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## CLUES TO THE MEDIEVAL DESTABILIZATION OF THE NEBRASKA SAND HILLS, USA, FROM ANCIENT POCKET GOPHER BURROWS

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### ABSTRACT

The Nebraska Sand Hills are a stabilized dune field in the central United States that reflect past conditions of drought. The most recent drought, known as the Medieval Climatic Anomaly, occurred from A.D. 900 to A.D. 1300 and had an enormous effect on the thriving prairie ecosystem, which included large populations of the plains pocket gopher (*Geomys bursarius*). Burrows of these organisms across a paleosol-eolian sand boundary in the Sand Hills indicate abrupt climate change during the transition from stabilized to active dune field and from humid to arid conditions. Medieval gophers tunneled at greater depths below the surface than do modern gophers, indicating the behavioral changes these animals underwent to survive during the transition. The gophers were likely surviving on roots remaining in the underlying soil as it was buried by sand; they tunneled >1 m up to the surface to deposit mounds of excavated soil and sand. Most of the burrows occur in areas of low-angle bedding, suggesting loss of vegetation occurred first on the crests of the newly formed dunes while vegetation persisted in the interdunes. Optically stimulated luminescence dates from a dune containing ancient gopher burrows are nearly identical throughout the height of the dune, indicating rapid accumulation of sand. As accumulation of sand was rapid, vegetative loss must also have occurred quickly, though not in a uniform pattern across the region. Pocket gophers were apparently able to survive in areas of remaining vegetation for a short time, but in a relatively short period of time, they were unable to reach their food sources and were forced ultimately to abandon the uplands in the region.

### INTRODUCTION

Trace fossils in marine sediments give powerful clues concerning the rate of sediment accumulation and erosion. Under slow rates, invertebrates are able to adjust their burrows upward or downward, generating spreite. If sediment accumulates rapidly (deposition by a turbidity current, for example), the upward paths of invertebrates through the sediment can be preserved as escape structures. Accumulations >30 cm thick typically exceed the ability of invertebrates to escape upward (Howard, 1975). In this paper we describe a somewhat analogous situation where eolian processes rapidly buried parts of a grassland landscape and deeply scoured other parts. These rapid changes destroyed a prairie soil and killed vegetation that had supported a sizable population of vertebrate burrowers. These burrowers, however, left behind a distinctive suite of sedimentary structures that chronicles their eventually futile efforts to mine sustenance from the buried soil.

The burrows occur in the Nebraska Sand Hills, United States, and are late Holocene (~800 years before the present). They are interpreted as pocket gopher burrows based on size, shape, orientation, and location. The burrows surround and intersect the boundary between a buried paleosol and overlying eolian sand and thus span the transition

from a stable prairie environment to a reactivated dune field. The extreme length of the burrows, extending upward into the overlying eolian sand, suggests the remarkable ability of the pocket gophers to survive under extreme conditions. Additionally, the distribution of the burrows throughout the ancient dunes suggests that vegetative loss was not uniform over the entire dune field during reactivation of the dunes within the Nebraska Sand Hills, providing important information about the transition from stabilized dunes to active dunes.

### GEOLOGIC SETTING

The Nebraska Sand Hills constitute the largest dune field in North America, occupying 57,000 km<sup>2</sup> (Fig. 1). Barchanoid, parabolic, and linear dunes are present in the Sand Hills, all of which are currently vegetated and stabilized. In the west-central Sand Hills, these dunes are ≤135 m tall (Ahlbrandt and Fryberger, 1980; Swinehart, 1998). Physical and biogenic sedimentary structures can be viewed in blowouts—areas where sand has become mobile due to disturbance of the vegetation (Ahlbrandt and Fryberger, 1980). Buried bison tracks have been recognized in many blowouts and are quite extensive throughout the Sand Hills (Loope, 1986; Loope and Swinehart, 2000). Boxwork clay coatings on the surfaces of sand grains allow for remarkable preservation of bison tracks and other features due to the increased cohesiveness of the deposits (Winspear and Pye, 1995).

Although the dune field was active during the Pleistocene, numerous reactivations during the Holocene have been identified and dated using optically stimulated luminescence dating throughout the dune field (Stokes and Swinehart, 1997; Miao et al., 2007). Megadroughts (droughts extending over a period of decades or longer) have occurred at least three times during the late Holocene and have caused complete dune reactivation over broad portions of the Nebraska Sand Hills. These megadroughts are centered at around 3.8 ka, 2.5 ka, and 0.7 ka. The most recent period of reactivation, known as the Medieval Climatic Anomaly, spanned from A.D. 900 to A.D. 1300 (Miao et al., 2007).

Three specific locations within the Nebraska Sand Hills served as study sites for this project (Fig. 1), all with exposures of buried paleosols and their contacts with overlying eolian sand. The majority of the research was conducted at Yao's Blowout, a blowout through a small linear dune superimposed on a large barchanoid megadune just south of the Middle Loup River (42°05' N, 101°22' W). Additional research was conducted at Mick's Slide, directly along the northern edge of the Middle Loup River (42°23' N, 101°01' W), and at Kroeger Blowout, located northwest of Valentine, Nebraska (42°57' N, 101°09' W). Additional location information is available from Goble et al. (2004). All sites have been previously dated using optically stimulated luminescence (OSL) dating, with the overlying eolian sands dated at ~800 years old. At Yao's Blowout, the OSL dates are nearly identical throughout the eolian sands, indicating extremely rapid accumulation (Goble et al., 2004). Exposed paleosols are significantly older. The paleosol at Yao's Blowout is a welded paleosol with ages averaging

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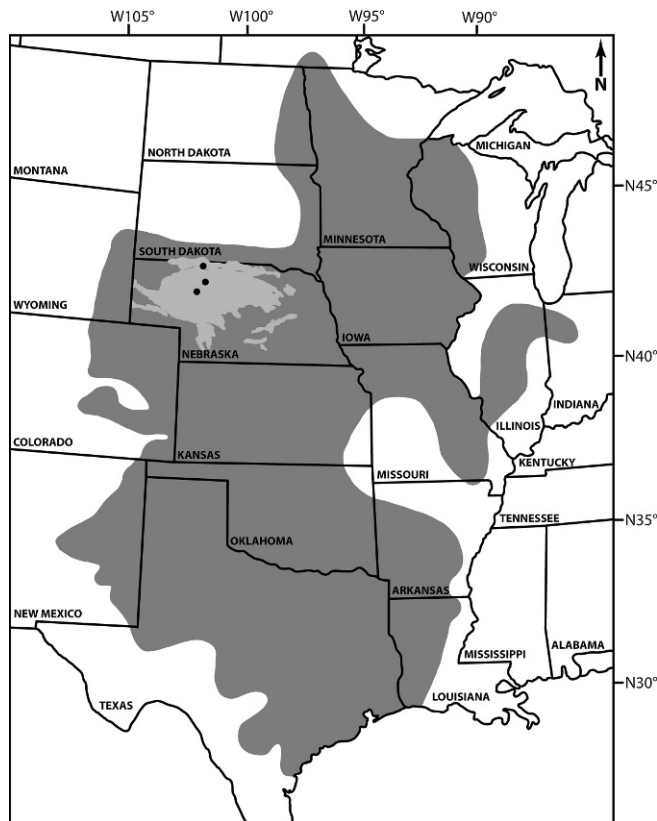


FIGURE 1—Map of central North America showing the distribution of the plains pocket gopher (*Geomys bursarius*) in dark gray (after Hall, 1981), the Nebraska Sand Hills in light gray, and localities described in this study (black dots).

~3800, 2700, and 1600 years (Goble et al., 2004, fig. 1). The single paleosol at Mick's Slide is dated at ~1180 years. Three paleosols are exposed at Kroeger Blowout, with sands between the second and third paleosol dated at ~2430 years (Goble et al., 2004). We searched for paleosols and ancient burrows in the southeastern part of the dune field but were unable to find either in this area.

Vertebrate burrows in each of the three study sites occur within both the eolian sands and the underlying paleosols. Where buried by dune sand, the bases of the paleosols were too deep to be determined at any of the localities. Hand augering around the perimeter of the dune at Yao's Blowout revealed a thin paleosol with lighter eolian sand above and below it, but only around the northwestern edge of the dune. All other auger holes revealed light-colored eolian sand with no indication of any transition. Eolian sands overlying the paleosol in blowout exposures were dominated by wind ripple lamination and inverse-graded bedding, and were deposited below the angle of repose. Areas of higher-angled bedding indicated the central portions of the dune, as confirmed by a cross-sectional view of each blowout, while more horizontal bedding indicated lower portions of the dune, from plinth to interdune.

## METHODS

One hundred thirty-seven burrows were photographed, mapped, measured, and described from Yao's Blowout, Mick's Slide, and Kroeger Blowout. Orientation of the tunnels was determined by digging further back into the exposure while following the tunnel. Optically stimulated luminescence samples were obtained by hand augering into interdune sediments surrounding the linear dune cut by Yao's Blowout. We drove light-resistant aluminum tubes into sand brought up in the auger bucket and capped both ends to prevent exposure to light.



FIGURE 2—Plains pocket gopher (*Geomys bursarius*) depositing excess soil on the side of a dune in the Nebraska Sand Hills (photo by Rebecca Schmeisser; July, 2007).

Samples were then processed at the University of Nebraska–Lincoln Geosciences Geochronology Laboratory to obtain quartz grains of the size fraction 90–150  $\mu\text{m}$  (for detailed methods, see Goble et al., 2004). Equivalent doses for the samples were calculated using the single aliquot regenerative protocol (Murray and Wintle, 2000).

We monitored soil carbon flux from two treatments in upland grasslands of the Sand Hills from 2005 to 2008 as part of a long-term dune destabilization experiment (see site description in Wang et al., 2008). The two control plots were kept ungrazed but otherwise undisturbed, while vegetation on the two plots receiving the experimental treatment were killed using the herbicide glyphosate on May 20, 2005, and thereafter kept free of living vegetation by herbicide application for the duration of the study (hereafter referred to as the press treatment). Above- and below-ground dead plant biomass was left undisturbed in the press plots. Soil carbon flux was measured approximately every 3 weeks using an LI-8100 automated soil  $\text{CO}_2$  flux system (Li-Cor, Inc., Lincoln, Nebraska). Measurements were taken at 15–20 locations in each of the 1.15 ha plots.

## GEOMYS BURSARIUS

Pocket gophers (Geomyidae) are small, fossorial rodents with external fur-lined cheek pouches used to transport food (see Fig. 2; Huntly and Inouye, 1988). Pocket gophers have a wide geographic distribution, extending from southern Canada to Panama, with the ranges of each genus rarely overlapping due to their individual soil preferences. In areas of overlap, the various geomyids live either in different soils or at different altitudes and therefore rarely interact (Best, 1973). All geomyids are active year round and obtain food (roots, shoots, forbs, and woody plants) by digging extensive tunnel networks below the surface (Huntly and Inouye, 1988).

*Geomys bursarius*, the plains pocket gopher (Fig. 2), is present throughout the Great Plains of North America (Fig. 1). Pocket gophers of the genus *Geomys* prefer sandy, friable soils (Davis, 1940; Hoffman et al., 2007) but will dig at greater depths when their ranges intercept other pocket gophers (Best, 1973). Fine soils, particularly hardpan soils, may even serve as a physical barrier to *Geomys* (Davis, 1940; Hoffman et al., 2007). Gophers within the genus *Geomys* have adapted to digging in softer soils by primarily using their claws. Gophers that dig in harder soils, such as *Thomomys*, primarily use their teeth for digging and are able to dig in harder substrates (Lessa and Thaler, 1989).

*Geomys bursarius* is typically solitary (Andersen, 1987) and active throughout the day, alternating periods of activity with slightly longer periods of rest (Vaughan and Hansen, 1961). To dig, the gopher braces itself with its hind feet and uses its modified foreclaws to shear soil from the face of the tunnel in front of it. Soil is kicked back by the hind feet



during digging and then is pushed forward using the head and forelimbs (Breckenridge, 1929; Andersen, 1988). Excavated soil is transported the shortest distance possible, either by filling an old side tunnel or by being pushed up to the surface, where it is deposited as a mound (Fig. 2; Andersen, 1988). The tunnels to the surface are almost immediately plugged, which protects the animal from predators (Werner et al., 2005).

The burrowing system of *G. bursarius* is relatively simple, consisting of one main foraging tunnel with several short, lateral tunnels to the surface (Fig. 3). The lateral tunnels lead to mounds of soil that the gopher deposits at the surface (Scheffer, 1940; Smith, 1948; Andersen, 1987), an action that is necessary to counter the increased volume that excavated soil occupies compared to *in situ* soil (Andersen, 1987). These mounds can be quite extensive, with one study indicating a total of 105 mounds associated with one burrow system (Scheffer, 1940). An average of 220 mounds can be deposited by one animal in 0.4 ha over a period of a year, leading to a total of 2.6 metric tons of soil deposited on the land surface (Kennerly, 1964). Below ground, one gopher may excavate >20 m of tunnels in a week, although each gopher typically leaves only ~35 m of open tunnel at a time. This limits the length of tunnel it is necessary to maintain and helps protect the gopher from possible predators (Thorne and Andersen, 1990).

In addition to lateral tunnels to the surface, some waste chambers and food-storage chambers are also constructed horizontally off the main tunnel (Fig. 3). These tunnels are typically loosely plugged (Scheffer, 1940; Smith, 1948). The main foraging tunnel is nearly round to slightly flattened in cross section and is ~7–8 cm in diameter (Scheffer, 1940; Smith, 1948; Best, 1973; Wilkins and Roberts, 2007). The main tunnel has a mean directionality of about zero. Digging in an approximately straight line with segments branching off the main tunnel at near-right angles allows for optimal foraging given the clumped distribution of plants typical in the plains pocket gopher's habitat (Andersen, 1988). The main tunnel is typically <25 cm below the surface (Scheffer, 1940). Other main tunnel depths reported are 15–23 cm for a burrow in eastern Kansas (Smith, 1948), a mean depth of 23 cm for several burrows in northeastern New Mexico (Best, 1973), and a mean depth of 23.7 cm for several burrows in Texas (Wilkins and Roberts, 2007). Significantly below the main tunnel lies a nesting chamber, which is anywhere from 35 cm (Scheffer, 1940) to 96 cm below the surface and is slightly expanded (Smith, 1948).

#### DESCRIPTION AND IDENTIFICATION OF BURROWS

Ancient burrows in the Nebraska Sand Hills are concentrated near paleosols (Fig. 4A), which are rarely exposed in the Sand Hills. The paleosols are structureless, indicating complete mixing. Burrows that are distributed across the boundary between the paleosol and overlying eolian sand are easily visible owing to contrasts in color between the fill and the matrix. The upper surface of the paleosol is typically uneven and wavy across our sections, with burrows appearing in both units. Very few to no burrows are seen in areas where the paleosol is not visible. Burrows are most common at Yao's Blowout but are similar in size and morphology at all localities. At Mick's Slide, the paleosol is more mottled in color, and the boundary with the overlying dune sand is significantly more irregular. Burrows at Kroeger Blowout extend higher up into the overlying eolian sand than at the other sites.

Burrows are clustered in areas of low-angle bedding of the overlying eolian sand, near the plinth and interdunes (Figs. 4A–B). Some of these areas are so heavily bioturbated that it is difficult to identify individual burrows. Burrows are much less common in areas of steeply inclined bedding, below the crests of the dunes (Fig. 4C). The majority of the burrows are clustered near the paleosol–eolian sand boundary, with very few burrows occurring near the tops of the dunes and very few occurring low in the paleosol. Still, many burrows with dark fill occur at a great height in the dune,  $\leq 1.36$  m above the boundary between the

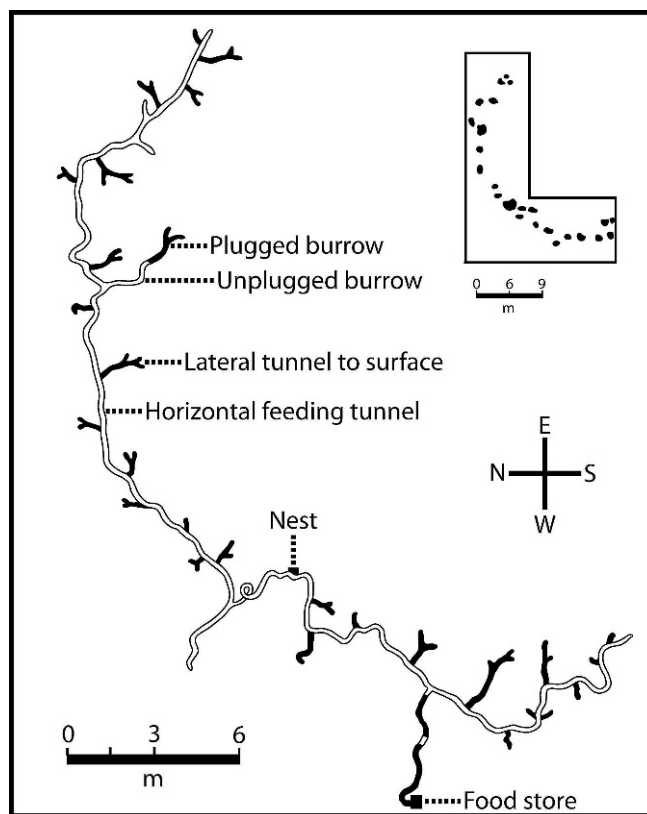


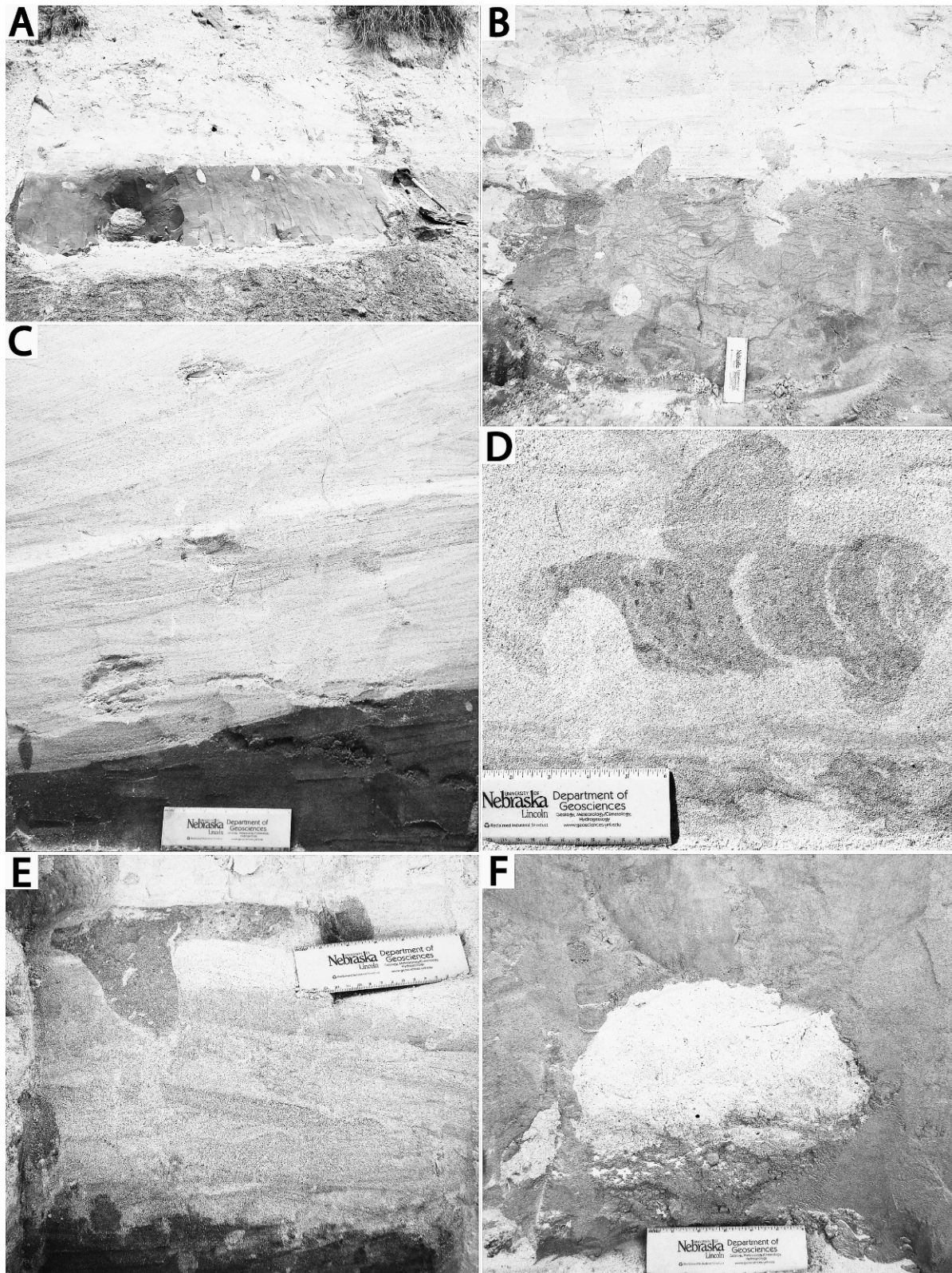
FIGURE 3—Plan view of a tunnel system of a plains pocket gopher (*Geomys bursarius*; after Smith, 1948). Tunnels with black shading are those plugged by the animal, tunnels with no fill are open. Inset shows the interpreted position of mounds as would be seen on the surface directly above the burrow system. Each mound correlates with a lateral tunnel leading to the surface, each of which was backfilled by the animal.

paleosol and eolian sand. More burrows are present along the northern side of Yao's Blowout, the side that is closest to the interdune, and away from the crest of the megadune. Burrow fills vary in color. Some burrows in the eolian sand have fill the same color as the surrounding sand, but most contain dark fill, matching the color of the underlying paleosol. Burrows in the dark material also have fill of both eolian sand and paleosol. A few of the tunnels in the dune sand are lined with darker material along the sides and bottoms of the tunnels.

The diameters of the tunnels are very consistent throughout the study area, indicating they were made by the same species. The burrows are nearly circular to slightly flattened in cross section, and the average minimum width is 6.5 cm. The angle of the lateral tunnels varies greatly, from ~30° to 70°. Grain size of the fill in the burrows ranges from fine to medium sand, with 75% of the burrow fills at least somewhat brecciated in appearance. Brecciated fills with meniscate structure consist of dark sand grains that are clumped and indicate active backfilling of loose, excavated soil by the burrower (Fig. 4D). The majority (82%) of the burrows described had relatively even edges, indicating that claw or tooth markings were either not present or were not preserved in most cases.

Orientation could not be determined for some of the tunnels. Both horizontal (Fig. 4D) and lateral tunnels were encountered, with lateral tunnels somewhat more prevalent (59% of the tunnels encountered). In some cases, lateral tunnels were recognized as joining with horizontal tunnels, indicating both tunnel types were part of the same network. In one instance, a possible spoil pile was discovered at the top of a lateral tunnel (Fig. 4E). The spoil pile extended horizontally away from the lateral tunnel and had a flat base parallel to the dominant bedding with a wavy upper margin. A possible nesting chamber was discovered in the





**FIGURE 4**—Photographs of pocket gopher burrows in the Nebraska Sand Hills. Ruler in B–F = 15 cm. A) Cutaway of the surface of the northeastern end of Yao's Blowout site showing the boundary between the underlying paleosol and overlying eolian sand (shovels = 1.0 m tall). Tunnels filled with lighter material may indicate necessary deposition by the animal during the process of digging through the eolian sand on their way to the surface. Tunnels filled with dark material likely indicate plugging of the lateral tunnels with excavated material from the paleosol as a measure of safety from predators. B) Close-up of gopher burrows along the paleosol–eolian sand boundary. C) Paleosol–eolian sand boundary near the center of the superimposed dune cut by Yao's Blowout. Note the wind-ripple lamination and distinct lack of bioturbation. D) Close-up of three horizontal burrows in eolian sand at Mick's Slide. Two tunnels are viewed in cross section, while the third is a longitudinal section. Backfilling by the animal is visible in this view, revealing a meniscate morphology and brecciated sediment that is mainly dark in color. E) Possible spoil pile (horizontal dark sand near the top of the photograph) and adjoining lateral tunnel (elongated dark oval reaching below the horizontal pile) directly above the paleosol–eolian sand boundary at Yao's Blowout. F) Possible gopher nest in the paleosol at Yao's Blowout.



paleosol at Yao's Blowout filled with light, unbedded eolian sand (Fig. 4F). The nesting chamber was 27 cm wide and 13 cm high and was 29 cm below the boundary between the paleosol and eolian sand. Further excavation revealed a single horizontal tunnel with a width of 8 cm and height of 7 cm extending into the hillside.

The identity of the medieval burrowers can be determined by comparing these ancient burrows with those of modern mammalian burrowers in the same region. Modern burrowers that inhabit the Nebraska Sand Hills include the plains pocket mouse, the hispid pocket mouse, Ord's kangaroo rat, and the plains pocket gopher. The plains pocket mouse (*Perognathus flavescens*) and the hispid pocket mouse (*P. hispidus*) are both present in sandy soils within the Nebraska Sand Hills (Jones et al., 1985) but are too small to have produced the burrows recognized in this study. Fossil pocket-mouse burrows in northeastern Nebraska are only 2–3 cm in diameter (Voorhies, 1974), as opposed to an average diameter of 6.5 cm in this study. Additionally, pocket mice produce straight, vertical burrows (Voorhies, 1974), which conflict with the more complex morphology of the ancient Sand Hills burrows. Ord's kangaroo rat is also an unlikely animal for the ancient Sand Hills burrows owing to the morphology of the burrow systems. Fossil kangaroo rat burrows from northeastern Nebraska are nearly circular, tubular burrows with a deep nest (Voorhies, 1975).

The plains pocket gopher (*G. bursarius*) is the most likely animal responsible for the ancient Sand Hills burrows. *Geomys bursarius* is currently common in sandy soils throughout Nebraska, including the Sand Hills (Jones, 1964; Jones et al., 1985; Freeman, 1998). A fossil skull of *G. bursarius* (age unknown) has also been identified from Nebraska, in loess or yellow marl along the Missouri River (Leidy, 1867). The diameter of modern pocket-gopher burrows is ~7–8 cm (Scheffer, 1940; Smith, 1948; Best, 1973; Wilkins and Roberts, 2007), while the average diameter of the ancient Sand Hills burrows is only slightly less. While studying the surface of a blowout in the Sand Hills, we observed a pocket gopher depositing soil onto the land surface (Fig. 2). The gopher left a tunnel measuring 7 cm high and 6 cm wide, a size consistent with that of the ancient burrows. While we were unable to excavate a complete ancient burrow system, the morphology of these tunnels is very similar to those of modern pocket gophers (Fig. 3), with a network of horizontal tunnels connected to lateral tunnels and deeper nesting areas (Scheffer, 1940; Smith, 1948; Andersen, 1987). One major difference between the modern and ancient burrows is the depth of the tunnel systems. Modern pocket-gopher burrow systems are typically <25 cm below the surface (Scheffer, 1940). Many of the dark-sediment-filled burrows are present at great heights above the boundary with the paleosol, the source for the burrow fill. The greatest height measured was 1.36 m, indicating a significant difference in burrowing activity, likely caused by differences in the location of available food.

## DISCUSSION

The pocket-gopher burrows recognized in this study were excavated during a climatic transition known as the Medieval Climatic Anomaly. During this period, the dunes in the Nebraska Sand Hills transitioned from being fully covered with vegetation and stabilized to being nearly or fully clear of vegetation and remobilized. Study of the burrows across this time period provides a clearer understanding of the transition as well as a greater understanding of the behavior of these fossorial animals during times of dune instability.

Burrowing is a costly lifestyle in terms of energy usage. Compared to foraging at the surface, greater amounts of energy are used during excavating and when pushing soil against gravity to plug old tunnels. Based on modeling, the cost of burrowing is 360–3400 times more than moving the same distance across the surface (Vleck, 1981). Pocket gophers are able to maximize the net energy gain for each section of soil excavated by keeping the tunnel radius and length as small as possible (Andersen, 1982). Additionally, pocket gophers fully exploit each food

source they encounter, an energy-efficient behavior (Vleck, 1981). The length of the ancient tunnels was likely kept to an absolute minimum, particularly during times of stress, such as when the animals had to burrow further upward to reach the surface.

Burrowing at greater heights above the food source than normal greatly increases the amount of energy used by the animal. The gophers likely tried to deposit as much excavated soil below ground as possible because of the massive energy requirement (Sparks and Andersen, 1988) to build lateral tunnels and push soil up to the rising dune surface. The gophers could not deposit all of their excavated soil below ground, however, given the increased volume of excavated soil compared to *in situ* soil, therefore they were forced to dig some lateral tunnels to the surface to backfill sediment. One way to minimize the energy used to dig such long lateral tunnels is to optimize the length of horizontal tunnel segments between the lateral tunnels. A length of 1.22 m is optimal for gophers burrowing at a depth of 27 cm (Vleck, 1981), but it is difficult to determine the optimal length of tunnel segments at a depth of >1 m. Building short segments between lateral tunnels uses more energy as greater volumes of soil are excavated as the frequency of laterals increases (Vleck, 1981). It seems more likely that in order to maximize energy gain while burrowing at such great depths, the gophers would create longer segments and therefore fewer tunnels to the surface. Each tunnel to the surface would be a massive effort with no energy gain, while horizontal networks provided opportunity for food intake. The ancient gophers also made steeply inclined lateral tunnels, made possible by the cohesiveness of the sand in the Sand Hills. The greater the incline on the lateral tunnels, the shorter they can be, and therefore less energy must be used (Vleck, 1981). In fact, nearly vertical tunnels created in strongly cohesive soil by one species of pocket gopher, *Thomomys*, diminishes the energy used by 30% (Vleck, 1981).

Times of food scarcity, as occurred during the Medieval Climatic Anomaly in the Nebraska Sand Hills, have a drastic effect on the burrowing behavior of pocket gophers. In experiments conducted in areas where food is scarce, pocket gophers spent more time foraging above ground, typically at night (Andersen, 1987). This may have been a good strategy for the pocket gophers during the initial stages of reactivation, but it would have proved fruitless as sand built up, covering the tops of the vegetation. At this point, the gophers likely foraged below ground using an area-restricted search, which conserves energy in areas of low food supply by decreasing the overall linearity of the burrow system and increasing the number or angle of directional changes (Benedix, 1993). This foraging pattern works best in areas of clustered resources (Benedix, 1993) and would have been ideal for pocket gophers foraging at times of vegetative loss in the Nebraska Sand Hills.

Soil-carbon flux (i.e., soil respiration) is an indicator of below-ground biological activity by autotrophs (i.e., respiration by living plant roots) and heterotrophs, which include bacteria, fungi, and soil invertebrates using detritus and soil organic matter as energy sources (Ryan and Law, 2005). Following the death of the vegetation, soil carbon flux dropped by 20%–30% within weeks in the press plots in the Nebraska Sand Hills, reflecting the loss of respiration by living plant roots (Fig. 5). The press plots continued, however, to have ~40% of the soil respiration observed in control plots through the third year of the study and ~25% in the fourth year. Thus, considerable below-ground biological activity persisted in these sand dune soils for at least 4 years following an extreme experimental disturbance. This has implications for the persistence of roots, plant detritus, and soil invertebrates beneath the dunes of the Nebraska Sand Hills during times of drought. Presumably, during the onset of a drought, vegetation would not be killed nearly as thoroughly or as quickly as occurred in our press treatment. The soil-carbon flux data indicate that organic material was likely still present beneath the surface of the sand dunes for several years after the vegetation perished on upland sites. Therefore a food source could have been present for the pocket gophers for several years after the transition to an active dune field was locally complete.

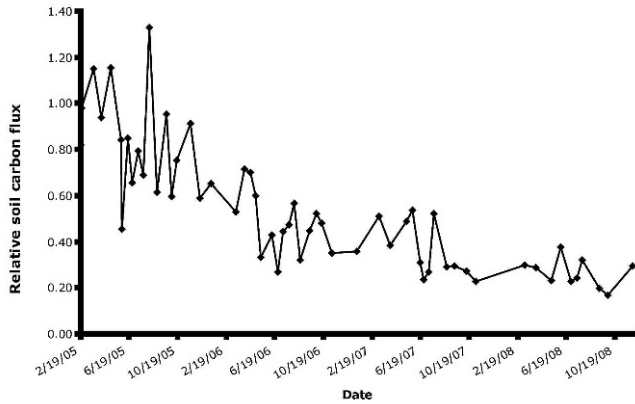


FIGURE 5—Bivariate fit of relative soil-carbon flux given as a ratio between a control plot (kept ungrazed) and a press plot (vegetation killed with herbicide in May 2005 and kept dead since then) in the Nebraska Sand Hills.

Hand augering through interdune sediments revealed the presence of a paleosol directly north of Yao's Blowout, but only light-colored eolian sediments were encountered in auger holes to the northwest and to the southeast of the blowout, on either side of the dune. Optically stimulated luminescence samples collected from the light-colored sediments provide the burial age of the sediment or the last time the grains were exposed to light (Table 1). To the southeast, where no paleosol was encountered, the ages are extremely old ( $12,900 \pm 788$  years and  $14,500 \pm 885$  years; see Table 1 and Fig. 6), indicating that the paleosol was eroded from the interdune and that little to no deposition occurred in the interdunes during the most recent reactivation during the Medieval Climatic Anomaly. To the northwest, on the other side of the linear dune, light-colored eolian sand is also much older than the dune itself ( $4,450 \pm 229$  years; see Table 1 and Fig. 6), which supports the hypothesis that the paleosol was eroded during the most recent reactivation. Sediments from the interdune areas were likely providing sediment to the superimposed linear dunes during the reactivation, as suggested in one model for the formation of linear dunes (Pye and Tsoar, 1990). The other model suggested by Pye and Tsoar (1990) allows for the extension of linear dunes by sand coming from upwind while the interdunes remain completely vegetated. Our OSL ages contradict this model because they indicate erosion of the interdune areas. It is still possible and likely that vegetation persisted in lower interdune regions for a short time as aridity increased because abundant pocket-gopher burrows in these areas suggest a remaining source of food. The eventual removal of the vegetation from the interdune, however, ultimately allowed for complete erosion of any soil and transport of these sediments up onto the growing linear dunes.

#### SEQUENCE OF EVENTS

The following is an interpretation of the sequence of events that occurred during the transition from stabilized to active dunes during the last reactivation in the Nebraska Sand Hills (A.D. ~900–1300):

1. Slightly more than 1000 years ago, the dunes were fully stabilized, with prairie grasses and other types of vegetation covering their surfaces

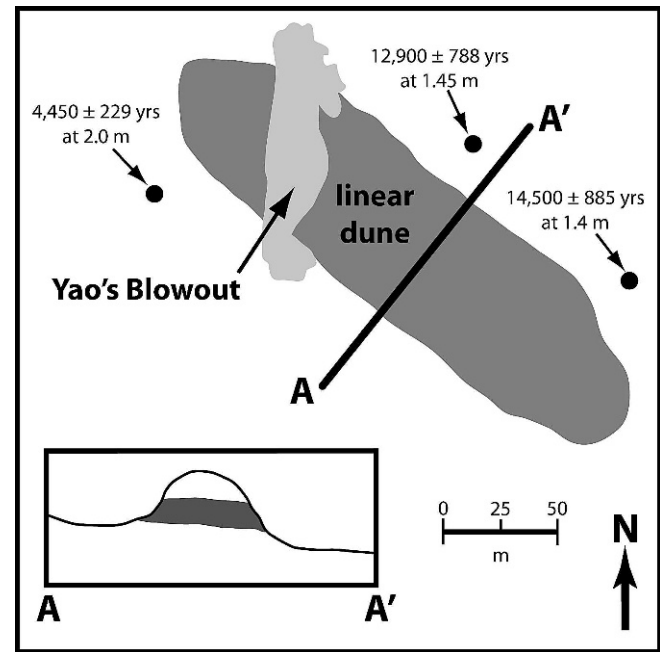


FIGURE 6—Optically stimulated luminescence dates from interdune sediments surrounding the superimposed linear dune (darker shading) cut by Yao's Blowout (lighter shading). Black circles represent locations of auger holes from which samples were taken. Inset shows hypothesized cross section of the linear dune with interpreted location of paleosol (dark shading; eroded and missing from interdune).

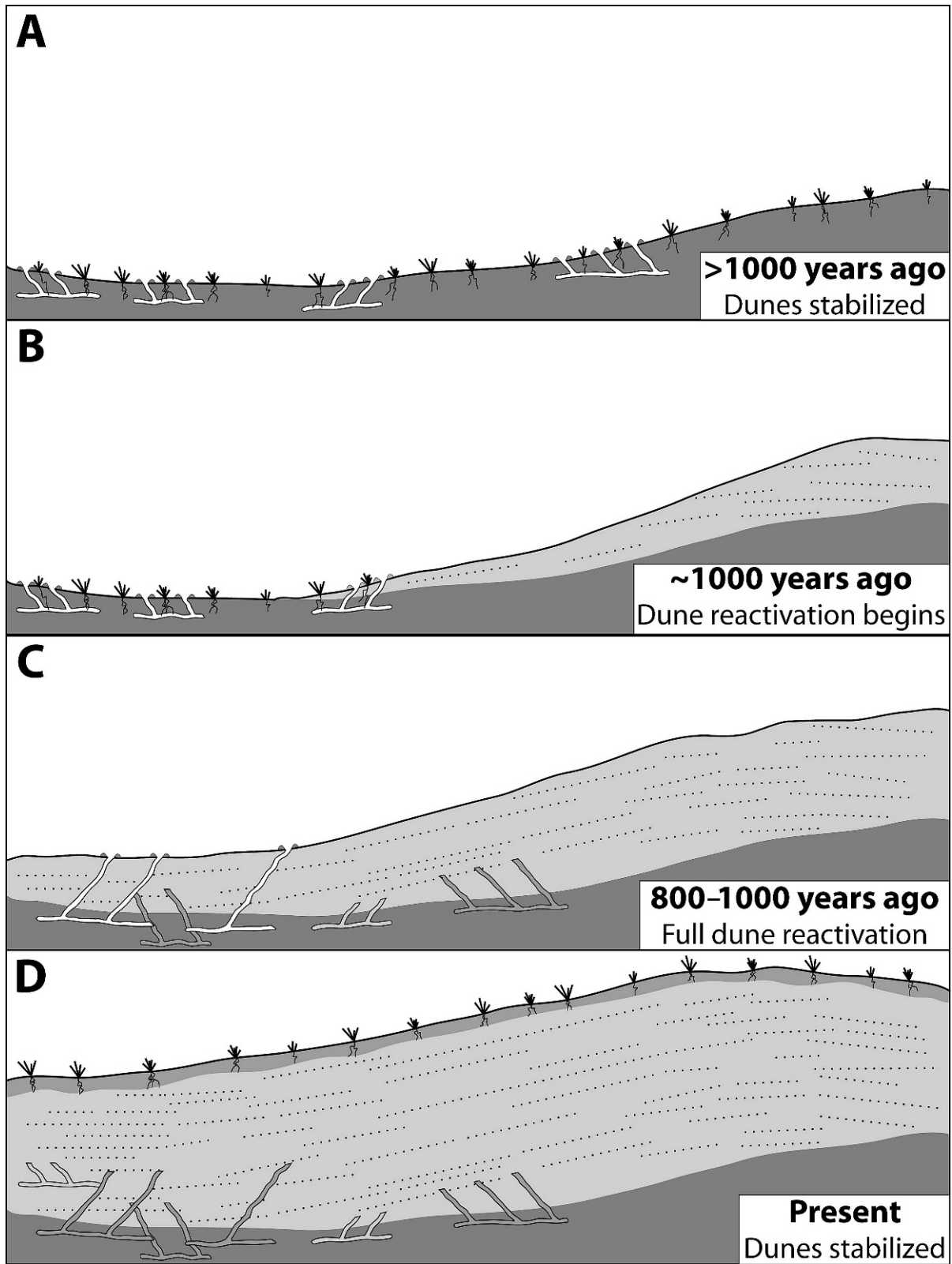
(Fig. 7A), not unlike the modern scenario. Pocket gophers burrowed beneath the entire land surface, with the roots of the vegetation providing an ample food supply. Mounds from the gopher burrow systems dotted the land surface, dark in color to match that of the soil the gophers were excavating.

2. Approximately 1000 years ago, the climate began to shift to a much drier condition, and vegetation began to disappear from the land surface (Fig. 7B). As vegetation thinned, sand was free to shift and began to build up into new dunes that covered broad areas. The pocket gophers were still able to survive in some areas, feeding on the roots of any remaining vegetation. In areas of sand accumulation, this required burrowing upward to greater heights than normal to reach the surface and deposit soil removed during the excavation of the burrows. In areas of patchy vegetation (small interdune regions), gophers were still able to deposit soil mounds on the surface. Gopher populations became concentrated in areas where vegetation remained and where the soil had not yet been eroded or deeply buried.

3. About 1000–800 years ago, during the middle of the Medieval Climatic Anomaly, the vegetation cover and much of the soil was completely removed from the upland regions (Fig. 7C). Small, superimposed dunes were fully formed on top of larger megadunes. Soil that was buried beneath the superimposed dunes was the only soil to escape erosion. Initially, gophers were still able to survive by using any remaining plant material from the now-buried soil below the sand. This required a huge expenditure of energy as the gophers had to burrow significantly higher to deposit their mounds and bring fresh air to their burrow systems. Gopher populations were concentrated in

TABLE 1—Data for optically stimulated luminescence samples taken from interdune sediments surrounding a small, superimposed linear dune in the Nebraska Sand Hills.

Field Sample #	UNL Sample #	Depth (m)	<i>In situ</i> moisture content (%)	K <sub>2</sub> O (%)	Th (ppm)	U (ppm)	D <sub>total</sub> (Gya-1 × 10 <sup>3</sup> )	D <sub>e</sub> (Gy ± 1σ)	Aliquots (n)	Age (a ± 1σ)
RLS08-4	2344	2.00	4.1	2.01	3.6	1.0	2.25 ± 0.08	10.0 ± 0.23	28	4450 ± 229
RLS08-6	2345	1.45	2.7	2.19	3.9	0.9	2.44 ± 0.08	31.6 ± 1.26	28	12,900 ± 788
RLS08-7	2346	1.40	6.3	1.93	4.0	1.1	2.19 ± 0.08	31.7 ± 1.26	25	14,500 ± 885



**FIGURE 7**—Interpretation of formation of superimposed dune and pocket-gopher burrows at Yao's Blowout. Burrows not to scale. A) Surface of the megadune during a stable period (gray shading = thick, bioturbated A soil horizon). No filled burrows are visible because all available sand is the same (dark) color. B) Sand movement and removal of vegetation began ~1,000 years ago, with a superimposed dune beginning to form. C) Between 800 and 1,000 years ago, a full superimposed dune (light gray) has formed over the surface of the megadune with the soil now buried (dark gray) and no vegetation. Newly deposited sand is lighter than the underlying material because saltation transport has removed the organic coatings. Gophers filled some lateral tunnels within the light-colored dune sand with dark soil (storage of spoil from extension of horizontal feeding tunnels). The gophers filled other burrows with dune sand to store spoil from new, very long laterals. Dark-filled burrows indicate fill of the underlying soil; light-filled burrows indicate fill of the surrounding eolian sediment. D) The modern setting, with restabilization and formation of a modern soil covering the superimposed dune and buried gopher burrows.



areas with the thinnest accumulation of sand, typically under the plinths and small interdunes, areas of low-angle bedding. Long lateral burrows were filled with the underlying darker material; the gophers brought it up to the surface to deposit mounds and then plugged the tunnel with the same dark material. Many tunnels within the dark paleosol were filled with lighter material while the long lateral tunnels were being excavated. Areas with higher sand accumulation, near the center of the superimposed dunes, were not populated by gophers owing to the severe energy requirements of burrowing through the huge thickness of sand.

4. Eventually, as sand continued to accumulate over the upland regions and the underlying plant material remaining in the buried soil decayed, gopher populations were forced to abandon the megadunes. These gopher populations may have migrated to areas between the larger megadunes, where water and vegetation seem to have been present throughout the period of reactivation (Loope, 1986). Finally, ~800 years ago, moist conditions returned to this part of the Nebraska Sand Hills, allowing vegetation to restabilize the upland regions and a thin modern soil to form (Fig. 7D). Gopher populations reinhabited the region, as clearly evidenced by the large number of gopher mounds that can be seen on the surface throughout the Sand Hills today.

### CONCLUSIONS

The precise conditions of the transition from stabilized to destabilized dunes in the Nebraska Sand Hills are difficult to quantify, but it is clear that these dunes represent a period of abrupt climate change. Examining the activities of animals during this transitional period provides information about where and when vegetation was lost. Bison tracks present in dune sediments along the eastern margin of the Sand Hills indicate that the bison may have been traveling across the dunes during times of drought in search of food and water (Loope, 1986). Loope (1986) suggested that the lowest interdunes likely supplied sufficient water and vegetation to sustain bison herds during times of drought.

In this study we used gopher burrows to determine that vegetation was lost progressively on the dunes of the Sand Hills during the Medieval Climatic Anomaly, A.D. ~900 to 1300 (Fig. 7). Although OSL dating provides very accurate ages and excellent resolution, the dunes were deposited too quickly to determine the precise timing of vegetation loss over the region. Prior to the transition, the Sand Hills were a thriving prairie ecosystem, with abundant vegetation and other animal life, not unlike the present environment. As the region became drier, vegetation gradually disappeared from the land surface. In the study area (the northwestern part of the dune field), burrowing activity ceased near the crests of the superimposed dunes but persisted longer on the plinths and interdunes between the superimposed dunes. Gophers were able to briefly survive on buried plant material but eventually migrated out of the upland portions of the region or perished. Eventually, all vegetation was lost on the superimposed dunes but likely remained in the large interdunes between the megadunes (Loope, 1986). In the southeastern part of the dune field, the lack of paleosols and burrows suggests that vegetation was lost completely across the dunes and interdunes.

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### REFERENCES

- AHLBRANDT, T.S., and FRYBERGER, S.G., 1980, Eolian deposits in the Nebraska Sand Hills: U.S. Geological Survey Professional Paper no. 1120A, p. 1–24.
- ANDERSEN, D.C., 1982, Belowground herbivory: The adaptive geometry of geomyid burrows: *American Naturalist*, v. 119, p. 18–28.
- ANDERSEN, D.C., 1987, *Geomys bursarius* burrowing patterns: Influence of season and food patch structure: *Ecology*, v. 68, p. 1306–1318.
- ANDERSEN, D.C., 1988, Tunnel-construction methods and foraging path of a fossorial herbivore, *Geomys bursarius*: *Journal of Mammalogy*, v. 69, p. 565–582.
- BENEDIX, J.H., 1993, Area-restricted search by the plains pocket gopher (*Geomys bursarius*) in tallgrass prairie habitat: *Behavioral Ecology*, v. 4, p. 318–324.
- BEST, T.L., 1973, Ecological separation of three genera of pocket gophers (Geomyidae): *Ecology*, v. 54, p. 1311–1319.
- BRECKENRIDGE, W.J., 1929, Actions of the pocket gopher (*Geomys bursarius*): *Journal of Mammalogy*, v. 10, p. 336–339.
- DAVIS, W.B., 1940, Distribution and variation of pocket gophers (Genus *Geomys*) in the southwestern United States: *Texas Agricultural Experiment Station*, v. 590, p. 1–38.
- FREEMAN, P.W., 1998, Mammals (of the Sand Hills), in Bleed, A.S., and Flowerday, C.A., eds., *An Atlas of the Sand Hills*: University of Nebraska–Lincoln, Lincoln, p. 193–200.
- GOBLE, R.J., MASON, J.A., LOOPE, D.B., and SWINEHART, J.B., 2004, Optical and radiocarbon ages of stacked paleosols and dune sands in the Nebraska Sand Hills, USA: *Quaternary Science Reviews*, v. 23, p. 1173–1182.
- HALL, E.R., 1981, *The Mammals of North America*: John Wiley & Sons, New York, 546 p.
- HOFFMAN, J.D., CHOATE, J.R., and CHANNELL, R., 2007, Effects of land use and soil texture on distributions of pocket gophers in Kansas: *Southwestern Naturalist*, v. 52, p. 296–301.
- HOWARD, J.D., 1975, The sedimentological significance of trace fossils, in Frey, R.W., ed., *The Study of Trace Fossils*: Springer-Verlag, New York, p. 131–146.
- HUNTLY, N., and INOUE, R., 1988, Pocket gophers in ecosystems: Patterns and mechanisms: *Bioscience*, v. 38, p. 786–793.
- JONES, J.K., 1964, *Distribution and Taxonomy of Mammals of Nebraska*: University of Kansas Publications, Museum of Natural History, Lawrence, 356 p.
- JONES, J.K., ARMSTRONG, D.M., and CHOATE, J.R., 1985, *Guide to Mammals of the Plains States*: University of Nebraska Press, Lincoln, Nebraska, 371 p.
- KENNERLY, T.E., 1964, Microenvironmental conditions of the pocket gopher burrow: *Texas Journal of Science*, v. 16, p. 395–441.
- LEIDY, J., 1867, Remarks on a fossil skull of *Geomys bursarius* from the loess of Nebraska: *Proceedings of the Academy of Natural Sciences of Philadelphia*, v. 19, p. 97.
- LESSA, E.P., and THAELE, C.S., 1989, A reassessment of morphological specializations for digging in pocket gophers: *Journal of Mammalogy*, v. 70, p. 689–700.
- LOOPE, D.B., 1986, Recognizing and utilizing vertebrate tracks in cross section: Cenozoic hoofprints from Nebraska: *PALAIOS*, p. 141–151.
- LOOPE, D.B., and SWINEHART, J.B., 2000, Thinking like a dune field: Geologic history in the Nebraska Sand Hills: *Great Plains Research*, v. 10, p. 5–35.
- MIAO, X., MASON, J.A., SWINEHART, J.B., LOOPE, D.B., HANSON, P.R., GOBLE, R.J., and LIU, X., 2007, A 10,000 year record of dune activity, dust storms, and severe drought in the central Great Plains: *Geology*, v. 35, p. 119–122.
- MURRAY, A.S., and WINTLE, A.G., 2000, Luminescence dating of quartz using an improved single-aliquot regenerative-dose protocol: *Radiation Measurements*, v. 32, p. 57–73.
- PYE, K., and TSOAR, H., 1990, *Aeolian Sand and Sand Dunes*: Unwin Hyman, London, 458 p.
- RYAN, M.G., and LAW, B.E., 2005, Interpreting, measuring, and modeling soil respiration: *Biogeochemistry*, v. 73, p. 3–27.
- SCHAEFFER, T.H., 1940, Excavation of a runway of the pocket gopher (*Geomys bursarius*): *Transactions of the Kansas Academy of Science Transactions*, v. 43, p. 473–478.
- SMITH, C.F., 1948, A burrow of the pocket gopher (*Geomys bursarius*) in eastern Kansas: *Transactions of the Kansas Academy of Science Transactions*, v. 51, p. 313–315.
- SPARKS, D.W., and ANDERSEN, D.C., 1988, The relationship between habitat quality and mound building by a fossorial rodent, *Geomys bursarius*: *Journal of Mammalogy*, v. 69, p. 583–587.
- STOKES, S., and SWINEHART, J.B., 1997, Middle- and late-Holocene dune reactivation in the Nebraska Sand Hills, USA: *Holocene*, v. 7, p. 263–272.

- SWINEHART, J.B., 1998, Wind-blown deposits, in Bleed, A.S., and Flowerday, C.A., eds., *An Atlas of the Sand Hills*: University of Nebraska–Lincoln, Lincoln, p. 43–56.
- THORNE, D.H., and ANDERSEN, D.C., 1990, Long-term soil-disturbance pattern by a pocket gopher, *Geomys bursarius*: *Journal of Mammalogy*, v. 71, p. 84–89.
- VAUGHAN, T.A., and HANSEN, R.M., 1961, Activity rhythm of the plains pocket gopher: *Journal of Mammalogy*, v. 42, p. 541–543.
- VLECK, D., 1981, Burrow structure and foraging costs in the fossorial rodent, *Thomomys bottae*: *Oecologia*, v. 49, p. 391–396.
- VOORHIES, M.R., 1974, Fossil pocket mouse burrows in Nebraska: *American Midland Naturalist*, v. 91, p. 492–498.
- VOORHIES, M.R., 1975, A new genus and species of fossil kangaroo rat and its burrow: *Journal of Mammalogy*, v. 56, p. 160–176.
- WANG, T., ZLOTNIK, V.A., WEDIN, D., and WALLY, K.D., 2008, Spatial trends in saturated hydraulic conductivity of vegetated dunes in the Nebraska Sand Hills: Effects of depth and topography: *Journal of Hydrology*, v. 349, p. 88–97.
- WERNER, S.J., NOLTE, D.L., and PROVENZA, F.D., 2005, Proximal cues of pocket gopher burrow plugging behavior: Influence of light, burrow openings, and temperature: *Physiology and Behavior*, v. 85, p. 340–345.
- WILKINS, K.T., and ROBERTS, H.R., 2007, Comparative analysis of burrow systems of seven species of pocket gophers (Rodentia: Geomyidae): *Southwestern Naturalist*, v. 52, p. 83–88.
- WINSPEAR, N.R., and PYE, K., 1995, The origin and significance of boxwork clay coatings on dune sand grains from the Nebraska Sand Hills, USA: *Sedimentary Geology*, v. 94, p. 245–254.

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