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Pedologic-biologic feedbacks on the Merced River chronosequence: The role of pocket gophers (*Thomomys bottae*) in Mima mound-vernal pool ecosystems of the San Joaquin Valley

by

Sarah Elizabeth Reed

A dissertation submitted in partial satisfaction of the requirements for the degree of Doctor of Philosophy in Environmental Science, Policy, and Management in the Graduate Division of the University of California, Berkeley

Committee in charge:

Professor Ronald Amundson, Chair
Professor Maggi Kelly
Professor William Dietrich

Fall 2013
Pedologic-biologic feedbacks on the Merced River chronosequence: The role of pocket gophers (*Thomomys bottae*) in Mima mound-vernal pool ecosystems of the San Joaquin Valley

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Abstract

Pedologic-biologic feedbacks on the Merced River chronosequence: The role of pocket gophers (Thomomys bottae) in Mima mound-vernal pool ecosystems of the San Joaquin Valley

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Sarah Elizabeth Reed

Doctor of Philosophy in Environmental Science, Policy, and Management

University of California, Berkeley

Professor Ronald Amundson, Chair

Distinctive Mima mound topography, found on all continents except Antarctica, has long inspired intense interest, both because of the uncertainty surrounding its origin, as well as the rich biodiversity often found in the adjacent depressional vernal pool wetlands. Emerging from the array of explanations proposed, a biological mechanism for mound formation has steadily gained strength. According to this model, subterranean animals such as pocket gophers build the small hillocks as a response to changes in soil thickness and permeability caused by pedogenesis (soil formation). However, the precise mechanics of the hypothesis – how soil weathering leads to changes in gopher soil movement and how the modified soil movement leads to the widespread Mima mound features – are not understood. To address this issue, this thesis presents three related efforts to document and explain Mima mound morphology and to elucidate the linkages between soil formation processes, mound form and distribution, and biotic sediment transport. The research targets the effects of pedogenesis by focusing on a set of alluvial terraces in the San Joaquin Valley of California, a chronosequence which ranges in age from a few thousand to a few million years old. In the first portion of the study, I designed a custom algorithm which automatically identifies Mima mounds from LIDAR (light detection and ranging) data in order to analyze the morphology and spatial patterns of the microtopography across the soil age gradient. I demonstrate that mound size changes systematically with soil age and with depth to a restrictive layer, consistent with the predictions of the biologic model. Further, I show that the nearly quarter-million mounds in the study are distributed in a highly regular pattern, on scales consistent with the home range of pocket gophers, adding further support to the proposal that gophers created the topography. In the second part of this dissertation, I developed a method to use radio frequency identification tags (as a proxy for soil particles) and periodic aboveground mapping of gopher soil movement to quantify gopher sediment transport vectors on each chronosequence surface. I found that gophers on Mima mounds move soil uphill and towards the center of mounds, and I show that this moundward tendency increases with soil age.
and the environmental pressure caused by soil formation over long time periods. Third, I combined the morphometric measurements with the sediment transport data from the first two parts of the study and developed a sediment transport model which estimates mound erosion and swale deposition rates. If the Mima mounds are steady-state landscape features, erosion must be balanced by a restorative upslope transport. I show that the erosion rates estimated for this study are largely counteracted by the observed rates of sediment mounding via pocket gopher burrowing, supporting the notion that bioturbation plays a dominant role in maintaining Mima mound terrain. Finally, I use LIDAR measurements and results from published gopher physiology research to develop a model that approximates the energy required for the formation of Mima mounds (shearing, pushing, and uplifting soil) and their maintenance (counteractions to erosion). This energy estimate was compared to estimates of energy available to gopher populations in the region. The results indicate that gophers have ample energy to build typical Mima mounds in as little as 100 years, thus strongly supporting a biotic mechanism of Mima mound development and maintenance.
Dedicated in loving memory of Bradley Edward Rozman

Stará láska nerezaví
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Chapter 1

Introduction

One of the most visually stunning, and scientifically puzzling, geologic features of North America are the small rounded hillocks called Mima mounds. While an individual mound is relatively inconspicuous (ranging from 1 to 50 m in diameter and 0.1 to 2 m tall), considered in aggregate the mounds cover large portions of North America (Figure 1.1), are aesthetically peculiar, and have inspired a heated debate for nearly two centuries (Johnson and Horwath Burnham, 2012). The first known writings on Mima mounds are the 1804 journals of Dunbar, who attributed the mounds of the Bayou des Buttes in Louisiana to the work of Native Americans. Since that time, numerous geologists, biologists and other scientists have puzzled over their origin. The diversity of explanations is remarkable – over 30 hypotheses have been proposed. However, scientists have not reached a consensus on the mounds' origin. For example, geologist G.K. Gilbert (1875) attributed their origin to animals, while Harlan Bretz (1913) proposed that the mounds are caused by debris filling in the holes in melting ice.

Alfred Wallace (1877), the co-founder of the theory of evolution, suggested the mounds of California were debris left behind from glacial meltwaters. He relays a usefully vivid description of the mounds:

[The mounds] may be represented on a small scale by covering the bottom of a large flat dish with eggs distributed so that their longer axes shall lie at various angles with one another, and then filling the dish with fine sand to a little more than half the height of the eggs. The surface of the sand and of those parts of the eggs which rise above it, gives a fair representation of hogwallow land. The mounds, which are represented by the eggs, vary from two to five feet in height, and from ten to thirty feet in diameter; some being nearly circular, some oval, while others are more irregular in shape. Those near the foothills are the largest, and they gradually diminish in size as they extend out into the plain. [Emphasis mine.]

The observation that the mounds decrease in size from foothill to the lower elevation plains serves as the main organizational structure for this thesis. I focus my study on a suite of soils in California which stretch from the foothills of the Sierra Nevada to the level surfaces of the Central Valley and which range in age from a few thousand to a few million years. As a chronologic sequence of soils (a chronosequence), they systematically vary in degree of soil
weathering, as a result of varying exposure to the elements. By designing the study around this age gradient, I strongly contribute to the growing evidence of a biologic hypothesis of mound origin and begin to unravel the linkages between soil formation processes, mound morphology, and animal behavior.

1.1 Background

1.1.1 Hypotheses of Mima mound origin

The various hypotheses of Mima mound formation fall into five general categories: erosional, depositional, seismic, biologic, and shrink-swell. Numerous explanations are based on fluvial or aeolian differential erosion or deposition in which vegetation such as shrubs act as anchors to retain sediment (Gabb, 1877; Kinahan, 1877; Hilgard, 1905 (for mounds in California); Rich, 1934; Page, 1977; Washburn, 1988; Rostagno and del Valle, 1988; Cramer et al., 2012). A large contingent of workers (Nikiforoff, 1941; Miller, 1994; Huss, 1994; Reider, 1996; Retzer, 1945) propose that the mounds are created through the action of hydrostatic processes in which groundwater flowing between two impervious layers develops pressure and leads to a release of water and sediment at the surface. A variety of proposals have been put forth relating the mounds to periglacial processes (Bretz, 1913, Pewe, 1948; Newcomb, 1952; Knechtel, 1952; Ritchie, 1953; Hubbs, 1957; Malde, 1965; Spackman, 1982). Most of these proposals are based on the idea that freezing of permafrost soil leads to polygonal cracking patterns around ice wedges. When the ice thaws, the material in the cracks surrounding the wedges results in Mima mounds. In 1990, Berg proposed that the mounds, many of which are located near active fault regions, were created via seismic shaking of unconsolidated sediment over a rigid substratum. While intriguing, this hypothesis has rarely been examined.

As with the hypotheses of mound formation, the list of names used to describe the low, roughly circular soil domes is lengthy (more than 250, Johnson, 2012 - Appendix C). Bretz (1913) coined the term ‘Mima mound’ after observing the relatively tall mounds on the Mima Prairie in western Washington. Similar microrelief in North America, Africa (Kenya and South Africa), South America (Argentina and Peru), Australia, and Asia is referred to as ‘pimple mounds’, ‘prairie mounds’, ‘heuweltjies’, ‘hogwallows’, ‘tumuli’, ‘Mima-like mounds’, among many other monikers (Johnson and Horwath Burnham, 2012). While it is certainly possible (and perhaps likely) that the genetic factors are different for mounds in different regions, I use the term ‘Mima mound’ to describe all small hillocks which fall into the range of size and shape which are normally attributed to Mima mounds: roughly circular soil mounds 1-50 m in diameter and 0.1-2 m in height. This is done for simplicity and following the tradition of many previous studies (Johnson and Horwath Burnham, 2012).

While the range of explanations is diverse, in the last several decades the preponderance of evidence implies that biologic forces play a key role. G.K. Gilbert (1875) was one of the first to offer a biologic explanation and stated there ‘is little question’ that the mounds of Arizona were created by burrowing animals. Koons (1926) formulated the concept further,
Figure 1.1: Map showing the approximate distributions and extensive overlap of Mima mounds (historical coverage, based on Johnson and Horwath Burnham, 2012) and pocket gophers (current coverage, based on Case and Jasch (1994) and Elrod et al. (1996)). Not all gopher species are represented (e.g., Geomys pinetis in Florida). In cases where gopher coverage and Mima mound coverage do not overlap, it is suspected that the regions previously supported gophers or other burrowing organisms, but now do not.
but the hypothesis was primarily developed by two biologists, Dalquest and Scheffer, in 1942. Recently Johnson and Horwath Burnham (2012) revised the model to include research from the second half of the twentieth century (with extensive contributions by G.W. Cox) and referred to it as the Dalquest-Scheffer-Cox (DSC) model.

According the DSC model, burrowing animals build Mima mounds in regions with thin, seasonally saturated soils. Given the higher risks of flooding and predation in such environments, the animals seek out deeper or better-drained locations. As they engage in foraging and burrowing, which involves dislodging and moving soil in order to create an extensive tunnel system, the animals move a collection of soil backwards, toward the center of their activity. Over time, this translocation results in a local accumulation of earth, which serves as preferred habitat for subsequent generations of burrowers. The mound grows with each turnover of residents and, ultimately results in a Mima mound. Johnson and Horwath Burnham (2012) extended the original model to include the effects of other biotic and abiotic influences, such as wind and water erosion, aeolian influxes, vegetation growth, shrink-swell, freeze-thaw, mass wasting, seismic and any other processes which may impact the form of the burrowing-created protuberances.

The organism most often implicated in this mound building is the pocket gopher (Rodentia: Geomyidae). The range of pocket gophers runs from Alberta, Canada to Panama and largely overlaps the historical distribution of Mima mounds (Fig. 1.1). In the United States, three genera of gophers are recognized (Thomomys, Geomys, and Pappogeomys), and in California the most common of those is Thomomys (in particular, the Thomomys bot-tae group). In 1923, Grinnell declared the pocket gopher California’s most widespread and abundant burrowing rodent and estimated their population to be 1 billion.

Pocket gophers are strikingly diverse in morphology and genetics (Nevo, 1979; Patton and Smith, 1981). The fossorial mammals spend nearly 100\% of their lives underground and have adapted to the conditions of the subterranean niche: negligible light, excess moisture, relatively constant temperatures, and low oxygen levels (Lacey et al., 2000). As a result, gophers provide an excellent opportunity to explore biologic response to changing soil conditions. Grinnell (1927) observed that gophers span an enormous range of conditions in California, being found nearly everywhere except the Mojave Desert and soil-free mountaintops. Building on Grinnell’s observations, Thaeler (1968) studied the distribution of pocket gophers in northeastern California and found that most species boundaries (which rarely overlap) demarcated regions with two divergent soil types. Given the intimate interplay between pocket gophers and their earthen habitat and given the proposal that biologic response to particular soil conditions has led to the widespread Mima mound features, this thesis focuses on an age gradient of soils in central California to test gopher response to changing soil conditions, clarifying issues of the Mima mound debate.

1.1.2 Merced River chronosequence

Within a dense region of Mima mounds in the eastern Central Valley of California, is a well-preserved soil chronosequence, a collection of soils which have similar parent material,
climate, topography, and biota, but which differ in age (Jenny, 1941). As soils age, pedogenesis occurs and includes chemical weathering (the formation of clays and metal oxides and their leaching from surface to subsurface horizons), changes in nutrient concentrations, accumulation of organic matter / inputs, and the formation of “pans” or other horizons that restrict the downward growth of roots and the infiltration of water (Brady and Weil, 2008). Known as the Merced River chronosequence, the landscape bears soils that span a three million year time range (Fig. 1.2). Decades of research have quantified soil and biogeochemical changes along the chronosequence and have generally shown that a significant association exists between soil properties and processes and geologic age. In particular, clay content, rubification, extractable iron, and bulk density generally increase with age, while soil thickness, net primary productivity, soil pH, soil organic carbon, and soil nutrients decrease with age (Arkley, 1962; Marchand and Allwardt, 1981; Harden, 1987; Brenner et al., 2001; Baisden et al., 2002b; White et al., 1996 and 2005). On the older surfaces, claypans or duripans (associated with restrictive Bt and Bqm soil horizons, respectively) have formed (Arkley, 1962; Harden, 1982).

Because pedogenesis leads to systematic changes in soil permeability and thickness, the Merced River chronosequence provides an opportunity to test the DSC hypothesis and to investigate whether and how changes in the suitability of gopher habitat lead to adaptations in burrowing behavior and, ultimately, to the Mima mound terrain.

1.2 Motivation

Although the evidence supporting the DSC model has rapidly increased in the last several decades, there remain many questions to explore. This thesis aims to conduct several novel tests of the biologic hypothesis of Mima mound origin and to more deeply explore lithosphere-biosphere feedbacks in Mima mound landscapes. Below, I address three key motivations for this work, with brief descriptions of the relative contributions of each chapter.

Resolve longstanding controversy

Controversy has defined the Mima mounds since their first observations by European explorers (e.g., Darby, 1816; Stuart, 1837; Wilkes, 1845; Agassiz, 1855; Hilgard, 1905; Washburn, 1988; Johnson and Horwath, 2012). Given that most studies of the mounds have involved small-scale, field-based observations, part of this controversy may be due to a narrow focus. For instance, the distribution map shown in Fig. 1.1 indicates that Mima mounds in the United States may cover up to 3.5 x 10^6 square kilometers. Using an average estimate of Mima mound density (2100 / km^2 (Johnson and Horwath Burnham, 2012)), there are likely more than one billion Mima mounds in the United States, and possibly up to 7 billion. However, the largest individual studies of Mima mounds have involved no more than 600 mounds (Vitek, 1978), and most were conducted in small areas within a single soil and geologic type. Recent developments in remote sensing technology such as LIDAR (light detection and ranging) (which uses lasers to create high resolution maps of the earth’s
Figure 1.2: Photographs showing the changing landscapes across the Merced River chronosequence. Main photographs show the increasing size of mounds with soil age, while the insets show changes in soil condition along the gradient. The terraces range in age from the \( \sim 0.01 \) million-year-old Upper Modesto formation shown in A (where no mounds exist) to the 3 million-year-old Laguna formation shown in C (with well-developed mounds). In B, the seasonal wetlands called vernal pools are visible in between the subtle mounds. While each of the chronosequence members bears soils of different ages, they all have similar climate (xeric moisture and thermic temperature regime), vegetation (grasslands dominated largely by nonnative annual grasses), topography (0-3% slopes), and parent material (granitic alluvium).
surface) offer an incredible opportunity to analyze wider regions of moundfields in order to gain the statistical strength to fully test hypotheses about their origin. Thus in Chapter 2, I analyze the patterns of mound form versus landform age on a 65 km$^2$ region across the chronosequence.

Much of the evidence supporting a biologic hypothesis of mound origin is circumstantial and points to inhabitation of mounds by burrowing animals (using preexisting topography as preferred habitat), but does not directly implicate them as the constructors of mounds. In addition, the precise mechanisms of how mounds might be built by burrowing animals and how changing environmental conditions might affect such ecosystems is underexplored. Part of the reason for this gap in our knowledge is that many burrowing organisms are cryptic and are rarely directly observed in their habitat (Lacey et al., 2000). If fossorial rodents are, in fact, the agents which built the Mima mounds, this invisibility likely contributed to the long-term debate on the mounds’ origin. What are needed are ways to directly or indirectly monitor their activity and behavior in situ. In Chapter 3, I emulate recent efforts at sediment tracing (e.g., Miller et al., 2011; Bertoni et al., 2012) and use radio frequency identification (RFID) technology to directly observe how gophers move sediment in Mima mound landscapes and how their sediment transport changes with increasing soil weathering.

A common argument against pocket gopher-created mounds is that the organisms are simply too small to have created such a widespread and cumulatively massive phenomenon. For example, Nikiforoff (1948) felt the hypothesis of gopher-built mounds was so implausible that it should be categorized as a fairy tale. In a critique of Dalquest and Scheffer (1942)’s original proposal for gopher-built mounds, Nikiforoff relayed a story from a California farmer which proposed that the mounds were created by Paul Bunyan (a fictional, giant lumberjack). He concludes by noting: “A skeptical reader will say that Paul Bunyan is a fiction, but, perhaps, so is the mound-building gopher - what is the difference?” To reject these notions, it is important to quantitatively test whether mounds built by burrowing animals are physically possible. In Chapter 4, I develop a quantitative energy budget to specifically address this issue.

Finally, the controversy in explanation is at least, in part, due to the fact that the mounds, similar to all landscapes, are likely polygenetic in origin. That is, the current observable form of Mima mounds is the outcome of a complex combination of biotic and abiotic processes over relatively long time periods. The effects of each of those processes leave an imprint on the soil surface, which is then observed and interpreted by researchers with different scientific expertise and bias, leading to the wide range of explanations (e.g., Washburn, 1988). In Chapter 4, in order to shift the focus from a strictly unary explanation for the mounds and instead begin to unravel the combination of processes which have led to their present state, I conceptualize the mounds as miniature hillslopes and develop a geomorphic model, which accounts for both downslope erosion and bioturbation (the mixing and movement of soils and sediment).

**Investigate life-landscape feedbacks**
Joseph Grinnell (1923, 1927) regarded pocket gophers as key agents in the formation of Cal-
California soils, likening them to Darwin’s earthworms in England (1881). In recent decades, renewed recognition of Darwin’s early idea has brought to light the possibility of the co-evolution of landforms and biological communities. Growing evidence details how organisms not only respond to their physical environment, but also reshape and constrain that environment in a manner that sustains their own existence. For example, bioturbation by marine organisms is suggested as one of the key factors driving the Cambrian explosion of life (the dramatic increase in global biodiversity occurring approximately 542 million years ago). The proposal is that after predation led to the evolution of skeletal structures, many organisms began to either take shelter or search for food by burrowing into the microbial mats on the ocean floor, ventilating the seafloor sediment and leading to the dramatic increase in oxygen seen during the late Precambrian (e.g., Thayer, 1979; McIlroy and Logan, 1999; Meysman et al., 2006; Rogov et al., 2012; Zhang et al., 2013). In a more localized example, Andersen and MacMahon (1985) demonstrated that pocket gophers facilitated plant succession following the 1980 eruption of Mount St. Helens. Pocket gophers were one of the few organisms to survive the eruption due to the protection provided by their underground habitat. As part of their subsequent burrowing, they exhumed underlying soil, covering portions of the relatively nutrient-poor tephra layer and enabling plant growth and distribution (Crisafulli et al., 2005). In addition, gophers’ underground burrows also served as refuge for other animals which survived the eruption, such as the Pacific tree frog (Lauber, 1993).

If a biologic model of Mima mound formation is correct, the widespread Mima mound topography is another example of these bio-physical feedbacks. Recent work has involved the development of landscape evolution models which incorporate feedbacks between biological and physical processes. Yoo et al. (2005) proposed a process-based sediment transport model which incorporated the dynamics of gopher populations. Roering (2008) built a model which explored the relationship between root density and soil depth. However, most geomorphic models do not explicitly incorporate biology (and vice versa) (Reinhardt et al., 2010, and references therein). This thesis attempts to add to the development of these models by linking direct observations of mammal activity with a geomorphic transport law and comparing the results to the extant mounded surfaces.

Protect endangered wetland biodiversity

In addition to the possibility that feedbacks between ecologic and geomorphic processes lead to Mima mounds, such interactions may also give rise to unique aquatic ecosystems. In many regions of Mima mounds, depressions directly adjacent to the mounds fill up seasonally with water, forming ephemeral wetlands called vernal pools. In California, the pools are relatively small, spatially discrete, and support a rich diversity of plant and animal species, including sixty species endemic to the state (Witham, 1998). The pools exist only in regions underlain by an impervious substrate (usually a hardpan or claypan) that prevents drainage and results in a seasonal perched water table. The mound-pool terrain, once a common feature in the Central Valley, is now reduced to isolated fragments after being eliminated in the push to convert the Valley into one of the most productive agricultural regions in the world (Kelly et al., 2005). More than 90% of the original vernal pool habitat has been
CHAPTER 1. INTRODUCTION

converted for agricultural or urban uses, and the remaining vernal pools are continuously threatened (Holland and Hollander, 2007; Holland, 2009).

In response to these losses and with the recognition that the vernal pools are regarded as one of the world’s biodiversity hotspots (Myers et al., 2000), researchers, conservationists, and land managers have waged an extensive effort to preserve the wetlands and mitigate against future losses. In 2005, the U.S. Fish and Wildlife Service designated more than 740,000 acres in California as critical vernal pool habitat. The greatest portion of this protected habitat (43%) is in the San Joaquin Valley (Economic and Planning Systems, 2003), where this study is centered. As part of the designation, several vernal pool recovery plans have been established which include actions such as conservation easements, land acquisition, habitat restoration (including the creation of artificial vernal pools), and continuous species monitoring (Warne, 2011). These recovery actions are projected to have nearly a $1 billion impact on the state’s economy, mostly in the form of preempted developments (Economic and Planning Systems, 2003). In this context, a comprehensive scientific understanding of these landscapes is critical to maximize conservation and minimize economic impact.

Yet, there is no clear understanding of how these landscapes developed or how they evolve over time. This is despite growing evidence that vernal pool species richness and distribution are highly sensitive to changes in mound-pool microtopography. For instance, Holland (1984) demonstrated that plant species are specialized to particular heights along mound-pool transects. He concluded that physical differences, namely the slope and surface area of vernal pools, are more important for determining species richness than competition between taxa. Other studies have similarly shown a strong correlation between microtopography and diversity of vernal pool species (e.g., DelMoral and Deardorf, 1976; Crowe et al., 1994; Platenkamp, 1998; Bauder, 2005).

In these grassland habitats where the soil surface is likely mixed by burrowing animals, insects, and plant roots every several hundred years – with gravity directing the mixed material downslope – the maintenance of strongly convex mounds with relatively soil-free, gravel-filled vernal pools points to the role of active restorative processes that maintain these landscapes. If gophers are indeed the creative and/or restorative agent, they must be considered the keystone species of this ecosystem, and must be at the heart of long-term management strategies. However, despite their possible vital function in vernal pool conservation, consideration of burrowing organisms is virtually nonexistent in the growing body of conservation plans, mitigation agreements and designs for artificial wetlands (Stebbins et al., 1996, DeWeese, 1998, Sutter and Francisco, 1998; Leidy and White, 1998; Ferren and Hubbard, 1998; Black and Zedler, 1998; EIP Associates, 2002; Moore et al., 2003; USFWS, 2005 (Critical Habitat Designation); USFWS, 2006 (Vernal Pool Recovery Plan); Airola, 2008; Mason and Ritenour, 2010; South Sacramento Habitat Conservation Plan, 2010; San Diego Recovery Plan draft documents, 2012; Buse, 2012)).

This thesis aims to contribute to the development of a scientific-based management strategy for these landscapes. I propose that Mima mounds and vernal pools are not static landforms, but are dynamic features that are maintained by an on-going process. In Chapter 4, I apply principles from hillslope geomorphology to place reasonable limits on the rate at
which the mounds are likely being eroded by gravity-driven processes, and then compare those rates to region-wide measurements of soil movement by gophers to determine if and how biological movement of soil serves as a mechanism for the maintenance and/or formation of the mounds.

1.3 Dissertation outline

This dissertation uses the framework of a soil age gradient to monitor Mima mound morphology, pedology and biology across landscape-wide scales. Remote sensing and fieldwork supports the development of a biogeomorphic sediment transport model, which is used to describe landscape evolution and clarify the role of burrowing organisms in building and conserving mound and pool topography.

In Chapter 2, I present the largest (by a factor of 400) and most detailed spatial analysis of Mima mound topography to date. I develop a local maxima algorithm which accurately identifies Mima mounds in a 65 km$^2$ LIDAR dataset. Using the classified data, I conduct an assessment of Mima mound abundance, size, and spatial pattern as a function of soil age and topography. I show that mound size changes systematically with soil age and with depth to restrictive layer, consistent with the predictions of the DSC model. In addition, I document a pattern of regularity (as opposed to randomness or clustering) in mound distribution on all terraces of the Merced River chronosequence. I compare the regularity in spacing with mound patterns documented elsewhere, with gopher territory distribution, and with plant dispersal and conclude that Mima mound spacing most closely conforms with the spacing of individual gopher territories (as measured by Howard and Childs (1959)).

In Chapter 3, I outline my development of a novel use of RFID (radio frequency identification) tracing technology to quantify gopher sediment transport vectors in Mima mound-vernai pool habitat. I document direct evidence that gophers engage in constructional processes in Mima mound terrain and quantify how their burrowing behavior changes with soil weathering. For five chronosequence landforms, I report the results of a two-year survey which monitored the direction of soil movement by gophers (as proxied by RFID markers) and demonstrate that the movement becomes more moundward (directed towards the center of the Mima mounds) as soil age increases. In addition, based on a seven-year survey, I estimate and compare rates of aboveground gopher sediment transport across a range of geologic types and topographic positions. Finally, I offer detailed observations of the spatial pattern of aboveground gopher sediment transport and of underground gopher burrows and use the information to infer details of gopher ecology and foraging strategies.

In Chapter 4, I combine data from Chapters 2 (curvature of mound-pool terrain) and 3 (gopher sediment transport vectors) to develop two models of mound formation. First, I use a linear diffusion model of hillslopes to estimate rates of Mima mound erosion and vernal pool deposition and compare the downwearing with rates of moundward-directed gopher sediment transport. Second, I develop a model which approximates the energy required for the formation (shearing, pushing and uplifting soil) and maintenance (counteractions to
erosion) of Mima mounds, and compare the amount to estimates of energy available to gopher populations in the Merced region. The results show that the building of mounds by gophers is feasible (on both an energetic and a mass-based level) in relatively short time periods, strongly supporting a biotic origin for construction and preservation of Mima mounds and vernal pools.

Lastly, in Chapter 5, I highlight the key results of this dissertation. Further, I consider the results in the context of vernal pool conservation efforts ongoing in the state of California. I propose several lines of future research which could shed further light on the role of burrowing organisms in the endangered wetland ecosystems.
Chapter 2

Mima Mound Form and Distribution Across a Soil Age Gradient

The coming of the airplane has awakened a new interest in the problem, because the mounds are much more conspicuous from the air than from the ground and because the aerial view or photograph brings out their pattern and their relations to other features so clearly that new possibilities are opened for the discovery of their secret. –J.L. Rich, 1934

2.1 Introduction

Mima mounds are small circular or elliptical hummocks located on grassland landscapes around the world. A single mound is small, ranging from 1 to 50 m in diameter and 0.1 to 2 m in height (Johnson and Horwath Burnham, 2012). When observing the mounds from a landscape-scale perspective, however, their density and regularity are notable. Named after mounds on Washington’s Mima prairie, Mima mounds cover large expanses of North America and can number more than 40 mounds per hectare (Cox, 1984). In many locations, the depressions adjacent to the mounds seasonally fill with water, forming ephemeral wetlands called vernal pools that, in California, support numerous endemic and endangered plant and animal species (Witham, 1998; Barbour et al., 2005). In spite of the global distribution, abundant biodiversity, and visual intrigue of Mima mounds, controversy over their origin has been ongoing for nearly two centuries (Washburn, 1988; Johnson and Horwath Burnham, 2012). As Higgins (1990) wrote, “they are a mystery that has been discussed for over 150 years and ... have generated a greater variety of hypotheses than any other geologic feature.”

Today, recent developments in remote sensing and GIS (geographic information systems) can be used to examine these landscapes quantitatively, across wide spatial scales incorporating a range of pedological and geological features.

Reports on the size, shape and spacing of mounds began in the 1800s and have continued to today (Table 2.1). While the great majority of studies have focused on ground-based
investigations at the local scale, a handful of studies have assessed the mounds on a regional or larger scale using remote sensing technologies, mostly aerial photography (Melton, 1929; Rich, 1934; Krinitzsky, 1940; Knechtel, 1952; Ritchie, 1953; Deal, 1972; Vitek, 1978; Spackman, 1982; Irvine et al., 2012; Cox, 2012). Vitek (1978) conducted one of the most extensive regional-scale analyses of the mounds to date. He studied the spatial pattern of 600 mounds in Colorado using aerial photographs and found a strong pattern of regularity (as opposed to randomness or clustering) in mound distribution. Vitek did not speculate as to how the regularity reflected the mounds’ origin. Spackman (1982) also found regularity in mounds in Wyoming, and concluded that the consistency in spacing was due to a combination of polygonal permafrost cracking and cryostatic pressure release through planes of weakness created by fossil sand wedges. More recently, Cramer et al. (2012) used Google Earth™ to quantify the pattern and size of thirty-four mounds in South Africa (locally referred to as heuweltjies) by manually measuring mound morphology. They determined that the mounds are the product of differential erosion in which bush-clump vegetation limited soil loss under and near vegetation. Cramer et al.’s result is in contrast to that of Lovegrove and Siegfried (1986, 1989) and Cox et al. (1987b) which concluded that the South African mounds are the result of the activity of mole rats.

The studies outlined above contributed insights to the analysis of mound origin, but the results are limited in scale and scope. Generally, the size and quality of the studies were constrained by the available technology. For instance, due to the subtle relief of the mounds and due to overlying vegetation, many areas of mounds are difficult to analyze with aerial photography. Furthermore, other remote sensing data (such as the National Elevation Dataset (NED, Resolution 3-30 m)) cannot adequately resolve the small features. As a consequence of these limitations, our view of Mima mounds to date may be far too magnified to observe useful patterns. This narrow focus may explain the large number of divergent explanations of mound origin, including those that reach different conclusions for mounds in the same area. Clearly, a more versatile tool is needed to thoroughly investigate these features.

The advent of commercially available airborne LIDAR (light detection and ranging) technology has provided unprecedented resolution and accuracy in determining surface features (Slatton et al., 2007; Glennie et al., 2013). LIDAR is a remote sensing technique that uses high-frequency pulsed laser beams to scan the land surface, measure distances from the laser source to the target surface, and ultimately enable the creation of large-scale, high-resolution digital elevation models (DEM). Achieving point densities of tens of locations per square meter and cm-scale (or better) resolution (Glennie et al., 2013), LIDAR provides an opportunity for detailed quantitative study of Mima mound terrain beyond the limited scale (less than one kilometer-squared) of most previous studies.
<table>
<thead>
<tr>
<th>Region</th>
<th>Source</th>
<th>Explanation for Mounds</th>
<th>Number Mounds Studied</th>
<th>Height (m)</th>
<th>Diameter (m)</th>
<th>Density (mounds / ha)</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>Colorado, South Central</td>
<td>Vitek (1978)</td>
<td>Undetermined process</td>
<td>600</td>
<td>0.14</td>
<td>10.5</td>
<td></td>
<td>Regular spacing. Slight a/b symmetry. Aspect effect in some areas.</td>
</tr>
<tr>
<td>Iowa, Kaslow Prairie</td>
<td>Ricks (1997)</td>
<td>Pocket gophers</td>
<td>59</td>
<td>0.23</td>
<td>3.7</td>
<td>0.91</td>
<td>Mounds are clustered. Most are round in shape, and approx. 40% are oblong.</td>
</tr>
<tr>
<td>Colorado, Blanca</td>
<td>Cox et al. (1987a)</td>
<td>Pocket gophers</td>
<td></td>
<td>0.25</td>
<td>12.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Texas, Gulf Coast</td>
<td>Udden (1906)</td>
<td>Uncertain origins, possibly ants</td>
<td></td>
<td>0.25</td>
<td>13.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gunnison County, Colorado</td>
<td>Scheffer (1958)</td>
<td>Pocket gophers</td>
<td></td>
<td>0.35</td>
<td>10.65</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Idaho, Eastern Snake River Plain</td>
<td>Tullis (1995)</td>
<td>Polygenetic during cold climates</td>
<td></td>
<td>0.35</td>
<td>11.0</td>
<td></td>
<td>Varies from regular to random to strongly linear</td>
</tr>
<tr>
<td>Saskatchewan, Little Manitou Lake</td>
<td>Mollard (1978); Irvine (2005)</td>
<td>Polygenesis, predominantly bioturbation</td>
<td>314</td>
<td>0.36</td>
<td>14.7</td>
<td>9.6</td>
<td>First evidence of gopher hypothesis outside of North America. Shape showed no consistent pattern with direction of slope.</td>
</tr>
<tr>
<td>Kenya, Aberdare Highlands (Kenyaatta Airport)</td>
<td>Cox &amp; Galahui (1983, 1985)</td>
<td>Mole rats</td>
<td>21</td>
<td>0.38</td>
<td>13.1</td>
<td>2.2</td>
<td></td>
</tr>
<tr>
<td>Texas, Coastal Plains</td>
<td>Koons (1948)</td>
<td>Pocket gophers</td>
<td></td>
<td>0.4</td>
<td>9.1</td>
<td></td>
<td>Spacing shows no regularity</td>
</tr>
<tr>
<td>Wyoming, Laramie Basin</td>
<td>Reider et al. (1999)</td>
<td>Groundwater vortex</td>
<td>3</td>
<td>0.4</td>
<td>15</td>
<td>26</td>
<td>LIDAR survey</td>
</tr>
<tr>
<td>California, Merced County</td>
<td>Reed &amp; Amundson (2012)</td>
<td>Pocket gophers</td>
<td>86400</td>
<td>0.44</td>
<td>7.3</td>
<td>49</td>
<td></td>
</tr>
<tr>
<td>California, San Diego</td>
<td>Cox (1984)</td>
<td>Pocket gophers</td>
<td>25</td>
<td>0.44</td>
<td>9.9</td>
<td>43</td>
<td>Strong positive relationship between neighboring mound volumes and intermound distance</td>
</tr>
<tr>
<td>Gulf Coast, Louisiana</td>
<td>Rich (1934)</td>
<td>Prairie bunch grass plays important role</td>
<td>Mounds observed along a ~400km flight-line from Dallas to Arkansas</td>
<td>0.45</td>
<td>8.1</td>
<td></td>
<td>First aerial survey of mounds. ‘Distinct tendency for mounds to occupy all available space’. Possibly aligned with drainage.</td>
</tr>
<tr>
<td>Missouri, Diamond Grove Prairie</td>
<td>Horwath &amp; Johnson (2006)</td>
<td>Pocket gophers</td>
<td>46</td>
<td>0.45</td>
<td>7.6</td>
<td></td>
<td>Mostly circular or elongate in N-S direction.</td>
</tr>
<tr>
<td>Location</td>
<td>Author(s)</td>
<td>Process Description</td>
<td>Mound Height</td>
<td>Mound Diameter</td>
<td>Method</td>
<td></td>
<td></td>
</tr>
<tr>
<td>--------------------------------</td>
<td>------------------------------</td>
<td>--------------------------------------------------------------------------------------</td>
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<td>-----------------------------</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Washington, Olympic Mountains</td>
<td>Cox (2012)</td>
<td>Pocket gophers</td>
<td>0.48</td>
<td>10.25</td>
<td>Google Earth and ground surveys</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wyoming, Laramie Basin</td>
<td>Spackman &amp; Munn (1984)</td>
<td>Cryostatic eruptions into sand wedges</td>
<td>0.5</td>
<td>6.5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Texas, Gulf Coast</td>
<td>Carty et al. (1988)</td>
<td></td>
<td>0.5</td>
<td>15.5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Washington, Mount Rainier</td>
<td>Cox (2012)</td>
<td>Pocket gophers</td>
<td>0.5</td>
<td>16.35</td>
<td>Closely packed and monotonously uniform in size, shape and spacing. Circular, with convex up surface. Mounds on slopes are elliptical downslope.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Idaho, Snake River Plain</td>
<td>Malde (1965)</td>
<td>Freeze-thaw of saturated soil</td>
<td>0.5</td>
<td>16.5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Iowa, Kaslow Prairie</td>
<td>Brotherson (1982)</td>
<td>Pocket gophers</td>
<td>128</td>
<td>0.51</td>
<td>6.6</td>
<td>1.97</td>
<td></td>
</tr>
<tr>
<td>Oregon, Lawrence Grassland Preserve</td>
<td>Cox &amp; Hunt (1990)</td>
<td>Pocket gophers</td>
<td>18</td>
<td>0.55</td>
<td>16.0</td>
<td>Mounds develop much flatter profiles than expected with increase in size, likely due to multiple occupancy at mound peripheries. Central depressions observed in very large mounds. Mound diameter correlated negatively with shape index.</td>
<td></td>
</tr>
<tr>
<td>Texas, Leon County</td>
<td>Robinson (2012)</td>
<td>Fluvial, requiring presence of accretionary ridge microtopography over point bar deposits</td>
<td>581</td>
<td>0.58*</td>
<td>21.1*</td>
<td>21</td>
<td>LIDAR survey</td>
</tr>
<tr>
<td>Washington, Eastern, Medical Lake</td>
<td>Piper (1905)</td>
<td>Water erosion and basalt weathering</td>
<td>0.6</td>
<td>4.6</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Missouri, Southwest</td>
<td>Spillman (1905)</td>
<td>Disintegrating flint concretions</td>
<td>0.6</td>
<td>7.5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oklahoma, East</td>
<td>Allgood &amp; Gray (1973); Allgood &amp; Gray (1974)</td>
<td>Combination of protective grass cover, burrowing organisms preference for higher vegetation under conditions of a perched water table</td>
<td>46</td>
<td>0.6*</td>
<td>15*</td>
<td>No definite pattern of arrangement except somewhat similar shapes, sizes, volumes, heights and intermound distances &amp; intermound distances</td>
<td></td>
</tr>
<tr>
<td>Minnesota, Dodge County</td>
<td>Johnson et al. (1999)</td>
<td>Pocket gophers</td>
<td>0.6</td>
<td>5.2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Iowa, Hayden Prairie</td>
<td>Johnson et al. (1999)</td>
<td>Pocket gophers</td>
<td>0.6</td>
<td>5.2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Location</td>
<td>Reference</td>
<td>Elevation</td>
<td>Mound Size</td>
<td>Slope</td>
<td>Mound Form</td>
<td></td>
<td></td>
</tr>
<tr>
<td>----------------------------------------------</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Minnesota, Northwest</td>
<td>Ross et al. (1968)</td>
<td>200</td>
<td>0.71</td>
<td>21.5</td>
<td>2.4*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>California, Fresno-area</td>
<td>Nikiforoff (1941)</td>
<td>173</td>
<td>0.72*</td>
<td>9.1*</td>
<td>56*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>California, Merced County</td>
<td>Arkley &amp; Brown (1954)</td>
<td>0.75</td>
<td>39</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Louisina / Texas, Gulf coastal plain</td>
<td>Krinitzsky (1949)</td>
<td>0.75</td>
<td>12.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>California</td>
<td>Barnes (1879)</td>
<td>0.76</td>
<td>9.0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Texas, Gulf Coast</td>
<td>Dietz (1945)</td>
<td>0.76</td>
<td>12.2</td>
<td>15</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Louisiana &amp; Texas</td>
<td>Aten &amp; Bollich (1981)</td>
<td>0.82</td>
<td>31</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oklahoma, Eastern</td>
<td>Knechtel (1952)</td>
<td>0.91</td>
<td>21.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>South Africa, Western Cape Region</td>
<td>Cramer (2012)</td>
<td>34</td>
<td>0.86</td>
<td>22</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Washington, Eastern, Channeled Scablands</td>
<td>Freeman (1926)</td>
<td>1.0</td>
<td>10.0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Washington &amp; Oregon, Columbia River Plateau</td>
<td>Waters &amp; Flagler (1929)</td>
<td>1.0</td>
<td>12.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oregon, Lawrence Memorial Grassland Preserve</td>
<td>Johnson (1982)</td>
<td>203</td>
<td>1.0</td>
<td>20.0</td>
<td>12.5</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Mounds most dense on higher, better-drained soils. Round to slightly oval, although occasionally elongated (2.5x) on slopes > 4 degrees.

In each field, mound size is rather uniform. Notes two distinct groups of mounds: thickly set, dense and conical and flat, less uniform and larger in diameter.

Regularly spaced, dispersion similar to both plant and termite distribution. Relatively circular with low eccentricity, exhibit down-slope; slumping with significantly greater down-slope than cross-slope dimensions.

Circular, polygonal and elongated mounds observed. Sorted stripes and nets also observed near mounds. However, no consistent relationship between shape and underlying slope. Minimum heights usually occur on smaller mounds and on the downslope of extremely elongated mounds. Asymmetrical cross-section in the downslope direction. Extremely long mounds are oriented with joints in the underlying basalt.
<table>
<thead>
<tr>
<th>Location</th>
<th>Author(s)</th>
<th>Process/Activity</th>
<th>Number</th>
<th>d</th>
<th>h</th>
<th>s</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kenya, Aberdare Highlands (Waunyomyu Ngeke Ranch)</td>
<td>Cox &amp; Galahau (1985)</td>
<td>Mole rats</td>
<td>23</td>
<td>1.0</td>
<td>14.3</td>
<td>3.4</td>
<td>Shape showed no consistent pattern with direction of slope.</td>
</tr>
<tr>
<td>Texas, Gulf Plain</td>
<td>Hobbs (1907)</td>
<td>Mud eruptions</td>
<td>1.05</td>
<td>18.25</td>
<td></td>
<td>Might be said to be regular but must be qualified by the degree of erosion that has shaped them. Cicular or oval in horizontal dimensions and flatly hemispheroidal in the vertical. Commonly asymmetric, with a steeper side facing up-gradient or, if in proximity to a prairie channel, facing that channel. Common maximum height in any one field.</td>
<td></td>
</tr>
<tr>
<td>Missouri</td>
<td>Bushnell (1905)</td>
<td>Polygenesis</td>
<td>1.06</td>
<td>15.5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Washington, Southwest</td>
<td>Ritchie (1953)</td>
<td>Running water that flowed across partially thawed, polygonally fissured ice fields</td>
<td>1.1</td>
<td>12.0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Washington, Thurston County</td>
<td>Washburn (1988)</td>
<td>Multiple explanations possible in different regions</td>
<td>1.2</td>
<td>7.25</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Washington, Tenino Area</td>
<td>Dahlquest &amp; Schefter (1942)</td>
<td></td>
<td>1.15</td>
<td>7.25</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>South Africa, Western Cape Region</td>
<td>Moore &amp; Picher (1991)</td>
<td>Evidence does not support pocket gophers</td>
<td>134</td>
<td>1.2</td>
<td>15</td>
<td>3.6</td>
<td>Majority of mounds had central depression and displayed a degree of asymmetry</td>
</tr>
<tr>
<td>Arkansas</td>
<td>Campbell (1906)</td>
<td>Burrowing animals</td>
<td>1.2</td>
<td>18.3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Washington, Thurston County</td>
<td>Del Moral and Deardorff (1976)</td>
<td>Large gophers</td>
<td>1.3</td>
<td>13.1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Washington, Thurston County</td>
<td>Dietz (1945)</td>
<td>Water deposition</td>
<td>1.3</td>
<td>13.1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wyoming, Laramie Basin</td>
<td>Spackman (1982)</td>
<td>Cryostatic eruptions into sand wedges</td>
<td>1.3</td>
<td>32.0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Washington, Tenino Area</td>
<td>Horner (1930)</td>
<td>Ripples of Noachian floods</td>
<td>1.35</td>
<td>7.25</td>
<td>12</td>
<td></td>
<td></td>
</tr>
<tr>
<td>California, Orange County</td>
<td>Kelly (1948)</td>
<td>Ripples of Noachian floods</td>
<td>1.35</td>
<td>7.0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>California, San Diego County</td>
<td>Kelly (1948)</td>
<td>Ripples of Noachian floods</td>
<td>1.35</td>
<td>7.0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oregon, Southern</td>
<td>Paeth (1967)</td>
<td>Depositional processes</td>
<td>1.35</td>
<td>24.4</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 2.1: Compilation of Mima mound studies which report on mound size, shape, and spacing, ranging from smallest in height to largest. In most cases, median values are reported, while mean values are noted by an asterisk.
CHAPTER 2. MIMA MOUND FORM AND DISTRIBUTION ACROSS A SOIL AGE GRADIENT

The use of LIDAR to evaluate Mima mounds is in its infancy. Robinson (2012) used spatial analysis of LIDAR data to test hypotheses of Mima mound formation in Texas, analyzing the microtopography of six geologic formations which comprise a chronosequence. (A soil chronosequence is a series of locations which vary in soil age but which are generally similar with respect to the other soil forming factors (climate, topography, biota, and parent material) (Jenny, 1941).) Robinson concluded the mounds are fluvial in origin: he proposed that the features resulted from erosion of accretionary ridge microtopography overlying point bar deposits.

While the general approach of the Texas study is useful, the capacity to rigorously evaluate hypotheses of origin is limited by the study's small sample size. The author used stratified sampling to analyze the heights of ∼500 mounds, but the results were statistically indistinguishable among five of the six geologic comparison groups. Manually identifying and measuring the mounds is very labor intensive and was likely the reason for the small selection of mounds analyzed. Automated classification methods could help fully utilize LIDAR data of Mima mounds for analyses of mound genesis and evolution.

2.1.1 Objectives and hypotheses

I use the spatial analysis of LIDAR data across a soil chronosequence in effort to explain how and when the Mima mounds of central California form, and why they persist. I focus on the Dahlquest-Scheffer-Cox (DSC) hypothesis (Johnson and Horwath Burnham 2012), which proposes that the mounds are the result of centripetal movement of soil by fossorial (burrowing) animals from established centers of habitation. According to the hypothesis, gophers living in regions with thin and/or poorly drained soils focus their activity on local areas with relatively favorable conditions (slightly thicker, less saturated soils). Concentration of burrowing in these areas of preferred habitat results in an accumulation of soil which, over time, leads to the formation of Mima mounds.

While the DSC model has been analyzed and tested in many locations and contexts (Table 2.1), I expand on these studies and test the model on a well-established soil age gradient, the Merced River chronosequence, in order to specifically explore the effect of soil formation processes on burrowing animal habitat and Mima mound morphology.

Since soil thickness (of mobile layers) and infiltration are known to decline with increasing soil age (Birkeland, 1999), I make the following predictions for mound form and distribution across the soil age gradient:

- In regions subject to extensive soil development, soil movement by gophers should be directed moundward (towards the center of a mound) and upward, as a consequence of nesting in and foraging outward from locations with comparatively thicker, less saturated soils, ultimately leading to mounded terrain.

- As soils age, and effective soil thickness and permeability decrease, moundward soil translocation will intensify, resulting in taller, narrower (smaller diameter) and more densely distributed mounds on older landforms.
Since gophers must use soil from intermound regions to build mounds, intermound spacing and mound diameter should be positively correlated.

Because gophers are territorial organisms (Howard and Childs, 1959), mounds should be uniformly spaced to reflect gopher home ranges (the area in which an animal lives and travels).

In this chapter, I: (1) develop an automated classification algorithm which maximizes the information that can be derived from LIDAR data of Mima mounds, (2) conduct the largest study, by several orders of magnitude, of Mima mounds to date, enabling a spatial analysis across a wide range of environmental conditions, (3) generate a detailed database of geomorphological metrics (mound height, diameter, slope, curvature, volume) of Mima mound-vernal pool terrain, (4) use the catalogue of terrain data, along with other environmental and GIS data to infer processes of formation from observed patterns, and (5) conclude that burrowing organisms (namely pocket gophers) are primarily responsible for the construction of Mima mounds along the Merced River chronosequence.

2.2 Methods

2.2.1 Study area

A 65 km² area in the watersheds of the Merced and Tuolumne Rivers was chosen for the study. Bordered on the east by the Sierra Nevada mountain range and on the west by the Central Valley, the study region contains a series of dissected river terraces and alluvial fans formed by glacial outwash from the Sierra Nevada (Marchand, 1976). The terraces and fan remnants range in age from a few hundred years (the active floodplain of the Merced River) to the several million-year-old China Hat member of the Laguna formation (Marchand, 1976). The sediments consist primarily of granitic alluvium. The soils are classified as Entisols on the lower, younger landforms (elevation ~50 m above sea level (asl)) and as Alfisols on the higher, older landforms (~250 m asl) (Arkley, 1962). On the older surfaces, claypans or duripans (associated with restrictive Bt and Bqm soil horizons, respectively) have formed (Arkley, 1962; Harden, 1982). Marchand (1976), Marchand and Allwardt (1981), Pavich et al. (1986), and Harden (1987) used C-14, K-Ar, U-series and Be-10 dating to establish age controls for the landforms. White et al. (2005) quantified decreasing soil permeability and increasing hydrologic heterogeneity associated with the formation of argillic horizons and silica duripans on the older formations.

The climate of the region is Mediterranean with strong seasonality. The mean annual precipitation is 310 mm, 90% of which falls between November and April. During the summer, the mean daytime temperature is 37°C, while the winter average is 7°C (Arkley, 1962; NOAA, 2013 (Station 045535)). The vegetation is dominated by European annual grasses and forbs (e.g., Bromus spp.; Hordeum spp.), which have largely overtaken the native perennial bunchgrass community (e.g., Poa secunda spp.; Aristida oligantha) (Ornduff and
CHAPTER 2. MIMA MOUND FORM AND DISTRIBUTION ACROSS A SOIL AGE GRADIENT

Faber, 2003; Barbour et al., 2007b; Stromberg et al., 2007). Due to the seasonal influx of rainfall and the development of restrictive soil layers, ephemeral wetlands called vernal pools support a variety of terrestrial and aquatic plant and animal species (e.g., *Lepidurus packardi*; *Neostapfia colusana*) (Laabs et al., 2002; Dittes and Guardino, 2002). Burrowing rodents are abundant, particularly the California ground squirrel (*Spermophilus beecheyi*) and the Botta pocket gopher (*Thomomys bottae*) (Laabs and Allaback, 2002). Cattle ranching and agriculture are the most common land use practices in the region (Robins and Vollmar, 2002).

The set of different-aged alluvial terraces and fan remnants described above comprise the Merced River chronosequence, which serves as the primary means by which to test the DSC model. Four chronosequence landforms were chosen for analysis, named for their corresponding geologic formation: Laguna (3 million years (My)), Riverbank (0.2 My), Modesto (0.03 My), and Holocene alluvium (<0.01 My). On the oldest landform (Laguna), two study areas were chosen: one on a level terrace top (Laguna level) and one on the slope descending to the next terrace level (Laguna sloping, slope ~20%).

The study region also includes outcrops of bedrock, which provide an additional opportunity to test the DSC hypothesis because they contain dense distributions of Mima mounds and have thin soil layers overlying a relatively impermeable surface. The regions include landforms derived from consolidated sand deposits, tuff deposits and andesitic mudflows, many of which have been reworked since their original deposition (Marchand, 1976). These additional mounded surfaces were used to test the DSC model by comparing changes in mound morphology with variation in effective soil depth (the depth of mobile soil layers above any restrictive layer). Five effective soil depth categories were analyzed: 20, 40, 80, 120 and 200 cm.

### 2.2.2 LIDAR acquisition and data processing

Topographic data were generated by two airborne LIDAR surveys totaling 65 km$^2$ (Fig. 2.1). First, in September 2006, the National Center for Airborne Laser Mapping (NCALM) conducted a laser altimetry survey of a 30 km$^2$ region of mounds approximately 10 km northeast of the city of Merced, CA. The data were collected with an Optech 1233 airborne laser terrain mapper (ALTM) mounted in a Cessna 337. The scan angle was a constant ±20 degrees and the scan frequency was 28 Hz for the duration of the flight. Two GPS (global positioning system) ground stations were used as reference stations for the flight, one inside the survey area on La Paloma Road and the other 35 km away at the Mariposa Airport. Average point density was 3 points/m$^2$. Second, in July 2010, Towill, Inc. collected LIDAR data of an additional 35 km$^2$ of landscapes surrounding the first study, using an Optech Orion M200 LIDAR system with a scan angle of 15 degrees and a scan frequency of 28 Hz. GPS base stations were established no more than 30 km away from the most remote areas of the study. The collection rate for this survey ranged from 50 to 200 kHz, with an average density of 10 points per square meter. All coordinates were recorded and processed using the Universal Transverse Mercator (UTM) coordinate system (Zone 10) in the 1983 North
Figure 2.1: Eastern Merced County regional map showing geologic units as mapped by Marchand (1976) and the outline of the LIDAR survey area (totaling 65km², in brown shaded relief). Formation age generally increases from west to east, with younger terraces in green and older in red. The LIDAR survey area is centered in the Yosemite Lake USGS (United States Geological Survey) Quadrangle, at latitude ~37.42°N and longitude 120.42°W.

Figure 2.2 gives a summary of the LIDAR data processing conducted. No filtering (removal of data) was performed on either dataset given the general absence of large vegetation or other obstructions. The data were gridded by point kriging using Surfer® software (Version 8) and 1 and 30 m grid spacing. A linear variogram model with a nugget effect of zero was used so the resulting digital elevations models (DEM) were created using exact interpolation. Surfer® was also used to calculate slope (maximum rate of change between a cell and its neighbors) and curvature (two-dimensional negative Laplacian of elevation, $-\nabla^2 z$) of the gridded data.

The study region encompasses a range of elevations (∼55-250 m above sea level), due to regional slope and post-depositional incision. Because these large-scale topographic changes can obscure the mound microtopography and hinder morphometric analysis, a 20 x 20 m moving window filter was used to smooth out the low frequency signals and accentuate the mounded features. Mounds were then identified on the high-pass-filtered data using the classification technique described below, but all other terrain data analysis was calculated using the original, unfiltered data.

The data from the NCALM survey reported consistently taller mounds than those from the Towill survey, even on closely adjacent areas (with the same soil type, slope and geology) (distance = 500 m). On average, mounds in the NCALM survey were 0.06 m taller than those from the Towill survey. Because this disparity was likely due to a height bias reported by the NCALM surveyors (Reed, 2006), all NCALM output was reduced by the bias difference.
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2.2.3 Image classification

An initial manual count of Mima mounds in a small portion of the LIDAR data indicated that there were hundreds of thousands of mounds included in the full dataset. In order to maximize the accuracy and amount of classified terrain data, three methods to automatically identify mounds were tested. Optimizing classification accuracy is important in order to improve the reliability of subsequent analyses (e.g., GIS analysis), discussed below.

The first two methods were object-based image analyses (OBIA), conducted using the eCognition® software program (Version 5.0, Definiens, Inc.). OBIA segments an image into groups of spectrally similar pixels and then classifies each resulting object based on a suite of object characteristics such as shape, position, and texture. This approach is distinct from pixel-based procedures which classify images based on the spectral information of individual pixels. OBIA is generally preferred over pixel-based image analysis when using high-resolution images (such as LIDAR) and for cases that require the integration of contextual information related to the phenomenon being studied (Blaschke, 2010). For each of the two methods, a multi-resolution segmentation was performed on the 1-m high-pass-filtered DEM: one level of segmentation (Scale Parameter = 10) was used to characterize the underlying topography, while the second level (Scale Parameter = 1) divided the image on the scale of the mounds. The first classification approach (the Definiens Fuzzy Membership routine) used a ‘fuzzy membership’ function which relies on image features to define inclusion/exclusion parameters for classification. The most useful features in this case were the contrast of object pixel values (mean and standard deviation) to neighbor values, where pixel values represent elevation. The second approach (the Definiens Local Maxima routine), used a local maxima search on pixel values (via the Process Tree utility, which allows for more complex class definitions), parametrized with a search radius on the order of average mound diameter.

For the final method, I developed a customized algorithm (referred to as the Custom Local Maxima routine, https://github.com/Thomomys82/Mima) to identify the mounds, using Python™ (Version 2.7.3). The algorithm searches the 1-m filtered DEM for local maxima and relies on a distinct morphologic definition of a Mima mound to ‘grow’ a mound outward from its high point by adding the highest neighboring cell at each point. Each cell can only be a member of a single mound. The definition employed was initially based on a range of statistics for mound size and shape taken from the literature (Johnson and Horwath Burnham, 2012). The parameters were iteratively adjusted until the highest mound classification accuracy was achieved, based on visual determinations comparing classification results with shaded relief imagery (created using ArcGIS (Version 9.3.1, Environmental Systems Research Institute, Inc. (Esri©))).

In this method, a Mima mound is defined as a feature satisfying the following requirements:

• Mound diameter ranges from 4-20 m
• Mound height ranges from 0.05-2 m
CHAPTER 2. MIMA MOUND FORM AND DISTRIBUTION ACROSS A SOIL AGE GRADIENT

- Mound shape is roughly circular:
  Mound plan area > semimajor axis * semiminor axis * 0.75
- Maximum re-rise (a ‘bump’ on a mound) is 0.2 m
- Overall maximum mound cell count is 120 (which represents a plan area totaling 120 m²)

The accuracy of each approach was assessed by visually comparing the classifications with the shaded relief imagery of nine hundred Mima mounds. The mounds were selected by generating nine hundred random points (across the entire survey area) and identifying the Mima mound closest to each point. The Custom Local Maxima algorithm yielded significantly higher mound identification accuracy than the other approaches (which will be further discussed in Sections 2.3.1 and 2.4.1). Therefore, the mound locations found via the custom classification were used in all analyses described below.

2.2.4 Landscape characterization and GIS analysis

2.2.4.1 Mound morphometry

Mound size and shape metrics (height, diameter, surface area, volume, slope, and curvature (negative Laplacian)) were calculated using mounds classified via the Custom Local Maxima algorithm.

Mounds can be accurately measured by identifying mound apices using the Custom Local Maxima routine. However, mound diameters are more difficult to estimate. Automatically delineating a mound edge using inflection points in slope or curvature is unreliable due to the noise in the second-order calculations. Because the mound definition is conservative (in order to maximize classification accuracy), diameter measurements generally reflected the maximum diameter limit (derived from literature) rather than actual diameters and tended to result in indistinguishable diameters across geologic and soil groupings. This was the case even when diameters at 50 and 70% of mound height were analyzed. Therefore, a subset of mound diameters was calculated manually. In ArcGIS, Hawth’s Tools (version 3.27, www.spatailecology.com) were used to select 900 random points from the set of mound centers, distributed evenly across the geologic and soil types represented in the survey area. Diameters were calculated using a shaded relief map (Azimuth angle = 315; Altitude = 45) to measure the semimajor and semiminor axes for each of these mounds. The same zoom level (150 x 150 m window) was used in effort to maintain consistency in measurements. The ‘edge’ of a mound was defined by noting areas of distinct pixel changes. If it was uncertain whether a point was, in fact, a Mima mound center, the diameter was not recorded.

Mound-pool volumetric relationships were assessed by randomly locating twenty mounds on the oldest formation (Laguna) and using Surfer™ to calculate the volume of each mound and the pool nearest to it. In several cases, the pools were not distinctly closed. In those instances, the volume of the depression reaching to the midpoint of all adjacent mounds was measured.
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The mound height and diameter calculations were field validated in May 2012 for twenty mounds on three geologic formations (5-10 mounds each, representing a range of size and shapes) using a tape, stadia rod and auto-level.

2.2.4.2 GIS analysis

Mound centers were classified by geologic type and effective soil depth to quantify if and how mound size, shape, and distribution vary with soil changes. The coordinates of each of the mound centers were imported into Geographic Information Systems (ArcGIS, Version 9.3.1, Environmental Systems Research Institute, Inc.©) and classified by intersecting the point centers with several layers of environmental data using Hawth’s Tools. The geologic formation and soil series type under each Mima mound center were derived from digitized 1:24,000 geologic maps (Marchand, 1976; Metz, 2006) and the Soil Survey Geographic (SSURGO) database (websoilsurvey.sc.egov.usda.gov), respectively. As mentioned above, the five geologic formations included in the chronosequence analysis were: Laguna (3 My), Riverbank (0.2 My), Modesto (0.03 My), and Holocene alluvium (<0.01 My). From SSURGO, the depth to the restrictive layer (20, 40, 80, 120 or 200 cm) was recorded for each soil type where mounds are located. In some cases, the depth to restrictive layer was not available. In those cases, information from relevant soil series publications was used to estimate the effective soil depth (Official Series Description, 2013; Arkley, 1962). The mound density (mounds / area) for each geologic formation was estimated using Hawth’s tools to count the number of mound centers per geologic polygon. Aspect (the horizontal direction which the underlying terrain faces) was calculated using the ArcGIS Spatial Analyst toolbox on a 30 m digital elevation model (DEM) of the study area. The aspect position of each mound was estimated by intersecting the mound center with the aspect map. Finally, to document the differences in mound morphology with underlying slope, elongation (ratio of semimajor ($a$) and semiminor ($b$) axes) was measured for ten mounds on each of five regional slope classes.

2.2.4.3 Statistical analysis

Data pre-processing, statistical tests, regression analyses, and point pattern analyses were conducted using R software (Version 3.0.0, http://www.R-project.org). All mounds that were not assigned to either a geologic formation, a soil series (or both) were excluded from the analysis.

The youngest geologic formations (Holocene alluvium and the Modesto formation) were subject to the largest number of false positive mound classifications. For clearly disturbed areas on these formations (e.g., roads, dredge tailings, agricultural activity), data were manually removed. For the other geologic formations, no data was removed as the area to assess would be too large, and the number of false positives was relatively small based on a small assessment of mounds on those regions.

Frequency and density histograms were calculated to assess the nature of the data. T-tests (confidence level = 0.99) were conducted on each geologic and effective soil depth
category in order to estimate the sample mean (for metrics such as mound height, curvature, slope, volume, density and diameter) and assess the reliability of that estimate. ANOVA (analysis of variance) and Tukey’s Honestly Significant Difference (HSD) tests were applied to confirm that the sample means are not equal and to determine which pairs of means are different within the stated significance level. These results were then used to evaluate hypotheses of mound formation. I propose that if mounds are created as a biologic response to changes in effective soil depth and/or permeability, then mound size should increase with decreasing soil thickness (of the biotically active, mobile layer) and increasing soil moisture and soil age. Given this, the null hypothesis states that differences in mound size should be indistinguishable between the geologic and soil groupings.

Heat maps, in which data is divided into bins and color-coded according to the number of data points in a given bin, were produced to examine connections between mound height and underlying slope and aspect. (Scatter plots were difficult to interpret due to the large number of mounds in the datasets.)

2.2.5 Point pattern analysis

If gopher transport of soil formed the mounds, the intermound and mound volumes should be roughly equal (assuming the original surface was relatively level) because gophers would have moved sediment from intermound areas in order to build the mounds. To test this prediction, mound dispersion (variation in inter-mound distance) was measured. Fifty-two points were randomly located on the oldest Laguna formation (slopes <15%), and one large mound and one small mound adjacent to each point were identified. Distances from each mound to all directly adjacent mounds were measured (mound apex to mound apex) and inter-mound distances were compared with mound diameters.

Point pattern analysis (PPA) is used to describe patterns of locations of mapped point events and is an important tool to understand ecologic processes (Wiegand and Moloney, 2004; 2013). Ripley’s $K$-function is a form of second order spatial point pattern analysis that summarizes spatial dependence over a wide range of scales (Ripley, 1981). This feature is relevant to this investigation because the processes responsible for mound formation may occur across many scales. Because gophers are territorial organisms (Howard and Childs, 1959), I predicted that mounds should be uniformly spaced to reflect gopher home ranges. Here, a Ripley’s $K$ approach was used on the point data representing mound centers in order to test the following null hypotheses: (1) the spatial distribution of mounds is random, and (2) the spatial distribution of mounds is indistinguishable between geologic and restrictive depth groupings.

The overall strategy of Ripley’s $K$ is to construct a set of concentric circles at defined distances around each point and count the number of neighboring points in each band. Ripley’s $K$-function, $K(r)$, is defined as the expected number of points within a distance $r$ of the center point ($E(r)$), divided by the intensity of the pattern ($\lambda$), or the mean number of points per area.

$$K(r) = \lambda^{-1} E(r) \quad (2.1)$$
A modified version of this definition, transformed $K(r)$, was used to enhance visual interpretability.

$$L(r) = \sqrt{K(r)/\pi} - r$$ (2.2)

To test whether the observed pattern differed from Complete Spatial Randomness (CSR), 99 Monte Carlo simulations were carried out on a random set of coordinates and $K$ values were calculated for each pair of coordinates within each subset, generating upper and lower bounds of significance. If the observed transformed Ripley’s function is above zero and within the 99 percent confidence envelope generated by the simulations, the mounds are clustered or aggregated and point-to-point distances are generally smaller than that of a random pattern. If the function is below zero and within the confidence interval, mound centers are dispersed in a regular distribution and interpoint distances tend to be larger than those characteristic of a random pattern. Ripley’s analysis was performed using R software (via the spatial library (Venables and Ripley, 2002) and the spatstat library (Baddeley and Turner, 2005)).

Due to land use change in the Central Valley in the last 200 years, large portions of the most fertile soils and youngest geologic formations have been converted to farmland or urban areas (Kelly et al., 2005). As a consequence, the largest contiguous areas on the younger landforms (Holocene alluvium, Modesto and Riverbank) are approximately 200 x 200 m regions. In effort to measure mound patterns on undisturbed regions, three 200 x 200 m regions were identified for each geologic and restrictive depth grouping. The areas were chosen to reflect the variety of density and distribution found within each grouping. In addition, to capture larger-scale patterns, four regions (ranging from 0.72-1.7 km$^2$) were analyzed on geologic formations where large, intact sections of densely distributed mounds are found (Laguna, North Merced Gravels, and Ione formations).

Despite the utility of Ripley’s $K$ function, most studies that quantified mound pattern report the Nearest Neighbor Index (NNI), also known as the $R$ statistic. For quantitative comparison with other Mima mound distributions, the $R$ statistic was also calculated for the regions described in the preceding paragraph. The formula for $R$ is as follows:

$$R = r_a/r_e.$$ (2.3)

$r_a$ is the mean observed distance to nearest neighbors:

$$r_a = N^{-1} \sum_{i\neq j}^N u_{ij}$$ (2.4)

for a set of $N$ points where the distance between the $i^{th}$ point and the $j^{th}$ point is $u_{ij}$.

$r_e$ is the mean expected distance in a random distribution of points. Complete spatial randomness for $N$ points in an area $A$ is described by the Poisson process. The expected average distance between nearest neighbors for this distribution is as follows:

$$r_e = 0.5 \sqrt{A/n}$$ (2.5)

Values of $R$ range from 0 (maximum clustering), through 1.0 (random pattern), to 2.0 (regularly spaced square lattice), to 2.1492 (hexagonal lattice) (Clark and Evans, 1954).
CHAPTER 2. MIMA MOUND FORM AND DISTRIBUTION ACROSS A SOIL AGE GRADIENT

<table>
<thead>
<tr>
<th>Classification approach</th>
<th>Overall error (%)</th>
<th>Overcount error (%)</th>
<th>Undercount error (%)</th>
<th>Cannot classify (%)</th>
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<td>Definiens - Local Maxima</td>
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<tr>
<td>Custom Local Maxima</td>
<td>18</td>
<td>2</td>
<td>16</td>
<td>8</td>
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Table 2.2: Comparison of three data classification approaches. The accuracy of these approaches was assessed by comparing the classifications with nine hundred randomly selected mounds (visualized via shaded relief imagery). Based on the significantly lower error rate, all point pattern and GIS analyses were conducted using the Custom Local Maxima classification.

2.3 Results

2.3.1 Mound classification accuracy

The classification of LIDAR point cloud data identified 223069-273982 mound centers, depending on the approach used. The accuracy of the classifications are given in Table 2.2, which also provides the percentage of the sample points for which a designation as mound or non-mound was not possible, due to irregularities in shape or due to limited visibility of the shaded relief image. Since the Custom Local Maxima approach achieved the highest accuracy, its classification was used for all reported analyses and results. A discussion of the differences between the three classification techniques is presented in Section 2.4.1.

2.3.2 Mima mound morphometry

Morphometric results for the entire dataset are summarized in Table 2.3. The survey area contains an estimated 242323 mounds, with an average height of 0.31 m and average diameter of 9.3 m. A typical mound profile on level terrain (Fig. 2.3) approximates a convexoplanar shape, with convex mound tops and more planar sideslopes. The average mound slope is 0.1 and curvature (negative Laplacian) is -0.10 m$^{-1}$. Taller mounds exhibit more convex profiles (Fig. 2.4). Mound and pool terrain on the oldest geologic formation in the chronosequence (Laguna formation) was analyzed on a select region (Fig. 2.5). Mound curvature is, on average, of greater magnitude than pool curvature, indicating that Mima mounds are slightly more convex than their vernal pool counterparts are concave. In addition, mound and pool volumes were highly correlated (Fig. 2.6).

The LIDAR mound measurements were field validated in May 2012 on twenty mounds in different geologic and topographic settings. LIDAR mound heights and diameters were consistently smaller than the ground-based measurements. Measured in the field, heights were 10 cm taller and diameters 1.3 m wider, on average, than the digital measurements. The discrepancy increased slightly with mound height.
Figure 2.3: Inset A shows a cross section of typical mound and swale topography on the Laguna formation, derived from a 1 m DEM of LIDAR data. Insets B and C show the changes in slope and curvature (negative Laplacian), respectively, along the cross section. D shows a shaded relief image of the Laguna formation, showing the context of the cross-section. North is at the top of the image.
Figure 2.4: Heat map showing relationship between mound curvature (negative Laplacian) and mound height for all mounds in the study. Curvature values generally become more negative (implying increasing convexity) with increasing mound height ($R^2 = 0.13$, $p < 0.001$).
Figure 2.5: Histogram showing the distribution of curvature (negative Laplacian) values calculated for 1600 points on both mounds and pools. Mound curvatures are more widely distributed and have a higher mean value than pool curvatures.
Figure 2.6: Relationship between mound volume and swale volume as calculated from the LIDAR dimensions of 20 randomly chosen mound-pool pairs on the 3 million-year-old Laguna formation. ($R^2 = 0.92$, $p < 0.001$)
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<table>
<thead>
<tr>
<th>Metric</th>
<th>Value ± Standard Deviation</th>
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<tr>
<td>Estimated total number of mounds in survey area</td>
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</tr>
<tr>
<td>Average mound density (mounds km$^{-2}$)</td>
<td>4089</td>
</tr>
<tr>
<td>Average mound diameter (m)</td>
<td>9.3 ± 2.8</td>
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<tr>
<td>Average mound height (m)</td>
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</tr>
<tr>
<td>Average mound volume (m$^3$)</td>
<td>10.3 ± 6.1</td>
</tr>
<tr>
<td>Survey-wide mound volume (m$^3$)</td>
<td>$2.5 \times 10^6$</td>
</tr>
<tr>
<td>Average mound surface area (m$^2$)</td>
<td>58.3 ± 19</td>
</tr>
<tr>
<td>Survey-wide mound surface area (m$^2$)</td>
<td>$14 \times 10^6$</td>
</tr>
<tr>
<td>Average mound slope (units)</td>
<td>0.1 ± 0.09</td>
</tr>
<tr>
<td>Average mound curvature (negative Laplacian) (m$^{-1}$)</td>
<td>-0.10 ± 0.08</td>
</tr>
</tbody>
</table>

Table 2.3: Data summary of the physical characteristics of Mima mounds in a 65 km$^2$ area near Merced, California. Data include morphometric values for mounds found on all geologic and soil types.

2.3.3 Relation to subsurface characteristics

Figures 2.7 and 2.8 provide a synthesis of results and environmental data for each of the five chronosequence terraces and for a range of effective soil depths, respectively. Each category of results is presented below and, in Section 2.4.3, the results are discussed in the context of the hypotheses of mound formation. Environmental data are from Arkley (1960, 1962), Marchand (1976), Harden (1987), White et al. (1996), Vollmar (2002), and NRCS (2012).

2.3.3.1 Mound morphology across a soil chronosequence

Figure 2.9 shows the histograms of height values (frequency and density) for each of the chronosequence landforms. The total number of mounds identified in the chronosequence analysis is 163775. The Laguna and North Merced Gravels formations comprise the two largest portions of the LIDAR chronosequence data (59 and 35%, respectively), while the younger formations made up smaller, but significant portions of the data (Riverbank = 3%; Modesto = 2%, and Holocene = 1%) (Fig. 2.9, top panel). The distributions of height data for each chronosequence landform approximated normal distributions, with slight deviations at the tails.

Mima mound height increased significantly with soil age (Fig. 2.9 (bottom panel) and 2.10). In addition, mound slope and density generally increase, and mound curvature (negative Laplacian) decreases (becomes more negative), with increasing soil age (Fig. 2.10.
Figure 2.7: Table of all LIDAR and environmental metrics across the soil chronosequence. Summary statistics in the upper portion of the table are based on data collected from 163775 mounds included in the chronosequence. Data in the bottom half of the table is from Marchand (1976), Harden (1987), and Vollmar (2002).
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Figure 2.8: Synthesis of LIDAR and environmental data for a sample of geologic formations with varying effective soil thickness (depth to restrictive layer). Summary statistics are based on data collected from all 242343 mounds identified in the survey area. Effective soil depth data (depths to restrictive layer) were estimated based on SSURGO data, official soil descriptions, and Arkley (1962). Simulations of soil profile data were generated in R using the aqp package available from the California Soil Resource Lab. The red line on each soil profile graphic estimates the depth of restrictive layer. The shaded relief images presented are meant to represent characteristic mound form and pattern observed on the various geologic formations.
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Figure 2.9: Frequency and density histograms of mound height values with terrace age. Geologic formations range in age from the <0.01 million year old (m.y.o.) Holocene alluvium (top of legend) to the ~3 m.y.o. Laguna formation (bottom of legend). Density histogram represents: frequency / (number of data points * difference between break points).
and 2.11). The second-oldest formation in the chronosequence, the North Merced Gravels formation (1 million years old), bears the most dense collection of mounds. Mean mound diameter decreased from young to old on the four oldest geologic formations, but did not differ significantly among the geologic groups (Figure 2.7).

2.3.3.2 Mound morphology across an effective soil depth gradient

Figure 2.12 shows the histograms of height values (frequency and density) for each of the five effective soil depth categories. The total number of mounds included in the effective soil depth analysis is 242323. (This includes the 163775 mounds in the chronosequence analysis.) The 80 cm restrictive depth category comprises the greatest portion of the group (64%), while the remaining depth categories make up the following proportions: 20 cm = 7%; 40 cm = 22%, 120 cm = 6%; and 200 cm = 1% (Fig. 2.12, top panel). The distributions of height data for each category approximated normal distributions, with a slight positive skewness.

Mounds increase in height (Fig. 2.12, bottom panel and Fig. 2.13) and decrease in curvature (Fig. 2.13) with decreasing soil thickness. Mound height and curvature were both significantly different between the effective depth categories, except for curvature between the 120 and 200 cm categories. Mound diameters did not vary significantly or systematically among effective soil depth categories.

2.3.4 Relation to underlying topography

Slopes of the underlying terrain range from 0-55%, with approximately two-fifths of the survey region having slopes of 3-10%. Mounds were observed on hillsides with slopes as great as 40%. Figure 2.14 illustrates mound height variation with changes in terrain for the oldest terrace (Laguna formation). Mounds on the level landforms are generally the tallest, while mounds on the hillslopes and bases of slopes are shorter. However, this height-slope relationship is weak when quantified across the entire dataset (Fig. 2.15, $R^2 = 0.1$). On smaller regions, the correlation is slightly stronger (e.g., for a 0.63 km$^2$ region of the Laguna formation, $R^2 = 0.19$).

Mounds on level terrain (slope <5%) are slightly elliptical in shape (average ratio of semi-major to semiminor axis length = 1.33), whereas mounds on sloping terrain are particularly elongated downslope (Fig. 2.16). Many of the Merced hillslope mounds were aligned linearly in near-parallel rows downslope (Fig. 2.17).

Mounds across the survey tended to be taller on north-facing slopes, shorter and least abundant on east-facing slopes, and most abundant on southwest facing slopes (Fig. 2.18). On one particular soil type (Hornitos soil series, classified as a Lithic Dystroxerupt), taller mounds are observed on eastern aspect slopes (Fig. 2.19). Figure 2.20 illustrates the pattern in one location, whereby taller, narrower mounds are observed on eastern-facing slopes and shorter, broader mounds are observed on the directly opposite western-facing slopes. This effect is observed at multiple locations within the Hornitos soil distribution.
Figure 2.10: Figures showing variation in mound height (top panel) and slope (bottom panel) with soil age. All values show mean ± standard error (SEM). N ranges from 695 to 97487. Means were significantly different among all groups (Tukey’s HSD test, 164926 df; p <0.0001).
Figure 2.11: Figures showing variation in density (top panel) and curvature (negative Laplacian) (bottom panel) with soil age. Curvature values show mean ± SEM. N ranges from 695 to 97487. Curvature means were significantly different among all groups (Tukey’s HSD test, 164926 df, p < 0.001).
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Figure 2.12: Frequency and density histograms of mound height values across a gradient of effective soil thickness.
Figure 2.13: Mound heights (top panel) (mean ± SEM) correlate strongly with effective soil thickness. Mound curvature (negative Laplacian, bottom panel) generally decreases (becomes more convex) with decreasing effective soil depth. N ranges from 2463 to 154334. Means were significantly different among all groups except for curvature between the 120 and 200 cm categories (Tukey’s HSD test, 243872 df, p < 0.001).
Figure 2.14: Locations of mounds on a portion of the 3 million-year-old Laguna formation, with color gradient showing mound heights overlying shaded relief imagery of mound terrain.
Figure 2.15: Across the entire 65 km² survey region, mound heights are weakly, inversely correlated with the slope of the underlying terrain \( (R^2 = 0.1, p < 0.001) \).
Figure 2.16: On each slope class, 10 mounds were randomly chosen and semimajor \((a)\) and semiminor \((b)\) axes were measured and averaged. Mound elongation \((a/b)\) increases with slope.
Figure 2.17: On many slopes greater than 20%, mounds tend to align in rows perpendicular to hillslope contours. In the top panel, a shaded relief image of the Mima mounds on the Laguna geologic formation is shown. In the lower image, a 1 m contour map is overlaid.
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Figure 2.18: Heat map showing mound height variation based on the aspect of underlying terrain, for the entire dataset. Mounds are taller on north-facing slopes, shorter and least abundant on east-facing slopes, and most abundant on southwest facing slopes. Zero degrees indicates north-facing slopes.
Figure 2.19: Heat map showing mound height variation with aspect for the Hornitos soil series. Unlike other soils, significantly taller mounds are observed on the eastern-facing slopes. On all other soil and geology types, there is a relative dearth of mounds on eastern-aspect slopes. Zero degrees indicates north-facing slopes.
Figure 2.20: Figures illustrate two distinct mound classes on the same landform (Ione sandstone with Hornitos soil series). The mounds are markedly different in size and shape between two aspect ranges. Taller, narrower mounds occur on the eastern aspect slopes (blue shades). Shorter and wider mounds are found on the western facing slopes (yellow shades).
2.3.5 Point pattern analysis

Mounds are typically uniformly spaced at an average intermound distance of 12 m. Where intermound spacing did vary, it was correlated with mound diameter (Fig. 2.21). A series of transformed Ripley’s K analyses was conducted to characterize Mima mound distribution. A clear pattern of regularity (even spacing) in mound location was observed for all geologic formations (on 200 x 200 m sample regions) on distances ranging from 4 to 15 m (Fig. 2.22). Regularity was generally more pronounced on the older landforms. In addition, on the older terrain there is the suggestion of a secondary regularity at approximately 20 m. Ripley’s analysis on larger regions (up to 1.7 km$^2$) (Fig. 2.23) also showed regularity in the 4-10 m range, and clustering beyond 20 m.

Nearest-neighbor indices (NNI or $R$ values) generally increased with increasing soil age, ranging from 1.2 on the youngest formations up to 1.6 on the oldest (Fig. 2.7). The North Merced Gravels formation showed the strongest dispersion, which is consistent with its higher mound density, as discussed previously (Fig. 2.9). Across large spatial scales (such as the region shown in Fig. 2.23), a typical $R$ value was 1.4.

2.3.6 Additional observations

Additional mound patterns were observed with close inspection of the data. Fig. 2.24 demonstrates the wide variety of mound shapes and patterns that can be found in a relatively small region. In some outcrops (especially on the Riverbank and Ione geologic formations), dense areas of mounds are surrounded by areas completely devoid of the microterrain (Fig. 2.25, top and middle panels). In addition, many areas (on a variety of soil and geologic types) demonstrate circular or arcuate patterns of mounds (Fig. 2.25, bottom panel) (including areas that do not appear to be aligned with drainage patterns). In general, besides mound size differences, there appear to be mound shapes that are unique to certain soil or geologic types. For instance, on the Hornitos soil (Lithic Dystroxept), distinctive, wide mounds are commonly observed (Fig. 2.20) and are not observed in other regions.

2.4 Discussion

2.4.1 Mound classification accuracy

Three classification approaches were tested (two using Definiens OBIA software and one developed specifically for the Merced Mima mounds). The Custom Local Maxima approach more accurately identified mounds in the terrain and was used for all analyses. Fig. 2.26 compares the three classification techniques on typical problem areas for the Definiens approaches. The Definiens Fuzzy Membership classification tended to undercount mounds, due to the effects of the underlying topography on the classification (even after high-pass filtering). The Definiens Local Maxima classification grossly overclassified mounds on level, non-mounded areas due to the prescribed local extrema search radius. However, in areas of
Figure 2.21: Comparison of mound diameter (semimajor axis) and intermound distance (average span between given mound apex and all directly adjacent mound apices) for 104 mounds randomly located on the oldest geologic formation (Laguna). \( R^2 = 0.47, \ p < 0.001 \)
Figure 2.22: The modified Ripley’s $K$ function for each of the geologic formations in the soil chronosequence, ranging from youngest at top to oldest at bottom. Point pattern distributions were analyzed across 0.05 km² areas for each formation. Negative values outside of the gray confidence envelope indicate a dispersed or regular pattern and positive values indicate a clustered or aggregated pattern. The significance of the clustering generally increases with soil age. On the older formations, a possible secondary regularity is observed at $\sim 20$ m.
Figure 2.23: Inset A is a shaded relief image of a 0.72 km$^2$ portion of the Laguna formation. In B, a map of mound heights is shown for the same region. Mound heights are represented both by the color scale (in meters) and variation in point size. Inset C shows the modified Ripley’s $K$ function for the mounds in the given area. Negative values outside of the gray confidence envelope indicate a dispersed or regular pattern and positive values indicate a clustered or aggregated pattern. Even across large spatial scales, Mima mounds are highly regular at distances of 5-10 m. Beyond 20 m, mounds are clustered. The clustering likely reflects the effects of the underlying topography on mound distribution.
Figure 2.24: Shaded relief image showing diversity of mound terrain on a single geologic formation (Ione). North points to the right hand side of the figure.
Figure 2.25: A sample of the varied patterns observed in the LIDAR data. Note the regions with dense mounds interspersed with flat, unmounded regions (top and middle images) and arcuate chains of mounds (bottom image).
relatively dense moundfields, the Definiens Local Maxima technique was highly successful in identifying mounds. The Custom Local Maxima algorithm occasionally reported false positive mounds in areas near channels or stream edges. More often, this approach would undercount mounds in instances where two mounds were very close together or nearly merging, especially on hillslopes (Figure 2.27); in this case, the algorithm would identify the larger mound and ignore the smaller. The Custom Local Maxima approach clearly achieved a more accurate classification. However, due to the Custom algorithm’s tendency to undercount small mounds, merged mounds, and/or mounds on hillslopes, reported size metrics may be overestimated, particularly in steeper terrain.

2.4.2 Mima mound morphometry

The mounds in this portion of California’s Great Central Valley are generally shorter, smaller, and more densely spaced than other Mima mounds (Fig. 2.28 and Table 2.1). The approximate mound density is 4089 mounds km\(^{-2}\), which is slightly larger than Arkley and Brown’s (1954) estimate of 3900 mounds km\(^{-2}\) for the greater Merced region.

Measurements of mound height and diameter were larger for the field-based measurements than the LIDAR measurements (Section 2.3.2). The difference in height values is likely due to the conservative mound-finding approach of the Custom Local Maxima classification. The mound definition (Sec. 2.2.3) was optimized to maximize the accuracy of the classification. However, this led to generally compact mound classifications - narrower mound boundaries - in order to avoid false positive mounds or two mounds classified as a single mound. The narrower mound boundaries result in undervalued height estimates. The underestimation in LIDAR-based diameter values is likely due to the shortcomings of measuring mounds through visual inspection of shaded relief imagery (900 randomly identified mounds were measured manually in ArcGIS, Sec. 2.2.4.1). While an effort was made to take consistent measurements (e.g., by maintaining a similar zoom level when viewing the shaded relief), the assessment is relatively subjective and prone to inconsistencies. Repeated diameter measurements on the same mound were commonly 0.5 m different from one reading to the next, and sometimes as great as 1.5 m variability. In addition, there are inherent difficulties in mound measurements, especially with regard to diameter. It is challenging to precisely delineate the mound edges (for both shaded relief and field measurements) because the topography is so variable and relatively slight around the perimeter. Future iterations of the Custom Local Maxima classification algorithm should better incorporate slope or curvature inflection points as a means of defining mound margins. This would likely improve the accuracy of both the diameter and height measurements.

2.4.3 Mound pattern with soil age, depth and topography: implications for mound origin

I proposed that Mima mounds are created by gophers as a response to soil changes caused by pedogenesis. Below, the results are discussed in the context of this proposal. Two alternative
Figure 2.26: Examples of classification error for the Definiens Fuzzy Membership routine (blue, upper left) and the Definiens Local Maxima routine (blue, lower left). The ‘fuzzy membership’ routine fails to identify mounds on ridgetops, even when a high pass filter is applied to the data to remove the effects of underlying topography. Level land is classified as ‘mound’ by the Definiens ‘local maxima’ classification routine due to the prescribed search radius. In contrast, the Custom Local Maxima routine more accurately identifies mounds in the same regions (yellow, upper and lower right).
Figure 2.27: The Custom Local Maxima technique achieves much higher identification accuracy than the two other approaches, but on hillslopes and in other areas where mounds appear to ‘merge’ together, the Custom technique fails to classify some mounds, usually ignoring the smaller mounds.
Figure 2.28: Diagram comparing Merced-area mounds with published data for other mounds in North America. Data for the Merced-area mounds (the number reported above the central tick marks on each scale) are the average of measurements made using LIDAR data for all soil and geology types. Data for the mound continuum are derived from various sources including Cox (1984a), Washburn (1988), and Johnson and Horwath Burnham (2012).

hypotheses (erosion with vegetation anchoring and deposition with vegetation anchoring) are consistent with the available evidence for mounds in California (e.g., Washburn, 1988) and are also considered here, in order to ensure a thorough assessment of potential explanations. The proposals that mounds form when vegetation either (1) protects sediment from erosion (especially fluvial) or (2) accumulates sediment during deposition have been supported by many studies (LeConte, 1874; Hilgard, 1884a; Shaw, 1937; Holland, 1952; Collins, 1975; Cain, 1974; Gangmark and Sanford, 1963; Page et al., 1977). Below, I will demonstrate that although some observations are compatible with all three proposals, the evidence strongly points to biologically formed Mima mounds along the Merced River chronosequence.

Mound morphology with soil age and effective soil depth

The mean values of mound height, slope, and curvature were all significantly different between the different-aged chronosequence terraces and effective soil depth categories (Fig. 2.7 and 2.8), leading to a rejection of the null hypothesis and strongly supporting the DSC model of mound formation. As soils age and/or soil effective depth decreases, environmental pressure on organisms inhabiting the soil increases, prompting a response via increasingly directional (and thus constructional) sediment transport. This should lead to an increase in mound height and density if gophers are responding to decreasing habitability, which was the pattern observed (Fig. 2.10, 2.11, and 2.13).

Both the vegetation anchoring hypotheses are inconsistent with the changes in mound form across the chronosequence and across the effective depth gradient. If erosion created the mounds in a discrete time period, the size of mounds is expected to scale with soil thickness in a manner opposite to that observed in the LIDAR data. That is, for shallower (older)
soils, erosion would lead to smaller mounds because of a lack of residual material. If the surfaces with taller mounds were eroded in a separate time period when the soil thickness was, in fact, greater than on the other formations, the observed pattern in mound height would require a systematic difference in erosion rate (higher erosion on the older landforms to erode down to create taller mounds). For deposition, if the depositional events occurred at different times on each formation, progressively larger volumes of depositional material would be required from young to old. If the mounds were built from a single depositional (or erosional) event, the observed pattern of mound size would require increasingly larger anchoring vegetation present on young to old landforms. Neither of these scenarios seems likely.

Mean mound diameter did not vary significantly among the geologic groups. This was likely due to the small sample size (N = 900) constrained by the limitations of manual diameter measurements. However, the general trend (decreasing diameters with increasing soil age (considering all but the youngest surface) (Fig. 2.7)), is consistent with the DSC hypothesis of mound formation: drawing from a thin and finite soil layer, gophers transport soil from the perimeter of their areas of activity towards the center of those areas. Therefore, the trend of increasingly taller, narrower, and steeper mounds with soil age may reflect the different stages in Mima mound formation over time.

The mounds on the North Merced Gravels formation are more densely packed than the mounds on other chronosequence members (Fig. 2.11). The soils on this formation are approximately the same depth as the Laguna formation, however the North Merced Gravels formation bears shorter, wider and denser mounds. The cobble content on North Merced Gravels is higher than Laguna (Arkley, 1962), which, if the DSC model is correct, could have an impact on the ability of gophers to construct mounds and might lead to more dense rather than taller mounds. Another possibility is that the North Merced Gravels landscapes could have more favorable habitat conditions (e.g., denser vegetation) than on the Laguna formation, which could lead to higher gopher populations (and denser mounds). For instance, Vollmar (2002) and Metz (2001) report higher densities of vernal pools and vernal pool species on North Merced Gravels than on the Laguna formation.

In contrast to the predictions of the DSC model, small mounds were detected on the youngest formation, Holocene alluvium, despite the relatively thick soils and the lack of a restrictive layer. One explanation for this apparent contradiction may be that the ‘mounds’ identified by the Custom Local Maxima algorithm are not the same type of features as mounds on the other formations. While a number of the features appeared to be Mima mounds based on visual inspection of the shaded relief images, none of the Holocene alluvium mounds were confirmed in the field. The existence of Mima-like mounds and gopher activity was, however, field-verified on regions of all other chronosequence formations. On the other hand, if Mima mounds do exist on geologic formations lacking a restrictive layer and/or shallow soils, this may indicate that the DSC model is incorrect or incomplete. For instance, changes in plant type, density and/or distribution may be the primary driver or an auxiliary driver (in combination with soil changes) of gopher foraging and burrowing behavior changes. Brenner et al. (2001) demonstrated that net primary productivity (NPP,
the amount of biomass generated from photosynthesis, minus the energy used for cellular respiration) generally decreases along the Merced River chronosequence, ranging from 913 g m\(^{-2}\) on a 3000 year-old formation (comparable to the Holocene alluvium) to 476 g m\(^{-2}\) on the 3 million-year-old Laguna formation. Such apparent reductions in food availability may induce gophers to engage in a foraging strategy which results in a region locally enhanced in biomass. In fact, Brenner et al. (2001) measured higher NPP on mound areas than in vernal pools. However, whether vegetation changes or soil changes are the key motivating factor for changes in gopher burrowing remains to be determined.

Robinson (2012) conducted the only other known quantitative study of LIDAR data of Mima mounds, examining mound morphometry across a chronosequence of six landforms in Texas. Robinson proposed a fluvial origin for the mounds. Based on frequency of observed features on the different terraces, he suggested that accretion ridges erode to Mima mounds and that Mima mounds eventually erode to smaller topographic features on the older landscapes. In contrast to the Merced study, Robinson did not observe a statistically significant difference in mound height among most age groups. Only one group was significantly different from the other five. This is likely because Robinson measured the heights of only 472 randomly located mounds, versus the 240000 in this study. If a larger sample size was measured on each terrace, a clearer picture of the morphology of the Texas mounds may have emerged. In addition, another possible explanation for the lack of observable pattern in the Texas study is that the ages of the various terraces are not well-constrained – their designation was based on terrace elevation levels. Furthermore, Robinson excluded mounds <30 cm and did not specify whether pocket gophers or other burrowing rodents are currently active on the studied landforms, making comparisons to this study more difficult. For instance, if pocket gophers are absent on the oldest terrace (in which a relatively smaller number of mounds were observed) but present on all other terraces, this could explain the difference in feature frequency compared with the younger terraces.

**Mound morphology with underlying topography**

One of the most perplexing considerations of Mima mounds, with respect to the DSC model, is the observation of mounds on hillslopes (Fig. 2.17). Perched water tables are not likely to occur and saturated soil conditions occur less frequently on the steep slopes (up to 40%) on which mounds are observed. The presence of mounds on these slopes then seems inconsistent with the DSC model. However, recently Marcy et al. (2013) showed that soil differences apropos to the study sites (changes in depth to restrictive layer, soil clay percent and linear extensibility (shrink-swell capacity)) prompt gophers in California to evolve into groups with distinct morphological adaptations. The researchers found that a subgenus of gophers developed a more efficient digging apparatus (tooth-digging versus claw-digging) to survive in shallower, higher clay, higher linear extensibility soils. If increasingly shallow and indurate soils induce distinct morphological changes, it may be possible that such soil conditions could also prompt burrowing animals to develop behavioral changes in the adapted subgenera, even if not experiencing the exact conditions that initially prompted the behavior (i.e., saturated soils). This may help explain why mounds are found on hillslopes even when
restrictive soil conditions are not.

In addition, mounds aligned with drainage patterns may seem contradictory to a hypothesis proposing pocket gophers as agents of formation. However, it is possible that the observed patterns are indicative of a response of burrowing rodents to pre-existing patterns in the terrain – for instance, the animals may take advantage of slight elevational differences associated with drainage patterns, or may adapt to restrictive boundaries, such as streams or rock outcrops (Scheffer, 1958; Washburn, 1988).

While a mound size-slope correlation and alignment of mounds with slope and drainage patterns are both consistent with the vegetation anchoring hypotheses (for fluvial erosion or deposition), the relationships observed here are fairly weak and inconsistent (Fig. 2.15). In addition, the density and regularity of mounds on level surfaces (and on the highest elevation terraces) weaken the erosion proposal. Other studies that have examined the connection between mound height and terrain slope have reported conflicting results. Cox (1990a) observed shorter, more asymmetric mounds on steeper slopes in Oregon, while Washburn (1988) surveyed many studies and concluded that there is a lack of consistent mound size-slope relationship (which may be due to different genetic factors). As Kaatz (1959) commented, the lack of a reliable relationship “constitutes an important refutation of the dominance of water erosion as the causal agency”. Instead, the variety of observed patterns with slope could reflect a combination of differences in soil movement by gophers in response to tunneling on slopes, varied erosion rates, soil thickness and subsurface drainage.

Many studies have demonstrated the effect of aspect on soil and vegetation development (Carson and Kirkby, 1972; Wilcox et al., 2003; Roering, 2004; Istanbulluoglu et al., 2008). Aspect modifies moisture retention, which subsequently governs vegetative distribution and erosion processes (Kirkby et al. 1990). Generally, large north-south contrasts are observed. For instance, in Wyoming, Walker (1948) observed more vegetated, steeper, and straighter north-facing slopes and more concave and grassy south-facing slopes. More recently, Istanbulluoglu et al. (2008) measured a similar effect in New Mexico, across a variety of geologies and elevation ranges.

The observed mound-hillslope aspect patterns (e.g., taller Mima mounds on north-facing slopes (Fig. 2.18)) could help explain the processes involved in mound formation. For instance, taller mounds on north-facing slopes are consistent with the DSC model: northern slopes receive less sunlight and undergo less evaporation, leading to more saturated soils and a relatively greater environmental pressure to build mounds. Additionally, denser vegetation is expected on north-facing slopes which could drive enhanced foraging and bioturbation, leading to taller mounds. On the other hand, the aspect effect is also consistent with the vegetation anchoring hypotheses: denser vegetation on the northerly slopes could result in larger volumes of retained sediment and reduced erosion or increased deposition, which would yield taller mounds.

The east-west aspect effect observed on the Hornitos soil type (Fig. 2.20) (taller, narrower mounds on eastern aspect slopes and shorter, wider mounds on western slopes) could be explained by aeolian processes. The prevailing wind direction for this region is west-northwest (NOAA, 2013). The taller mounds on the eastern-facing slopes could be positioned such that
they are protected from the prevailing winds, while the shorter western-facing mounds may be exposed to and flattened by strong westerly winds. The fact that this effect is limited to a single soil type may be due to the relatively fine particle size of the Hornitos soil, which is derived from sandstone, and may be more affected by aeolian processes. However, it is important to note that aeolian forces are not likely to have created mounds – many studies in California and elsewhere have rejected the hypothesis via an examination of particle size distributions (Cox, 1984; Cox et al., 1987a, b; Horwath and Johnson, 2006). Instead, in this example, aeolian processes may affect the development of mounds subsequent to their formation.

Point pattern analyses
Here, the spacing and distribution of the Merced River chronosequence Mima mounds are compared with that of other regions of Mima mounds, and gopher and plant distributions in order to determine the origin of the mounds. In addition, the nature of and reasons for gopher territoriality are discussed.

The highly regular pattern of Mima mounds in the Merced area (Fig. 2.23) is consistent with the DSC model in that the pattern may represent a signature of the territoriality of gophers. Alternatively, the regularity is also consistent with a vegetation-anchoring hypothesis, whereby vegetation (likely shrubs) may have served as sediment reservoirs by either preventing erosion and/or capturing sediment in transport. In this case, the spacing and pattern of mounds should match that of the anchoring vegetation. To explore these possibilities further, Table 2.4 compares all reported nearest neighbor indices (NNI, Sec. 2.2.5) for Mima mounds as well as for gopher territory and vegetation distribution.

The range of Merced-area Mima mound nearest neighbor indices (NNI) bounds the median value for gophers in California (Table 2.4). Furthermore, the Merced Mima mound NNI (1.2-1.5) more closely match the gopher NNI (1.3) than the vegetation NNI (1.1 or 1.8). Thus, the DSC model is more consistent with Merced-area Mima mounds than are the erosion / deposition vegetation anchoring hypotheses. However, the range in vegetation NNI is wide (highly regular spacing for shrubs in Africa vs. random distribution in California) and it is possible that a different type of vegetation with a distribution pattern more closely matching that of the mounds may have existed in the study region in the past and served as a sediment anchor. Pollen analysis indicates that greasewood (Sarcobatus spp.) and saltbrush (Atrixplex spp.) were present (at 28000-5000 yr. B.P. and 7000-1000 yr. B.P., respectively) in the Central Valley in a location 140 km south of the study area (Davis (1999). However, the spatial pattern of greasewood and saltbrush are not well-documented in the literature. Therefore the NNI values reported by Cox (1987) for creosote bush (Larrea tridentata) in San Diego (Table 2.4) are the closest estimate found for plant dispersion in the Central Valley. In addition, while some plant spatial distribution studies report strong spatial regularity (e.g., Rietkerk and van de Koppel, 2008), many others (which did not report NNI, but which used Ripley’s K function) describe a random or clustered plant distribution (e.g., Haase et al., 1997 (shrubs in semiarid Spain), Garcia-Feced et al., 2011 (trees in California)). Furthermore, the fluvial deposition / vegetation anchoring hypothesis is not consistent with
the observations that intermound distance scales with mound diameter (Fig. 2.21) and that mound-pool volumes are highly correlated (Fig. 2.6).

Additional observations also support the DSC model. Zinnel and Tester (1994) observed that gophers in Minnesota grasslands maintain a distance of approximately 10 m between individuals, closely matching the average intermound spacing of 12 m. Bandoli (1987) measured an average gopher home range of 150 m$^2$, which corresponds to the sum of average combined mound and swale areas in the Merced region (156 m$^2$). Howard and Childs (1959) measured a range of territory sizes for gophers in the San Joaquin Valley, CA, of 120-250 m$^2$.

The close correspondence between mound spacing and gopher spacing is consistent with a biologic explanation of Mima mound creation, in that each mound designates the territorial sphere of gopher burrowing and foraging activity. In addition, intermound distance and diameter are positively correlated (Fig. 2.21), as are mound and pool volumes (Fig. 2.6). These findings are also compatible with the biologic model, which predicts that the rodents use soil from the intermound areas to build the mounds.

The NNI value for gopher distribution was estimated using the territory maps published by Howard and Childs (1959) for 330 gophers (*Thomomys bottae mewa*) studied over seven years near Fresno, CA. *Thomomys bottae mewa* is suspected to be the same subspecies of gophers that lives within the Merced study region (Jim Patton, pers. comm.). The area studied by Howard and Childs did not bear Mima mounds but did support a dense gopher population. They mapped regions of territory by connecting outer points of capture with repeated trappings. The authors noted that the ‘orderly spacing of individuals is apparent’ and observed that there was rarely overlap in territory boundary, especially for gophers of the same sex. (They also noted that there was a strong correlation between soil depth and gopher abundance - most gophers preferred regions with soils greater than one-half meter in thickness.) Strong intra-species and inter-species aggression and territoriality has been documented in laboratory experiments. For instance, Baker (1974) observed consistent aggression between *Thomomys talpoides* and *Thomomys bottae* and determined the species which inhabits a wider variety of environmental conditions, *Thomomys talpoides*, was more aggressive than its narrow-niched counterpart. Within a single species, *Geomys attwateri*, Gregory et al. (1987) also found highly agonistic behavior between individuals and reported that fighting only ended when one or both of the gophers had created a soil partition between their respective burrows.

The reasons for this strict territoriality are likely based on the energetic and logistical limitations faced by subterranean organisms. Tenacious burrow defense is expected due to the extremely high energetic costs required by foraging, mating, and breeding almost entirely in an underground soil environment (Vleck, 1979). Romanach et al. (2005a) studied three species of gophers in a variety of soil and vegetative environments and found burrow geometry to be generally similar across species, sexes, ages, and habitats. This indicates that, across species, gophers may optimize their spacing to maximize individual foraging efficiency. For instance, Reichman et al. (1982) found strict tunnel spacing within a single gopher’s burrow and between different burrows, despite a doubling in plant productivity across study areas. In addition, in a simulated gopher environment, Seabloom and Reichman (2001) found
that annual plant abundance increased with gopher density in the long term (beyond forty years). These optimizations in burrow spacing and gopher density and feedbacks between gopher density and plant abundance may result in large-scale self-organized ecosystems (e.g., Rietkerk and van de Koppel, 2008) such as the Mima mounds and vernal pools under study.

**General observations**

Finally, several other mound patterns were observed within the dataset (Sec. 2.3.6). If the DSC model is correct, the patterns may provide further insight into the nature of mound formation and persistence. For instance, several regions included dense patches of mounds interspersed with flat, mound-free areas (Fig. 2.25, top and middle panels). It remains to be established whether the mound-free areas are due to human disturbance and leveling of mounds, or another cause. Inspection of the areas on Google Earth™ did not provide insight and ground inspection of these regions was not attempted. The pattern could be the result of fluvial erosion or deposition flattening pre-existing areas of mounds. In some cases, mounds are observed in the middle of the flat, voided areas (see circled portion of middle panel Fig. 2.25) and may have formed recently after the flat regions were created.

Circular or arcuate chains of mounds are observed in many locations (Fig. 2.25, bottom panel). Some of these forms appear to line up with drainage patterns, while others do not. It is possible that the arcuate patterns may reflect subsurface conditions that gophers respond to in the process of building Mima mounds.

In many cases, larger surface features appeared to be in the process of being divided into smaller component Mima mounds (e.g., Fig. 2.24 and 2.25, middle panel), supporting the DSC model. However, it has also been suggested that the mounds are the result of differential erosion of such larger topographic structures. Contradicting the erosion proposal, many of the mounds overlying the larger forms are oriented in several directions and not necessarily aligned with the direction of fluvial or aeolian movement (Fig. 2.24).

**2.5 Conclusion**

This work provides the some of the strongest evidence to date in support of a biologic model of Mima mound formation. I documented clear landscape-wide patterns of mound morphology which are consistent with gopher-built mounds. In particular, mound height and density (mounds per area) systematically increased along the Merced River chronosquence, likely reflecting the different stages in mound formation as soils age. While many of the previous Mima mound studies have yielded results which are consistent with multiple explanations, the clear pattern of mound change with pedogenesis is only predicted by the biologic model. In addition, widespread regularity in mound distribution closely matches the strict habitat spacing of territorial gophers. Finally, the LIDAR analysis provided insight regarding how macrotopographic changes might relate to mound formation and gopher ecology. For instance, mounds are commonly taller on north-facing slopes which could reflect changes
### Chapter 2. Mima Mound Form and Distribution Across a Soil Age Gradient

<table>
<thead>
<tr>
<th>Region</th>
<th>Source</th>
<th>Dispersion Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Argentina (Tuco-tucos)</td>
<td>Cox &amp; Roig (1986)</td>
<td>0.75</td>
</tr>
<tr>
<td>Imperial County, CA (Creosote bush)</td>
<td>Cox (1987)</td>
<td>1.1</td>
</tr>
<tr>
<td>Merced, CA (Young soils) 10 k.y. - 50 k.y.</td>
<td>This Study</td>
<td><strong>1.20</strong></td>
</tr>
<tr>
<td>Kenya (Kenyatta Airport) (Mole rats)</td>
<td>Cox &amp; Gakahu (1985)</td>
<td>1.29</td>
</tr>
<tr>
<td>Oneals, CA (Gophers)</td>
<td>Howard and Childs (1951)</td>
<td><strong>1.30</strong></td>
</tr>
<tr>
<td>South Africa (Termite mounds)</td>
<td>Levick et al. (2010)</td>
<td><strong>1.45</strong></td>
</tr>
<tr>
<td>Wyoming</td>
<td>Spackman (1982)</td>
<td>1.49</td>
</tr>
<tr>
<td><strong>Merced, CA (Old soils) 200 k.y. - 3000 k.y.</strong></td>
<td>This Study</td>
<td><strong>1.50</strong></td>
</tr>
<tr>
<td>San Diego, CA</td>
<td>Cox (1984)</td>
<td>1.52</td>
</tr>
<tr>
<td>Kenya (Waunyomu Ngeke) (Mole rats)</td>
<td>Cox &amp; Gakahu (1985)</td>
<td>1.53</td>
</tr>
<tr>
<td>South Africa (Mole rats)</td>
<td>Cramer et al. (2012)</td>
<td>1.60</td>
</tr>
<tr>
<td>Colorado</td>
<td>Vitek (1978)</td>
<td><strong>1.61</strong></td>
</tr>
<tr>
<td>South Africa (Mole rats)</td>
<td>Love &amp; Siegried (1989)</td>
<td>1.70</td>
</tr>
<tr>
<td>Oklahoma</td>
<td>Vitek (1978)</td>
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<tr>
<td>Idaho</td>
<td>Vitek (1978)</td>
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</tr>
<tr>
<td>Iowa</td>
<td>Brotherson (1982)</td>
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</tr>
<tr>
<td>Washington</td>
<td>Vitek (1978)</td>
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<tr>
<td><strong>South Africa (Bush clumps)</strong></td>
<td>Cramer et al. (2012)</td>
<td><strong>1.80</strong></td>
</tr>
<tr>
<td>Niger (Bush clumps)</td>
<td>Rietkerk &amp; van de Koppel (2008)</td>
<td>1.80</td>
</tr>
<tr>
<td>Texas</td>
<td>Robinson (2012)</td>
<td>1.82</td>
</tr>
</tbody>
</table>

*Table 2.4: Mound dispersion for Mima mounds in North and South America and Africa (in non-colored rows). Dispersion value (nearest neighbor index (NNI)) of 1 indicates a random pattern and a value of 2.5 signifies maximum dispersion (regularity). NNI less than 1 indicate a clustered pattern. Values in colored rows represent spatial distribution for plants (green), pocket gophers (inhabitating non-mounded terrain) (brown), and termite mounds (blue). The animals listed in parentheses in the non-colored rows are the resident burrowing animals found in the Mima mound regions listed. The resident burrower is a gopher unless otherwise noted. Median values for reported ranges are asterisked.*
in gopher sediment transport in response to denser vegetation and/or more saturated soils caused by differences in solar radiation.

Given the likelihood that gophers play a key role in the formation of Mima mound topography, it is also important to address their role in the creation and maintenance of the adjacent vernal pool wetlands, a global biodiversity hotspot (Myers et al., 2000) that is rapidly disappearing due to land use change and increasingly threatened by climate change. The utility of the LIDAR data could be further expanded by using the digital terrain models for habitat modeling and wetland mitigation. For instance, many agencies in California are focused on predicting vernal pool habitat in order to optimize conservation planning (e.g., Vollmar et al., 2013). LIDAR data of Mima mounds and vernal pools would be valuable tools in these applications, allowing conservationists to more precisely predict the locations of the many vernal pool species which inhabit very specific regions along pool basin transects (Crowe et al., 1994; Bauder, 2005). In Chapter 4, the LIDAR data is used to model erosion and deposition on the grassland landscapes in further effort to characterize the role of gophers in the persistence of mound-pool ecosystems.
Chapter 3

Pocket Gopher (Thomomys bottae) Sediment Transport on the Merced River Chronosequence

The element of time granted, we are able to conceive of vast accomplishments on the part of even so humble a contributor as the pocket gopher. –Joseph Grinnell, 1923

3.1 Introduction

Small soil hillocks up to 2 m tall and 1-50 m in diameter cover large portions of western North American grasslands, as well as scattered regions around the world. Generally referred to as Mima mounds, after their type locality on the Mima Prairie in Washington, the origin of the features has been debated for more than two centuries (Johnson and Horwath Burnham 2012). More than thirty hypotheses have been proposed for Mima mound origin, most of which fall into one of five general categories: erosional, depositional, shrink-swell, seismic, or biotic. While recent studies have presented evidence supporting aeolian (Seifert et al., 2009) and erosion-vegetation anchoring (Cramer et al., 2012) hypotheses in Arkansas and South Africa, respectively, the proposal that burrowing organisms play a primary role in creating the mounds is becoming more widely accepted. The first proponent of a biologic hypothesis was Darby (1816) who suggested mounds in central Louisiana were created by ‘some kind of mole’. The biotic proposal was formalized by Dalquest and Scheffer in 1942, further developed by Cox (1984, 1987, 1990) and is referred to as the Dalquest-Scheffer-Cox (DSC) model (Johnson and Horwath Burnham, 2012).

The DSC model proposes that Mima mounds are created by subterranean mammals (in most cases, pocket gophers (Rodentia: Geomyidae)) that build up raised nest centers in regions with thin soils. According to the model, burrowing animals like gophers establish centers of activity for reproduction, foraging, estivation, hibernation, and predator avoidance.
As fossorial organisms, the animals are strongly impacted by thin or water-logged soils because such conditions affect thermo-regulation and exposure to predators (McNab, 1966). Accordingly, the DSC model suggests that the animals initially locate nesting centers in local areas with slightly thicker soil and better drainage. Outward burrowing from those centers results in a portion of soil being directed centripetally backwards. When a small amount of that back-transported sediment is accumulated, it results in preferable habitat for future generations of animals. The process, continued over many years, leads to Mima mounds.

While the DSC model has garnered fairly extensive support, much of the evidence is circumstantial. For instance, many studies focus on particle size distributions (e.g., Horwath and Johnson, 2006) or compare the geographic distributions of Mima mounds with those of the various explanatory factors (distribution of gophers, glaciers, expandable clays, etc.) (e.g., Ricks, 1997). This evidence is important for understanding Mima mound origin, but often the observed patterns are consistent with multiple hypotheses, or are likely the result of a combination of geomorphic and/or biologic events, making conclusive assignment of agency difficult. A few studies have reported qualitative observations of mound building by gophers. For instance, Price (1949) reported that “a mature Mima mound has been built in 5 years” in Texas. On the Carrizo Plain in California, Johnson and Horwath Burnham (2012) reported the formation of a number of mounds on terrain which had been cultivated until the 1980s. These reports are illuminating, but are limited in scope and don’t provide quantitative information about how the mounds were built.

Cox (1984) and Cox and Allen (1987) are the only known studies to directly and quantitatively document constructional soil transport by gophers. They inserted soil plugs containing metal markers into gopher burrows in Mima mounds near San Diego, California, and found that the net movement of sediment by gophers was moundward (towards the center of Mima mounds), presumably in response to saturated conditions in the thin soils. Direct observations such as these are a more powerful line of evidence for explaining the existence and persistence of Mima mounds. Since Mima mounds are a global phenomenon, replication of such studies in more than one location is critical.

A better understanding of the trajectory of gopher sediment movement is important not only to demonstrate the generality of Cox and Allen’s findings with respect to Mima mound development, but also to quantify land surface evolution processes. Recent studies have highlighted the role of biologic processes in landscape modification (often referred to as bioturbation). In particular, burrowing organisms have been shown to strongly impact soil mixing rates, increase erosion, increase landscape heterogeneity, modify soil fertility, and affect plant productivity and distribution (Black and Montgomery, 1991; Huntly and Inouye, 1988; Gabet 2000; Reichman and Seabloom, 2002; Hall and Lamont, 2003, Johnson et al., 2005; Zaitlin and Hayashi, 2012). The effects of bioturbation can have significant ecosystem-wide impacts. For instance, changes in pocket gopher burrowing in response to Medieval climate change may have destabilized ancient Nebraskan sand hills (Schmeisser et al., 2009). More recently, bioturbation has been shown to increase pollination (by raising the elevation of flowers) (Yoshihara et al., 2010) and fungal biodiversity (Taylor et al., 2009). If it is the case that gophers are responsible for building and/or maintaining Mima mounds, then their
CHAPTER 3. POCKET GOPHER (THOMOMYS BOTTAE) SEDIMENT TRANSPORT ON THE MERCED RIVER CHRONOSEQUENCE

sediment transport also leads to the development and preservation of the basins adjacent to Mima mounds, that in many places (especially in California) are seasonally filled with water. These ephemeral wetlands, called vernal pools, provide habitat for 60 species endemic to California (Witham, 1998), many of which are threatened with extinction (Alexander and Schlising, 2011).

Several studies have clarified the need to quantify biotic-abiotic interactions (Dietrich and Perron, 2006; Amundson et al., 2007; Reinhardt et al., 2010). Many 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 (e.g., Fernandes and Dietrich, 1997; Gabet, 2000). Other work highlights the importance of differentiating direction in biotic sediment transport (Roering et al., 1999, Yoo et al., 2005). In the last decade, radio frequency identification (RFID) technology has increasingly been used in sediment transport studies (e.g., Nichols, 2004; Allan et al., 2006; Curtiss et al., 2009; Miller et al., 2011; Bertoni et al., 2012). The technology involves the use of radio-frequency electromagnetic signals to transfer data between small transponders (passive integrated transponder (PIT) tags, cm-scale length) and a signal receiver in order to track movement. To date, it has been primarily used in stream and marine studies to trace the trajectory of clasts along riverbeds and beaches. Applying PIT tag technology to the study of biotic sediment transport in Mima mounds could aid in the development of a more complete model of Mima mound dynamics and could contribute to the recent focus on biotic-abiotic interactions in geomorphology.

3.1.1 Objectives and hypotheses

This study extends the methods of the Cox and Allen (1987) Mima mound sediment transport study, but broadens the approach to include a diversity of soil types in one of the largest remaining grasslands of the Central Valley of California. The range of soil types comprise a soil chronosequence and is meant to represent discrete stages of soil formation and, presumably, biologic response to changing soil conditions. In this diversity of soil, I test the following hypotheses:

- As soil formation occurs and landform age increases, soil permeability and effective soil thickness (depth of the mobile layer) will decrease.
- In response to the soil changes, gophers will seek out better drained, thicker soils on which to concentrate their nesting and foraging.
- Soil movement by gophers will become increasingly moundward (directed towards the center of the mound) and upward as landform age increases, due to nesting in and foraging outward from locations of relatively reduced soil saturation and increased soil thickness, ultimately leading to mounded terrain.
Soil movement by gophers should be directed moundward at the base of mounds and this trend should decrease at the mid and tops of mounds, where soil is thicker and less saturated.

In this study, I use sediment tracer technology and long-term field measurements to: (1) Develop a novel use of RFID sediment monitoring, to quantify gopher soil transport pathways in Mima mound-vernal pool habitat, (2) Quantify the potential differential response of gopher burrowing to soil condition along a soil age gradient, (3) Measure and compare rates of gopher sediment transport across a range of geologic types and topographic positions, (4) Create detailed maps of the spatial pattern of aboveground gopher sediment movement and use the information to infer details of gopher ecology and foraging strategies, and (5) Analyze soil conditions and confirm that soil profile characteristics are consistent with the DSC model of mound formation.

3.2 Methods

3.2.1 Study area and focal species

Pocket gopher sediment transport was monitored at five sites in the San Joaquin Valley (Fig. 3.1), near Merced, California (CA). The sites include a dense distribution of Mima mounds and vernal pools on a series of landforms which range in age from 0.01 to 3 million years (My) old (Marchand, 1976; Pavich, 1986; Harden, 1987). The terraces formed from river incision driven by glacial outwash from the neighboring Sierra Nevada. The fluvial sediments that cap the terraces consist primarily of granitic alluvium, and the soils are classified as Entisols on the lower, younger terraces and as Alfisols on the higher, older terraces (Arkley, 1962). On the oldest surfaces, claypans or duripans (associated with restrictive $Bt$ and $Bqm$ soil horizons, respectively) have formed (Arkley, 1962). Mima mounds are found on four of the five landforms. The sites are named for their corresponding geologic formation: Laguna (3 My), Riverbank (0.2 My), Lower Modesto (0.05 My), and Upper Modesto (0.01 My). No Mima mounds are found on the youngest site, Upper Modesto. On the oldest landform (Laguna), two study areas were chosen: one on a level terrace top (Laguna level) and one on the slope descending to the next terrace level (Laguna sloping, slope $\sim$20%). 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 $^\circ$C (NOAA, 2013 (Station 045535)). Annual grasslands, dominated by non-native species, cover the landscape, which has been grazed for over a century (Vollmar, 2002).

Pocket gophers are fossorial (burrowing) herbivores that create large tunnel systems through digging with their teeth and/or front claws. The subspecies $Thomomys bottae mewa$ occurs in a range from Sacramento, CA, to south of Fresno, CA (Grinnell, 1927), and is likely the subspecies inhabiting the sites in this study (Jim Patton, Pers. comm.). $Thomomys bottae mewa$ is notably different from its neighboring species in that it has a smaller body, darker pelage, and distinctly procumbent incisors, enabling more powerful digging (Patton
and Smith, 1990). This suggests that the subspecies has resided in relatively thin, high clay, low permeability soils for a long period of time and therefore provides an opportunity to test whether gophers have developed any behavioral adaptations to sediment transport in order to adapt to limiting soil conditions.

### 3.2.2 Soil profile observations

Baisden et al. (2002a) dug a trench through a Mima mound on the Laguna Formation using a backhoe (Latitude = 37.55°; Longitude = −120.44°; Elevation = 220 m). For this study, the outer 15-30 cm of material were removed from the trench face in order to re-expose and examine the profile of a typical mound. In addition, the adjacent intermound region was excavated to the depth of the apparent water-restrictive layer. Descriptions of the soil profile were made following Schoenenberger et al. (2002).

To assess differences in soil strength along the age gradient, a Rimik CP40 cone penetrometer was used to measure soil hardness. At least ten measurements were made on each landform. Soil hardness was measured to the maximum possible depth, although on many locations, the penetrometer was not able to breach the soil surface. On the mounded terraces, measurements were made on both mound tops and basin bottoms. Both maximum and average hardness measurements were recorded. Measurements were made in December 2012, in a two-day period following a rain event (0.3 cm) (NOAA, 2013).

### 3.2.3 Direction of gopher sediment transport

If gophers are responsible for creating the mounds, they must systematically move sediment in the upslope direction and towards the center of the mound, against the force of gravity. In addition, while much discussion has focused on the origin of the mounds, an equally important question is: what maintains the mound and swale topography? Using principles from hillslope geomorphology (Gilbert, 1909; Culling, 1960, 1963), I consider Mima mounds to be miniature gentle, convex hillslopes. These hillslopes undergo slope-dependent, downward soil creep through a combination of physical and biological processes (such as gopher burrowing or tree turnover). For the mounds to persist, there must be an upslope/moundward movement which must exceed downslope transport generated by biotic activity and wind and water erosion (Fig. 3.2). To test the proposal that gophers build and maintain Mima mounds, I tracked gopher soil movement on each of the five study sites. Study plots (8000-10000 m²) were delineated on each of the landforms and six surveys of gopher activity were conducted on each site from July 2010 to December 2012.

The direction of movement was monitored using small RFID (radio frequency identification) or PIT (passive integrated transponder) tags. For each survey, two to three mounds were chosen to represent a range of mound size (height and diameter) classes. A unique set of mounds was chosen for each of the six surveys on each of the five study areas. Three evenly-spaced concentric zones were designated on each mound: top, middle, and base of mound (Fig. 3.2 and 3.3). The edge of a mound was estimated to be at the inflection point
Figure 3.1: Eastern Merced County regional map showing geologic formations as mapped by Marchand (1976). Five gopher monitoring locations are marked with blue circles and located on surfaces ranging from 0.01 m.y. to 3 m.y. Formation age generally increases from west to east, with younger terraces in green and older in red. The study area is centered in the Yosemite Lake USGS (United States Geological Survey) Quadrangle, at latitude $\sim$37.49°N and longitude 120.44°W. Shaded relief outlines of the LiDAR survey areas from Chapter 2 are also shown.
in which the mound slope changes from clearly inclined to nearly level. Therefore, mound delineations did not extend into the adjacent basins. A steel marker was inserted at the center of each mound in order to serve as a consistent benchmark from which to make displacement measurements. On the youngest formation, on which there are no Mima mounds, I defined “mounds” by outlining areas of gopher activity, via surface tailings (small semicircular piles of loose soil which cover tunnel openings, hereafter referred to as ‘tailings’). It was assumed that the region of activity for one gopher could be defined by identifying areas in which no surface gopher activity was visible ∼1 m beyond the edge of a cluster of tailings.

Two types of PIT tags (23mm rod-shaped and 30mm disk-shaped) were used to represent a range of soil particle sizes (Fig. 3.5). PIT tags were mixed with ∼900 cm$^3$ of loose, local soil. The soil-tag mix was placed in one gopher burrow in each of the designated mound zones (top, mid, or base) (Fig. 3.4) and the opening was covered with sod. Tags were placed in tunnels with a minimum clearance of 15 cm and an average clearance of 50 cm. One to two months after the tags were emplaced, they were re-located using the PIT tag reader (Oregon RFID, www.oregonrfid.biz) and their position and displacement were recorded with a differential GPS (global positioning system, Trimble GeoXH®) and with a measuring tape, following the methods of Cox and Allen (1987). A low-frequency, half-duplex RFID system was used. In order to improve the accuracy of PIT tag detection, a 30 x 30 cm PVC square was placed on the ground in the vicinity of the signal and was used to iteratively pinpoint the tag location. All mounds adjacent to the study mounds were also surveyed for PIT tag detection in order to avoid biasing against long distance tag movements.

Tags that moved closer to the mound apex from the implant location were identified as ‘moundward’ movements and displacements (original distance less final distance from apex) were recorded as positive values, while tags that moved away from the mound center were considered ‘edgeward’ movements and recorded as negative values. Note that the displacement measurements reflect the overall proximity to the mound apex. That is, if a PIT tag is moved such that it ends up closer to the apex compared to its implant location, the displacement is ‘moundward’, even if the PIT tag moves from one side of the mound to the other, but is still closer to the apex on a net basis. Statistical tests were conducted using R software (Version 3.0.0, http://www.R-project.org). T-tests (confidence level = 0.90) were conducted across several categories (geologic formation, mound position (top, middle, or base), mound height (measured via LIDAR data discussed in Chapter 2), PIT tag type, and time of survey) in order to estimate the sample mean for tag displacement values and assess the reliability of that estimate. ANOVA and Tukey’s Honestly Significant Difference (HSD) tests were applied to assess whether sample means are equal and to determine which pairs of means are different within the stated significance level. Transport dynamics were then evaluated in the framework of the DSC model. I propose that if mounds are created as a biologic response to changes in soil depth and/or permeability, soil movement (as assumed to be represented by PIT tag movement) should become more moundward with decreasing soil thickness and increasing soil moisture and soil age. Given this, the null hypothesis states that differences in PIT tag displacement would be indistinguishable between the geologic formations and mound positions.
Figure 3.2: A conceptual model treating a Mima mound as a miniature hillslope, subject to slope-dependent, gravity-driven soil creep (red arrow). The soil creep occurs as a combination of physical and biological processes. For Mima mounds to exist and persist, there must be a restorative soil movement which counteracts the downslope erosion. The restorative movement is hypothesized to be due to upward (and moundward) sediment transport by gophers (green arrow). To test the hypothesis, mounds were divided into three, equal concentric zones (top, mid, and base) as indicated by the blue lines. PIT (passive integrated transponder) tags were implanted in each zone and their movement was tracked.
Figure 3.3: Mounds were divided into three, equal concentric zones (top, mid, and base). PIT (passive integrated transponder) tags were implanted in each zone and their movement was tracked. Base shaded relief image is derived from a 1 m DEM of LIDAR data of the region (Ch. 2). Red points show locations of recent gopher activity (gopher tailings).
Figure 3.4: Illustration demonstrating the technique for inserting PIT (passive integrated transponder) tags (reproduced with permission from Case and Jasch, 1994). As shown in the top panel, a pointed metal stake was used to perforate the soil surface in between recent gopher tailings until a tunnel was found. Tunnels were verified using a flexible metal rod and used for the experiment only if a tunnel clearance of at least 15 cm was confirmed. The tags were mixed with approximately 900 cm$^3$ of soil, placed in active gopher tunnels (lower panel), and tracked using an RFID (radio frequency identification) reader, following the methods of Cox and Allen (1987).
Figure 3.5: Main photograph shows the larger PIT (passive integrated transponder) tag in comparison to the sediment in a gopher tailing on the ∼0.2 My Riverbank soils. Inset shows size of smaller PIT tag used, relative to a grain of rice (Wikimedia Commons, 2013). Two sizes of PIT tags were used in order to more adequately represent the range of soil particle sizes found at the study sites.
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3.2.4 Magnitude and distribution of gopher sediment transport

The quantity of soil moved by gophers was estimated by counting, weighing, and mapping soil surface tailings piles on each landform. Tailings (Fig. 3.6) were identified, flagged, and their locations were recorded using a Trimble Geo XH™ GPS (Fig. 3.7). Regions mapped were \( \sim 10000 \text{ m}^2 \) in area, except on the sloping Laguna formation, where a \( \sim 8000 \text{ m}^2 \) region was monitored. Four smaller (3500 m²) surveys of gopher soil movement conducted in 2005-2008 in a pilot study on the Laguna formation are also reported. Gopher tailings were identified as loose piles of soil on the ground surface, with no vegetation growing on them. If any uncertainty existed about whether a soil mound was caused by recent gopher activity (or by activity during an earlier measurement period), it was not flagged. I note there is a relatively clear distinction between “fresh” tailings and older tailings (tailings that had been subject to a rain event or events) based on the degree of hardening of soil on the gopher tailing surface. Thus, the number of tailings reported is a likely minimum.

Measurements of the magnitude of gopher activity were made on nine occasions between 2005 and 2012, during a range of climate conditions. On three of these occasions (November 2005, November 2010, and March 2011), 30 tailings piles on each landform were selected (in a manner meant to represent a range of positions along mound-pool transects) and weighed with a field spring balance in order to obtain estimates of mass movement associated with burrowing. The tailings mass measurements were not corrected for soil moisture content. In addition, as the direction and magnitude of gopher sediment transport was monitored, general characteristics of gopher tunnel architecture were also recorded.

The data describing density and mass of gopher tailings were combined, along with published bulk density data (Harden, 1987; White et al., 1996), estimates of tailings age (based on time since last rainfall at time of survey), and the PIT tag survey results, in order to estimate rates and vectors of biotic soil movement. All reported estimates of tailings volume, mass, and concentration are the average of all measurement periods. The volume of gopher soil movement (m³ ha⁻¹) across each site was calculated using the average individual gopher mound mass, the average concentration of gopher mounds (tailings per area), and the average soil bulk density for each landform (Harden, 1987 and White, 1996). The average rate of above-ground gopher sediment movement (m³ ha⁻¹ yr⁻¹) was estimated using the assumption that the measured gopher mound material had been produced since the time since last rainfall, informed by meteorological data collected at nearby weather stations (NOAA, 2013). The vector of gopher sediment transport (moundward soil movement rate, cm / 1000 year) was estimated by adjusting the rate of above-ground sediment movement to reflect the proportion of soil that is moved moundward on each geologic formation (based on PIT tag movements). Note that the tunnels in which PIT tag movements were emplaced were almost always ‘feeding’ tunnels, which gophers use for underground root foraging (Cridle, 1930). Because the feeding tunnels run parallel to the mound surface (Arkley and Brown, 1954), PIT tags that are moved moundward are also assumed to represent (at least in part) upward, constructive transport which counteracts soil erosion.

Point pattern analysis (PPA) is used to describe patterns of locations of mapped point
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events and is an important tool for interpreting ecologic processes (Weigand and Moloney 2004; 2013). Several methods of PPA are commonly used, including Nearest Neighbor Index (NNI) and Voronoi diagrams, but Ripley’s K-function is a form of second order spatial point pattern analysis which gives an effective summary of spatial dependence over a wide range of scales (Ripley, 1981). Here, I use a Ripley’s K approach on the point data representing gopher tailings locations in order to test the following null hypotheses: (1) the spatial distribution of gopher tailings is random, and (2) the spatial distribution of gopher tailings is indistinguishable between geologic and restrictive depth groupings. I conduct this test in order to explore whether there are differences in gopher burrowing behavior across the chronosequence.

The overall strategy of Ripley’s K is to construct a set of concentric circles at defined distances around each point and count the number of neighboring points in each band. Ripley’s K-function, \( K(r) \), is defined as the expected number of points within a distance \( r \) of the center point \( (E(r)) \), divided by the intensity of the pattern \( (\lambda) \), or the mean number of points per area.

\[
K(r) = \lambda^{-1} E(r) \tag{3.1}
\]

A modified version of this definition, transformed \( K(r) \), was used to enhance visual interpretability.

\[
L(r) = \sqrt{K(r)/\pi} - r \tag{3.2}
\]

To test whether the observed pattern differed from Complete Spatial Randomness, 99 Monte Carlo simulations were carried out on a random set of coordinates, and \( K \) values were calculated for each pair of coordinates within each subset, generating upper and lower bounds of significance. If the transformed Ripley’s function is above zero and within the 99 percent confidence envelope generated by the simulations, the tailings are clustered or aggregated and point-to-point distances are generally smaller than that of a random pattern. If the function is below zero and within the confidence interval, gopher tailings are dispersed in a regular distribution and interpoint distances tend to be larger than those characteristic of a random pattern. Ripley’s analysis was performed using R software (Version 3.0.0, via the spatial library (Venables and Ripley, 2002) and the spatstat library (Baddeley and Turner, 2005)).

Despite the utility of Ripley’s K function, many ecological studies report the Nearest Neighbor Index (NNI), also known as the \( R \) statistic. In order to enable better quantitative comparison between tailings distributions along the soil age gradient, the \( R \) statistic was also calculated for the tailings on each terrace. The formula for \( R \) is as follows:

\[
R = r_a/r_e \tag{3.3}
\]

\( r_a \) is the mean observed distance to nearest neighbors:

\[
r_a = N^{-1} \sum_{i \neq j} u_{ij} \tag{3.4}
\]
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for a set of \( N \) points where the distance between the \( i^{th} \) point and the \( j^{th} \) point is \( u_{ij} \).

\( r_e \) is the mean expected distance in a random distribution of points. Complete spatial randomness for \( N \) points in an area \( A \) is described by the Poisson process. The expected average distance between nearest neighbors for this distribution is as follows:

\[
    r_e = 0.5\sqrt{A/n}
\]

Values of \( R \) range from 0 (maximum clustering), through 1.0 (random pattern), to 2.0 (regularly spaced square lattice), to 2.1492 (hexagonal lattice) (Clark and Evans, 1954; from Vitek).

3.3 Results and Discussion

3.3.1 Soil profile

Figure 3.8 shows the profile of the excavated mound on the Laguna formation. The upper 25 cm is an \( A \) horizon, characterized by a darker color value and more homogeneous matrix than the lower horizons. This layer also contains a higher concentration of small gravels and a relative absence of large gravels and cobbles compared to the horizon directly below it. These characteristics suggest significant bioturbation and sorting by burrowing organisms, likely gophers. Although the trenched mound was not currently occupied by gophers, gopher tailings nearby indicate that they are active in the region. In addition, gopher-sized tunnels were observed at several locations in the soil profile.

The \( Bt \) horizon, located beneath the \( A \) horizon, (25-88 cm; approximately 30% clay) has prismatic structure and an irregular lower boundary. Such features generally require \( 10^4 \)-\( 10^5 \) years to develop (Birkeland, 1999). The \( Bt \) layer did not extend into the intermound region.

Based on these observations, several scenarios could be proposed. For instance, the mounds may have existed in roughly their current form since the late Pleistocene. On the other hand, the mound stratigraphy could also reflect a time when the formation rates of the prismatic structure of the \( Bt \) horizon exceeded bioturbation rates, or could reflect the attenuation of biotic activity with depth. In addition, a \( Bt \) layer could have been already in place across the landscape when mound-building began, and the gophers may have extracted the \( Bt \) horizon sediment from the intermound regions and redeposited it in the mounded areas.

Further constraining the age controls on mound formation and comparing them to records of gopher activity and inhabitation could help untangle the factors of formation. Davis (1999) conducted a pollen analysis of sediments in Tulare Lake, a currently dry lakebed \( \sim 140 \) km south of the field region. The results of the analysis are the best known proxy to provide a chronology of vegetation and climate for this study region. The study found that Great Basin-like vegetation (giant sequoia and greasewood) dominated the low elevation interior from roughly 28000-8500 B.P., with vegetation similar to present-day vegetation (grassland) occurring around 7000 B.P. Gophers likely began to inhabit the region around the time of this vegetation shift. Potter Creek Cave and Samwel Cave, both located in
Figure 3.6: Typical tailings piles from pocket gopher (*Thomomys bottae*) tunneling. An average gopher tailings pile is \( \sim 25 \) cm in diameter. A variety of ages of tailings can be seen, ranging from older piles of sediment, which are hardened over by past rain events and/or overgrown with vegetation to new tailings piles, composed of loose soil and no overlying vegetation.
Figure 3.7: A photograph of Mima mound and vernal pool landscapes where the small mounds generated by gopher activity (tailings) have been mapped. A Trimble® differential Global Positioning System (GPS) was used to create detailed tailings maps on ~8000-10000 m² plots on each landform. A representative subset of the tailings was weighed on each geologic formation to estimate the magnitude of gopher sediment transport.
Figure 3.8: Mima mound cross section (latitude 37.46°N; longitude 120.37°W) with pick, 65 cm in length, for scale. Mound apex is near left-hand side of photo. Relict gopher burrows were observed in the A and B horizons, down to 70 cm. Mounded region in the background shows tailings pile from trenching. The cobble layer is continuous from the base of this mound to an adjacent swale. (Photo courtesy of A. Heimsath.)
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north-central California in Shasta County, are the source of most gopher fossils collected in the northern half of the state (MVZB, 2012). *Thomomys* emplacement is dated to the late Pleistocene, during the last glacial maximum (Feranec et al., 2007). These observations support gopher presence on a time scale long enough to build the mounds according to this study’s stratigraphic observations and models of mound formation (Reed and Amundson, 2012; This volume (Ch. 4)). However, given the sparse paleontological record, gophers or a related species may have inhabited the region prior to the present interglacial period.

The layer (88-120 cm) underlying the *Bt* horizon has a concentration of large cobbles. This layer is a continuous strata which crops out in the adjacent vernal pools, and has been observed by other studies in the region (e.g., Arkley, 1962). A biotic mechanism of mound creation should result in a two-layered biomantle: a concentration of small clasts, those that can readily be transported by animals (in this case, gophers) in the mounds, and a layer of cobbles and large clasts below the mounds (Horwath and Johnson, 2006), as is observed here. Gophers have been shown to burrow around and under unmanageable clasts (Grinnell and Storer, 1924; Murray, 1967) which can undermine the large particles and cause them to settle into a lower stone-rich layer. At the same time, gophers preferentially move smaller sediments into their zone of burrowing (the typical size range of particles moved by gophers is 0.6-2.5 cm (Hansen and Morris, 1968) and the maximum particle size transported by gophers is 5-7 cm (Dalquest and Scheffer 1942; Murray, 1967; Johnson, 1989)). Cox (1984b) found a higher concentration (1.8 times) of small stones (long axis < 5 cm) in the mounds near San Diego as compared with the intermound regions. The observed particle size distribution is inconsistent with several alternative proposals for mound origin. If the mounds were formed by wind deposition, they would be composed of sand-sized or smaller particles and would not contain gravel. Differential erosion would concentrate gravels and cobbles in the intermound regions, however, it would not cause that concentration to extend continuously underneath the mounds.

Below the cobble layer lies a dense, hard, clay-rich layer which impedes water percolation and burrowing by gophers. In 1941, Nikiforoff made observations of hundreds of mounds in grasslands approximately 175 km south of the study region. Both he and Arkley and Brown (1954) noted that the water-restrictive layers did not parallel the microrelief surface. Further, Nikiforoff noted that many mounds had at their base a “window” in the hardpan surface, which ranged in size from 0.3-3.7 m across. Generally, the soil underlying the mound at the level of the hardpan was more friable than that in the depressions. He also observed that gophers were “able to bore even through the firmest hardpan”. (Nikiforoff was an opponent of a biotic mechanism of mound formation.) I interpret the sum of these observations to indicate that the windows were either preexisting and expanded by gophers or originally created by them in effort to establish a nest. A significant advantage was then conferred to subsequent generations to re-use such nests, creating point centers from which generations of gophers foraged, eventually creating the mounds.

In addition to the soil profile observations, soil induration was measured across the chronosequence. Soil hardness measurements were highly variable. On the oldest formations, soils were often so hard and large cobbles so abundant that it was difficult to find
locations in which the penetrometer could breach the soil surface. Fig. 3.9 demonstrates that generally, the only subsurface measurements that were attainable on the oldest landforms (Riverbank and Laguna) were those that penetrated through multiple gopher burrows. For this reason, only maximum soil hardness measurements are reported as average measurements were unreliable. Maximum soil hardness measurements increased systematically with soil age (Table 3.2).

In conclusion, the clear presence of a continuous cobble layer at depth, a concentration of small clasts in the A horizon, gopher burrows throughout the profile, a dense, clay-rich layer at the base of the mounds, and more indurate soils on older formations all support the proposal that the mounded terrain results from directed (moundward) soil movement by gophers in response to low soil permeability and hardpan restrictions to burrowing.
3.3.2 Directional movement of soil by gophers

Sixty-six mounds (including the gopher activity areas designated as ‘mounds’ on the youngest Upper Modesto formation) were monitored for directional gopher activity between 2010 and 2012. Mound heights ranged from 0.12 to 0.34 m and diameters ranged from 6 to 23 m. A total of 871 PIT tags were deployed, 74% of which were recovered. Of those recovered, 51% moved more than 15 cm from the location of implant. Pocket gophers were most active in moving PIT tags in surveys conducted in the winter and spring months, with an average of 63% being relocated in the wetter months of the year (October-April), while only ~20% of tags were moved in the hotter, drier months (May-September). Significant differences in movement with respect to PIT tag type and mound size were not observed.

Movement of PIT tags on mounded terrain exhibited patterns similar to the results of Cox and Allen, 1987 (Table 3.1). An example of typical tag movement for one mound on the 0.05 My Lower Modesto landform is shown in Figure 3.10. Recall that the displacement measurements reflect the overall proximity to the mound apex. That is, if a PIT tag is moved such that it ends up closer to the apex compared to its implant location, the displacement (original distance less final distance) is ‘moundward’, even if the PIT tag moves from one side of the mound to the other, but is still closer to the apex on a net basis. The average distance moved (not accounting for direction) was 100 cm and the maximum displacement was 470 cm. The majority of tags emplaced on mounded terrain moved toward the center of the mounds rather than towards adjacent basins (Fig. 3.11). Across all mounded sites, the average horizontal displacement was 5 cm moundward and the net displacement (the sum of all signed movements (+ for moundward and - for edgeward)) was 1278 cm moundward.

PIT tag movement by gophers shows a trend of becoming more moundward as soil age increases (Figure 3.12). Average displacements ranged from 30 cm edgeward (away from the mound apex) on the youngest, non-mounded site to 28 cm moundward (towards the mound apex) on the oldest, level site. Net displacements (sum of all movements, accounting for direction) ranged from 18.0 m edgeward to 18.3 m moundward on the youngest and oldest landforms, respectively. PIT tag displacements were also correlated with position along mound-basin transect (top, mid, or base zone) (Fig. 3.13). With increasing distance from mound center, tag movement became moundward, ultimately reaching an average of 13 cm and a net 15 m of moundward-directed movement for the tags implanted in the lowest elevation, ‘base’ zones.

These results provide strong evidence that biotic sediment transport changes in response to the environmental effects of pedogenesis and provide information on how these changes may lead to the creation of Mima mounds. According the the DSC model, Mima mounds occur in regions of shallow, poorly drained soils in which burrowing rodents must create nest chambers in thicker soil regions in order to secure tolerable habitat. This study indicates that moundward soil movement is greatest in regions where soils are thinnest and most saturated (unpublished observations using volumetric water sensors) - on the oldest landforms and at mound edges. This, along with recent accounts of direct mound-building by gophers and kangaroo rats (Johnson and Horwath Burnam, 2012), provide evidence that burrowing
rodents build and regularly maintain Mima mound-vernai pool topography in California.

Despite the overall trend of increasingly moundward movement with soil age and proximity to mound edge, gopher transport dynamics were highly variable and complex, resulting in high standard errors. Mean displacements were only significantly different between the oldest and youngest landform. In order to ensure more generally significant results, the number of PIT tags deployed would need to be quadrupled, at minimum.

On the 0.05 million-year-old Lower Modesto formation, on which short, wide mounds are observed, the net PIT tag movement is edgeward, which contradicts the DSC model. If the overall direction of gopher-mediated sediment transport on this geologic formation is, in fact, towards the edges of mounds, the features should not persist. One reason for this inconsistency may be due to the relatively low number of PIT tags displaced on the Lower Modesto formation. On this formation, a marked decrease in gopher activity was observed over the course of the study (discussed further in Section 3.3.3). It may be the case that a reduction in the local gopher population (via migration or disease) led to the reduced activity at that site (Howard, 1961). Likely for this reason, the Lower Modesto formation had one of the highest rates of unmoved PIT tags (60%). This increased the standard error of the measurements at this site and indicates that the character of movement reported may not be representative of gopher activity on this soil age category. On the other hand, if the average edgeward displacement is characteristic of this landform, it may indicate that the DSC model is incorrect or incomplete and that other factors besides soil age and thickness drive the directional movement on these landforms.

An effort was made to delineate distinct regions of gopher activity on the non-mounded landscape (Upper Modesto), in order to compare with gopher sediment transport on mounded landscapes. However, it is not clear how accurately the defined regions reflect individual gopher home ranges (the area in which a gopher lives and travels). For instance, if gopher home ranges were underestimated, the net ‘edgeward’ movement observed on this landform might be overestimated. Nevertheless, the regions identified were significantly larger than Mima mound plan areas (15-40% larger, on average), which should reduce the likelihood of mischaracterizing the net movement as ‘edgeward’. Using RFID technology to tag and monitor individual gophers would significantly improve the characterization of gopher home range on the non-mounded site.

Recent studies have reported the successful use of RFID technology in the tracking of particles in fluvial and marine environments (e.g., Nichols, 2004; Allan et al., 2006; Curtiss et al., 2009; Miller et al., 2011; Bertoni, 2012), but there are limitations to this method. While this study shows trends similar to Cox and Allen (1987), who used metal tracers, the results are not as robust because of the smaller sample size and relatively low recovery rate (Table 3.1). The smaller sample size was dictated by the relatively high costs of the PIT tags ($2-5 per tag and >$2000 for the RFID reader system), when compared with other tracing systems (e.g., painted clasts or metal markers). Many PIT tag surveys report higher recovery rates compared with other tracers (e.g., Sear et al., 2000; Nichols, 2004). However, this study had a lower overall recovery rate (74%) than Cox and Allen (1987) (98%). One explanation is the importance of tag orientation in signal detection. For instance, no signal
is transmitted if two or more PIT tags are in contact. This constraint is more problematic for this study than for the stream and marine applications which typically embed PIT tags inside individual clasts, preventing tag contact.

In addition, it is possible that the PIT tags may not serve as a good proxy for gopher soil transport as gophers may treat them in a different manner than they do actual sediment. For example, one PIT tag was observed on the soil surface with teeth marks that appeared to roughly match the size of gopher incisors. In addition, a set of tags was detected and excavated from a location ∼40 cm below the surface in what appeared to be a food storage nest. If gophers collect the PIT tags in subterranean compartments, this may explain the relatively low recovery rate since tags can only be reliably detected at a maximum depth of ∼80 cm.

A large advantage of PIT tags in surveys of biotic sediment transport is the ability to track subsequent movement of the markers after implantation, while minimizing disturbance to habitat, important in studies such as this in which the focus ecosystems support many endangered plant and animal species. Approximately 10% of the markers were moved multiple times after implantation (that is, they have been displaced repeatedly to several, distinct locations). The character of these secondary movements is similar to the first measurement results.

3.3.3 Magnitude and distribution of soil movement by gophers

Magnitude of gopher soil movement

While moundward displacement supports the DSC model, information on the quantity of soil moved is also necessary to fully understand the role of gophers in Mima mound landscapes. Table 3.2 summarizes the data describing the abundance and distribution of gopher tailings, in addition to reporting the directional transport metrics. A map of tailings distribution is shown in Figure 3.14, for the level Laguna site. For comparison, a map of gopher surface activity for the youngest Upper Modesto formation (on which no Mima mounds are found) is shown in Figure 3.15, along with the ‘mound’ edge designations that were used for the RFID survey. In total, 6100 individual tailings were mapped and 300 tailings were weighed on the five terraces during ten surveys between 2005 and 2012.

Average gopher tailing mass was 1.54 kg and average tailings concentration ranged from 0.09 mounds m$^{-2}$ across all study sites to more than 20 mounds m$^{-2}$ on small regions of dense activity. Tailings concentrations were highest on the most saturated (Riverbank) (unpublished volumetric water content data) and steepest (Laguna sloping) landforms, indicating that in addition to adjustments to the direction of soil movement with respect to soil age, gophers may also vary the intensity of tunneling in response to changing soil conditions.

The overall biotic sediment transport rate for this study (2.8 m$^3$ ha$^{-1}$ yr$^{-1}$, not accounting for direction) is low compared to other *Thomomys bottae* rates (Table 3.3). This rate indicates that, in the Merced region, the biologically active A horizon (25 cm thick) would be fully mixed in several hundred years, which is slower than the turnover rates estimated in other regions of California (e.g., Yoo et al., 2005). Biotic soil movement for this study
Figure 3.10: A map of typical PIT tag movement on a mound on the ~0.05 m.y. Lower Modesto landscape, surveyed in November 2010. A set of PIT tags was implanted into each of three concentric zones (top, mid and base). The crosses are the locations where five PIT tags each were mixed with local soil and inserted into a gopher burrow. A number on a cross indicates the number of PIT tags remaining at the implant location. The large circles indicate the location of a PIT tag after movement by gophers and the color indicates the location of origin. A number on the circle indicates the number of tags in approximately the same location (within 15cm). Note that 26% of the tags deployed in all surveys were not detectable after implant. The small circles represent a mapping of gopher tailings piles, with color indicating an age designation based on appearance and shape of tailings and timing since last rainfall. Note the large distances that some tags are moved (>3m in this case).
### Table 3.1: Comparison of results of current study and previous study by Cox and Allen (1987) (and Cox (1984b), asterisked results). The first section of the table shows results for all surveys (mounded and non-mounded). The second section reports the PIT tag survey results for only the oldest landform (Laguna level and Laguna sloping), which has mounds that are most comparable in size to the Cox and Allen (1987) and Cox (1984b) studies. Net movement is the sum of all movements, accounting for direction. *Vertical displacement for this study was measured only during a pilot study using metal markers and a metal detector on the 3 My Laguna formation.

<table>
<thead>
<tr>
<th>Category</th>
<th>Metric</th>
<th>This study</th>
<th>Cox &amp; Allen (1987)</th>
</tr>
</thead>
<tbody>
<tr>
<td>All sites</td>
<td>Numbers of markers emplaced</td>
<td>871</td>
<td>4659</td>
</tr>
<tr>
<td></td>
<td>Maximum marker displacement</td>
<td>4.7 m</td>
<td>5.1 m</td>
</tr>
<tr>
<td></td>
<td>% of markers recovered</td>
<td>74</td>
<td>98</td>
</tr>
<tr>
<td></td>
<td>% of markers moved from implant location (of % recovered)</td>
<td>51</td>
<td>28</td>
</tr>
<tr>
<td>Laguna sites (mounds on oldest terrace)</td>
<td>Number of mounds in study</td>
<td>26</td>
<td>24</td>
</tr>
<tr>
<td></td>
<td>Average horizontal displacement (+ represents moundward movement)</td>
<td>25 cm</td>
<td>41 cm</td>
</tr>
<tr>
<td></td>
<td>Net horizontal displacement (+ represents moundward movement)</td>
<td>2800 cm</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>Average vertical displacement* (+ represents upward movement)</td>
<td>1 cm</td>
<td>4 cm</td>
</tr>
<tr>
<td></td>
<td>Net vertical displacement* (+ represents upward movement)</td>
<td>100 cm</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>% of markers moved moundward (of markers moved)</td>
<td>60</td>
<td>65**</td>
</tr>
<tr>
<td></td>
<td>% of markers moved edgeward (of markers moved)</td>
<td>40</td>
<td>35**</td>
</tr>
<tr>
<td></td>
<td>% of markers redeposited at surface (of markers moved)</td>
<td>15</td>
<td>12</td>
</tr>
</tbody>
</table>
Figure 3.11: Distribution of PIT tag displacements after implantation in pocket gopher tunnels at the four sites on which Mima mounds are found (Laguna level, Laguna sloping, Riverbank and Lower Modesto). Darker gray bars represent the number of markers that were moved >15 cm towards a basin adjacent to the mound (away from the mound apex) and bars in lighter gray represent the number of markers that were moved >15 cm towards the center of the mound. Movements smaller than 15 cm were not included in the analysis due to the resolution limits of the RFID reader. A slightly larger portion of the PIT tags were moved moundward (53%) than were moved edgeward (47%).
Figure 3.12: Gopher PIT tag movement patterns, with respect to soil age. Top panel shows average displacements (mean ± SEM) and bottom panel shows net movement (sum of all movements on each landform (average 13 mounds per landform), taking into account direction). Movement ranged from edgeward on the youngest landforms to moundward on the oldest. Means were significantly different only between the oldest and youngest terraces (Tukey’s HSD test, p <0.05).
Figure 3.13: Gopher PIT tag movement patterns with respect to mound position (includes movement on all mounded landforms). Top panel shows average displacement (mean ± SEM) and bottom panel shows net movement (sum of all movements on each landform (average 290 movements per position class), taking into account direction). Movement was generally moundward at the base of mounds and edgeward at the mound tops. Means were not significantly different between position groupings.
was measured over large regions, long time scales, and a range of soil and topographic conditions. As such, the measurements capture a wider range of conditions than most other gopher sediment transport studies. This broader representation may, in part, explain the lower soil movement rates. Furthermore, in general aboveground sediment transport measurements underestimate the excavation work done by gophers. Several studies (e.g., Miller, 1957; Andersen, 1978; Cox, 1990c) have shown that up to 70-80% of excavated sediment gets redeposited belowground and is therefore not represented in these surface-based measurements.

Measurement of gopher activity is also complicated by inaccurate counting of gopher mounds. For instance, mounds can be missed due to grass re-growth or leveling by rainfall. Especially on the youngest Upper Modesto landform, mounds were sometimes obscured by the relatively denser vegetation. In addition, gopher mounds have been observed to exist without vegetation for longer than three years (Robert Holland, pers. comm.), and thus it is possible that mounds were double-counted between successive surveys. As mentioned previously, the mound counts in this study are conservative in that only mounds composed of vegetation-free, loose soil were counted. In addition, usually at least one rainfall occurred between surveys, making tailings identification easier.

Another factor which may affect the accuracy of the gopher activity measurements are the soil bulk density estimates, based on values measured for the chronosequence terraces (Harden, 1987; White et al., 1996). The values were probably overestimated because 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, tailings concentrations, total tailings volumes, and gopher sediment transport rates are probably underestimated.

**Combined rate (magnitude and direction) of sediment transport**

Combining the measurements of soil movement (magnitude and direction), along with environmental data and the time period over which the tailings were produced, the rate of moundward gopher sediment transport (cm/1000yr) is estimated for each landform in Fig. 3.16. Net moundward transport is highest on the most saturated (Riverbank, 23 cm / 1000 yr) and steepest (Laguna sloping, 26 cm / 1000 year) landforms. On the oldest level site, the rate of soil transport (tailings piles produced per area) was lower than expected (32 cm / 1000 year, not accounting for direction), but the proportion of upward movement was the highest (66%), perhaps indicating that gophers on the terminal landform have adapted to soil and vegetative conditions caused by long-term chemical weathering.

This study’s focus on directional rates of sediment transport provides an important constraint on gophers’ long-term ability to move soil. 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. In order to fully understand the sediment transport dynamics of these landscapes, rates of other geomorphic processes need to be constrained and compared with rates of biotic movement. In Chapter 4, the high-resolution topographic measurements
Distribution of gopher activity and relevance to gopher ecology
The DSC model proposes that each Mima mound represents the habitat of a single gopher, as an outcome of the fossorial mammal’s highly territorial nature (Baker, 1974; Gregory, 1987). If this is true, changes in gopher activity over time on a given mound may reflect fluctuations in populations of gophers within the areas of study. Classification of activity/occupancy level on a per-mound basis was based on observations of gopher surface activity (tailings densities). If fewer than five recent tailings were observed on a mound, it was classified as ‘inactive’ or ‘unoccupied’. On all sites, observed Mima mound occupancy shifted significantly over time, ranging from as low as 34% to as high as 74%. Fig. 3.17 shows a map of estimated mound occupancy for the Laguna sites (both level and sloping). At the Lower Modesto site (Fig. 3.18), a marked decrease in gopher activity was observed since the beginning of the study,
Figure 3.15: Above-ground gopher tailings mapping on the 0.01 My Upper Modesto formation. Mima mounds are not observed on this surface. In order to compare movement on this formation with soil movement by gophers on mounded terrain, an attempt was made to identify the habitats of individual gophers by mapping discrete regions of gopher tailings. Fresh gopher tailings are represented by pink points. Estimated regions of individual gopher activity are represented by blue circles.
### Table 3.2: Table summarizing data on gopher activity and environmental conditions collected across the soil chronosequence.

<table>
<thead>
<tr>
<th>Category</th>
<th>Measurement</th>
<th>Upper Modesto (0.01 my)</th>
<th>Lower Modesto (0.05 my)</th>
<th>Riverbank (0.2 my)</th>
<th>Laguna (Sloping) (3 my)</th>
<th>Laguna (3 my)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Direction</strong></td>
<td>Average PIT tag movement (cm) (+ represents moundward movement)</td>
<td>-30</td>
<td>-14</td>
<td>-2.0</td>
<td>23</td>
<td>28</td>
</tr>
<tr>
<td></td>
<td>Net of all PIT tag movements (cm) (+ represents moundward movement)</td>
<td>-1800</td>
<td>-1400</td>
<td>-87</td>
<td>963</td>
<td>1830</td>
</tr>
<tr>
<td></td>
<td>% of movements directed moundward</td>
<td>44</td>
<td>45</td>
<td>56</td>
<td>51</td>
<td>66</td>
</tr>
<tr>
<td><strong>Magnitude</strong></td>
<td>Average mass individual gopher tailing (kg)</td>
<td>1.3</td>
<td>1.7</td>
<td>1.9</td>
<td>1.6</td>
<td>1.3</td>
</tr>
<tr>
<td></td>
<td>Average density gopher tailings (tailings / m²)</td>
<td>0.1</td>
<td>0.05</td>
<td>0.12</td>
<td>0.16</td>
<td>0.08</td>
</tr>
<tr>
<td></td>
<td>Average gopher sediment transport rate (cm / 1000 yr)</td>
<td>20</td>
<td>20</td>
<td>40</td>
<td>52</td>
<td>32</td>
</tr>
<tr>
<td><strong>Spatial pattern</strong></td>
<td>Average distance between gopher tailings (cm)</td>
<td>49</td>
<td>46</td>
<td>80</td>
<td>45</td>
<td>102</td>
</tr>
<tr>
<td></td>
<td>Dispersion (nearest neighbor index) of tailings</td>
<td>0.36</td>
<td>0.20</td>
<td>0.46</td>
<td>0.36</td>
<td>0.46</td>
</tr>
<tr>
<td></td>
<td>% of mounds with recent evidence of gopher activity (average)</td>
<td>N/A</td>
<td>57</td>
<td>67</td>
<td>63</td>
<td>56</td>
</tr>
<tr>
<td><strong>Environmental data</strong></td>
<td>Maximum soil hardness (kPa)</td>
<td>3025</td>
<td>3347</td>
<td>3827</td>
<td>4048</td>
<td>4883</td>
</tr>
</tbody>
</table>
Figure 3.16: Comparison of rates of soil movement by gophers (proportion moved moundward, derived from PIT tag surveys and mapping and weighing of gopher tailings) along the Merced River chronosequence.
### Table 3.3: Collection of reported *Thomomys bottae* sediment transport rates (as soil volume per area per time, for the purposes of comparison with other studies). The transport rate for this study is the lowest compared to all other rates. In general, *Thomomys bottae* rates are lower than other gopher species (*Thomomys talpoides*, *Thomomys monticola*, and *Geomys* spp.) (Smallwood and Morrison, 1999a). A few studies have estimated belowground transport and report that the belowground portion makes up 70-80% of all sediment transport (Miller, 1957; Cox, 1990c).

<table>
<thead>
<tr>
<th>Region</th>
<th>Source</th>
<th>Average sediment transport rate ( \text{m}^3 \text{ ha}^{-1} \text{ yr}^{-1} )</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>Merced, CA</td>
<td>This study</td>
<td>2.8</td>
<td></td>
</tr>
<tr>
<td>Marin, CA</td>
<td>Black and Montgomery (1991)</td>
<td>3.1</td>
<td></td>
</tr>
<tr>
<td>Miramar mounds, CA</td>
<td>Cox (1990c)</td>
<td>5.8</td>
<td>Surface</td>
</tr>
<tr>
<td>Miramar mounds, CA</td>
<td>Cox (1990c)</td>
<td>14.4</td>
<td>Subsurface</td>
</tr>
<tr>
<td>New Mexico</td>
<td>Hakonson et al. (1982)</td>
<td>8.42</td>
<td></td>
</tr>
<tr>
<td>Davis, CA</td>
<td>Miller (1957)</td>
<td>13.6</td>
<td>Surface</td>
</tr>
<tr>
<td>Arizona</td>
<td>Bandoli (1981)</td>
<td>15.6</td>
<td></td>
</tr>
<tr>
<td>Miramar mounds, CA (total)</td>
<td>Cox (1990c)</td>
<td>20.24</td>
<td>Total (surface + subsurface)</td>
</tr>
<tr>
<td>Arizona</td>
<td>Reichman et al. (1982)</td>
<td>37.6</td>
<td></td>
</tr>
<tr>
<td>Davis, CA</td>
<td>Miller (1957)</td>
<td>67.0</td>
<td>Subsurface</td>
</tr>
<tr>
<td>Davis, CA</td>
<td>Miller (1957)</td>
<td>80.6</td>
<td>Total (surface + subsurface)</td>
</tr>
</tbody>
</table>
which is reflected in the low soil transport rates in Figure 3.16. It may be the case that a reduction in the local gopher population (via migration or disease) led to the low tailings production rates at that site.

The changes in activity level over time certainly also reflect seasonal shifts in burrowing and foraging. Romanach et al. (2005b) reported that gophers near Santa Barbara, CA, are most active following the first seasonal rain. In central California, this generally occurs in the months of October-December (NOAA, 2013). After the initial rain spurs a flurry of gopher activity, tailings production declines and plateaus until the summer months when almost no new activity is observed. Romanach hypothesized that gophers take advantage of more pliable soils during the early wet weather in order to build or maintain burrow systems. Subsequent, steady-state burrowing reflects the minimum amount of burrowing required to maintain adequate energy intake.

Stark fluctuations in gopher activity were observed on the Merced River chronosequence under different seasonal conditions, consistent with Romanach et al. (2005b)'s observations. For instance, on one small region, tailings densities ranged from 0.04 to 0.1 tailings m$^{-2}$ from dry period to wet period, respectively (Fig. 3.19). Climatic differences may also explain large disparities in tailings production between different regions in California. For example, the gopher mound concentrations in this study (0.09-0.3 mounds m$^{-2}$) are lower than the concentrations Black and Montgomery (1991) measured for a coastal site in Marin County, California (0.16-2.88 mounds m$^{-2}$), which is both cooler and wetter.

In general, gopher tailings were found on convex rather than concave portions of the landscape. On average, approximately 55% of the tailings were found on convex areas, 42% were found on concave areas, and 3% were found on planar surfaces. On the convex portions, the gopher mounds were predominantly on the side slopes of the Mima mounds, rather than on the summits. 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 tailings are highly clustered on all landforms (Fig. 3.20) at distances ranging from 5-15 m. On the mounded landforms, this distance is likely related to the average intermound spacing of 12 m (Chapter 2), consistent with the minimum spacing that gophers have been observed to maintain (e.g., Howard and Childs, 1959). Tailings are most evenly spaced and one of the lowest in concentration on the oldest level landform, Laguna (Table 3.2). (The Lower Modesto formation also has low tailings density. This is likely due to the apparent decrease in gopher population that occurred over the course of the study, as mentioned above.) Differences in tailing heaps pattern and density may reflect variation in foraging approaches in response to changes in vegetation and/or soil quality along the age gradient. Gophers have been observed employing a strategy of area-restricted searching (ARS) (Benedix, 1993), in which they concentrate digging in food-rich patches. ARS would lead to dense concentrations of tailings piles. Romanach et al. (2007) demonstrated, through a spatially explicit foraging model, that ARS is the most energetically efficient strategy, compared to random approaches. Net primary productivity (NPP, the amount of biomass generated from photosynthesis, minus the energy used for cellular respiration)
generally decreases along the chronosequence (Brenner et al., 2001). Therefore, an increase in clustering with age is predicted (in order to maximize foraging efficiency through ARS), but was not observed - on the oldest terrace, tailings are most evenly spaced and lowest in concentration. However, the burrowing and foraging pattern observed on the oldest landform may ultimately be a more energy efficient approach. On the oldest landform, which bears the lowest biomass and the hardest, most cobble-rich soils, gophers may be limited in their ability to burrow for long stretches in order to find a food-rich patch (as in ARS). Instead, it may be most efficient to search and forage in a more regularly spaced pattern in order to increase the likelihood of overall energy intake and to avoid cobbles. Consistent with this idea, the character of tunnels in this study seemed to differ between young and old landscapes, in a way that may reflect such hypothesized adaptations in foraging strategy. On younger landforms, long stretches of tunnel (>1 m) were commonly observed. On older landforms, tunnels often traversed a more complicated course, frequently changing direction as often as every 15 centimeters (Fig. 3.21). This pattern may reflect a difference between longer burrows that are part of the ARS strategy on the younger landforms, and a different approach on the oldest landform.

In addition to information about sediment transport direction, magnitude and distribution, general observations about gopher habitat and activity were made. Based on more than 200 measurements taken during PIT tag implantation, average gopher burrow depth was 13.8 cm (to bottom of burrow), and ranged from 4-45 cm deep. No significant difference in burrow depth between landforms was found. Furthermore, the majority of active tunnels (57%) were located on the south side of mounds and were most frequently oriented east to west. Seventeen instances of gravels greater than 5 cm in diameter were observed both in active gopher tunnels and in tailings piles. On a few occasions, tunnels near the soil surface were angled downward steeply, at more than 45 degrees. In addition, tunnels which ran a spiral course from the soil surface to more than 20 cm belowground were observed on the oldest Laguna formation. The tunnels resembled that of a ‘spiral staircase’, in which three or more circular turns were observed stacked on top of the other. The diameter of the loops was approximately 20 cm. Brown and Hickman (1973) reported widespread occurrence of spiral tunnels built by gophers (Geomyys pinetis) in Florida. They observed these looping burrow structures in approximately 70 percent of individual gopher systems observed. They speculated that the tunnels may serve as protection from predation in that such burrows would slow down or confuse potential predators. The spiral tunnels may also be an optimally engineered way to travel vertically in a small lateral distance. Studies of gophers in California have reported near-vertical tunnels which serve to link shallow and deep burrows (Seton, 1929; Criddle, 1930; Scheffer, 1931), but this appears to be the first study to report spiral burrow structures in the gopher systems of California.
Figure 3.17: Shaded relief image of the oldest landforms (Laguna formation (3 My, sloping (at top of image) and level (at bottom of image)) showing occupancy (classified via activity level) of mounds in the study areas. Red circles indicate mounds which display a significant level of recent gopher activity. Blue circles represent mounds on which no recent gopher activity was observed. On both regions shown, measured in October 2010, ∼60% of mounds, on average, appeared to be occupied by gophers. The apparent occupancy of Mima mounds shifted over time, ranging from as low as 34% to as high as 74%.
Figure 3.18: Shaded relief image of the youngest, mounded landform (Lower Modesto (age 0.05 m.y.) showing occupancy (classified via activity level) of mounds in the study area. Red circles indicate mounds which display a significant level of recent gopher activity. Blue circles represent mounds on which no recent gopher activity was observed. On this formation, activity substantially decreased over the course of the study, from 65% in October 2009 to 52% in October 2011. The results of a survey of mound activity taken in October 2011 are shown here.
Figure 3.19: Contour map showing seasonal changes in gopher activity. The number of tailings ranged from 221-323, activity increased with rain events, and, in this case was highest in May 2006, following a recent rain. Recent gopher tailings were identified by noting degree of overgrowing vegetation and whether surface of tailings were hardened due to rain. Map generated using data from GPS survey points gridded by Kriging.
CHAPTER 3. POCKET GOPHER (THOMOMYS BOTTAE) SEDIMENT TRANSPORT ON THE MERCED RIVER CHRONOSEQUENCE

Figure 3.20: Insets A and B show the modified Ripley’s $K$ function and a map of the locations of the gopher tailings, respectively, mapped in March 2012 on the oldest Laguna formation (3 My, level terrain). Insets C and D show the Ripley’s function and tailings distribution for the Upper Modesto formation (0.01 My, which does not support Mima mounds) in December 2012. Gopher tailings are clearly clustered on both mounded and non-mounded terrain at distances ranging from 5-15 m.
Figure 3.21: Inset A shows the typical course of a gopher burrow on older terrain, as shown by blue arrows representing the zig-zag tunnel observed on the Laguna formation (3 My). In B, tunnels were straighter for longer courses on the younger and less cobbly terrain, such as shown here on the Lower Modesto formation (0.05 My). Distance between endpoint stakes is approximately 150 cm in Inset A and 300 cm in Inset B.
3.4 Conclusion

Evidence presented in this chapter suggests that gophers play a crucial role in the evolution of Mima mound-vernal pool landscapes, likely both during the inception of the mounds as well as part of their upkeep against forces of erosion. On younger landscapes with either no Mima mounds or with small, subtle mounds, the net direction of biotic sediment transport is away from the center of activity or the mound center, respectively. As soils age, the net orientation of soil movement shifts upward and towards the center of mounds, as predicted by the biologic model. This supports a potential designation of gophers as keystone species – specifically keystone habitat modifiers – in mound-pool systems: any change in gopher populations could have a marked affect on the other species in the habitat. However, the critical function of gophers in wetland conservation is often ignored in the conservation and mitigation of vernal pools in California. In 2005, the United States Fish and Wildlife Service designated 740,000 acres as critical vernal pool habitat (USFWS, 2005) in California. The critical habitat designation is projected to have nearly a $1 billion impact on the state’s economy (Economic Planning Systems, 2003). Since then, several regions in the state have developed habitat conservation plans in order to manage remaining vernal pool habitat. However, most conservation plans do not mention pocket gophers, nor consider their role in vernal pool preservation. For instance, in a survey of fifteen vernal pool monitoring and conservation documents from various nonprofit, government, and research agencies (Stebbins et al., 1996, DeWeese, 1998, Sutter and Francisco, 1998; Leidy and White, 1998; Ferren and Hubbard, 1998; Black and Zedler, 1998; EIP Associates, 2002; Moore et al., 2003; USFWS, 2005 (Critical Habitat Designation); USFWS, 2006 (Vernal Pool Recovery Plan); Airola, 2008; Mason and Ritenour, 2010; ; South Sacramento Recovery Plan, 2010; San Diego Recovery Plan draft documents, 2012; Buse, 2012), only one (DeWeese, 1998), mentions pocket gophers.

While gophers are known to be resilient animals, the effort to eradicate them (which includes trapping, fumigating, biocontrol, and the use of rodenticides such as styrpyazine and 1080) has been intense and ongoing in California for nearly two hundred years because of the large-scale damage to agricultural crops and forests that gophers cause (Marsh, 1992). In addition, Kelly et al. (2005) estimate that more than 500 metric tons of small mammals were lost, annually, in grassland land use conversion in the Central Valley and they note that: “When we consider the interrelated population dynamics of small mammals and the many predatory species that largely depend on them (e.g. carnivores, raptors, owls, snakes), this loss in biodiversity is compounded significantly.” In the case of gophers and their likely role in creating and maintaining Mima mound-vernal pool ecosystems, this effect is especially salient. The detailed sediment transport rates and vectors generated in this study can be used to fully clarify gophers’ role in the endangered ecosystems. Given the evidence supporting their key place in vernal pool preservation, it is critical that the function of gophers be better integrated into habitat conservation plans and other preservation efforts.
Chapter 4

A Biogeomorphic Model of Mima Mound Evolution

...when one contemplates the fact that there are about 15 mounds per acre, or nearly 10,000 mounds per square mile, the amount of work expended in this one small area is seen to be tremendous. To attribute this colossal earth-moving feat to small rodents certainly appears ridiculous at first glance. –R.J. Arkley, 1948

4.1 Introduction

The Pleistocene and Pliocene landscapes of the Great Valley of California support an assemblage of peculiar and compelling topographic features called Mima mounds (Fig. 4.1). The gently sloping alluvial fans and stream terraces in the region are, in many locations, continuously mantled with a multitude of low mounds and intervening depressions. Where slopes are low, the depressions fill with water during winter and spring months, and become vernal pools, which support an endemic and endangered suite of plant and animal species (Holland, 1978; Zedler, 1987; Barbour et al., 2007a). These microtopographical features once covered several million acres in California, but have been largely eradicated through conversion to agriculture and urban land uses (Holland, 1978; Holland, 2009). The remaining tracts, particularly large expanses of rangeland near Merced, California, are protected by the Endangered Species Act (16 U.S.C. 1531 et seq. (2000)) and, as a result, are at the center of an intensive regulatory and conservation effort (e.g., Witham et al. (Eds.), 1998; USFWS, 2005; Schlising and Alexander (Eds.), 2007; Alexander and Schlising (Eds.), 2011). Yet, despite their biologic and historical importance, questions remain about the details of why and how these features formed, how they are maintained, and the role of burrowing animals in the mounds’ evolution.

Arkley and Brown (1954) studied the mounds on the alluvial terraces near Merced and concluded that a hypothesis proposed by Dalquest and Scheffer (1942), which attributes the microtopography to the work of fossorial (burrowing) rodents, mainly pocket gophers (Ro-
dentia: Geomyidae, hereafter referred to as ‘gophers’), is “undoubtedly correct”. Recently Johnson and Horwath Burnham (2012) revised the hypothesis (and named it the Dalquest-Scheffer-Cox (DSC) model) to include research from the second half of the twentieth century and to more fully incorporate the range of geomorphic processes occurring in these landscapes. A key element of the DSC model is that the existence of either restrictive hardpan layers (caused by long-term changes in vadose zone hydrology) or coarse gravel layers compels burrowing animals, being unable to dig downward, to escape wet and/or shallow soil and minimize predation by burrowing laterally. Lateral burrowing preferentially moves soil such that more soil is transported toward the animal’s nest than away from it, and it is in this way that biologically created mound and swale topography is proposed to occur. Despite Arkley and Brown’s conviction, questions remain about the origin of the Merced and similar microtopography, questions that lie at the heart of several historic genetic uncertainties. The Mima mound type-locality is found in Washington state, but many other mound regions similar in form and distribution are found in the grasslands and open forests of North America and elsewhere around the world. I note that while it has not been shown conclusively that the different mound regions are related, in this study I discuss the Merced-area mounds in the context of other mound regions because of their potential genetic associations. For simplicity, I refer to all similar microtopography, like ‘pimple’, ‘prairie’, and similarly named mounds, as Mima mounds, while noting that differences of origin and environment may exist between different mounded terrains.

The origin of Mima mounds has long been at the center of a lively debate, with many, diverse explanations proposed for the mounds since their discovery (e.g., Wallace, 1877; LeConte, 1877; Hilgard, 1905; Branner, 1905; Campbell, 1906; Bretz, 1913; Nikiforoff, 1941; Dalquest and Scheffer, 1942; Stallings, 1948; Grant, 1948; Arkley, 1954; Paeth, 1967; Vitek, 1978; Cox, 1984a; Washburn, 1988; Berg, 1990; Cox, 1990b; Horwath and Johnson, 2006; Seifert et al., 2009; Cramer, 2012; Johnson and Horwath Burnham (Eds.); 2012; Gabet et al., 2013). Of these suggested mechanisms for formation, five general groupings of viable hypotheses exist: erosional, depositional, shrink-swell, seismic, and biotic. Washburn (1988) conducted an analysis of the most feasible hypotheses and deduced that an erosion-vegetation anchoring hypothesis was most consistent with the evidence for the majority of mound sites in the U.S. It is clear from Washburn’s writings that he was generally not supportive of the idea that small burrowing animals, like gophers, constructed the mounds. He pointed out that much of the evidence in support of gopher-built mounds suggests that the animals may have simply used pre-existing topography to their advantage. Further, he outlined the arguments of several authors who proposed that typical gopher burrowing patterns would accelerate mound erosion rather than lead to the pimpled topography (Hubbs, 1957; Nikiforoff, 1941; Paeth, 1967). Despite these arguments, there is extensive support for a biological interpretation. For example, Cox and colleagues (1984a; 1984b; 1987; 1990c) and other workers (Horwath and Johnson, 2006; Reed and Amundson, 2007; 2012) have conducted studies that support the proposal for burrowing animal-built mounds. Recently, a special volume on the Mima mounds (Johnson and Horwath Burnham (Eds.), 2012) provided a comprehensive view of Mima mound research and concluded that while a variety of geomorphic processes
have led to the current form of Mima mounds, the action of burrowing animals is the primary mechanism explaining the topography.

Subterranean habitats are low-oxygen, low primary productivity environments with high energy demands. Digging requires 360-3400 times more energy than above-ground locomotion (Vleck, 1979). Gophers have developed thermoregulatory and digging adaptations in response to these limitations (e.g., McNab, 1966; Thaeler, 1968; Darden, 1972; Nevo, 1979; Lessa and Thaeler, 1989; Buffenstein, 2000). Given this evidence of a close relationship between soil conditions and gopher morphology, I investigated Mima mound form and distribution (Ch. 2) and gopher sediment transport (Ch. 3) on a variety of soil types to explore whether gophers develop behavioral adaptations to soil environment, ultimately leading to the creation of Mima mound topography. Here, I apply those findings to the development of a simple model of Mima mound formation and evolution. The high-resolution LIDAR (light detection and ranging) data (Ch. 2) allow me to precisely quantify the morphology of the mounds and to estimate rates of their downwearing. Long-term, regional measurements of biotic activity (Ch. 3) enable realistic estimates of biologic soil movement across seasons, soil types and relief. Furthermore, the analysis is inspired by recent studies (e.g., Yoo et al., 2005; Phillips, 2009) that have included quantitative considerations of biological energy within geomorphic models. My work thus includes conservation of energy analyses to assess whether populations of burrowing mammals have produced these features.

4.2 Methods

4.2.1 Merced River chronosequence

An early record of California Mima mound topography was written by Hilgard (1884b), who noted that:

...certain landscapes of the Central Valley are dotted with the singular rounded hillocks, popularly known as ‘hog-wallows’, from 10 to 30 feet in diameter and from 1 to 2 feet high, which are evidently the result of erosion, but precisely under what conditions it is difficult to explain. These hillocks are usually most abundant near the foothills....They occur on all kinds of soil, and even on the rolling foothill lands themselves....In some cases they are so thickly set, abrupt, and resistant as to render the land valueless for ordinary cultivation.

Eastern Merced County harbors one of the largest remaining tracts of the landscape that Hilgard described, located in the watershed of the Merced River. The study area contains a series of river and stream deposits spanning a wide range of ages (Arkley, 1954; Arkley, 1962; Marchant and Allwardt, 1981; Pavich et al., 1986; Harden, 1987a). Rivers originating in the Sierra Nevada mountain range drain into the San Joaquin Valley. During the Pleistocene, periodic glaciation and continuous uplift of the Sierra Nevada (e.g., Stock et al., 2004; Clark, et al., 2005) created an array of glacial outwash deposits downstream
Figure 4.1: Photographs showing the Merced-area Mima mound landscape. (A) A wide view of the mounds on the ~3 million-year-old Laguna formation. B details the linear alignment on hillslopes. In C, cobbles fill the intermound regions and have been shown to form a continuous layer extending underneath the mounds. (D) The seasonal wetlands, called vernal pools, which are commonly found in the intermound swales in the winter and spring. Cattle ranching is a common land use practice, especially on the older terraces. Here, the cattle are grazing on the 1 million-year-old North Merced Gravels formation. The Sierra Nevada mountain range is visible in the background.
and incised valleys upstream (Marchand and Allwardt, 1981; Weissmann et al., 2002). The result is a collection of inset river terraces and nested alluvial fans that span the Quaternary. One set of such terraces, the Merced River chronosequence, is notably well-preserved and is the focus of this study. The soils of the chronosequence range in age from a few hundred years (the active floodplain of the Merced River) to the several million-year-old China Hat member of the Laguna formation (Marchand, 1976). The fluvial sediments consist primarily of granitic alluvium, and the soils are classified as Entisols on the lower, younger terraces and as Alfisols on the higher, older terraces (Arkley, 1962). Effective soil thickness (depth of mobile layer) varies across the chronosequence, measuring more than 2 m thick on the youngest terrain and becoming thinner with age, averaging less than 0.5 m on the oldest surface. On the older surfaces, claypans or duripans (associated with restrictive $B_t$ and $B_{qm}$ soil horizons, respectively) have formed beneath the biologically active $A$ horizons (Arkley, 1962; Harden, 1982). Four of the terraces were selected for analysis in this study: Upper Modesto (~0.01 million years (My)), Lower Modesto (~0.05 My), Riverbank (~0.2 My), and Laguna (~3 My). On the oldest, Laguna formation, two regions were examined – both a nearly level terrace top and a side slope of ~20%. Ages are constrained based on carbon-14 dating of the younger terrain (Harden, 1987) and beryllium-10 dating of the older surfaces (Pavich et al., 1986).

The climate of the region is Mediterranean, characterized by strong fluctuations between two seasons. In summer (between May and October), conditions are hot and dry (mean daytime temperature = 37°C and precipitation = 30 mm) and in winter (between November and April), the climate is cool and wet (mean daytime temperature = 7°C and precipitation = 280 mm) (Arkley, 1962; NOAA, 2013 (Station 045535)). The vegetation is dominated by European annual grasses and forbs (e.g., Bromus spp.; Hordeum spp.), which largely overtook the native perennial bunchgrass community (e.g., Poa secunda spp. secunda; Aristida oligantha) (Ornduff and Faber, 2003; Stromberg et al., 2007). In addition, due to the seasonal influx of rainfall and the development of restrictive soil layers, ephemeral wetlands support a variety of terrestrial and aquatic plant and animal species (e.g., Lepidurus packardi; Neostapfia colusana) (Laabs et al., 2002; Dittes and Guardino, 2002). Burrowing rodents are abundant, particularly the California ground squirrel (Spermophilus beecheyi) and the Botta pocket gopher (Thomomys bottae) (Laabs and Allaback, 2002) (Fig. 4.2). Cattle ranching and agriculture are the most common land use practices in the region (Robins and Vollmar, 2002) (Fig. 4.1d).

### 4.2.2 Modeling Mima mound development

According to the argument for rodent-built mounds, a restrictive stratum must exist in the soil. This layer hinders vertical water transport and prompts fessorial rodents to construct the mounds in an effort to secure protection from predators in the thin soils and/or to avoid a perched water table or low permeability conditions. In many cases, the obstructive layer is a consequence of long-term soil formation processes. These layers include argillic horizons and duripans, which are present in the study area.
Figure 4.2: (A) Typical tailings piles from pocket gopher (*Thomomys bottae*) tunneling in the region. An average gopher tailings pile is \(\sim 25\) cm in diameter. (B) A tailings heap created by ground squirrels (*Spermophilus beecheyi*), which normally leave their burrows open (as opposed to the closed openings of gophers). The long axis of the ground squirrel tailings pile shown is 90 cm.

Harden (1982) found that the soils of the Merced River chronosequence show consistent changes in soil development with landscape age, particularly an increase in clay in the B horizons. Fine-textured subsoils generally have lower permeability, leading to soil water retention and, potentially, to saturation or perched water tables. Gophers spend nearly the entirety of their lives in intimate contact with the soil (Ingles, 1951) and must be keenly sensitive to differences in permeability. Gophers have high rates of gas exchange, because of their thermoregulation requirements (McNab, 1966). As soil textures become finer, air exchange decreases, and gophers would likely need to make behavioral or physiological adaptations to compensate. For instance, McNab (1966) observed that in areas cohabitated by large and small gophers, the small gophers were relegated to the shallower soils due to the greater gas exchange requirements of the larger gophers, even though smaller gophers would choose deeper soils in areas without competition for habitat. In addition, McNab (1966) concluded that increased burrowing by gophers during wet periods (Miller, 1948; Ingles, 1949; Hansen and Morris, 1968; Cox and Hunt, 1992) could be a response to decreased air exchange in burrows, due to decreased permeability. Furthermore, in a simulated gopher environment, Romanach et al. (2007) found that gopher survival decreased significantly as soil clay content increased. Thus, soil permeability is of particular importance to gophers, because the gas required by fossorial rodents must be derived via soil diffusion.

How, then, do the gophers on the Merced River chronosequence adapt to the limitations imposed by decreased permeability? Gophers are plentiful on even the oldest and most
developed of the alluvial terraces (Laabs and Allaback, 2002). In Ch. 3, I presented evidence that preferential soil movement is their response to changing soil conditions. Yet, it is still important to develop a detailed understanding of how gopher sediment transport may ultimately lead to mound creation. To approach a solution, I begin with a review of previous work, which describes and models the processes by which rodents may build the mounds.

Dalquest and Scheffer’s (1942) original description of their gopher-based hypothesis was largely qualitative. They observed that gophers inhabiting mounded regions on Scott’s Prairie of Western Washington (near the type locality Mima Prairie, which is not currently inhabited by gophers) regularly burrow out “exploratory” tunnels which reach roughly 3 meters out from the mound center. They assumed the mound centers are located at points which may have originally been better drained or had thicker soil profiles. Dalquest and Scheffer measured five of these active tunnels; more than half of the soil emptied from the passageways did not get transported to the surface and was thus assumed to be incorporated into the mound. According to the authors, this shuttling of earth, long continued, accounts for the sunken contour of the inter-mound area and for the greatest part of the volume of the Mima mound. Five years later, Scheffer (1948) conceded that the model they presented did not wholly account for the building of the mounds:

In fancy, it is easy to picture the start of a Mima Mound. It is less easy to account for its growth. For reasons that may never be known, the gophers carried more dirt toward the nest than away from it. Perhaps some biologist will suggest an experiment whereby the growth of a Mima-type mound can be studied from start to finish. At present, we do not know whether the mounds on the Puget Sound and other prairies are still growing, whether they are in equilibrium with the forces tending to reduce them, or whether they are shrinking.

A group of researchers responded to this challenge by closely monitoring gopher activity in mounds near San Diego. In 1987, Cox and Allen tracked, over the course of one year, the directional movement of small iron pellets emplaced in soil plugs which were implanted into gopher burrows. They found that the net movement of the markers was largely moundward (average 41.3 cm) and slightly upward (average 4.9 cm). In a subsequent study, Cox (1990c) measured the quantity of soil mined (and deposited both aboveground and belowground) in the mound terrain and found that deposition of surface heaps per unit area was greatest at the center of the mounds, and was reduced toward the mound edge and intermound areas. Cox (1990c) combined the results of these two studies to develop a model which predicts the net deposition or removal of soil at given points along the mound-intermound gradient, and for mounds with differing heights.

Horwath and Johnson (2006) proposed a qualitative model of Mima mound evolution based on observations and analyses of gravelly Mima mounds in seasonally wet Diamond Grove Prairie Preserve, Newton County of southwestern Missouri. The mounded prairie is underlain by a dense claypan, and a substantial stonelayer that, like the Merced moundfield, is exposed in seasonally wet and stony intermound swales. The authors drew on particle size
analyses, included gravel fractions, and trench-exposed horizonation assessments to hypothesize how a combination of biotic, pedogenic, aeolian depositional, and erosional (surface washing) forces led to the current mound profiles, which include bimodal clay-rich horizons and two stonelayers (Horwath Burnham et al., 2012). The authors concluded that gophers, which had recently inhabited the moundfield – evidenced by gopher-sized soil krotovina (refilled burrows) and the presence of gophers in nearby counties – were the primary force in creating the polygenetic mound-intermound terrain.

Gabet et al. (2013) recently developed a spatially explicit, rule-based model of Mima mound formation using measurements of Mima mound size, soil thickness and gopher behavior in California. The model predicted that Mima mounds reached steady state within 500 years and successfully recreated (when compared with the Merced-area LIDAR data (Reed and Amundson, 2006)) a number of key mound features such as mound size and spacing, and intermound depressions. Gabet et al. (2013) proposed that the mounds are an example of spatial self-organization created by feedbacks between changing soil conditions and gopher activity and concluded that, on the basis of organism weight, Mima mounds are the largest structures created by (non-human) mammals.

These observations and models provide conceptual representations of biologically-built Mima mounds, and they are supported by considerable evidence. However, Cox (1990c)’s empirical model only directly applies to the mounds in the San Diego region, and also does not address mound erosion. Gabet et al. (2013)’s model is parametrized using measurements from Cox and Allen (1987) and Cox (1990c) of moundward gopher sediment transport in existing Mima moundfields. The model, as it was constructed, does not help explain how or why the moundward movement develops or why Mima mounds do not emerge in all gopher-inhabited landscapes. In addition, many other studies have demonstrated that numerical models similar to Gabet et al.’s and based on abiotic-biotic interactions lead to spatial self-organization (e.g., Kefi et al., 2010; Barbier et al., 2014). It is possible that similar topography could have emerged from a model based on an erosion-vegetation anchoring hypothesis, for example. Finally, burrowing is a costly activity which makes up a large fraction of rodents’ energy budgets (Vleck, 1979; Du Toit et al., 1985; Perissonotti et al., 2009), and these models do not demonstrate that mound creation or maintenance by gophers is energetically feasible. Thus, I use energy as the metric to test the possibility that gophers build and sustain Mima mounds. The model outlined below, which combines geomorphic and biologic models and observations, is a simple representation of mound evolution, but is a step towards an analytic model that could be applied to other regions where mounded topography exists.

4.2.3 Diffusive sediment transport

In the last half century, hillslope geomorphology, building on G.K. Gilbert’s (1909) conceptual model of soil-mantled hillslopes, has moved towards a quantitative, process-based theory of landscape evolution (e.g., Culling, 1960, 1963; Dietrich et al., 1995; Roering et al., 1999; Yoo et al., 2005; Roering, 2008; Furbish et al., 2009; Heimsath, 2012). Based on these devel-
opments, I consider Mima mounds to be miniature, convex, soil-mantled hillslopes. However, unlike most soil-mantled hillslopes, the mounds in the Merced study area are not underlain by bedrock, but by several soil layers, which I refer to as “parent material”, for purposes of description. Transport in the upper layer is assumed to be dominated by slope-dependent creep, driven by biotic disturbance (mixing and perturbation by rodents). Biogenic sediment transport (especially on convex, soil-mantled hillslopes) is commonly modeled using a linear, diffusive transport law (Equation 4.1), in which sediment flux is proportional to hillslope gradient. The model was originally introduced by Davis (1892) and Gilbert (1909) and was formalized by Culling (1960, 1963), using an analogy with Fick’s law of diffusion (in which flux is proportional to a concentration gradient):

\[ q_s = -K \nabla z \]  

(4.1)

where the sediment flux \( q_s \) [(length)\(^2\) (time)\(^{-1}\)] is proportional to the hillslope gradient, \( \nabla z \), and \( K \) is equivalent to a diffusion coefficient with dimensions (length)\(^2\) (time)\(^{-1}\) and embodies factors such as climate, soil type, and vegetation. While the vegetation in the study ecosystem is important from both a conservation and a geomorphic perspective, I simplistically incorporate the entire effect of vegetation on erosional processes into the diffusion coefficient. Equation 4.1 was applied to the Mima mounds in order to model soil movement on them. Based on studies conducted in California grasslands where, similar to the Merced region, bioturbation is the main transporter of sediment (Dietrich et al., 1995; Heimsath et al., 1997; McKean et al., 1993; Reneau, 1988), \( K \) values in the Merced region are assumed to range between 25–75 cm\(^2\) yr\(^{-1}\).

There has been considerable recent work showing that transport on soil mantled slopes may be more accurately modeled with non-linear functions which involve some dependency on soil thickness or disturbance magnitude (Roering et al., 1999; Gabet, 2000; Roering, et al., 2001; Roering, 2004; Furbish et al., 2009). Thus, soil creep on mounds is likely not fully described by a simple linear model. However, the traditional creep model is used here because the linear model likely provides a reasonable approximation for the gentle slopes of Mima mounds (see Chapter 2).

In order to estimate the erosion rates of convex Mima mounds and the subsequent deposition into the concave vernal pool regions, I use the mass continuity equation (Equation 4.2) of soil thickness:

\[ \rho_s \frac{\partial h}{\partial t} = -\rho_{pm} \frac{\partial e}{\partial t} - \rho_s \nabla \cdot q_s \]  

(4.2)

where \( \rho_s \) and \( \rho_{pm} \) are the bulk densities of the mobile soil layer and the “parent material”, respectively, \( h \) is the soil thickness (measured from the soil surface to the top of the parent material), \( e \) is the elevation of the soil-parent material interface, and \( q_s \) is the sediment transport vector. Here, \( \rho_{pm} \frac{\partial e}{\partial t} \) represents the production of soil from the parent material (assumed here to be primarily due to disruption and transport of sediment by rodents) and \( \rho_s \nabla \cdot q_s \) represents soil removal. If the mounds are persistent, and thus at steady state
(constant mobile layer thickness and hillslope shape, $\frac{\partial h}{\partial t} = 0$), then the expression (Equation 4.3) for landscape lowering ($E = \frac{\partial e}{\partial t}$):

$$E = -\frac{\rho_s}{\rho_{pm}} K \nabla^2 z$$  \hspace{1cm} (4.3)

shows that erosion can be calculated using curvature values ($\nabla^2 z$). The ratio of the bulk density of soil in the mobile layer (the upper layer, above the parent material) and the bulk density of the parent material ($\frac{\rho_s}{\rho_{pm}}$) was assumed to be equal to 0.75, based on work by Reichman and Seabloom (2002), who stated that the density of material in gopher tailings piles is generally 10-40% lower than the underlying consolidated soil.

Reed and Amundson (2007; 2012) used topographic data derived from differential GPS (global positioning system) and LIDAR surveys, respectively, to calculate curvature values on a region of mounds and pools, in order to use Eq. 4.3 to determine how rapidly mounds would erode, in the absence of a preserving force. It was found that, without an active agent maintaining this topography, the landscape would be largely flattened by biogenic, gravity-driven erosion in $\sim 10^3$ years (assuming minimal aeolian deposition). These initial studies were conducted on select regions of the oldest chronosequence member, the Laguna formation.

Here, I expand the work to estimate erosion across the soil age gradient using mound curvature values measured from LIDAR in Chapter 2 for each geologic formation. I compare the estimates of downwearing with the rates of moundward gopher sediment transport measured in Chapter 3 (using RFID (radio frequency identification) technology). I use the results to quantify the role of gophers in counteracting erosion for a range of Mima mound and vernal pool terrain on the Merced River chronosequence.

### 4.2.4 Mima mound energy balance

The mass balance approach to hillslope evolution described above, in which land surface changes are represented by mass fluxes in the form of erosion and deposition, does not directly consider the effect of biota on resultant topography. Thus, I combine the mass balance model with studies of gopher behavior and physiology in order to determine if there is sufficient energy available to the burrowing animals to produce and maintain the mounds.

#### 4.2.4.1 Energy requirements for mound building and maintenance

I assume that the mounds are built when gophers forage centripetally (radially) outward from what were perhaps originally better-drained portions of the landscape. Such locations would likely function as nest areas, and thus become main activity centers for gophers and other organisms. I further assume that burrowing outward from the center should result in slightly more soil being moved back toward the starting point, than to the distal end point. Repeating this process over multiple generations produces Mima mounds.
While the model below does not address exactly how this preferential transport occurs on a particle-by-particle basis, it does represent aggregate transport. It was constructed to represent the maximum energy required for mound building, providing a test of the feasibility that gophers build mounds. In order to estimate the upper bound on the energy required for mound building, I used mound morphology measurements (from Chapter 2) for the oldest terrace which has the tallest and most convex mounds. To begin, the energy required to build and preserve a mound is defined:

\[ E_{\text{mound}} = E_{\text{lift}} + E_{\text{burrow}} + E_{\text{maintain}} \]  

(4.4)

The component energy terms are converted into energy density values \([E L^{-2} T^{-1}]\) and used to represent biologic and geomorphic energy storage and expenditures. The definition and quantification of these terms are discussed below.

**Lift Energy** \((E_{\text{lift}})\)

For a terrace surface that is approximately level and unmounded, the change in potential energy required to lift sediment from below base level (in what ultimately becomes a swale) to a position above the base level (to form the mound), is determined by the following equation:

\[ \Delta PE = mg \Delta h = \rho V g \Delta h \]  

(4.5)

where \(m\) is the soil mass, \(\rho\) is soil bulk density, \(V\) is soil volume, \(g\) is the gravitational constant, and \(\Delta h\) is the change in height of the sediment. Restated, the mound sediment is assumed to be derived from the inter-mound depressions, and the model allows one to calculate the change in potential energy for uplifting sediment. The mounds in the Merced region are slightly ellipsoid in shape (Ch. 2); thus by integrating over the volume of a half ellipsoid, the potential energy change involved in lifting a mound’s volume of sediment against the force of gravity is:

\[ E_{\text{lift}} = \frac{1}{2} \rho g \int \int \int z dx dy dz \]  

(4.6)

where \(z = c \sqrt{1 - \frac{x^2}{a^2} - \frac{y^2}{b^2}}\) (the formula for an ellipse), \(a\) is the semimajor axis of the mound, \(b\) is the semiminor axis, and \(c\) is mound height. Bulk density \((\rho_{\text{avg}} \sim 1.7 \text{ g cm}^{-3}\) for the Laguna formation) is from Harden (1987).

Solving this integral from base level to the top of a mound yields:

\[ E_{\text{lift}} = \frac{1}{4} \pi \rho g abc^2 \]  

(4.7)

This value was simply doubled to estimate the total change in potential energy due to the lift from below base level to above base level. The actual \(E_{\text{lift}}\) would be less because when the soil volume is inverted from concave up (below base level) to concave down (above base level), the potential energy change diminishes with distance from mound center. Thus, the calculated
$E_{\text{lift}}$ represents a maximum because it reflects the energy required to raise a concave down volume of soil from below to above base level. The energy expressed in Equation 4.7 (after doubling) is the lift energy for one mound. To measure the total change in potential energy caused by soil redistribution across a given area ($\text{J m}^{-2}$), Equation 4.7 was multiplied by the average mound concentration (mounds per area, Ch. 2) for the Laguna formation. In order to calculate the energy density of mound lifting work ($\text{J m}^{-2} \text{ yr}^{-1}$), it is necessary to estimate the time required for the mound-building process. A range of timescales (10-10$^4$ years) is applied to the energy calculations in order to assess the likelihood of different mound-building scenarios.

**Burrowing Energy ($E_{\text{barrow}}$)**

Several studies have shown that shearing and pushing soil are the most energetically costly activities associated with biotic soil transport (Vleck, 1979; Du Toit, et al., 1985; Seabloom et al., 2000). Vleck (1979) developed a model to estimate the energy needed to shear the soil from the face of an individual burrow (cross-sectional area approximately equal to gopher body diameter) and to push loose soil along the burrow length. He parameterized the model by measuring gopher oxygen consumption during burrowing for different distances and in different soils. In order to estimate mound-building costs, I modified Vleck’s model and assumed a gopher creates multiple burrows within the swale soil, such that the sum cross-section of all burrows is, over time, equal to the cross-section of a mound or swale. Then, the gopher pushes that soil from the basin area to the mound area. Cox (1990c) estimated, based on his observations of the direction and magnitude of gopher-driven soil movement, that the mean soil displacement distance during mound formation is 4.4 m. In order to place upper bounds on the amount of soil sheared and the distance it is subsequently pushed, the average mound diameter (across all mounds measured in Ch. 2) is used to estimate the shear and push distance parameters. This value is meant to represent an upper-limit average on the distance of soil movement, including upward movement (through surface-access tunnels) and movement from pools on all sides of a given mound. The energy required for a gopher to fully burrow out an area equal to the size of a mound cross-section and transport it (ultimately building a mound) is:

$$E_{\text{barrow}} = \pi \rho acd(K_s + \frac{1}{2}K_p d)$$

where $a$ is the semimajor axis of the mound, $c$ is mound height, $d$ is the mound diameter (assumed to be equal to swale diameter), and $\rho$ is soil bulk density. $K_s$ represents the energy cost ($\text{J m}^{-2} \text{ yr}^{-1}$) of shearing one gram of loose soil, while $K_p$ represents the energy cost of pushing one gram of loose soil 1 m in distance. (Note these $K$ parameters are different than the diffusion coefficient used in Equation 4.1.) The energy required to move soil for a range of time frames (10-10$^4$ yr), and for both sandy loam and clay soils, was calculated. While this model clearly does not offer a detailed particle-based representation of precisely how gophers may move soil from basin areas to form mounds (e.g., how burrow architecture
changes with time), it does represent an upper bound on the energy required to loosen and push an equivalent amount of soil from source (pool) to resultant form (mound).

**Maintenance Energy (E\text{maintain})**

Apart from the nuanced dynamics of how gophers might form mounds, modeling (Reed and Amundson, 2007; 2012) indicates that, assuming zero or minimal aeolian infall, the mounds would not persist long-term against erosion without a conserving force. I use the erosion rates calculated with Equations 4.1 and 4.2 to estimate the energy required to maintain mound form against erosive forces. Given an erosion rate ($m\ \text{yr}^{-1}$), the rate of release of potential energy ($J\ \text{m}^{-2}\ \text{yr}^{-1}$) is calculated by multiplying the erosion rate, soil bulk density and gravitational constant (following Phillips, 2009). The geomorphic model I described neglects the change in mound form (curvature values) that would result as erosion occurs over time and thus likely overestimates the maintenance energy required.

### 4.2.4.2 Energy available for mound building and maintenance

**Available energy (E\text{gopher})**

Using the approach outlined above, the energy required for the formation of mounds from a level surface can be estimated. The question I hope to address is, “Given the energy budget for mound formation, are biologically built mounds feasible?” To determine whether gophers are capable of doing this work, I used the literature to estimate total ecosystem biological energy stores and the proportion of that energy which is partitioned to gophers. Net primary productivity (NPP) is the amount of biomass generated from photosynthesis, minus the energy used for cellular respiration. NPP measurements from Brenner et al. (2001) for the Laguna formation (the average of mound and intermound values) were used to estimate the total stored biological energy available in the study region. On the Merced River chronosequence, NPP decreases with soil age and is lower in vernal pool areas than mound areas (Brenner et al., 2001). Using the Laguna values yields a minimum potential energy intake value and therefore a highly conservative estimate on gophers’ ability, energetically, to create the mounds. Previous studies, which have compared biotic and geomorphic processes, have used NPP as the primary biologic comparison metric. These have shown that NPP stores are many orders of magnitude greater than the energy required for most geomorphic processes (Devlin, 2003; Yoo et al., 2005; Phillips, 2009), supporting the notion of biologic influence on landscape evolution.

However, because the energy densities of NPP are generally so much greater than that of geomorphic work, it is necessary to further constrain the bioavailable energy in order to determine if gophers, in particular, have enough energy in reserve to build (and maintain) mounds. Thus, a budget of the energy available to gophers for sediment transport processes was calculated, using previous studies of gopher physiology and Merced-area field measurements (Ch. 3), and compared to the energy required for mound building. Gettinger (1984) measured energy flux through gopher populations being fed a natural diet in the laboratory. He partitioned assimilated energy (energy consumed less energy excreted) into “existence”
energy (resting metabolism and nonthermal regulatory maintenance) and “activity” energy. He further estimated that \( \sim 20\% \) of the activity energy is used for locomotion (nonburrowing movement, including through burrows and, rarely, aboveground). The remaining activity energy (activity energy less locomotion) is the energy available for all burrowing activities, from which the energy for mound building would be derived.

In order to convert the burrowing-available energy value into an energy density, an estimate of the population density of gophers in the Merced region is required. Howard (1961) and Richens (1965) both demonstrated that periodic measurements of gopher tailings (small mounds of soil generated by gopher activity and located on the soil surface) are highly correlated with gopher population density. Although gopher populations likely fluctuate in both space and time, the Merced-area gopher density can be estimated by dividing measurements of the aboveground gopher transport (tailings production per gopher) by an average estimate of tailings production per gopher (110 tailing heaps yr\(^{-1}\)) (Miller, 1948; Bandoli, 1981). For the Merced estimate, I used the average rate of aboveground transport for the Laguna formation calculated in Chapter 3 (0.57 tailing heaps m\(^2\) yr\(^{-1}\)). The burrowing-available energy estimated from Gettinger (1984) is then divided by the gopher concentration estimate to calculate the density of energy (J m\(^{-2}\) yr\(^{-1}\)) available to gophers for soil movement \( (E_{\text{gopher}}) \) in the Merced region. The energy expenditure \( (E_{\text{mound}}) \) and storage values \( (E_{\text{gopher}}) \) were then compared, on various time scales and within different substrates (clay and sandy loam, as parametrized by Vleck (1979)), to explore whether gophers could be responsible for both building and/or maintaining the mounded terrain.

### 4.3 Results and Discussion

The 65 km\(^2\) LIDAR survey region examined in Chapter 2 contains \( \sim 240,000 \) Mima mounds. Based on mound distribution maps (Cox, 1984a; Johnson and Horwath Burnham, 2012), \( \sim 30\% \) of California (127,000 km\(^2\)) was historically (conservatively) covered by Mima mounds. Calculations based on the LIDAR data indicate that mounds in the survey area are comprised of more than five million metric tons of sediment. Extrapolating this figure to the estimated Mima mound coverage in California and assuming the same concentration as the Laguna formation mounds (likely a maximum), the mounds in the state originally totaled roughly 11 billion metric tons of soil. In contrast, a single gopher \( (Thomomys bottae) \) weighs an average of 120 g (Howard and Childs, 1959; Vleck, 1979) and measures roughly 19 cm in length (Daly and Patton, 1986). To imagine such small organisms creating the mounded topography by moving an amount of sediment nearly equal to the annual sediment discharge of the world’s rivers (12.2 billion metric tons, Milliman and Meade, 1983) can be perplexing. However, the results of the modeling work show that mound creation and maintenance by gophers is a plausible mechanism for this mass movement under reasonable environmental scenarios.
4.3.1 Mass balance results

Using the region-wide average mound curvature value (0.10 m$^{-1}$), Equation 4.3, and the previously mentioned range of $K$ values, erosion rates off of the Mima mounds range from 18-56 cm kyr$^{-1}$. An illustration of mound erosion and pool deposition on the Laguna formation is shown in Figure 4.3, using $K = 50$ cm$^{-2}$ yr$^{-1}$. Curvature values and erosion rates calculated from the landscape-wide LiDAR terrain data indicate that, in the absence of a conserving force, the mounds would be leveled on time scales of $10^3$ years.

Figure 4.4 compares erosion rates (based off of LiDAR curvature data, Ch. 2) and moundward sediment transport rates (based off of RFID sediment monitoring, Ch. 3) for each terrace in the chronosequence. Note that because the tunnels in which RFID tags were emplaced are parallel to the mound surface (as discussed in Ch. 3), moundward movement represents, at least in part, upward, constructive transport which counteracts soil erosion. Erosion rates (using $K = 50$ cm$^{-2}$ yr$^{-1}$) increase from 15 to 38 cm kyr$^{-1}$ with increasing soil age, while gopher soil transport (moundward portion) ranges from 8 to 26 cm kyr$^{-1}$. Since the moundward sediment transport rates consist of both a lateral and a vertical component, the strictly upward gopher soil movement is less than the rate reported here. While the gopher sediment transport rates are not large enough to completely counter the estimated erosion of the mounds, these region-wide rates of biologic soil movement are the same order of magnitude as surface downwearing, supporting the proposal that gophers play a crucial role in offsetting the long-term erosion of Mima mounds. Additionally, the aboveground sediment transport measurements also likely underestimate the excavation work done by gophers, as several studies (e.g., Miller 1957; Andersen, 1978; Cox, 1990c) have shown that up to 80% of excavated sediment gets re-deposited belowground and is therefore not represented in the measurements reported here. If it is conservatively assumed that total gopher soil movement on the Merced mounds is twice the amount measured on the surface (using an estimate that 50% of all movement is belowground and assuming the same moundward component), then moundward gopher sediment transport would exceed erosion on all landforms.

While a slope-dependent linear diffusion model describes soil transport in landscapes with low-gradient soil-mantled hillslopes reasonably well (McKean et al., 1993; Roering et al., 2002; Roering, 2008), the erosion model used here is simplistic and likely does not adequately capture the range of processes occurring. For instance, while most hillslope models consider only physical transport processes, the impact of chemical weathering on landscape evolution is important (Mudd and Furbish, 2004; Mudd et al., 2013), especially for the Merced region. The oldest endmembers of the Merced River chronosequence have undergone soil weathering for long periods of time, resulting in large chemical weathering losses and volumetric collapse (Harden, 1987; White et al., 1996). Chemical weathering would therefore likely contribute to overall landscape lowering rate and would increase the degree of sediment movement needed to maintain the Mima mound topography.
Figure 4.3: Map showing results of modeled erosion off mounds (in red tones) and deposition into swales (in green tones). Erosion patterns are overlaid on a shaded relief image of the local terrain. Region-wide erosion values averaged 24 cm kyr$^{-1}$). Values shown were calculated using a diffusion coefficient of 50 cm$^2$ yr$^{-1}$ and a soil-to-parent material bulk density ratio of 0.75.
Figure 4.4: Comparison of rates of soil movement by gophers (proportion moved moundward, derived from RFID sediment tracking surveys and mappings of gopher tailings (Ch. 3)) with mound erosion rates (estimated using a linear diffusive model of transport and average curvature values derived from LIDAR data, Ch. 2). Values shown were calculated using a diffusion coefficient equal to 50 cm$^2$ yr$^{-1}$ and a soil-to-parent material bulk density ratio of 0.75.
4.3.2 Energy analysis results

Just as the mass balance results (Sec. 4.3.1) suggest gophers could build and maintain mounds, the energy analysis also supports the hypothesis. The relationship between the biological energy allocated to gopher burrowing activities and the energy needed for mound-building is summarized in Fig. 4.5 for the case of a mound composed of sandy loam sediment that is built in \(10^3\) years. Figure 4.6 summarizes the energy budgets for a selection of mound-building scenarios. With respect to mound-building costs, the energy required for lifting soil against gravity to build mounds is the smallest component of the mound-building budget and ranges from 95 to 0.095 J m\(^{-2}\) yr\(^{-1}\) for 10-10\(^4\) year construction scenarios, respectively. The shear and push costs for mound building (sandy loam) range from 4.4 x 10\(^5\) to 440 J m\(^{-2}\) yr\(^{-1}\) for the same range in time periods. For a mound composed of clayey sediment, the range is 2.8 x 10\(^6\) - 2800 J m\(^{-2}\) yr\(^{-1}\). Using the average erosion rate reported above, the cost of counteracting diffusive erosion of existing mounds is 3.0 - 9.1 J m\(^{-2}\) yr\(^{-1}\), for a range of diffusivity values (25-75 cm\(^{-2}\) yr\(^{-1}\)). Thus the total cost of lifting, shearing, pushing, and maintaining soil in the shape of a mound ranges from 4.4 x 10\(^5\) - 440 J m\(^{-2}\) yr\(^{-1}\) for sandy loam and 2.8 x 10\(^6\) - 2800 J m\(^{-2}\) yr\(^{-1}\) for clay.

The energy available to gophers for burrowing activities was estimated using gopher sediment transport measurements as a proxy for gopher population density and using the energy partition outlined in Fig. 4.5 and developed by Gettinger (1984). The Merced gopher population density was calculated to be 52 gophers ha\(^{-1}\). From this, the remaining activity energy available for sediment transport processes, \(E_{\text{gopher}}\), was estimated to be 5.4 x 10\(^4\) J m\(^{-2}\) yr\(^{-1}\), which is 1% of NPP for the area.

For a sandy loam mound built in 1000 years, the costs of building are 8% and 0.1% of burrowing-available energy and NPP, respectively (Fig. 4.5). For a clay mound built in the same time period, the costs are 52% and 0.8% of burrowing-available energy and NPP. Based on this calculation, there is insufficient energy for gophers to build mounds within 10-year (both clay and sandy loam, not shown in Fig. 4.6) and 100-year clay mound scenarios (Fig. 4.6). However, for thousand-year timescales and longer, there clearly does exist adequate biological energy to produce and preserve these landscape features.

Pedologic processes increase clay content over time (e.g., Birkeland, 1999). As soils develop, then, the energy requirement for gopher sediment transport would increase. Therefore, soil weathering is expected to work against the persistence of mound-pool topography in a number of ways: increased chemical denudation increases landscape lowering (as discussed above), increased energy required for burrowing (Vleck, 1979), and decreased bioturbation rates (due to decreased NPP). Yet despite these limitations, the tallest mounds are found on the most weathered terraces (Ch. 2). Gophers may develop both morphologic and behavioral adaptations to compensate for chemical-weathering induced mound depletion and soil hardening. Recently, Marcy et al. (2013) demonstrated that California gophers divide by subgenera on the basis of soil conditions and that gophers in harder, thinner soils developed a more energetically efficient tooth-digging skull morphology. This adaptation may serve to decrease the burrowing energy requirement, mitigating the high metabolic costs of
digging. Furthermore, the evidence that sediment movement by gophers is net moundward in Mima mound landscapes (Ch. 3) lends additional support to the idea that gophers adjust to pedogenic changes.

4.3.3 Considerations for model improvement

While there are reports of relatively rapid Mima mound development (Price, 1949; Koons, 1948; Ross et al., 1968; Johnson and Horwath Burnham, 2012), the data for Merced suggest processes that operate on geologic time scales. In 1949, Price reported that “a mature Mima mound has been built in 5 years”. Similarly, Ross et al. (1968) report accounts of black silt loam mounds reappearing 4-5 years after being plowed. Based on this time frame and the reported size of the mound discussed in Price (1949) (19 m diameter and 0.6 m height (sizes reported in Ross et al. (1968) are comparable)), the energy required for construction by a single gopher is $2.23 \times 10^6 \text{ J m}^{-2} \text{ yr}^{-1}$. This is nearly 4000% of energy that a gopher can expend for burrowing, for semi-arid Merced. The mound-building account on the Carrizo Plain is more consistent with the energy constraints calculated for the Merced grasslands. In order to build the 0.25 m tall mounds that Johnson and Horwath Burnham (2012) reported emerging in 30 years, $1.8 \times 10^5 \text{ J m}^{-2} \text{ yr}^{-1}$ is required (for clay soils). This is nearly six times more than the energy available for gopher burrowing using the parameters discussed above.

The direct accounts of mound building are not energetically possible using the approach here, but several considerations may explain the disparity, especially for the Carrizo Plains. First, the model was constructed to estimate maximum bounds on mound building costs and realistic approximations of bioavailable energy. In particular, the distance soil is pushed and sheared during mound building was estimated to be equal to one mound diameter. This was intended to represent an upper-limit average on the distance of soil movement, including upward movement (through surface-access tunnels) and movement from pools on all sides of a given mound. This conservative approach likely leads to an overestimate of the amount of energy required to shear and push soil. For instance, Cox (1990c) estimated that the mean soil displacement distance during burrowing is 4.4 m (based on observations in the San Diego Mima mounds). If Cox’s average displacement distance is used (instead of mound diameter), mound building under the Carrizo Plain conditions requires $2.2 \times 10^4 \text{ J m}^{-2} \text{ yr}^{-1}$, which is only 40% of the energy available for burrowing. Therefore, if the average soil displacement that occurs during mound building is closer to the Cox estimate, the construction of Mima mounds by gophers is reasonable even on short time scales. This result is more consistent with the output of Gabet et al.’s (2013) numerical model which yielded mounds strikingly similar in size to the Carrizo Plain mounds after 30 years of model time.

In addition, given Cox and Hunt’s (1990) observations of multiple gophers occupying larger mounds, it is possible that more than one gopher may contribute to mound building, reducing overall energy costs. (However, most studies (Dalquest and Scheffer, 1942; Hansen, 1962; Murray, 1967) report that each Mima mound is usually occupied by a single gopher.) Furthermore, on the Carrizo Plain, kangaroo rats inhabit Mima mounds and are thought to
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Figure 4.5: Flow diagram showing how biologically available energy is incorporated and allocated under the scenario that gophers build Mima mounds made of sandy loam on a 1000-year time scale. Net primary productivity estimate is from Brenner et al., (2001) for the Laguna formation. Gopher energy uptake was measured by Gettinger (1984) and was estimated for the gophers in the Merced region using population density estimates. The partitioning of available activity energy is calculated through various methods detailed in the text. All units are J m\(^{-2}\) yr\(^{-1}\). Relative sizes of energy pools are not necessarily drawn to scale.
Figure 4.6: The energy costs of various scenarios of mound building by gophers (expressed as the logarithm of energy density [$J \text{ m}^{-2} \text{ yr}^{-1}$]) for different soil types and time scales. The lightest gray represents the energy required for gophers to shear and push soil from the intermound region into the shape of a mound (based on model by Vleck, 1979). The black quantity indicates the energy required to lift the soil against the force of gravity to build mounds. Finally, the dark gray indicates the energy required to maintain the mounds against diffusive erosion. The black horizontal line represents the estimated energy available to gophers from biomass intake to do the mound-building work (based on Gettinger, 1984). Note that these are conservative estimates for building the some of the tallest mounds in the region.
CHAPTER 4. A BIOGEOMORPHIC MODEL OF MIMA MOUND EVOLUTION

engage in mound construction. As more social, less fossorial mammals, kangaroo rats may have lower mound building costs (Lacey et al., 2000). Finally, especially given the evidence that gophers in California develop morphologic adaptations to challenging environments (e.g., procumbent incisors for shearing high linear extensibility smectite soils (Marcy et al., 2013)), gophers in Mima mound terrain may represent a subspecies that is more efficient at burrowing than those in non-Mima mound terrain such as those observed by Vleck (1979) and Getttinger (1984) (which were used to parametrize the model). Investigations of genetic and/or morphologic changes among gophers on the different chronosequence terraces (in addition to the sediment transport differences reported in Chapter 3) could serve as a basis to explore whether pocket gophers evolve along with Mima mound form and distribution as pedogenesis shapes the substrate habitat.

In addition to the inconsistency between the model results and direct reports of mound building, other issues associated with the model should be addressed. First, estimated gopher densities for the Merced region (52 gopher ha\(^{-1}\)) are considerably lower than reported in other regions (e.g., Seabloom et al., 2000, \(N = 119\); Smallwood and Morrison, 1999b, \(N = 53\pm 49\); Howard and Childs, 1959 (\(N = 360\) (pre-population crash) and \(N = 64\) (post-population crash))). However, the low population density is reasonable considering the eastern Merced County grasslands receive less rainfall than most other U.S. grassland regions (Dukes et al., 2005). If the gopher population density is underestimated here, then it is possible that \(E_{\text{gopher}}\) is even higher than reported, more strongly supporting the conclusion that rodent-built mounds are energetically possible.

Next, the analysis assumes that gophers are the region’s primary subterranean organism. However, other fossorial rodents are found in some regions of Mima mounds and their presence in an ecosystem undoubtedly impacts sediment transport processes and community ecology. Ground squirrels (\(Spermophilus beecheyi\)), for example, are prevalent in the Merced region (Laabs and Allaback, 2002) and while their burrowing behavior is different from gophers in that their burrows are generally larger and left open after excavation (Fig. 4.2), they also must affect land surface processes. Other organisms also likely impact the dynamics of mound erosion and upbuilding. American badgers (\(Taxidea taxus\)) prey on gophers and ground squirrels and also excavate burrows for their own protection (Orloff, 2002). Several studies indicate that the San Joaquin kit fox (\(Vulpes macrotis mutica\)) may enlarge ground squirrel and badger burrows for their own use, especially in regions where hardpans exist (Jensen, 1972; Morrell 1972; Orloff et al. 1986). The digging activities of these other animals would likely affect rates of mound erosion/construction, although the extent of the effects remains to be quantified.

Furthermore, nearly 150,000 acres within and surrounding the study region are used for cattle grazing (Robins and Vollmar, 2002), and the effects of this practice are likely to affect sediment transport processes and gopher behavior and ecology. For instance, I have observed that some mounds in the study region (at least 20%) exhibit mid-mound deflation, in which the top center of the mound is a concave depression. Nikiforoff (1941) speculated these were caused by the sinking of gopher tunnels at the mound apex, perhaps due to the weight of cattle, although this sinking could also be due to burrowing by other rodents or
predators. He concluded that both the burrow collapse and the tailings piles created by gophers should be expected to cause a gradual destruction and leveling of the mounds rather than their upbuilding. Grazing may also affect gopher density (and mound density) (e.g., through changes in soil density or forage supply), although the reported impacts of grazing on gopher populations are contradictory. Several studies have shown a decrease in gopher densities in grazed areas (Hansen, 1965; Turner et al., 1973; Hunter, 1991), while other have reported an increase (Buechner, 1942; Richens, 1965) or equal densities in grazed and un-grazed areas (Turner, 1969).

Although the model warrants improvements, several other studies of gophers support the results reported here. Previous workers have shown that although burrowing is expensive, gopher diet generally provides ample calories for soil digging, even in challenging environments (e.g., Gettinger, 1984; Romanach et al., 2007-simulation). Seabloom et al. (2000) showed that gophers do not adjust their sediment transport behavior even on slopes as steep as 30% because the costs associated with shearing and pushing the soil are so much greater than lifting soil against gravity. Huntly and Inouye (1988) demonstrate that the energy flow-through rates of gopher populations rival those of large grazers, indicating that gopher populations have large amounts of energy available to them.

4.3.4 Implications for conservation biology

The state of California and various non-profit agencies have waged a sizeable effort to protect remaining vernal pool ecosystems (Alexander and Schlising, 2011). One common mitigation tactic is to construct artificial pools to replace natural pools lost through development (Sutter and Francisco, 1998; Moore et al., 2003). While this approach is important to the pools’ preservation, there is, as yet, no fundamental scientific understanding of how these landscapes have developed, or what mechanism maintains the topography that is critical to the species that live in the pools. Given that mounting evidence suggests that gophers are the key species that both forms and preserves the terrain, these mitigation efforts may be neglecting a key component of mound-pool function, which could hamper long-term conservation success. For instance, Bauder (2005) showed that small (cm-scale) changes in mound and pool topography (which could occur through changes in gopher sediment transport) can have significant impacts on pool hydrology and on the resident plants and animals, which are finely calibrated to specific hydrological (i.e., topographic) conditions (Pyke, 2005).

Besides maintaining mound-pool form, gopher presence can have other effects on life within vernal pools. It has been shown (Loredo et al., 1996, and references within) that tiger salamanders (*Ambystoma tigrinum*), endangered vernal pool amphibians, use ground squirrel and gopher burrows as habitat during their non-breeding season. Furthermore, gophers may have an effect on maintaining vernal pool plant life via their dietary habits. Hunt (1992) showed that gophers eat vernal pool plants sparingly, mainly in late spring, and instead focus their foraging on grass and forb shoots. This feeding behavior could help keep European grasses and forbs from encroaching on vernal pools, similar to the effect that is observed to occur via livestock grazing (Marty, 2005; Robins and Vollmar, 2002). In
addition, soil mixing by gophers may support vernal pool invertebrate species richness by regularly excavating dormant cysts (Brendonck and De Meester, 2003; Croell and Kneitel, 2011).

The trapping, gassing, and poisoning of gophers has been practiced by farmers and ranchers in California’s Central Valley for more than a century because gophers are considered pests which eat and bury agricultural and feed plants, disrupt irrigation flow, and disturb the soil surface, causing problems for farm machinery (Rhoads, 1898; Miller, 1950; Smallwood et al., 2001; Laabs and Allaback, 2002). The practice of gopher eradication may impact mound and pool form and overall ecosystem function (e.g., Smallwood and Morrison, 1999b) and warrants further study.

4.4 Conclusion

Mima mounds, which have captivated researchers for more than a century, along with their adjacent vernal pools, provide a unique opportunity to study linkages between biotic and abiotic processes. LIDAR data of mound and swale surfaces makes it possible to build and test models to better understand landform evolution, and the rates and energy involved. In this chapter, I used a linear diffusion model of hillslopes to estimate rates of Mima mound erosion and vernal pool deposition and compared the downwearing with rates of moundward-directed gopher sediment transport. I also developed a model which approximates the energy required for the formation (shearing, pushing and uplifting soil) and maintenance (counteractions to erosion) of Mima mounds, and compared the amount to estimates of energy available to gopher populations in the Merced region. The results show that the building of mounds by gophers is feasible (on both an energetic and a mass-based level) in relatively short time periods, strongly supporting a biotic origin for construction of Mima mounds.
Chapter 5

Conclusion

5.1 Summary

This thesis sheds light on the formation of Mima mound-vernal pool topography and provides strong evidence that gophers are keystone species in central California. In Chapter 2, I documented clear landscape-wide patterns of mound morphology which are consistent with a biologic model of mound formation. In particular, mound height and density increase along the chronosequence, likely reflecting the different stages in mound formation as soils age. Furthermore, I demonstrated widespread regularity in mound distribution which matches the strict habitat spacing of territorial gophers. In addition, the LIDAR analysis yielded clues about how mound evolution is affected by macrotopographic changes and how that might relate to gopher ecology. For instance, mounds are commonly taller on north-facing slopes which could indicate effects related to how gopher sediment transport changes with denser vegetation and/or more saturated soils caused by differences in solar radiation.

In Chapter 3, I provided insight as to how gopher soil movement changes with soil age. On younger landscapes with either no Mima mounds or with small, subtle mounds, the net direction of biotic sediment transport is away from the center of activity or the mound center, respectively. As soils age, the net orientation of soil movement shifts towards the center of mounds, as predicted by the biologic model. In addition, long-term sediment transport rates were estimated for each alluvial terrace. When compared with other rates of transport for California and other regions in the U.S., the rate of Merced-area biologic soil movement is lower. While this disparity may be caused by a number of factors (e.g., differences in survey size and time period of survey), it may also provide clues about how burrowing intensity changes in mounded regions.

In the final core chapter of this thesis, I developed a model which combines biotic and physical processes in mound-pool systems to estimate rates of Mima mound erosion and vernal pool deposition. This made it possible to compare the physical downwearing with rates of moundward-directed gopher sediment transport. The results are consistent with the model that gophers counteract the leveling of Mima mounds by erosion. In this chapter, I
also developed a model which approximates the energy required for the formation (shearing, pushing and uplifting soil) and maintenance (counteractions to erosion) of Mima mounds, and compared the amount to estimates of energy available to gopher populations in the Merced region. The results show that the building of mounds by gophers is feasible in relatively short time periods, strongly supporting a biotic origin for the construction of central California Mima mounds.

5.2 Future work

While this dissertation begins to identify the mechanisms by which Mima mounds are formed, it also exposes a number of future directions for investigation.

The ever-increasing availability of LIDAR datasets enables the application of the methods described here to other Mima mound regions. In particular, the local maxima algorithm I developed in Chapter 2 can be used to conduct rapid, automated analyses of other mound-fields. For instance, one of the largest databases of publicly available LIDAR data, Open Topography, contains data for several regions with Mima mound features. These data could be interpreted to explain mound origin and compared to the Merced-area mounds.

The Mima mound LIDAR data could be used to develop several other models. For instance, the detailed surface maps generated in this study could be used to model vernal pool hydrology and, in turn, predict species distribution, on very fine scales. As discussed previously, each vernal pool plant species resides in remarkably narrow habitat zones based on the inundation levels in a given pool (e.g., Bauder, 2005). The high-resolution LIDAR-generated surface maps can be used by biologists to predict species occurrence on a per-pool, cm-scale basis, greatly improving the focus and quality of conservation actions. Given that species divergence has been documented between pools separated by very small distances (Aguilar, 2011, 2012), such high resolution species mapping also provides a basis for subsequent studies of evolutionary biology.

Given the significant role that gophers play in Mima mound-vernal pool systems, it is important to consider the effect that climate change may have on gopher populations, and as a result, on the persistence of mound-pool topography. For instance, in California, climate change is expected to increase temperature and precipitation levels overall (Kueppers et al., 2005), which is likely to increase the induration of soils with shrink-swell minerals such as those in Mima mound terrain (Reid-Soukup et al., 2002). Such changes could lead to gopher relocation or general population decline. For instance, Hadly (1997) revealed a 50% decline in the population of pocket gophers during the Medieval Warm Period when compared with other, cooler periods. A reduction in gopher populations would increase the overall erosion rate (given the moundward transport documented in Chapter 3) and lead to changes in vernal pool surface area and inundation levels.

One key aspect of the Mima mound-vernal pool systems not fully addressed in this thesis involves the question of precisely why gopher sediment transport changes with pedogenesis. Dalquest and Scheffer originally postulated that the thinner and more saturated soils on
hardpan landscapes would invoke pressure on the gophers to seek more favorable habitat, but the role of plants in their proposal is largely unexplored. Species richness often increases dramatically with soil age (e.g., Laliberte et al., 2013) and net primary productivity decreases (e.g., Brenner et al., 2001), indicating that plants are also affected by soil formation processes. Changes in plant distribution and abundance with soil development may serve as an additional driver for changes in gopher foraging and sediment transport vectors which then ultimately lead to the creation of mound-pool topography. Studies of the relationship between vegetation and gopher foraging across soil age gradients would help to home in on the precise driving factors of gopher-created Mima mounds.

In Chapter 3, using a field experiment investigating gopher sediment transport across a range of soil ages, I demonstrated that gophers move soil (using PIT (passive integrated transponder) tags as a proxy) towards the center of Mima mounds, on a net basis, indicating they serve an essential role in maintaining the topography responsible for the vernal pool ecosystems. However, I also observed substantial variability in direction of PIT tag movement, reducing the significance of the results. Employing a larger number of tracers would improve the transport signal but would be expensive and labor intensive. Therefore, developing new ways to monitor gopher soil movement would be fruitful for Mima mound studies and for the many other studies which examine bio-physical feedbacks. For instance, the use of ground-penetrating radar (GPR) has advanced in the last decade and would likely provide useful insight about the relatively invisible underground world of fossorial animals. GPR could help quantify burrow structure and sediment movement over time.

5.3 Relevance to conservation efforts

In a recent decision by the U.S. Court of Appeals for the Ninth Circuit (Home Builders Association of Northern California vs. U.S. Fish and Wildlife Service, 2010), the designation of 850,000 acres of critical vernal pool habitat in California and Oregon was upheld. The case was brought by a group of developers who opposed the vernal pool protections based on the economic impacts they are expected to cause. In their finding, the Court identified the mound-swale microtopography as one of three key factors necessary for the formation of vernal pools and the endangered species therein. Without a clear understanding of how that topography was originally formed or is currently maintained, the management and conservation of the vernal pool wetlands is in jeopardy.

This thesis provides strong evidence that gophers are the active agents that maintain and likely form the mound-pool systems in California’s Central Valley. My research is consistent with studies (e.g., Davidson et al., 2012) which have begun to highlight the role of burrowing organisms in maintaining ecosystem stability (e.g., by increasing biodiversity), and I argue that it is imperative that the role of gophers in Mima mound-vernai pool ecosystems is studied in far greater detail and the results integrated in the ongoing effort to protect vernal pool wetlands.
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