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FORM OF MIMA MOUNDS IN RELATION TO OCCUPANCY BY POCKET GOPHERS

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Mima mounds are widespread west of the Mississippi River from southern British Columbia, Canada, to northern Sonora, Mexico (Cox, 1984). These mounds, formed of soil and small stones ≤ 50 mm in maximum diameter, commonly reach heights of 2 m, diameters of 20 m, and densities of 25-50/ha (Cox and Gakahu, 1986).

Much of the Columbia Plateau of eastern Washington, northeastern Oregon, and southwestern Idaho is covered by Mima-mounded grassland. The mounds and intermound areas differ markedly in vegetation. Deeper silt-loam soils of the mounds are dominated by grassland species such as *Agropyron spicatum* and *Festuca idahoensis*, and shallow intermound soils by an *Artemisia rigida*-*Poa secunda* association (Dauenbire, 1970; Winward and Youtie, 1978).

Investigations of Mima mounds in western North America support the hypothesis that mounds are formed by the gradual translocation of soil by pocket gophers (Rodentia: Geomyidae) toward deep, well-drained microsites (Cox and Gakahu, 1986; Cox et al., 1987). Pocket gophers center their activities and locate their nests in such microsites. Moundward translocation results from the backward displacement of soil that occurs during outward tunneling from activity centers. Tunneling into intermound areas leads to translocation of soil from intermound areas to mounds, thus maintaining the thin soils of the intermounds.

Several studies of occupancy of mounds by pocket gophers indicate that a mound typically is occupied by one animal. Dalquest and Scheffer (1942) noted that the mounds at Mima Prairie, Washington, were spaced similarly to territories of pocket gophers on deep-soil, unmounded sites. R. M. Hansen (Scheffer, 1958) trapped only single gophers, or single adults plus one subadult, on individual Mima mounds at Black Mesa, Colorado, suggesting that the mounds tended to be territories of single pocket gophers. Hansen and Miller (1959) recorded plural occupancy of some mounds in early summer, when animals were breeding and when territories were weakly defended. From studies at Black Mesa, Hansen (1962) concluded that each mound tended to be a territory of one adult gopher. He noted that two adults rarely were found in single mounds during late summer and that two animals never were found on small mounds surrounded by stony intermound zones. From observations of mounds at Rocky Flats, Colorado, Murray (1967) also suggested that mounds were territories of single pocket gophers.

Studies of composition and form of Mima mounds in north-central Oregon (Cox et al., 1987) showed that these mounds vary from a few meters to >30 m in diameter. In addition, large mounds often show widely separated areas of digging activity of pocket gophers, suggesting that more than one territory is present. These observations led us to investigate the occupancy of mounds to determine how numbers of individuals of different sex and age vary with mound size. In addition, we examined the pattern of variation in cross-sectional form of mounds with mound size and animal occupancy to ascertain how mound development might be influenced by plural occupancy.

Studies were conducted at the Lawrence Memorial Grassland Preserve and on adjacent ranchland, southern Wasco Co., Oregon (44°57'N, 120°48'W), 15-23 June 1988. This site is representative of mounded grasslands of the Columbia Plateau region of northern Oregon and eastern Washington. The preserve lies at elevations of 1,036-1,060 m on the Shaniko Plateau and has a cold semidesert climate, with an average annual precipitation of 280 mm. The surface of the plateau is mounded scabland with Mima mounds that range to about 1 m in height and >30 m in diameter. Mound soils are "Condon eolian silt loams," whereas intermound soils are "Bakeoven residual very cobbly loams" (Green, 1970:8-10). The vegetation of mounds and deeper upland soils is dominated by Idaho fescue (*Festuca idahoensis*) and bluebunch wheatgrass (*Agropyron spicatum*). Shallow intermound soils are dominated by scabland sagebrush (*Artemisia rigida*), Sandberg bluegrass (*Poa scabrella*), several species of biscuitroot (*Lomatium* sp.), and bitterroot (*Lewisia rediviva*). The northern pocket gopher (*Thomomys talpoides*) is abundant throughout the preserve.

We selected 18 mounds for detailed sampling. We used as criteria for selection of a mound separation from neighboring mounds on all sides, location on a level to gently sloping site ($<5^\circ$), and presence of recent digging activity. We sought mounds that spanned the full range of sizes occupied by pocket gophers. Trapping

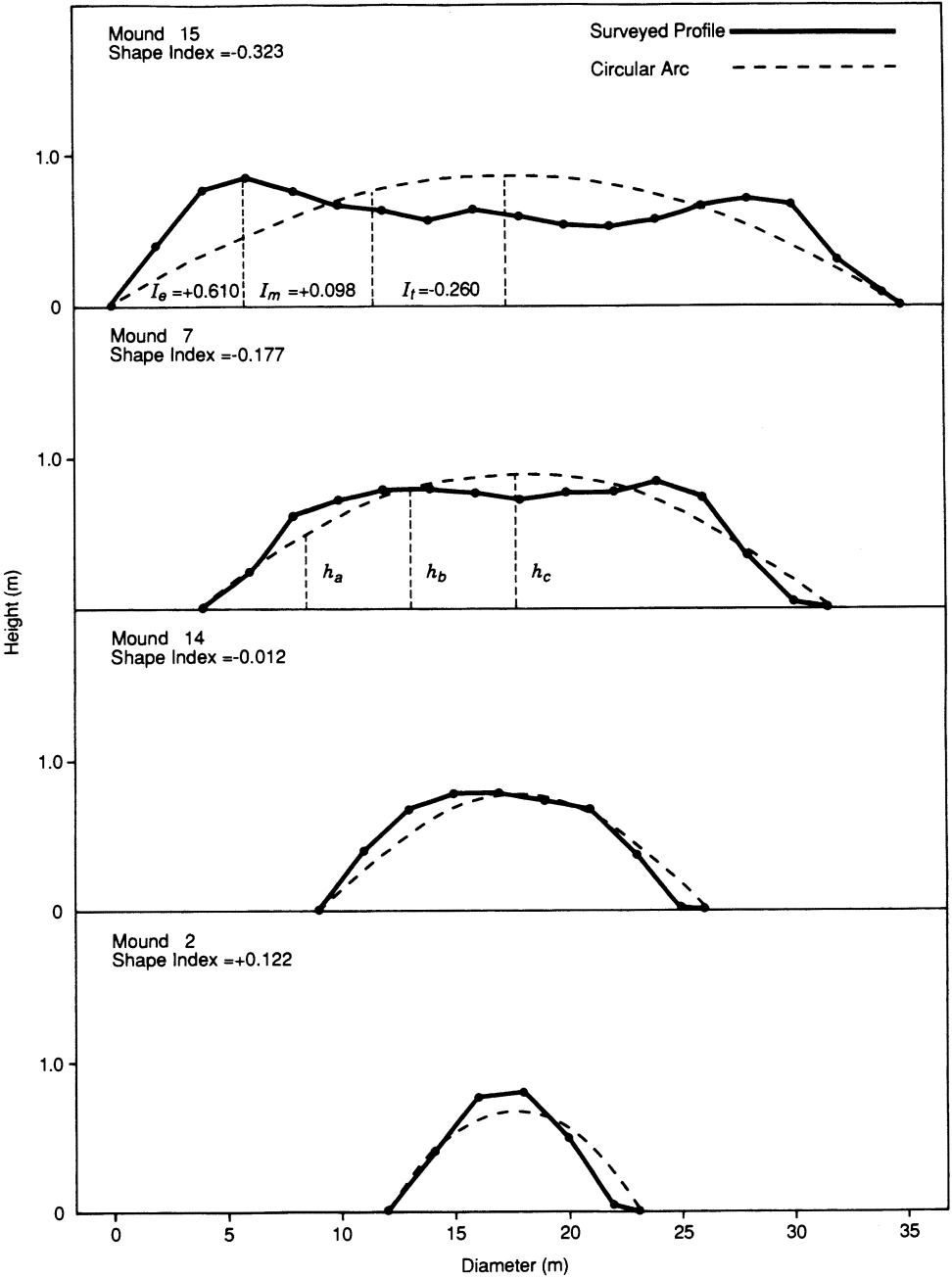


FIG. 1.—Cross-section profiles of representative *Mima* mounds at the Lawrence Memorial Grassland Preserve, Wasco Co., Oregon, compared to cross-section profiles of equal-area segments of circles.

on each mound was conducted for 3 days. Pairs of unbaited Macabee traps were placed in tunnels and examined at 24-h intervals. Animals were removed from traps and processed within 1 h of removal. Sex, age (juvenile, subadult, adult), reproductive status, and body mass were recorded for all animals captured. We examined tunnels for untrapped animals during and after the trapping period; plugged tunnels indicated the presence of one or more additional animals.

Cross-sectional profiles of the study mounds were mapped along major and minor axes of mounds. Elevations were determined at 2-m intervals (1-m intervals for mounds <10 m in diameter) along these axes with a Wild automatic level.

To describe and compare the cross-sectional profiles of mounds (Fig. 1), we first determined the cross-sectional areas of these profiles along the major and minor diameters of each mound. We computed the area below each 2-m measurement interval, using the mean of height readings at each end of the interval, and summed these values along the full diameter. We then calculated expected height measurements for the cross-sectional profiles. From the diameter and area of the measured cross-sections, height profiles of circular segments of equal area and base were computed by use of basic geometrical relationships of circles. The maximum height of the circular segment having a chord equal to the mound diameter, and an area equal to the mound cross-section, was first determined. This required iteration of the equation for the area of a segment of a circle (Hodgman, 1954:315) with trial values of maximum height, h_c . This procedure also gave the radius, r , of the circle represented by the segment. When the maximum height of the circular segment and the radius of the circle were known, heights of points on the arc of the circle at distances one-third, h_a , and two-thirds, h_b , the mound radius were calculated from relationships of chord lengths and distances from the center of the circle. The heights of comparable points on the actual mound surface were determined by interpolation of field data.

Actual and expected height measurements were used to derive indices of the heights of mound sectors as deviations from values for corresponding circular segments. Height indices were determined for the edge sector (I_e , edge to one-third radius from edge), the mid-zone (I_m , one-third radius to two-thirds radius), and the mound top (I_t , two-thirds radius to mound midpoint) for each mound. The difference between actual height (mean of values at inner and outer edges) for these sectors and that for the corresponding circular segment was determined and expressed as a fraction of the height of the circular segment; values were negative if the actual height was less and positive if greater. Sector indices were averaged for the two halves of the mound profile.

An index of overall mound shape was determined by combining sector indices into a single index. This index was designed to range from positive values, when a mound was more peaked in the center and lower at the edges than a circular segment, to negative values, when the mound was flatter than a circular segment. This index was calculated by the equation:

$$\text{Shape Index} = [(\text{Top Index}) - (\text{Mid-zone Index}) - (\text{Edge Index})] / 3 \quad (1)$$

A strongly peaked mound, with a positive top index and negative mid-zone and edge indices thus yielded a sum of three positive values, which were averaged to yield the shape index. A highly flattened mound, with a negative top index and positive mid-zone and edge indices similarly yielded a sum of three negative values, and a negative average. Mathematically, this index can vary between +1.0 and -1.0, but geomorphic possibilities place constraints that make it almost impossible to obtain values beyond about +0.5 and -0.5.

The 18 study mounds ranged in size from 73.0 m² to 727.7 m². We trapped 23 gophers on these mounds, and identified 19 additional areas of activity after trapped animals were removed. On two mounds no animals were captured and no activity was noted at opened tunnels. On the remaining 16 mounds, from one to six animals were present, based on animals trapped and areas of continued activity. The number of animals per mound closely correlated ($r = 0.935$, $P < 0.001$) with mound area. The mean area per animal did not change with increase in mound area. For the 16 occupied mounds, the mean area per animal was 104.65 m² ($SE = 6.68$). The number of animals occupying a mound, n , was related to the area of the mound by the regression relation:

$$n = 0.60 + 0.0071a \quad (2)$$

Adults were present on the smallest occupied mounds and on larger mounds. Adult males in breeding condition were trapped on single-animal mounds 90.7 and 100.8 m² in area. Several mounds contained more than one adult animal of the same sex; two adult males were trapped on each of two mounds. One of these mounds was estimated to contain four, and the second six, animals. One adult male and two adult females were trapped on a third mound judged to contain three animals.

No significant relationship was evident between mean body size and mound size. Animals of small to medium size were trapped on mounds of all sizes. However, the three largest males, ranging in mass from 77.5 to 89.5 g, were obtained from the three largest mounds, which ranged in area from 516.5 to 727.7 m².

All three indices of heights of sectors of mounds correlated strongly with mound diameter. The mound top index, I_t , was positive for small mounds and negative for large mounds ($r = -0.897$, $d.f. = 35$, $P < 0.001$),

ranging from +0.214 for a mound with a diameter of 10.0 m to -0.260 for a mound with a diameter of 34.7 m. The mid-zone index, I_m , was negative for small mounds and positive for large mounds. Omitting one outlying value, this index ranged from -0.055 for a mound 10.4 m in diameter to +0.132 for a mound 27.4 m in diameter ($r = 0.815$, $d.f. = 34$, $P < 0.001$). The edge index, I_e , also was negative for small and positive for large mounds, varying from -0.528 for a mound 11.6 m in diameter to 0.610 for a mound 34.7 m in diameter ($r = 0.878$, $d.f. = 35$, $P < 0.001$).

Indices of overall mound shape ranged from +0.302 to -0.323, showing that mounds develop much flatter profiles than expected with increase in size. Mound diameter correlated negatively with shape index ($r = -0.882$, $d.f. = 35$, $P < 0.001$).

Large mounds (>200 m²) were inhabited by as many as six pocket gophers. Because of the strong territoriality of pocket gophers (Hansen and Miller, 1959; Tryon, 1947), the cross-sectional form of a growing mound changes as its area increases and it becomes occupied by more than one animal. Our findings suggest the following changes in shape as mounds grow in area. As long as soil is mined and moved by a single animal, having a center of activity located near the mound center, soil translocation should be strictly centripetal, and the mound should grow in height and diameter according to a particular relationship. When a mound reaches a certain diameter, however, it becomes possible for two animals to occupy it, at least temporarily. These animals tend to locate their territories peripherally. As a consequence, soil is translocated toward the mound margin from the intermound zone, and even from the mound center, so that the mound tends to broaden and grow more slowly in height. As mound diameter increases, and the potential for occupancy by more than two animals develops, flattening is accentuated. In larger mounds, this process eventually produces a central depression from which soil has been translocated toward centers of peripherally located territories (Fig. 1).

We also suspect that this process depends on the degree to which the size of territory varies with the sex and body size of individual pocket gophers. If little variation exists, mounds may grow only to a size corresponding to the territory of a single individual. If, conversely, sizes of territories are variable, occupancy of mounds by more than one animal may occur more frequently, and the tendency of mounds to grow in diameter becomes stronger. Mounds may grow under the influence of individuals with large territories until they are vacated by death or dispersal. These mounds then may be occupied by two or more animals with small territories. Animals with small territories also may occupy mounds too small for individuals with large territories or for multiple occupancy. Thus, the potential exists for development of a mosaic of large (>200 m² in area) multianimal mounds and small single-animal mounds if the territory sizes of individuals of different sexes or body sizes vary greatly. Differences in mound size, shape, and density in different locations therefore may reflect differences in territorial behavior of the resident pocket gophers.

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CHROMOSOMES OF FIVE SPECIES OF VESPERTILIONID BATS FROM AFRICA

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Vespertilionidae, with 37 genera, is the second largest chiropteran family (Koopman, 1984a); 15 of these genera, comprising approximately 80 species, are represented in Africa (Hayman and Hill, 1971; Nowak and Paradiso, 1983). Until recently, work on African bats has been of a survey and distributional nature (Aggundey and Schlitter, 1984; Harrison, 1961; Hayman and Hill, 1971; Kingdon, 1974; Koopman, 1965, 1975; McLellan, 1986; Schlitter et al., 1982). Based on current morphological studies, presently recognized taxonomic boundaries may not be accurate in several groups (Koopman, 1984b; Robbins, 1978; Schlitter and Aggundey, 1986; Schlitter et al., 1980). Although karyological data may shed light on taxonomic relationships, such data are unavailable for most species of African bats; chromosomal studies of vespertilionid taxa mostly are restricted to Holarctic species (Bickham, 1979a; McBee et al., 1986, 1987).

Herein, we present karyotypes of five species of African vespertilionids (chromosome terminology follows that of Bickham, 1979a, 1979b). These include the first reported karyotypes for *Nycticeius schlieffenii*, *Scotophilus nux*, and *Miniopterus inflatus*. Differentially stained karyotypes are presented for *S. dinganii* and *S. nux*, showing lack of interspecific variation. Results of these investigations increase understanding of the patterns of chromosomal evolution within the Vespertilionidae.

Karyotypes from bone marrow were prepared by the methods described by Baker et al. (1982). Sterile-tissue biopsies from *Scotophilus dinganii* and *S. viridis* were taken in the field and placed in medium F-10 (KC Biological DM-322) fortified with 20% fetal bovine serum (Gibco 200-6140AJ), 1% penicillin-streptomycin (10,000 units penicillin G/ml, 10,000 µg streptomycin/ml, in normal saline; Irvine Scientific 9366), and 1% neomycin sulfate (10,000 µg/ml in normal saline; Irvine Scientific 9360). Monolayer cultures were established in the laboratory, harvested, and karyotypes prepared (Baker et al., 1982). G-bands were produced with the technique of Seabright (1971). Q-bands were produced by staining with quinacrine dihydrochloride (1 mg/50 ml distilled deionized water) for 10 min at room temperature, rinsing with distilled deionized water for 5-10 min, and mounting in sucrose mountant (Ellison and Barr, 1972) modified by addition of 3% formaldehyde; this mountant is self sealing and long lasting, with a high refractive index. Slides also were stained in 4'-6-diamidino-2-phenylindole by placing 5-6 drops stain (1 mg stock solution/30 ml absolute ethanol) under a coverslip for 2-5 min (Bickham, 1987). Staining with chromomycin A3 followed Amemiya and Gold (1986). Fluorescence photomicrography was accomplished as described by Bickham (1987). The three fluorochromes used in this study are known to be specific for certain types of DNA (Comings, 1978). The fluorochrome 4'-6-diamidino-2-phenylindole is a nonintercalating compound that binds to sequences rich in adenine and thymine (Schweitzer, 1976). Chromomycin A3 stains DNA sequences rich in guanine and cytosine (Schweitzer, 1976), and nucleolar-organizer regions (Amemiya and Gold, 1986). Quinacrine also stains sequences rich in adenine and thymine but binds to DNA differently than 4'-6-diamidino-2-phenylindole (Comings, 1978; Distèche and Bontemps, 1974). The two fluorochromes that stain sequences rich in adenine and thymine often enhance different chromosomal regions.

Specimens examined.—Abbreviations used are CM, Carnegie Museum of Natural History; TCWC, Texas