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Digging Behavior of Four Species of Deer Mice (*Peromyscus*)

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The substrate is an important component of the environment of terrestrial mammals, and there are numerous examples of the selective influence of substrate characteristics on locomotor patterns and other aspects of the biology of many species. Recognition and utilization of appropriate habitats also may often be dependent on cues provided by the nature of the substrate.

The present study is concerned with possible ecological correlations in the extent of total digging activity and the relative amount of digging on different substrates in populations of four species of deer mice (*Peromyscus*) and the possible adaptive significance of such relationships. The species involved are the Florida mouse (*P. floridanus*), cotton mouse (*P. gossypinus*), wood mouse (*P. leucopus*), and oldfield mouse (*P. polionotus*). The Florida mouse is assigned to the monotypic subgenus *Podomys,* and the remaining species belong to the subgenus *Peromyscus.* Within the latter group, *P. gossypinus* and *P. leucopus* are most closely related. In addition to the differences in their taxonomic affinities, they also differ to varying degrees in habitat specificity, homesite preferences, and other aspects of their ecology and behavior. Two populations of

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each of three of the species (*floridanus*, *gossypinus*, and *polionotus*) were studied to provide some indication of the magnitude of intraspecific variation to be expected in digging behavior in relation to the amount of ecological divergence and gene flow between populations. With the exception of *leucopus*, both individuals caught in the field and first generation laboratory-reared individuals of all stocks were tested in an attempt to assess the relative influence of genetic and environmental factors on digging behavior.

King and Weisman (1964) and King, Price, and Weber (1968) have previously investigated certain aspects of sand digging behavior in the genus *Peromyscus*.

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MATERIALS AND METHODS

Description of Stocks

Peromyscus floridanus: This species occurs in certain parts of Florida and is limited in its ecological distribution to a few types of relatively xeric woodland or scrubby vegetation on well-drained, sandy soils (Layne, 1963). It appears to be exclusively burrow dwelling but apparently seldom, if ever, excavates its own burrows. Burrows of such animals as the gopher tortoise (*Gopherus polyphemus*) and pocket gopher (*Geomys pinetis*) seem to be of the type preferred by the Florida mouse (Blair and Kilby, 1936; Layne, 1966). When utilizing such burrows, the mice may dig short side tunnels in order to construct a nest chamber off the main burrow, and individuals in the laboratory have been observed to plug the entrances to nest boxes with sand and debris (Layne, 1966).

Subjects representing the two populations of *P. floridanus* included in the present study were collected within 10 miles of Gainesville, Alachua County, and near the town of Cedar Key, Levy County. These populations (hereafter referred to as the "Alachua" and "Levy" stocks) are almost or completely isolated from each other by unfavorable habitats and are appreciably divergent in morphology and ecology.

Peromyscus gossypinus: The cotton mouse ranges widely throughout southeastern United States. Although primarily a deciduous forest species, it is found in a variety of habitat types (Hamilton, 1943). The soils of the typical habitats of this species are comparatively rich in organic matter and relatively moist, although the species regularly occurs on sandy, well-drained soils as well. Subjects for this study were collected at the same two localities in Levy and Alachua counties mentioned above. Unlike the case in *floridanus,* there is no evidence of restricted gene flow between the two *gossypinus* populations, and they exhibit no important differences in morphology or ecology. At both localities, mice were collected on the same sandy soils as *floridanus,* as well as in nearby more humid forest habitats with richer soils.

The cotton mouse exhibits great diversity in nest sites. Although the same type of burrows preferred by *floridanus* may be used on occasion (Layne, personal observation), this species more commonly nests in holes in stumps, logs, or trees; underneath objects on the ground; and in dwellings (Hamilton, 1943; Ivey, 1949).

Peromyscus leucopus: The wood mouse ranges widely throughout eastern United States, and extends west to Kansas, Arizona, and into Mexico. Like *gossypinus,* it is fundamentally a deciduous forest species but occurs in various other habitat types. Its nesting requirements are essentially similar to those of *gossypinus.* The subjects used in this study were collected in the vicinity of Ithaca, Tompkins County, New York.

Peromyscus polionotus: This species occurs in southeastern United States and is typically found in open, early successional habitat types with sparse vegetative cover and generally sandy soils. It appears to be exclusively subterranean in its nesting habits and constructs its own highly characteristic type of burrow (Hayne, 1936). In areas in which these mice are abundant, many partially completed as well as occupied burrows are found.

The two populations represented in this study were *P. p. leucocephalus* from Santa Rosa Island, Escambia County, Florida, and *P. p. subgriseus* from the Ocala National Forest in Marion County, Florida. The former population occurs in sparsely vegetated white sand dunes (Blair, 1951), whereas the *subgriseus* were collected along sandy road shoulders, predominantly in areas of dense scrub vegetation.

Procedures

Subjects were placed individually into an open-field box containing a layer of approximately two inches of dry, fine white sand or finely shredded peat and observed for a five-minute period. In addition to descriptive notes on all responses to the substrate, as well as actual digging behavior, the following quantitative data were also recorded: 1. number of separate digging bouts; 2. total amount of time spent digging; 3. elapsed time (latency) between introduction to the box and first digging bout.

The open-field box was 24 inches in width, length, and height. It was provided with a hinged top fitted with a reflector and 25-watt bulb and a viewing port of one-way glass. The interior was painted neutral gray. Subjects were transferred from their home cage to the box by means of a glass jar. All tests were conducted between 9 A.M. and 4 P.M. Mice used in the experiments were kept in a room with natural light and temperatures ranging from approximately 72°–80° F. Three or four individuals were usually housed together in opaque plastic cages with wire tops. Wood chips served as litter; food and water were provided ad lib.

The laboratory-reared subjects born to wild-caught pairs were removed from the parental cage within several weeks of weaning. Only fully adult males were used to avoid the possible complication of sex differences in digging behavior per se or in other aspects of behavior, such as general activity, which in turn might influence digging performance. A total of 364 mice was used in the study; sample sizes of the various stocks tested are listed in table 1.

Statistical comparisons were by means of the t-test, utilizing, where necessary, the correction for nonhomogeneous variances given by Steel and Torrie (1960).

RESULTS

Qualitative Differences in Digging Behavior

All species that were studied employed the same basic mode of digging, although there were relatively pronounced differences between species in particular details. No differences in digging methods were noted among populations of *floridanus, gossypinus,* and *polionotus* nor between field and laboratory stocks of the same population.

When digging, the mice typically assume a posture in which the hind feet are widely spread and located well forward, although in some cases the body may be greatly extended when material is being gathered in with the forefeet. The forefeet are employed in unison to loosen the substrate and move it back beneath the body. In some cases, the forefeet also throw the accumulated material to the rear between the hind legs. Typically, however, the hind feet perform this function. The hind feet may be used alternately to kick material behind the body, but generally they function in unison.

In some cases mice dug only superficially and briefly, in which instances typical postures were not assumed. The following descriptions of interspecific differences in digging behavior refer to actively digging individuals.

Peromyscus floridanus: Much of the digging of this species consists of short bouts with little excavation. When actively digging, the Florida mouse uses the forefeet both for excavating and propelling material to the rear. The forefeet are extended far forward and drawn back together in a long, powerful stroke that throws the material back through the arch of the body and between the hind legs with considerable force. On occasion, sand was thrown 15 to 16 inches behind the body. The

TABLE 1
SUBJECTS FROM EACH STOCK OF *Peromyscus* USED IN DIGGING EXPERIMENTS

Species	Population	Status	Substrate	Total Number
P. floridanus	Alachua	Field	Sand	15
			Peat	12
		Laboratory	Sand	12
			Peat	12
	Levy	Field	Sand	15
			Peat	12
		Laboratory	Sand	15
			Peat	11
P. gossypinus	Alachua	Field	Sand	15
			Peat	15
		Laboratory	Sand	15
			Peat	12
	Levy	Field	Sand	15
			Peat	15
		Laboratory	Sand	15
			Peat	15
P. leucopus	New York	Field	Sand	8
			Peat	8
P. polionotus	*subgriseus*	Field	Sand	15
			Peat	15
		Laboratory	Sand	17
			Peat	12
P. polionotus	*leucocephalus*	Field	Sand	21
			Peat	15
		Laboratory	Sand	17
			Peat	15

tempo of the forearm thrusts is rather slow, averaging two to three strokes per second. The hindquarters are elevated with each backward stroke of the forelimbs, producing a distinct bobbing motion of the rump and tail during vigorous digging bouts.

The hind feet are only rarely employed in kicking accumulated substrate to the rear. We often counted 150 to 175 forearm strokes before observing use of the hind limbs. The hind-foot thrusts of this species do not appear to be very powerful, and the general impression is that the hind limbs are not so well integrated into the total digging pattern as in the other species studied.

Peromyscus gossypinus: As in the case of *floridanus,* much of the digging of this species was of the superficial type. In addition, *gossypinus* subjects occasionally scratched, dug, or "shuffled" with the hind feet without first excavating material with the front feet and sometimes dug a hole only to turn around and refill it with hind-foot strokes as they moved away. Several subjects also burrowed into the loose substrate during the tests on peat, burying the anterior portion of the body beneath the surface. Cotton mice in standard laboratory cages often tunnel into the litter as well. Such variations in digging behavior were not observed in *floridanus.*

In typical digging, *gossypinus* moves the forefeet much more rapidly than does *floridanus.* Although the strokes are too fast to count accurately, we estimate the rate at five to eight per second. The forefeet may throw the substrate behind the body, but the hind limbs are chiefly used for this purpose. During the tests, sand or peat was often thrown as far as 12 inches away with the hind feet. The hind feet were also brought into play more frequently than in *floridanus,* bouts of three to five hind-foot strokes usually occurring after six to 10 forearm strokes. Unlike *floridanus,* there is no conspicuous up and down movement of the hindquarters in digging *gossypinus.*

Peromyscus leucopus: Digging behavior of this species was not observed in detail. However, both forelimbs and hind limbs are regularly employed, and the general pattern appears to be similar to that of *gossypinus.*

Peromyscus polionotus: In sharp contrast to the other species, *polionotus* spent much of the time in the open-field apparatus engaged in intensive digging. As in the other species, the forefeet are used primarily to loosen and draw the substrate back beneath the body (fig. 1A). During a given digging bout, the later strokes tend to bring the substrate farther to the rear than the initial ones (fig. 1B). The stroke rate of the forelimbs in this species is very rapid, an estimate being eight to 12 strokes per second. The hind limbs are also much more highly integrated into the total digging pattern, as one to three hind foot strokes regularly alternate with a series of eight to 12 forefoot strokes (fig. 1C). The hind-foot thrusts that propel the excavated sand or peat behind the body are especially powerful. They literally blast the material to the rear, often to a distance of from 24 to 26 inches. When observing a digging mouse from above, it is not unusual to catch a glimpse of the plantar surfaces of the hind feet when they are engaged in kicking material to the rear.

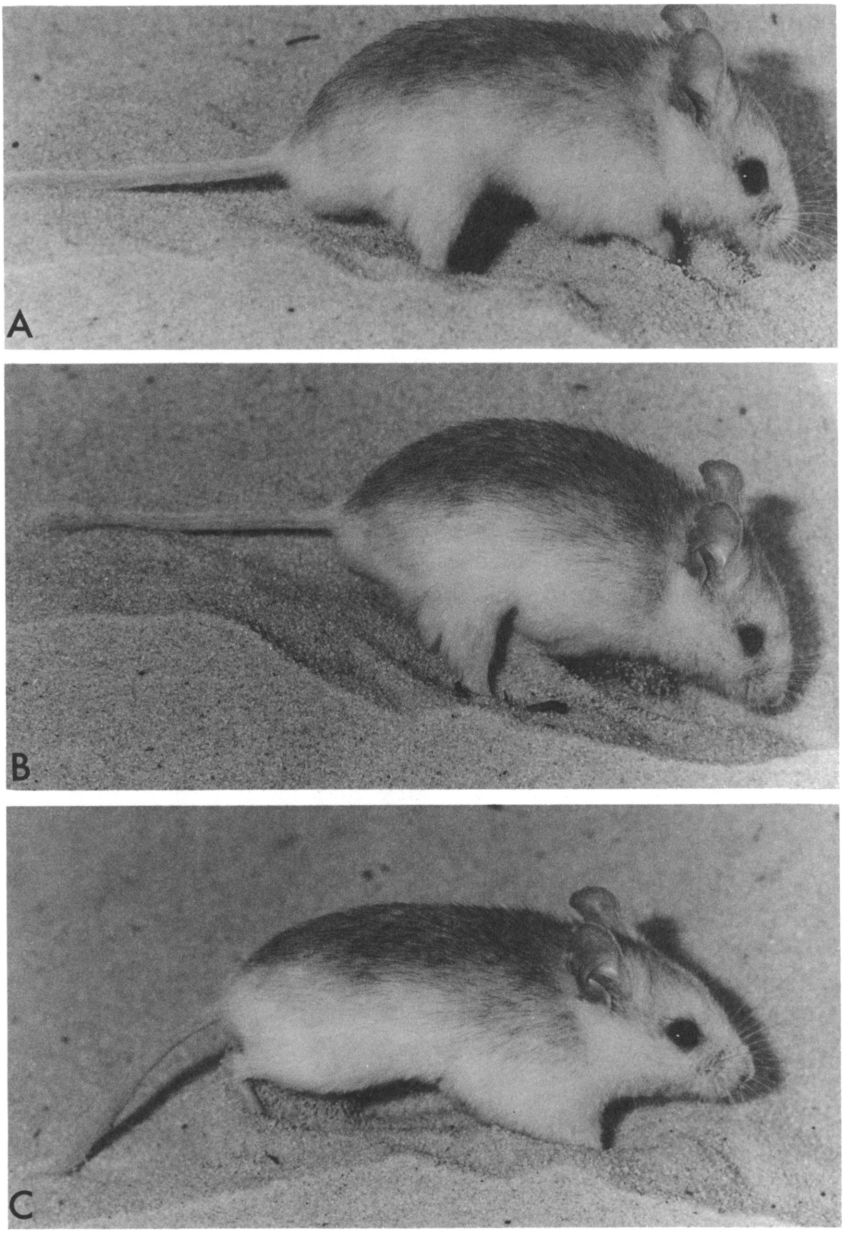

FIG. 1. Digging sequence in *Peromyscus polionotus leucocephalus*. A. Excavating sand with forelimbs. B. Pushing sand back beneath body with forelimbs. C. Beginning of hind foot stroke to propel substrate to rear.

There was no pronounced bobbing action of the hindquarters accompanying digging by this species.

Quantitative Differences in Digging Behavior

Differences between the various stocks in number of bouts, total time spent digging, and latency are presented in figure 2. In these analyses, no distinction is made between superficial and more intensive digging bouts.

Peromyscus floridanus: This species did the least amount of digging and had the longest latencies of any of the species studied. With the exception of the Levy/laboratory group with a higher number of bouts and greater time digging on peat and Alachua/laboratory subjects with a slightly higher mean latency on sand, all groups of the Florida mouse exhibited somewhat more digging activity on sand. However, the differences between substrates are not significant in any case. In addition, there are no clear differences between the two populations in regard to total digging activity on both substrates combined.

In the case of Alachua *floridanus* on both sand and peat and Levy *floridanus* on sand, field subjects had a lower mean digging latency and higher mean number of bouts and total digging time than did laboratory individuals. The reverse was true in Levy *floridanus* on peat. These differences between field and laboratory stocks are not significant in any case.

Peromyscus gossypinus: Compared with *floridanus,* this species is a more active digger. Cotton mice had a slightly lower mean latency and slightly higher mean number of bouts and total digging time than *floridanus* on both substrate types. However, the only statistically significant difference ($p < .05$) between the two species is in over-all mean number of bouts.

As in the Florida mouse, there was a general tendency for all groups of *gossypinus* to exhibit a preference for sand. The only exception was the Alachua/field group, which had a higher mean number of bouts on peat. Differences between substrates were significant only in the case of mean number of bouts ($p < .01$), total time digging ($p < .02$), and latency ($p < .01$) in Levy/field *gossypinus,* and latency ($p < .01$) in the Levy/laboratory group. There were no significant differences in the over-all digging activity of the two *gossypinus* populations.

Laboratory subjects had higher average latencies (except for the Alachua group on sand and the Levy group on peat), fewer bouts, and less total time digging than field groups on both substrates. However, these differences were significant at the .05 level only in the case of number of bouts and total time for the Levy stock on sand.

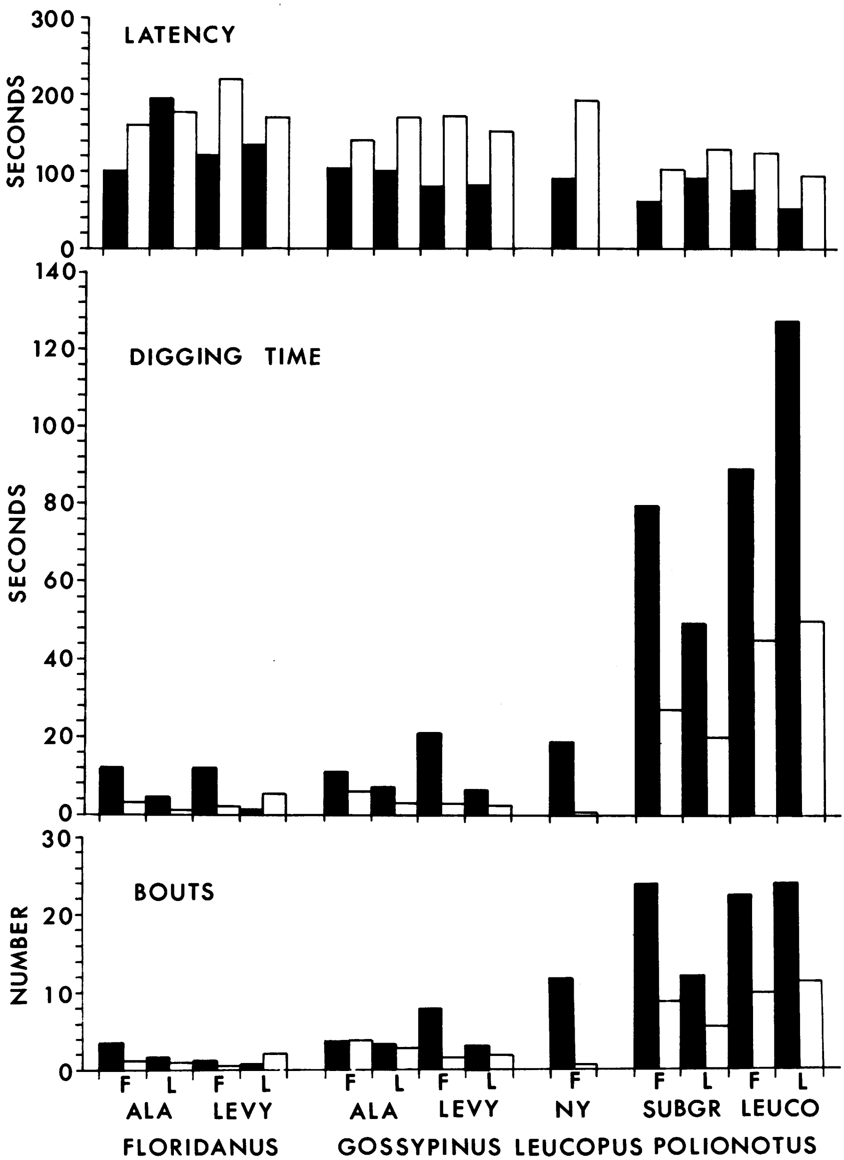

FIG. 2 Mean number of digging bouts, cumulative digging time, and digging latency in stocks of four species of *Peromyscus*. Solid and open bars represent performance on sand and peat, respectively. "F" denotes field-caught subjects and "L," laboratory-reared animals.

Peromyscus leucopus: The wood mouse showed a somewhat higher over-all level of digging activity and a more pronounced difference between substrates than either of the preceding species. In over-all performance, it compared most closely with *gossypinus.* In mean number of bouts on sand, *leucopus* differed highly significantly ($p < .01$) from *floridanus* and significantly ($p < .05$) from *gossypinus.* Differences in total digging time and latency on sand were not significant. There were no significant differences between *leucopus* and *floridanus* in any of the measures on peat. The mean number of bouts in *leucopus* was significantly higher ($p < .05$) than *gossypinus;* the two species did not differ significantly in any of the other measures.

With regard to substrate preference, mean number of bouts and total digging time were considerably higher on sand than on peat, and latency was lower, these differences being significant at the .01, .05, and .01 levels, respectively.

Peromyscus polionotus: This species differed strikingly from the other three in showing a much higher level of digging behavior in the testing situation. Latency periods also tended to be shorter. The differences between *polionotus* and the other species in mean number of bouts and mean total digging time on both sand and peat were highly significant. *Polionotus* did not differ significantly from *floridanus* or *gossypinus* in latency on sand or from *leucopus* in latency on sand or peat. The differences in latency on peat between *polionotus* and *floridanus* and between *polionotus* and *gossypinus* were significant at the .01 and .05 levels, respectively.

At the subspecific level, none of the differences between field *leucocephalus* and *subgriseus* was significant, although the former tended to spend more time digging on both substrates. However, the laboratory group of *leucocephalus* had a significantly ($p < .01$) greater number of digging bouts and total digging time on sand and a significantly greater ($p < .05$) number of bouts on peat than *subgriseus.* The two populations did not differ significantly in digging latency.

The *subgriseus* laboratory group agreed with the other species tested in having greater latency, fewer bouts, and less total digging time compared with the field group on both sand and peat. The differences between bouts and cumulative digging time on sand were significant at the .01 and .05 levels, respectively. A distinct reversal of this trend was exhibited by *leucocephalus,* where laboratory subjects exceeded field animals in mean number of bouts and total digging time on both substrates, the differences being significant ($p < .05$) in the case of both mean number of bouts and digging time on sand.

DISCUSSION

Over-all digging activity in the four species included in this study is more strongly correlated with their nesting habits than with the substrate characteristics of their natural habitats. Thus, although both *polionotus* and *floridanus* are narrowly restricted to sandy soils, they were at opposite extremes in the present tests, *polionotus* being the most active digger of all species and *floridanus* the least active. *Peromyscus gossypinus* and *P. leucopus,* which occur on a much broader range of soil types than *polionotus* or *floridanus,* were not markedly different from *floridanus.* On the other hand, *polionotus* is the only ground-dwelling species that typically constructs its own burrows. Neither *gossypinus* nor *leucopus* commonly nests in burrows, whereas *floridanus,* although a burrow dweller, appears on the basis of presently available evidence typically to rely on the burrows of other animals.

In regard to relative activity on different substrates, there was a consistent preference in all of the stocks tested for sand over peat. This suggests that a sandy substrate provides a strong stimulus for digging in any species regardless of its particular natural environmental relationships. This general "base-line" of sand preference must be taken into account when considering the possible adaptive significance of differences in digging performance on different substrates.

Peromyscus polionotus greatly exceeded all other species in absolute amount of digging on sand and, except for *leucopus,* exhibited the greatest relative preference for sand as well. The pronounced differential substrate response of this species may be indicative of greater selection for substrate discrimination as a result of the critical importance of the proper kind of substrate for burrow construction. As in the case of total digging activity, the absence of significant substrate preference in *floridanus* may be related to the fact that this species uses the burrows of other animals and hence is not faced with the problem of selecting the proper substrate for excavating its own. It might thus be speculated that habitat selection in *floridanus* depends more upon response to appropriate types of burrows than substrate characteristics per se. We can find no plausible ecological explanation for the relatively high level of sand digging displayed by *leucopus* in the present study.

Only in *polionotus* was there a marked difference in quantitative aspects of digging between the two populations of the species tested. Such variation at the population level may be a further indication of strong selective pressures for digging behavior in this species. The intraspecific differences may be related to greater problems of burrow construction and maintenance, procurement of food, and avoidance of predators facing *leucocephalus,* as a result of which there has been increased selection for digging behavior in this population. General observation suggests that the looser surface sands of the *leucocephalus* habitat may make digging a burrow more difficult. Blair (1951) noted that *leucocephalus* burrows are also frequently covered by drifting sand, and that the mice apparently make an effort to keep them open. He found that "after a blow had drifted the holes shut with sand, several or all of the normally utilized holes in the home range would be visited and cleared out in the course of a night's wandering." The wind-blown sand may also cover a large proportion of fallen seeds and other food items. In addition, one of the varieties of escape behavior of transient and immigrant mice observed by Blair was that of hiding in shallow holes and sometimes partially covering the body with sand. He found evidence that in at least some cases the holes were actually dug by the mice. Such behavior might be more prevalent in *leucocephalus* than in *subgriseus* as a result of the sparser vegetative cover of the former's habitat. It is of interest in this connection that *leucocephalus* has a relatively large hind foot, which has been considered a possible adaptation for more efficient digging in loose sand (Hayne, 1950; Bowen, 1968).

Although laboratory stocks exhibited essentially the same trends in digging behavior as that of the field groups, thus indicating that the behavioral differences in question have a genetic component, there were differences between field and laboratory groups within every stock. Except in the case of *P.p. leucocephalus,* laboratory subjects performed more poorly in the tests. As there is no evidence to suggest accidental selection for reduced digging behavior in the field animals producing the laboratory young used in the study, the differences may be assumed to reflect environmental effects. Such effects might involve either the lack of experience on natural substrates, with resulting failure of the full expression of genetic tendencies for digging, or changes in activity, temperament, or other aspects of behavior influencing digging performance produced by the relatively monotonous laboratory environment under which the young were raised. In regard to the latter possibility, Denenberg and Morton (1962) found increased emotionality in albino rats raised under standard laboratory conditions as compared with individuals reared in larger "free-environment" boxes. The persistence of a high level of digging in laboratory-raised *leucocephalus* may thus be indicative of either a stronger genetic basis of digging behavior in this stock as compared with *subgriseus* or to a lesser effect on its behavior of the stimulus-poor laboratory environment, perhaps because of its more homogeneous natural habitats as compared with the other populations studied.

King and Weisman (1964) and King, Price, and Weber (1968) studied digging behavior of several species of *Peromyscus,* including three (*floridanus, leucopus,* and *polionotus*) of the species involved in the present investigation. In contrast to our results, King and Weisman found no ecological correlations in the sand digging behavior of five stocks of *Peromyscus.* Digging tendencies were measured by the amount of sand removed from a dispenser by a subject confined to a relatively small cage. The sand removed from the dispenser fell through the wire mesh floor of the cage. A possible explanation of the lack of agreement in the two studies is that the type of apparatus used by King and Weisman provided such a strong stimulus for digging in an attempt to escape or as an outlet for excess energy that species-specific differences in normal digging tendencies were obscured. The excessive quantities of sand removed by some of the mice in these experiments (up to 94.3 pounds in a 24-hour period) argues in favor of this interpretation.

King, Price, and Weber (1968) measured the tendency of mice to dig through a sand-filled plastic tunnel in order to move from one cage to another. The results of these experiments agree with ours in showing *polionotus* to be the most active digger of all species tested. However, unlike our findings, *floridanus* also emerged as an active digger in this study, being second only to *polionotus.* Although the *floridanus* stock used by King, Price, and Weber represents a different population from those we studied and has been bred in the laboratory for a number of generations, the discrepancy in the two studies more likely results in greater part from differences in the tests rather than in the subjects. Other than in foraging for food, much of the active digging done by *floridanus* may be assumed to consist of underground modification of existing burrows of other species, such as construction of short side tunnels and nest chambers and perhaps plugging entrances to its nest chamber. It is thus possible that the apparatus of King, Price, and Weber more closely approximated the conditions under which *floridanus* naturally digs than did ours, and thus provided a more effective stimulus for digging. The performance of *floridanus* in the apparatus of King, Price, and Weber also suggests that its particular style of digging, with greater emphasis on the forelimbs than other species, may somehow be adaptive for digging in underground situations.

The slight tendency to dig on the surface, as well as the lack of strong differences in digging activity on sand and peat exhibited by *floridanus* in our study, supports the contention that this species does not regularly burrow from the surface and suggests that the substrate per se does not play a primary role in its habitat selection and utilization.

SUMMARY

Certain aspects of digging behavior in four species of deer mice, *Peromyscus* (*P. floridanus, P. gossypinus, P. leucopus,* and *P. polionotus*), were studied to determine the relationships between the level of digging activity and ecological factors and the possible adaptive significance of such correlations. Two populations of each of three of the species (*floridanus, gossypinus,* and *polionotus*) were included to provide some indication of the magnitude of intraspecific variation in digging activity, and both field and first generation laboratory-raised subjects of the same species were studied in an attempt to distinguish between the relative influences of genetic and environmental factors on this behavior. Mice were placed individually into an open-field box containing either sand or peat and observed for a five-minute period. In addition to descriptive notes on digging behavior, number of bouts, total time spent digging, and latency (time elapsed between introduction to the apparatus and beginning of first digging bout) were recorded. *Peromyscus floridanus* dug relatively slowly, using the forefeet for excavating and moving material beneath the body and also to propel the substrate to the rear. In contrast to the other species, the hind feet were rarely used to kick accumulated material backward. *Peromyscus gossypinus* moved the forefeet more rapidly in excavating material than did *floridanus* and generally used the hind limbs to throw the substrate behind the body. Details of digging in *leucopus* were not clearly observed; but it appears to resemble *gossypinus* in its style of digging. *Peromyscus polionotus* appeared to be the most efficient digger of the four species. It moved its forefeet more rapidly than the other forms, and the hind limbs were more closely integrated into the total action pattern. Quantitatively, *floridanus* dug less than the other species, *gossypinus* and *leucopus* were slightly more active, whereas *polionotus* far exceeded all other species in mean number of bouts and total time digging and had distinctly shorter latencies. The well-developed digging behavior of *polionotus* is correlated with burrowing habits. All species exhibited a tendency to dig more actively on sand rather than on peat, but only in *leucopus* and *polionotus* was the discrepancy pronounced. The higher level of digging of *polionotus* on sand may reflect selection for substrate recognition as a result of the importance of the proper type of soil for burrow construction in this species. There seems to be no obvious adaptive basis for the sand preference of *leucopus*. Only

in *polionotus* were there appreciable differences between populations in digging behavior, with *leucocephalus* tending to do more digging than did *subgriseus.* This difference may reflect more intense selection for digging in the *leucocephalus* population as a result of more difficult burrow construction and maintenance, constant covering of food items by blowing sand, and greater use of shallow holes to avoid predation. In general, laboratory-raised stocks fell into the same relative position as field groups in the aspects of digging behavior studied, indicating a genetic basis of the differences observed. However, in all stocks except *P. p. leucocephalus* there was a tendency for reduced digging in laboratory-reared subjects. The differences between field and laboratory-raised groups appear to be of environmental origin, either reflecting the absence of experience on natural substrates or an effect of the homogeneous laboratory environment on other aspects of behavior, such as activity, temperament, etc., which in turn influence digging performance. The fact that laboratory-reared *leucocephalus* actually dug more than did field subjects may indicate either a stronger genetic basis for digging in this stock or a lesser effect of laboratory conditions, perhaps because of the relative homogeneity of the natural environment of this population compared with that of the other stocks. Differences in the present results and those of previous studies of digging behavior in *Peromyscus* dealing with some of the same species appear to be attributable to the types of testing apparatus and procedures utilized.

LITERATURE CITED

BLAIR, W. FRANK
1951. Population structure, social behavior, and environmental relations in a natural population of the beach mouse (*Peromyscus polionotus leucocephalus*). Contrib. Lab. Vert. Biol. Univ. Michigan, no. 48, pp. 1–47.

BLAIR, W. FRANK, AND JOHN D. KILBY
1936. The gopher mouse—*Peromyscus floridanus.* Jour. Mammal., vol. 17, pp. 421–422.

BOWEN, W. WEDGWOOD
1968. Variation and evolution of Gulf Coast populations of beach mice, *Peromyscus polionotus.* Bull. Florida State Mus., vol. 12, pp. 1–91.

DENENBERG, VICTOR H., AND JOHN R. C. MORTON
1962. Effects of environmental complexity and social groupings upon modification of emotional behavior. Jour. Comp. Physiol. Psych., vol. 55, pp. 242–246.

HAMILTON, WILLIAM J., JR.
1943. The mammals of eastern United States. New York, Comstock Publ. Co., pp. 1–432.

HAYNE, DON W.

1936. Burrowing habits of *Peromyscus polionotus*. Jour. Mammal., vol. 17, pp. 420–421.

1950. Reliability of laboratory-bred stocks as samples of wild populations, as shown in a study of the variation of *Peromyscus polionotus* in parts of Florida and Alabama. Contrib. Lab. Vert. Biol. Univ. Michigan, no. 46, pp. 1–56.

IVEY, ROBERT D.

1949. Life history notes on three mice from the Florida east coast. Jour. Mammal., vol. 30, pp. 157–162.

KING, JOHN A., EDWARD O. PRICE, AND PETER L. WEBER

1968. Behavioral comparisons within the genus *Peromyscus*. Papers Michigan Acad. Sci., vol. 53, pp. 113–136.

KING, JOHN A., AND RONALD G. WEISMAN

1964. Sand digging contingent upon bar pressing in deer mice (*Peromyscus*). Animal Behavior, vol. 12, pp. 446–450.

LAYNE, JAMES N.

1963. A study of the parasites of the Florida mouse, *Peromyscus floridanus*, in relation to host and environmental factors. Tulane Studies Zool., vol. 11, pp. 1–27.

1966. Postnatal development and growth of *Peromyscus floridanus*. Growth, vol. 30, pp. 23–45.

STEEL, ROBERT G. D., AND JAMES H. TORRIE

1960. Principles and procedures of statistics. New York, McGraw-Hill, pp. 1–481.