

rather permanent. Animals as well as plants migrate with changing conditions.

I am amazed at the statement that the burrowing habits of the squirrel, mole, and pocket gopher are "similar." I cannot name three better examples of diametrically different uses of the earth by digging animals. The ground squirrel lives in colonies, burrows only for protection, and forages above ground by day. It has good eyesight, moderately developed nails for digging, and does not use its teeth for digging. The spoil is deposited at the mouth of the unplugged burrow. The mole, nearly blind, possesses a remarkably specialized body for forcing its way along under the sod in search of worms and insects. It seldom burrows, does not leave spoil dumps along its unplugged tunnel, and does not forage above ground. The pocket gopher plugs his burrow and can feed only over a radius of his body length around a forage hole—never completely emerging. (The young and males do travel above ground at certain seasons at night to start a new territory or to find a mate.) Its teeth and toenails are modified for digging and its pouches for carrying soil.

16. "... mounds are found only where . . . a thin layer of workable soil [overlies] a dense substratum."

Dr. Scheffer quotes Vernon Bailey as stating that mounds occur in southwestern Louisiana. There is no hard substratum there.

17. "... in deep sandy soil . . . [gophers] never form Mima-type mounds."

There is no proof that they produce mounds in shallow soil either. There are great areas of mounds where no gophers occur and vice versa.

18. According to Dr. Scheffer, the mounds are not deposits since they are unoriented and occasionally occur on slopes.

Dr. Scheffer's figure (1947, p. 286) shows that the mounds have a marked orientation. The fact that the mounds differ in texture from their bases proves that they were *built* by some means.

19. According to Dr. Scheffer, the mounds are not due to erosion because the interspaces are frequently closed depressions.

The most obvious disproof of dissectional residue is that the substratum differs from the mounds.

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MIMA MOUNDS: A REPLY

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Major Grant believes that gophers behave in one way, and we¹ believe that they behave in another—or we admit that we do not know exactly how they behave. I have plainly stated

¹ In 1942 Walter W. Dalquest and I developed the theory of origin of the Mima Mounds by gopher activity. Since Mr. Dalquest is in Mexico and unable to enter the present discussion, I am taking the liberty of defending his views as well as my own.

(1947, pp. 293, 294) that our evidence is indirect; that we have not seen gophers building a giant mound; that we do not know whether mound building is a contemporary or a historic process; and that we do not know whether the stimulus for mound building is a hardpan or a high water table or both.

Our main contentions are (1) that mounds of the Mima type occur only within the range of

gophers, living or extirpated, and (2) that only a living, adaptable force, not a physical agency, could have produced the Mima-type mounds out of widely varying materials and in widely varying environments from Mexico to Puget Sound. We note that Chapman Grant does not propose an alternative theory for the origin of the mounds.

In his introduction Major Grant has paraphrased our arguments quite well. We disclaim the statement: "All mounds are gopher-made whether gophers now inhabit the area or not." There are, of course, many kinds of mounds. We claim only that the Mima-type mound or pimple mound, as illustrated in our article, is gopher-made. Furthermore, the only place on the West Coast where we have seen Mima-type mounds unassociated with living gophers is Mima Prairie, a small opening of perhaps 10 square miles. Major Grant, later in his paper, emphasizes the fact that there are no gophers here. As we have explained (1942, p. 81; 1947, p. 293), the absence of living gophers on this specific prairie is unimportant. Rather than selecting Mima Prairie as the type locality of the pimple mounds, we could as easily have selected Tenino Prairie, where there *are* mounds inhabited by living gophers, 1 mile southeast of Mima Prairie.

We shall attempt to answer Major Grant's criticisms, numbered for easy reference, as follows:

1. The depth of a gopher nest varies. The nests with which Major Grant is familiar may be shallow, but

. . . on the gravelly prairies of western Washington the feeding runs of [the gopher], as they approach the vicinity of the nest, descend almost vertically to depths of 2, 3, and even 5 feet. . . . In excavating four burrow systems of this species, the writer found the nests at depths of 26, 29, 34, and 36 inches, respectively [Scheffer, 1931, p. 13].

2. The specific enemies or adverse conditions that a gopher avoids in nest building are unimportant in our discussion. The pertinent facts are that a gopher always builds a nest, the nest is the focal point of the home territory, and the nest is deeper than the average foraging runway. Fish and Wildlife Service records of stomach examinations show, however, that gophers *are* eaten by bear, wolf, and wildcat; but, again, these facts are unimportant.

3. Major Grant raises an interesting question in connection with the shape and spatial relations of the foraging territory. It is true that the foraging territory, or burrow system, is more

linear than circular, *at any given time*. Enough burrow systems have been excavated to prove this point. The burrow system is constantly changing, however, as the gopher searches for plant roots. New tunnels are made, old ones are filled; a gopher dies and another takes its place; subadult gophers leave the nest and seek new territory. We believe that the effect over many gopher generations is a honeycomb-like spacing of the mounds.

In this connection the areal distribution of other mammals is significant. On the Pribilof Islands, Alaska, the male fur seals gather in the spring, each taking up a territory on the beach and jealously guarding it from newcomers. The seals are not spaced with the regularity of checkers on a board, and yet they are certainly not spaced at random. Here we have a visible example of the fairly uniform spacing of family territories. We cannot see the spacing of gophers because they live underground, but we can infer that the individual territory tends to be circular or, more precisely, hexagonal in shape. The tightness or looseness of the network of home territories probably varies with the kind of soil and vegetative cover; that is, a gopher family requires more foraging ground where food plants are scarce than where they are plentiful.

In previous accounts we have stated our belief that the mound is developed around the center of an old nest burrow. We do not mean to imply that each mound is still the hereditary castle of a family of gophers. At any given time some mounds are occupied, and others are not. Were all the mounds occupied at once, Major Grant could reasonably feel that the gophers were overcrowded.

4. We did not state or imply that the gopher uses reasoning power. When it moves dirt from the side or top of a boulder, the boulder remains at rest. When it moves dirt from beneath the boulder, the boulder tends to settle. The evidence is a layer of coarser materials at the base of the Mima-type mound.

5. The intermound cobbles, or boulders, on the Puget Sound prairies were not moved out of mounds by gophers. They are more or less *in situ*, although many of them have been bared by the removal of silt gravel.

6. We feel that this is a matter of opinion.

7. Major Grant has understood us correctly. We believe that, where soil and climatic conditions are favorable to mound building, gophers *do* push more dirt toward the nest. In addition to mounds, of course, one can see the small spoil

heaps or gopher hills scattered on and between the mounds.

8. It is true that gophers do not everywhere make their spoil dumps toward the center. We believe, though, that over periods of time, in the shuttling of dirt as the gopher digs for plant roots and for nest and food-storage chambers, there is a differential movement of materials favoring the growth of the mound.

9. We inadvertently cited Lugn. We should have cited C. Bertrand Schultz who, in 1942, stated that "most palaeontologists now believe . . . that *Daimonelices* are the casts of rodent burrows."

10. A shallow depression occurs on the top or flank of many mounds on Mima Prairie. On this prairie, the reader will recall, there are no living gophers. We interpret the depression as the collapse of an old nesting chamber somewhere in the mound. It may, however, represent the recent activity of moles or livestock. J Harlen Bretz (1913, p. 101) referred to "occasional . . . sunken areas a foot or so across on these mounds. . . . The small sunken areas are so recent that the sod has not healed over the marginal cracks."

Major Grant states that "gophers do not seek out high ground for nest sites." We have been given two photographs taken in Texas, showing mounds sliced open to reveal nest chambers well above the surrounding ground level. Here winter flooding evidently obliges the animals to build their nests out of danger. Pennoyer F. English (1932, p. 127, pl. 9) has published a photograph of a similar Texas mound, with the statement that the gopher here "builds its nest not deep in the ground but in an enormous mound."

11. We find it easy to fancy the beginning of a mound as a center of activity in the vicinity of the nest. Others, with equal freedom, may fancy the beginning of a mound as a platform on which the gopher attempts to raise its nest out of the mud at a certain season.

12. The size of a Mima-type mound in a particular locality probably depends upon many factors. We are more concerned, though, with establishing the fact that the mounds are of gopher origin than with the ultimate size to which the mounds may grow. The industry of the gopher as a mover of soils is perhaps greater than many realize. According to Lincoln Ellison (1946, p. 113):

In what is considered to be a representative part of the subalpine zone of the Wasatch Plateau in central Utah, annual displacement of soil to the surface

by pocket gophers was found in 1941 to be at least 5 tons per acre and to cover 3½ per cent of the surface. The base population of pocket gophers is estimated to be somewhere between 4 and 16 animals per acre.

13. See No. 3.

14. See our introduction, paragraph 3.

15. We do not "propound a theory that the range of a species is rather permanent." In fact, we once published a paper describing the migrational history of gophers (1944, pp. 308-333, 423-450).

Use of the word "similar" here is a semantic privilege. The mole, ground squirrel, and pocket gopher are similar in that they make tunnels and throw out excavated soil in mounds.

16. We have clearly posed the question (1947, p. 294): "Does ground water at certain times of the year and in certain localities act in the same way that a soil hardpan does. . . ?" We have not seen the mounds of Louisiana, but, from the evidence of aerial photographs and from correspondence with Vernon Bailey, we believe them to be of the Mima type. *If* they actually are of the Mima type and *if* there is no hard substrate there, the water table may act as hardpan does on certain other mound prairies.

17. Major Grant states that "there are great areas of mounds where no gophers occur and vice versa." We have pointed out that the absence of living gophers in Mima-type mounds does not invalidate the theory of their origin in past years by gophers. We have also pointed out that there are many smooth prairies where gophers are living but where conditions do not favor the formation of mounds (1942, pp. 81, 84; 1947, p. 293).

18. Bretz's map, which we used as a figure (1947, p. 286), perhaps suggests slight orientation. Bretz himself stated that, while there is commonly an elongation of the mound, it "does not conform to any definite orientation" (1913, p. 83).

Major Grant discusses orientation, but he does not comment on our point that the mounds occasionally occur on slopes. Here is a phenomenon difficult to account for, unless one accepts the theory that the mounds are built from within, by animals. We quite agree with his statement: "The fact that mounds differ in texture from their bases proves that they were *built* by some means."

19. Major Grant's criticism is not clear.

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