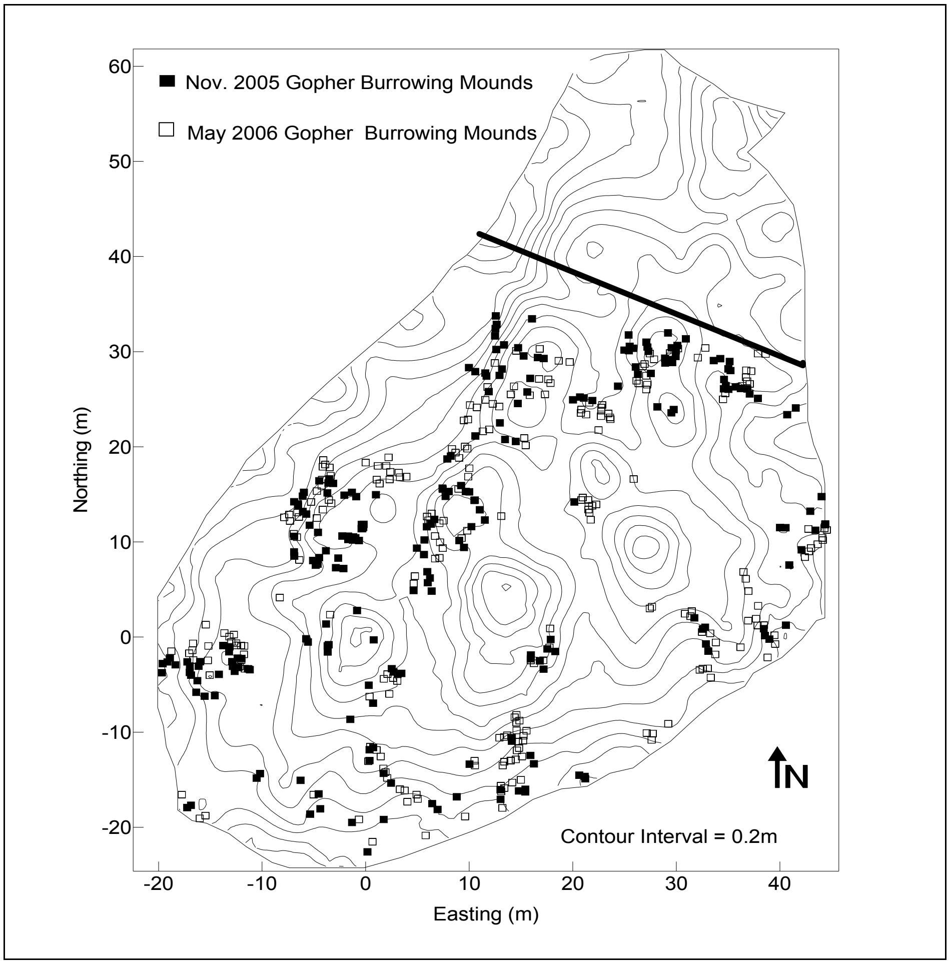

FIGURE 2. Contour map showing the study site, distribution of Mima mounds, and November 2005 and May 2006 above-ground gopher activity. Gopher activity above the solid line was not included in the gopher mound survey. Note the relative absence of gopher activity on the two largest Mima mounds.

(Note that the erosion rates off of the overall landscape are significantly inhibited by the underlying hardpan, but off of the mounds, downslope erosion occurs due to biological activity.) Our erosion rates, simply interpreted, suggest that Mima mounds would level out by natural erosive processes on 10^3 to 10^4 year time scales (the true rate of leveling would decline with time due to a progressive reduction in mound curvature). The erosion rates estimated for the Mima mounds (8-23 cm/1,000 yr) were slightly higher than the erosion rates (2-10 cm/1,000 yr) estimated by Heimsath et al. (1997) for Tennessee Valley, California. These differences are primarily attributable to the higher curvature values at the Mima mound site.

Another potential source for variation in erosion values is that, as discussed above, the actual ρ_s/ρ_r value may differ from the median value used (0.75). However, even if the extreme values (0.9 and 0.6) reported by Reichmann and Seabloom (2002) are applied, the endmembers of the possible erosion values are 6 and 27 cm/1,000 yr, which are not widely different than the reported values.

To our knowledge, no previous measures of the rate of gopher activity have been made in the San Joaquin region near our site. The gopher mound concentrations at this site (0.089-0.287 mounds m^{-2}) are lower than the concentrations Black and Montgomery (1991) measured for a site in Marin County, California (0.16-2.88 mounds m^{-2}). One important reason for these differences is climate: Marin is both cooler and wetter. Several investigations (e.g., Cox and Allen, 1987) have concluded that gophers are significantly more active during wet seasons in what appears to be a response to increased soil moisture levels. In addition, more food is available when conditions are wetter, which could also lead to in-

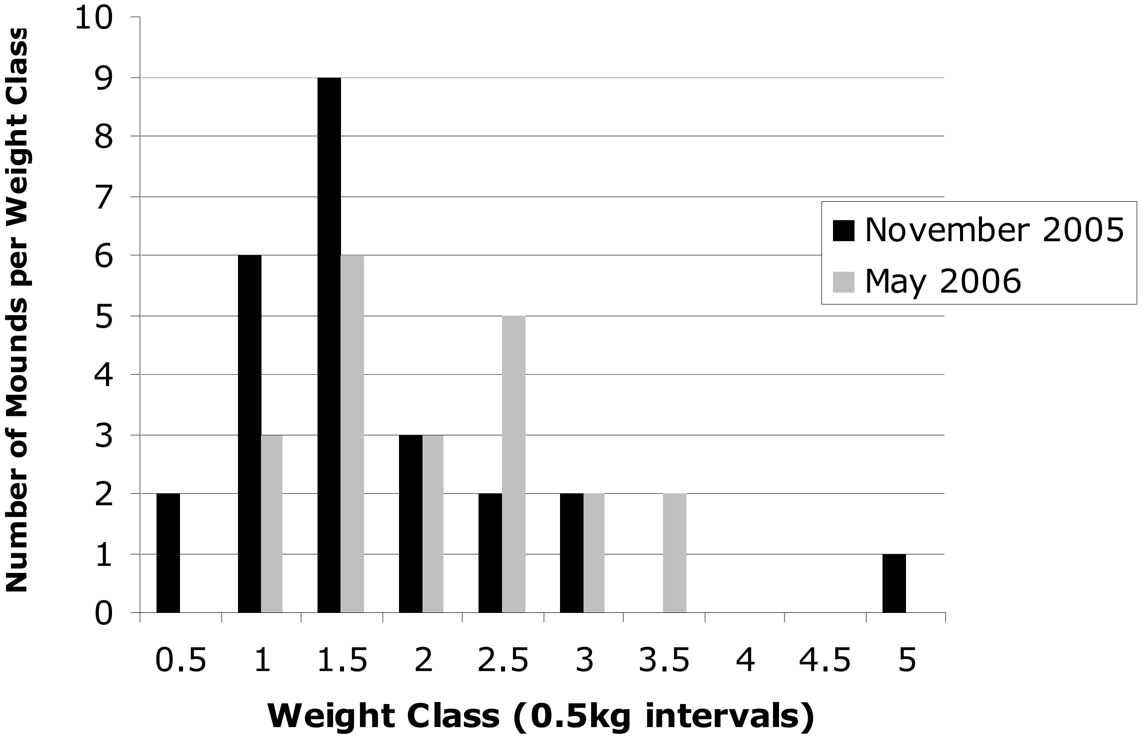

FIGURE 3. Gopher mound mass distribution showing twenty-five mass measurements taken in November 2005 and twenty-one mass measurements taken in May 2006. Average mass over the two time periods is 1,638 grams.

creased gopher activity during that time (Huntly and Inouye, 1988).

Measurement of gopher activity is complicated by potentially inaccurate counting of gopher mounds. For instance, we may have missed mounds due to grass re-growth or leveling by rainfall. On the other hand, gopher mounds have been observed to exist without vegetation for longer than three years (Holland, personal communication, 2007), and thus it is possible that we double-counted mounds between the two survey periods. As mentioned previously, we regard our counting of mounds to be conservative in that we only counted mounds composed of vegetation-free, loose soil. Thus we consider the number of mounds reported to be a minimum, but it should be noted that more frequent measurements of gopher activity should be made in order to infer more accurate information about gopher activity. However, regardless of our inability to capture temporal variations in gopher activity, our focus here on net activity provides an important constraint on their long-term ability to move soil. Another factor which may affect the accuracy of our gopher activity measurements is the soil bulk density used for the site, based on an average of values for the region (Harden, 1987). This value was probably overestimated because, as mentioned, the action of burrowing out and redepositing the soil at the surface generally decreases the density of the gopher mound material (Gabet et al., 2003; Reichmann and Seabloom, 2002). For the aforementioned reasons, mound concentrations, total gopher mound volumes, and gopher activity rates are probably underestimated.

The gopher activity and erosion rates are the same order of magnitude (57 cm/1,000 yr and 8-23 cm/1,000 yr, respectively), suggesting that gophers may be active agents in maintaining the mound—pool complexes, if, indeed they participate in directional sediment transport as Cox and Allen's (1987) results suggest. Determining how the erosion and gopher activity rates are related will require a more clear understanding of directional sediment movement by gophers. Most geomorphic studies of soil creep by biological processes assume (or show empirically) that sediment movement by biota is randomly oriented, but on hillslopes is net downward due to the force of gravity (Fernandes and Dietrich, 1997; Gabet, 2000). However, Cox and Allen (1987) conducted experiments with soil plugs containing metal markers and found that for Mima mounds in southern California, the net movement of

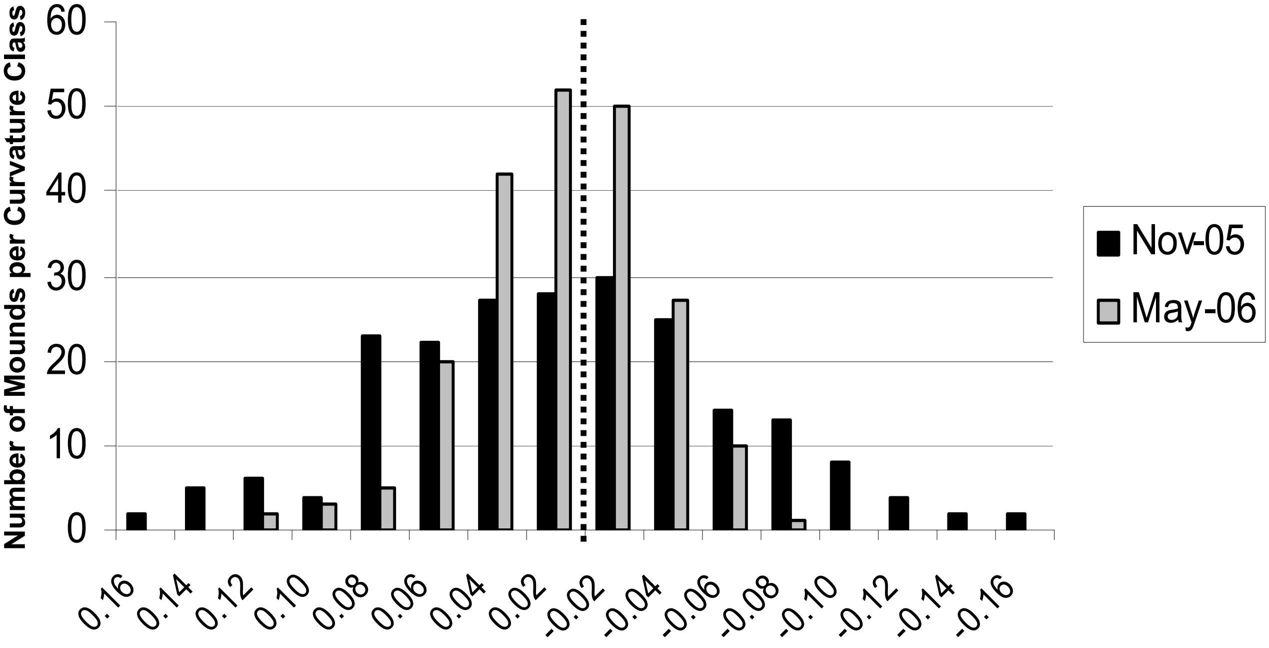

FIGURE 4. Gopher mound curvature distribution showing relative proportions of gopher burrowing mounds found on convex areas and concave areas for November 2005 and May 2006. On average across the two time periods, 55% of the gopher mounds were found on convex areas, 42% were found on concave areas, and 3% of mounds were found on level areas with level being defined as areas with curvature magnitudes < 0.002.

sediment by gophers was moundward presumably in response to hydrological conditions in the inter-mound, vernal pool region. Clearly, understanding the trajectory of gopher sediment movement in the Great Valley is important to demonstrate the generality of Cox and Allen's findings; however, the spatial location of the gopher mounds found here certainly suggests a topographic control on their distribution, and as a result, the direction of their movement.

While gophers may expend energy to "move soil uphill," the placement of loose soil on the surface of mounds may, in large part, contribute to the net downward erosion driven by gravity. Several studies have shown that downslope sediment transport in certain areas is facilitated by the presence of gopher mounds (Black and Montgomery, 1991; Gabet, 2000; Litaor et al., 1996; Sherrod and Seastedt, 2001). Gabet (2000) and Yoo et al. (2005) found that a simple linear diffusive transport model, as used here, does not completely represent biogenic sediment transport at two sites in California. Thus, several key modifications of the mass balance model will likely be required for it to be fully applicable to Mima mounds and vernal pools in the Great Central Valley. However, the linear approach chosen here provides first order constraints on the magnitude of the rates of these processes.

Roering et al. (1999) developed a nonlinear diffusive sediment transport model which differentiates the downslope and upslope components of sediment flux. Roering et al.'s model works under the assumption that (due to the driving force of gravity) downslope sediment transport is greater than upslope sediment transport, but if the gophers in this study move sediment directionally, then the sediment transport terms will need to be modified accordingly. Combining Dietrich et al.'s (1995) and Roering et al.'s (1999) work results in the following expression describing Mima mound form and development:

$$\rho_s \frac{\partial h}{\partial t} = -\rho_s \nabla \cdot q_{gross,downward} + \rho_s \nabla \cdot q_{gross,upward} \quad (4)$$

where $q_{gross,downward}$ is the sum of downward sediment transport, and $q_{gross,upward}$ is the sum of upward sediment transport.

This model can be used to more clearly infer erosion rates, which can then be compared to the measured rates of biological processes. The rate, and form, of the upslope transport term must be determined by

TABLE 1A-D. Data summary highlighting the physical characteristics and sediment transport processes of a Mima mound—vernal pool landscape near Merced, California. Note that gopher mound masses were not corrected for soil moisture content. Surface area of active gopher areas was estimated by designating and then measuring areas in which there are distinguishable clusters of gopher activity.

1A. Gopher mounds

	November 2005	May 2006	2005-2006 Average
Number of mounds in survey area	241	268	255
Number of mounds massed	25	21	23
Average mound mass (g)	1470	1800	1638
Average soil bulk density (g/cm^3) (Harden, 1987)	1.70	1.70	1.70
Average individual mound volume (cm^3)	868	1059	963
Total site-wide volume of gopher mounds (m^3)	0.21	0.28	0.25
Surface area of gopher survey (m^2)	2869	2869	2869
Surface area of active gopher areas (m^2)	858	858	858
Mound concentration over surveyed area (m^{-2})	0.084	0.093	0.089
Mound concentration over active area (m^{-2})	0.281	0.312	0.297
Percentage of mounds on convex areas	54	56	55
Percentage of mounds on level areas ($\lvert\nabla^2 z\rvert < 0.002$)	1	5	3
Percentage of mounds on concave areas	45	39	42

1B. Mima mounds

Number of full mounds surveyed	12
Total volume of mounds (m^3)	220
Total surface area of mounds (m^2)	537
Average slope of mound (site-wide)	0.096

1C. Erosion rates

Average negative curvature of Mima mounds (1/m)	0.04
Erosion: $-(\rho_s/\rho_r)\ K\ \nabla^2 z$ (cm/1,000 yr) $K = 25$ cm^2/yr, $(\rho_s/\rho_r) = 0.75$	8
Erosion: $-(\rho_s/\rho_r)\ K\ \nabla^2 z$ (cm/1,000 yr) $K = 50$ m^2/yr, $(\rho_s/\rho_r) = 0.75$	15
Erosion: $-(\rho_s/\rho_r)\ K\ \nabla^2 z$ (cm/1,000 yr) $K = 75$ cm^2/yr, $(\rho_s/\rho_r) = 0.75$	23

1D. Gopher activity rates

Volume of gopher mounds (m^3)	0.25
Area of gopher activity (m^2)	858
Assumed time period of gopher activity (yr)	0.5
Rate of gopher activity (cm/1,000 yr)	57

field measurements of soil movement by gophers. Therefore, our future work will involve surveying in new gopher mounds on a periodic basis, and weighing them. In addition, Cox and Allen's methods (1987) will be used, along with short-lived isotopes and Mima mound cross-section observations to determine the dynamics of gopher-driven sediment transport. The resultant information will be used to further constrain sediment transport values, q_s.

CONCLUSIONS

One of the vexing, and certainly interesting, questions of the ancient Great Valley grasslands is the origin of the upland Mima mounds and vernal pools and how they are maintained over time. In grassland habitat where the soil surface is likely mixed by burrowing animals, insects, and plant roots every several hundred years, the maintenance of strongly convex mounds with relatively soil-free, gravel-filled vernal pools is not only puzzling, but points to the role of some (very) active restorative processes that maintain this fascinating landscape. Here, we applied recent advances in hillslope geomorphology to place reasonable limits on the rate at which the mounds are likely being eroded by gravity-driven processes, and we then compared these rates to very short-term measurements of soil movement by gophers to determine if biological movement of soil is at all a plausible mechanism for the maintenance and/or formation of the mounds. We found that (1) erosion rates off of the mounds range from 8-23 cm/1,000 yr, and (2) the rate of above-ground sediment movement by gophers was, on average, 57 cm/1,000 yr. Even taking into account the potential variability in the parameters used to constrain these rates, the order-of-magnitude similarity points to gophers playing a significant role in sediment transport in these landscapes.

Our preliminary analysis contains numerous assumptions and uncertainties, the most important being the direction which the observed gopher mounds on the land surface have traveled prior to being deposited. Previous work suggests upslope transport, and the distribution of gopher mounds clearly indicates gophers do not inhabit the intermound areas, but instead predominantly reside within the well-drained, convex areas.

Paradoxically, the placement of loose soil on the land surface by gophers is likely an important contributor to the net downslope movement of soil by gravity. Thus, the gophers may be the key agents in a complex pattern of sediment movement. If the gophers are indeed the forces that maintain the Mima mound terrain, then their very presence is required for the long-term existence of this unusual and diverse ecosystem. Management and/or climate changes that reduce or eliminate these organisms would cause, based on reasonable estimates of erosion rates, the complete leveling of the landscape on the order of a few thousand years. As such, the origin of Mima mound—vernal pool systems is of great ecological, as well as geomorphic interest and deserves additional quantitative research.

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