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INTRODUCTION

Pine voles (*Microtus pinetorum*) have long been recognized as a pest species in fruit orchards of the eastern United States (Hamilton 1935). These semifossorial rodents construct tunnel systems beneath apple trees where they eat entire roots or strip roots of bark and cambium. Hamilton (1938) reported numbers of pine voles within apple orchards as high as 200-300 voles per acre which is in sharp contrast to the relative scarcity of pine voles outside orchard situations (Crain and Packard 1966; Goertz 1971). These findings suggest that orchard habitat provides excellent conditions for pine vole growth and reproduction, although the specific components which are attractive to pine voles and facilitate their proliferation remain poorly understood.

Prior studies have suggested that pine vole habitat selection is based on preference for a complex of habitat components including cover density (Benton 1955; Paul 1970; Goertz 1971), food resources (Noffsinger 1976), soil texture (Fisher and Anthony 1980), and soil moisture (Haines and Gier 1951; Miller 1964). With regard to the latter two variables, Miller (1964) and Best (1973) have presented evidence indicating that soil texture is a primary factor limiting the distribution of some fossorial mammals but soil moisture content may also be of importance (Miller 1948). The extent to which these soil properties influence the distribution and abundance of pine voles is presently unclear. Similarly, pine vole response to soil temperature remains unexplored. Thus, in this study we examine the influence of soil texture, moisture, and temperature on nest site selection and burrowing activity of the pine vole, *Microtus pinetorum*.

MATERIALS AND METHODS

Soil Temperature Selection

The influence of soil temperature on pine vole nest site selection was assessed by means of a device which offered a dichotomous choice in soil temperatures. Two ten gallon aquaria with one end of each replaced with hardware cloth, were connected by means of a 0.5 m length of hollow (diameter = 5 cm), plexiglass tubing and filled to a depth of 15 cm with potting soil. Straw was added in quantities sufficient to cover the soil surface. The soil temperature of one aquarium was regulated at the desired level by means of an electric heating tape wrapped around the aquarium and connected to a variable voltage source: the soil of the alternate aquarium was kept at room temperature (19°C). Soil temperatures were measured with a YSI probe and Markson digital thermometer. Water was added as necessary in order to keep the soil in a mouldable condition. Food (Charles River RMH 1000) and water were provided in both aquaria.

When the soil of the heated aquarium reached the desired temperature, a male-female pair of pine voles was introduced into one of the aquaria (previously selected by coin toss) and the animals were left undisturbed for 24 hours. All pairs of voles constructed nests during this period. At the end of this period, the aquarium selected as the site of nest construction was noted as well as the surface or subsurface location of the nest. The animals were then removed from the apparatus, all tunnels destroyed by thoroughly mixing the soil, and straw replaced as necessary. Ten to eleven pairs of voles were tested for each of three soil temperatures (25°, 30°, and 35°C) in the heated aquarium. An additional 11 pairs of voles served as controls when the soil temperatures of both aquaria were 19°C.

Soil Moisture and Texture Selection

To examine soil moisture and texture preference by pine voles, they were placed in 3.66 m (12 ft) x 4.88 m (16 ft) x 0.4 m (16 inches) wooden enclosures with hardware cloth bottoms and which were filled to a depth of 15 cm with three soil types. The three soil types were arranged in adjacent 1.22 m x 4.88 m strips. One strip consisted of a base mixture of loam and peat moss (3:1 volume/volume) alone, while the other two strips consisted of the base mixture with the addition of either #1A gravel (3:2 v/v) or #2 stone (1:1 v/v). The positions of the strips differed in each of the three enclosures in order to reduce the potential influence of center strip (open area) avoidance by the voles. Apples placed beneath three plywood squares (20 cm x 20 cm) evenly distributed along the length of each strip provided food and water for the voles during each trial. A thin layer of straw provided cover and nesting material.

Soil water content in the enclosures was regulated by means of two sprinkler hoses suspended across the top of each enclosure and perpendicular to the enclosure's long axes. One hose was placed across the end of each enclosure and the second at 1.7 m from the first (approximately one third the length of the enclosure). This hose arrangement produced a water flow pattern which resulted in a gradient of water content within each soil type. For the purposes of this study, three zones of soil moisture were recognized, each corresponding to one-third the length of the enclosures. Soil water content in the wet, moist, and dry regions of the strips averaged 1.15 ± 0.12, 0.71 ± 0.05, and 0.16 ± 0.03 grams water per gram dry weight soil, respectively. Daily watering for one hour sustained the level of soil moisture. Four removable, plastic-covered lids prevented entrance of rain water.

To investigate the importance of soil moisture content to site selection and use by pine voles, the enclosures were watered as described above. Single male-female pairs of pine voles were released in the center of each enclosure and left for five days. Apple use was noted every two days to ensure that sufficient food was available for the animals. On day five, the pair of animals was removed from each enclosure, their nest locations noted, and the lengths and locations of all subsurface tunnels and surface runways recorded. Prior to the introduction of the next pair of voles, all existing tunnels and runways were destroyed by thoroughly raking the soil. Soil water content was assessed at the start of each five day trial by randomly selecting five soil samples from each of the three moisture zones within each strip. Water content was determined as the difference in weight of the samples before and after drying. Twelve pairs of voles were used in these trials.

Statistical Analyses

All nesting data were analyzed by means of chi-square goodness-of-fit tests.

A two-way analysis of variance followed by Duncan's multiple range was employed in analyzing data for surface runway and subsurface tunnel lengths.

RESULTS

Soil Temperature Selection

Soil temperature influenced nest-site selection by pine voles. In this instance, the number of nests constructed in the heated aquarium decreased with increasing soil temperature (Fig. 1). Significantly fewer nests were located in the aquarium containing soil kept at 30°C (X^2 = 4.54; d.f. = 1; $p<0.01$) than in the aquarium containing soil maintained at 19°C. Furthermore, each of the nests built in the aquarium containing 30° - or 35°C - soil was located on the soil surface, which contrasts with the subsurface location of all nests constructed in cooler soil.

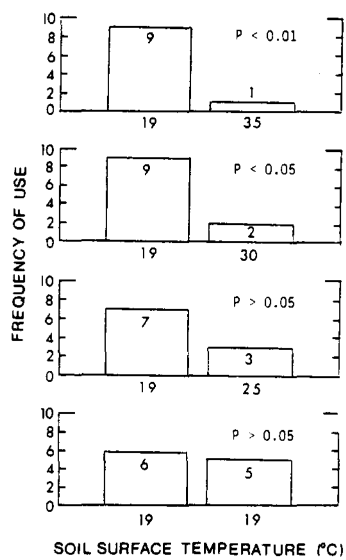

Figure 1. Influence of soil temperature on nest-site selection by the pine vole, *Microtus pinetorum*. Numbers within rectangles indicate the number of voles selecting a particualr soil temperature; soil temperatures are indicated below each graph.

Soil Moisture and Texture Selection

The three soil mixtures employed in this study differed in their acceptability to pine voles (Fig. 2). In this instance, 11 (92%) of a total 12 pairs of voles selected the soil strip as a nest site whereas only a single pair built a nest in the gravel strip; no voles established nests in the stone strip. Comparison of the number of nests located within each of the three soil types indicates that significantly more nests were located in the soil strip than in the other soil types ($X^2 = 18.5$; d.f. = 2; $p<0.01$).

In addition, soil moisture strongly influenced nest-site selection by pine voles (Fig. 2). Ten (83%) of a total 12 pairs of voles constructed nests in the center, or moist zone, of the strips and the majority of these nests (9 of 10) were located in the soil strip. Comparison of the number of nests located in each of the three moisture zones indicates that significantly more nests were constructed in the moist zone than in the dry or wet zones of the strips ($X^2 = 9.5$; d.f. = 2; $p<0.01$).

Comparison of means for subsurface tunnel lengths in each region of the enclosures indicates that significantly more tunneling occurred in the moist zone of the soil strip than in any other area of the enclosures; no subsurface tunnels were found in the stone strips. Surface runways were present in similar amounts in all regions of the enclosures.

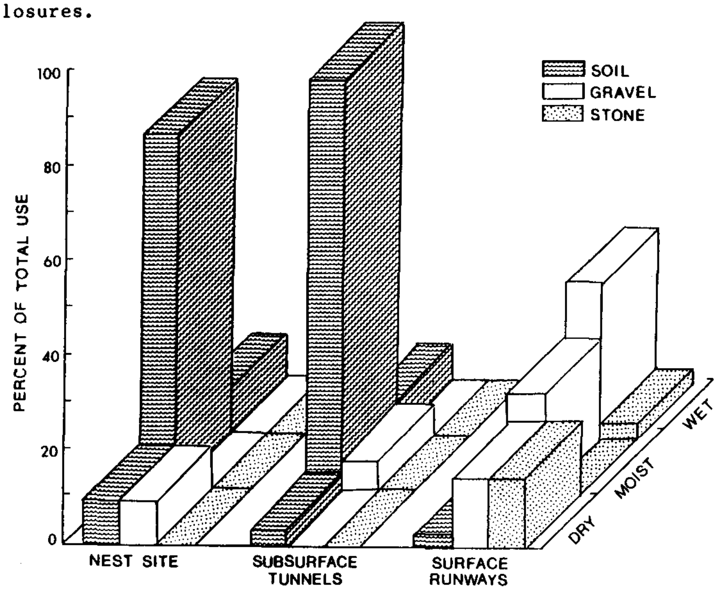

Figure 2. Influence of soil moisture and texture on nest-site selection and burrowing activity by the pine vole (n = 12 pairs). Height of rectangles represents mean.

DISCUSSION

Soil temperature influenced nest-site selection by pine voles. In this instance, pine voles presented with a choice of soil temperatures always selected soil maintained at 25°C or less in which to construct a subsurface nest. Conversely, pine voles responded to soil temperatures of 30°C or 35°C by complete avoidance or by constructing nests on the soil surface. These findings are consistent with those of other studies in which measured nest temperatures for a number of microtines were found to lie below each species respective thermal neutral zone (Daniel 1964; Gebczynski 1966; Cotton and Griffiths 1967). With regard to the pine vole, selection of cool soils in which to build nests may be a function of these vole's thermoregulatory physiology. Pine voles are characterized by high rates of metabolic heat production (Bradley 1976) which must be offset by an equivalent rate of heat loss in order to maintain constant body temperature. Under laboratory conditions, evaporative water loss is one important component of heat loss in this species as evidenced by the findings that evaporative water loss is elevated 135% in 30°C- exposed voles relative to animals exposed to 15°C (Rhodes and Richmond 1981). However, in the water-saturated air of a subsurface burrow system (Getz 1965) evaporative water loss from these animals may be much reduced, thereby suppressing this route of heat loss. In the absence of effective evaporative cooling mechanisms, pine voles may be incapable of tolerating high soil temperatures without incurring increases in body temperature. Thus, it is not surprising to find that pine voles select soil of low temperature in which to establish subsurface nests and burrows.

When presented with a selection of three soil types in which to construct a nest and tunnel system, the majority of pine voles in this study selected soil strips without gravel or stone in which to establish themselves. These results are consistent with results generated from human attempts at tunnel construction in the gravel and stone strips. In the former soil type, tunnels formed with a one-inch diameter dowel collapsed unless the gravel was moist, whereas in the latter soil types, the large stones always prevented tunnel formation; subsurface tunnels were easily formed in the soil strip. In this regard, the characteristics of the soil strip were similar to soil characteristics present in areas inhabited by free-ranging voles. Specifically, these animals are found in association with light, friable soils both within (Fisher and Anthony 1980) and outside of (Haines and Gier 1951; Goertz 1971) orchards.

In contrast to the pronounced use of the soil strip, the stone strips were never selected by pine voles as a nest site although the presence of surface runways indicated that the stone strips were explored by the voles. The spatial distribution of other fossorial mammals is also known to be influenced by soil texture. For example, the mole, _Talpa europea_, is common in areas of deep, light soil but is absent from areas of identical soil composition when stones are abundant (Milner and Ball 1970). Similarly, Miller (1964) and Best (1973) have presented evidence indicating that members of the family Geomyidae have geographic distributions limited by soil texture. Moreover, these studies point out that morphology is an important indicator of the soil types in which a fossorial rodent can persist. In the present study, the pine vole is a small rodent (avg. wt. 24 g) which lacks many of the specialized adaptations for a fossorial life style characteristic of the talpids and geomyids. Moreover, because the energy costs of burrowing are related to soil properties (density, cohesiveness, shear strength) (Vleck 1979), it is not surprising to find that the majority of pine voles in this study selected the soil mixture which presented the least resistance to burrowing activity in which to establish themselves.

Soil moisture content also influenced pine vole selection of a nest site. In the present study, ten (83%) of a total 12 pairs of voles chose the moist zone of the strips whereas only 2 (17%) of 12 pairs established nests in the wet or dry ends of the strips. Pine voles may select moist soil as a center of activity because of the reduced energy costs of burrowing in moist soil coupled with better tunnel integrity (Collis-George 1959). With regard to these possibilities, a positive correlation between soil water content and burrowing activity has also been noted for the pocket gopher, _Thomomys bottae_ (Miller 1948; Miller 1957). In those studies, burrowing activity was reported to be most pronounced during reasonably wet periods (Miller 1948) and also subsequent to flood irrigation of alfalfa fields (Miller 1957). However, Miller and Bond (1960) found no correlation between seasonal burrowing of _T. bottae_ and soil moisture and suggested that breeding status and feeding habits were more important determinants of burrowing activity in this species.

Additionally, selection of moist soil ensures that the burrow air is at saturation or is nearly saturated with water vapor (see previous discussion). As a consequence, the vapor pressure deficit for water between air and animal is reduced which results in a decrease in evaporative water losses from the voles. For a small mammal with high daily water requirements such as the pine vole, reductions in evaporative water loss may play an important role in maintaining water balance.

In conclusion, when presented with a selection of soil temperature, moisture, and texture, the majority of pine voles established nests and subsurface tunnel systems in a light, friable, moist soil maintained at less than 30°C. However, further studies are required to establish the relevancy of these findings to habitat selection by free-ranging voles.

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