

THE EVOLUTIONARY SIGNIFICANCE OF
CERTAIN BEHAVIORAL, PHYSIOLOGICAL,
AND MORPHOLOGICAL ADAPTATIONS
OF THE OLD-FIELD MOUSE,
Peromyscus polionotus

By
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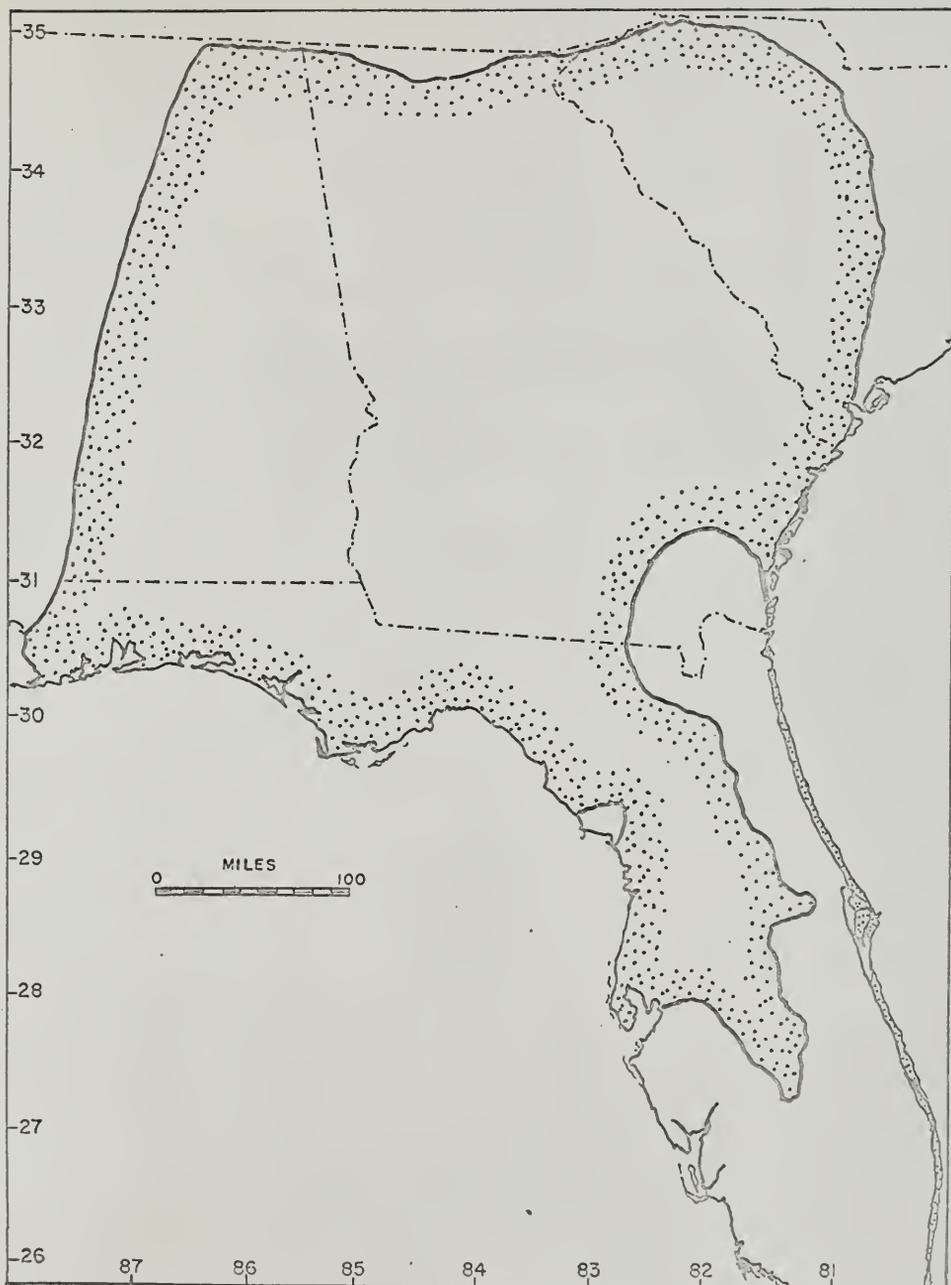
INTRODUCTION

The old-field mouse, Peromyscus polionotus, shows more variation in morphology within a limited geographical area than any other species in the genus (Blair and Howard, 1944; Hayne, 1950; Blair, 1951; Schwartz, 1954). The degree of divergence within a species is limited by the amount of genetic exchange between populations and by the nature and intensity of the selective pressures they are being subjected to (Dobzhansky, 1951; Mayr, 1963). This study represents an attempt to gain an understanding of some of the effects and interactions of variation, selection, and isolation as they relate to the intraspecific evolution of the old-field mouse.

Systematic relationships

Peromyscus polionotus is a small, semi-fossorial, nocturnal rodent of the subgenus Peromyscus and the maniculatus species group (Osgood, 1909; Blair, 1950; Hall and Kelson, 1959). It is endemic to the southeastern United States (Fig. 1) and may have been isolated from its parental stock, P. maniculatus, since the period of Pleistocene glaciations (Blair, 1950). There are two other species of Peromyscus in Florida, P. floridanus of the subgenus Podomys and P. gossypinus of the subgenus Peromyscus. Ochrotomys nuttalli is excluded because it is no longer considered a Peromyscus (Hooper and Musser, 1964).

Fig. 1. The approximate range of the old-field mouse,
Peromyscus polionotus, in the southeastern United States.



There are no known hybrids between species of different subgenera of Peromyscus. Peromyscus polionotus is able to hybridize with P. maniculatus in the laboratory, but it does not hybridize with P. gossypinus or P. leucopus (Dice, 1933; Watson, 1942; Dawson, 1965). Possible hybridization occurs in the field between P. maniculatus and P. leucopus (Waters, 1963) and between P. leucopus and P. gossypinus (Howell, 1921; Dice, 1940; McCarley, 1954; Golley, 1962). It appears that P. leucopus, P. gossypinus, P. maniculatus, and P. polionotus are closely related. Even if this were not the case, it is evident that P. polionotus is more closely related to P. gossypinus than to P. floridanus (Hooper and Musser, 1964). Despite the close relationship of P. polionotus to several other species, it can be easily identified as the smallest species of Peromyscus in the United States (Blair, et al., 1957, p. 708).

ECOLOGICAL ASPECTS

Collecting methods

Many species of Peromyscus spend the daylight hours in an underground nest. However, P. polionotus is exceptional among the semi-fossorial members of this genus in that it digs its own burrow and does not depend upon the chance occurrence of suitable shelters. The burrow entrances are conspicuous, thus, facilitating collection of these animals in the field (Sumner and Karol, 1929; Hayne, 1936; Smith, 1939; Rand and Host, 1942; Laffoday, 1957; Smith and Criss, in press).

Range of the old-field mouse

A revised range map was drawn up using the field data, as well as pertinent references (Chapman, 1893; Bangs, 1898a, 1898b; Osgood, 1909; Howell, 1921; Sumner, 1926; Sumner and Karol, 1929; Dice, 1934, Hayne, 1936; Coleman, 1939, 1948; Rand and Host, 1942; Moore, 1946; Ivey, 1949; Schwartz, 1954; Hall and Kelson, 1959; Golley, 1962), and data from specimens in the Florida State Museum. Collections were made in Florida, Georgia, and South Carolina in places where it was reasonable to expect that a sample of 20 adult animals could be taken (Table 1). Otherwise, the geographical location of the burrows was noted. The revised map differs from that of Hall and Kelson (1959) in several respects (Fig. 1). The mice occur as far

Table 1. Collecting locality and habitat

Locality	County	State	Location of Burrows	Predominant Vegetation
Lake Placid	Highlands	Florida	primarily road shoulders	scrub and orange groves
Vero Beach	Indian River	"	beach and road shoulders	sea oats
Lake Wales	Polk	"	road shoulders	turkey oak and orange groves
Haines City	"	"	"	"
Eustis	Lake	"	old-fields and road shoulders	orange groves and grassy fields
Ocala National Forest	Parts of Marion, Putnam and Lake	"	cleared fields and road shoulders	sand pine scrub
Citra	Dixie	"	"	turkey oak, long leaf pine and grassy fields
Junction of Highways 484 and 200	"	"	road shoulders	turkey oak
Inverness	Citrus	"	"	"
Zephyrills	Pasco	"	"	orange groves

Table 1. (continued)

Locality	County	State	Location of Burrows	Predominant Vegetation
Williston	Levy	Florida	cleared fields and road shoulders	crops and turkey oak
Manatee State Park	"	"	"	turkey oak and long leaf pine
Archer	Alachua	"	"	crops, turkey oak and long leaf pine
Newberry	"	"	"	"
Gainesville	"	"	"	crops and turkey oak
Cross City	Dixie	"	road shoulders	long leaf pine flatwoods
Bell	Gilchrist	"	cleared fields and road shoulders	crops, grassy fields, turkey oak and long leaf pine
Lake City	Columbia	"	"	grassy fields and long leaf pine
Falmouth	Suwannee	"	"	grassy fields and crops
Asheville	Jefferson	"	cleared fields	crops
Miccosukee	Leon	"	"	"

Table 1. (continued)

Locality	County	State	Location of Burrows	Predominant Vegetation
Thomasville	Thomas	Georgia	cleared fields	crops
Ludowici	Long	"	road shoulders	turkey oak
Claxton	Evans	"	cleared fields and road shoulders	grassy fields and crops
Savannah River Plant	Aiken	South Carolina	old-fields and road shoulders	turkey oak, long leaf pine and grassy fields
Allendale	Allendale	"	old-fields and cleared fields	grassy fields and crops
8 km south of Camden	Kershaw	"	cleared fields and road shoulders	grassy fields and long leaf pine

south as Highlands County in the central part of Florida, and they were not found in the Cedar Key area, nor around the Okefenokee Swamp, nor east of the Saint Johns River except on the sand dunes along the beach. The locality south of Camden, South Carolina, is a new range extension (Table 1, Fig. 1).

Ocala National Forest

The majority of the field work was done in the 146,497 hectare (362,000 acre) Ocala National Forest located on the Florida peninsula between Ocala and Daytona Beach. The area is bounded on north and west by the Oklawaha River, on the east by Lake George and the Saint Johns River, and by state highway 42 on the south. Parts of Marion, Putnam, and Lake County make up the forest. Approximately 184 km (115 miles) of paved roads and about four times as many maintained dirt roads lead through the forest. The grass on the road shoulders is mowed at regular intervals. About 99 percent of the specimens came from burrows on the road shoulders where they were concentrated and conveniently located.

To minimize the effects of sampling, mice were never taken twice from the same stretch of road within any six-month period. Some active burrows were not touched to insure repopulation of the area. Along one five-mile section of highway 316 between Eureka and Salt Springs, all the burrows were dug out and the occupants captured. New burrows were excavated on subsequent field trips. The approximate age, sex and reproductive status were recorded for each animal. Females that were perforate, pregnant, or lactating and males that had their testes in a scrotal position or sperm in the epididymes were considered sexually active. Sexual

inactivity was indicated by the absence of these conditions (also see Smith and Criss, in press).

Twelve to 36 occupied burrows of the old-field mouse were dug up in the Ocala National Forest plus or minus ten days from the first of each of the following months: December, 1962, April, July, August, September, October, November, and December, 1963, January, February, March, April, May, June, September, October, November, and December, 1964, January, February, March, April, July, August, September, 1965, and on May 15, 1965. The number of occupants, approximate age, sex and reproductive status of each occupant, presence or absence of a nest, or uneaten food, and other species of vertebrates and invertebrates in occupied burrows were noted. The temperature of the soil at the depth of the nest cavity was recorded for at least five occupied burrows each month. From July, 1963, to June, 1964, the temperature and occasionally the percent oxygen of the burrow air in the nest cavities were recorded. Oxygen concentration was measured with a Beckman oxygen electrode. Air temperatures and the percent oxygen in the nest cavity were obtained by taping the probes onto a two-foot rod and inserting it down the entrance tube into the nest cavity immediately after the sand plug was removed. The entrance tube was again closed with sand, and the readings were taken within three minutes. The dimensions of the five burrows were recorded during each of the 12 months. The angles between the horizontal plane and the escape tube as it left the nest cavity or the entrance tube just behind the sand plug were measured with a protractor and a level.

The mice sacrificed in the field were placed in a plastic bag and kept on ice. The width and length of the testes of each adult male were measured with a caliper; the epididymes were microscopically checked for sperm, and the length of the seminal vesicles were measured after the method of Jameson (1950). Females were checked for the presence of embryos.

Habitat relationships

Mice were collected in a variety of habitats primarily in north central Florida (Table 1). Monk (1965) divides the vegetation of this area into swamp forests, mixed deciduous and evergreen forests not periodically flooded, and pine forests. The mice were never found in swamp forests, nor in forests predominated by evergreen trees. The pine forests, which are fire sub-climaxes, are subdivided into sandhill, sand pine scrub, and pine flatwoods (Laessle, 1958a; Edmisten, 1963; Monk, 1965). The pine flatwoods frequently occur on poorly drained soils; sand pine scrub and sandhill are confined to well-drained upland soils. The mice were found in old-fields, cleared farmland, sand dunes along the beach, sand pine scrub, sandhill, and pine flatwoods (mostly long leaf pine) in decreasing abundance in the order listed.

Abundance is correlated with soil type, amount of soil drainage (Table 2), type and amount of vegetation. All of the habitats occupied by this species are characterized by sparse vegetation and relatively well-drained or recently plowed soils, except pine flatwoods. In this habitat, burrows were rarely found, and the mice were probably transients; no permanent popu-

Table 2. Relative abundance of mice as it relates to the physical and moisture retention data for some of the common soil types found in Florida. Soil data were taken from Stewart, et al. (1963) and Bryan (1960)

Soil Type	Hydraulic Conductivity (cm/hour)		Percent Water at 15 Atmospheres (Volume Percent)		Depth of Hardpan	Abundance of Mice
	Shallow Depth*	Deep Depth*	Shallow Depth*	Deep Depth*		
Saint Lucie Sand	138.4	173.0	2.2	2.1	none to 1.3 m	high
Lakewood Fine Sand	89.4	89.7	2.6	2.8	none to 2 m	moderate
Lakeland Sand	103.4	152.7	1.7	2.7	none to 2 m	high
Immokalee Fine Sand	41.1	5.6	3.0	5.4	.3 to .7 m	rare
Archer Fine Sand	13.2	20.4	3.1	20.4	none to 1.3 m	rare
Gainesville Fine Sand	24.1	81.3	5.4	4.5	none to 1.3 m	rare
Plummer Fine Sand	22.4	14.0	5.1	1.8	none to 1.3 m	none
Leon Fine Sand	5.1	20.1	11.9	1.9	.3 to .7 m	none
Saint Johns Fine Sand	32.2	1.8	8.6	9.2	.3 to .7 m	none

* shallow = 5 to 15 cm and deep = .6 to 1 m

lations were found in the pine flatwoods. An inverse relationship between the density of animals and the amount of ground cover may exist (Rand and Host, 1942).

Distribution of burrows and soil characteristics

Certain soil characteristics appeared to be important in limiting the distribution of mice. In relatively undisturbed habitats, the mice occurred primarily on fine sand including the well-drained, acid Saint Lucie, Lakewood, Lakeland, and Kershaw soils which have a low clay content, low moisture retention capacity, and high hydraulic conductivity (Stewart, et al., 1963; Table 2). Mice never occurred in high densities on poorly drained soils. In addition, they never constructed burrows in hard soils where digging was difficult, nor in areas where the hardpan was close to the surface of the ground.

Burrows were built on the sloping banks of sand dunes on the beaches. In the Ocala National Forest, they were usually found on the slopes of sand hills, probably remnants of old sand dunes (Laessle, 1958b; Fig. 3). Occasionally, they were located on the road shoulders at the top of these sand dunes but rarely in the low ground between the dunes.

Deposits of sorted sands have been laid down in several ways in Florida (Laessle, 1958b). Wind was an important agent along the beach dunes. The action of water was important along the flood plains of large rivers, the shore lines of lakes and small islands, and submerged offshore bars. All areas above the current water level were at one time part of the Florida shoreline. As the water level fell during glacial periods, numerous

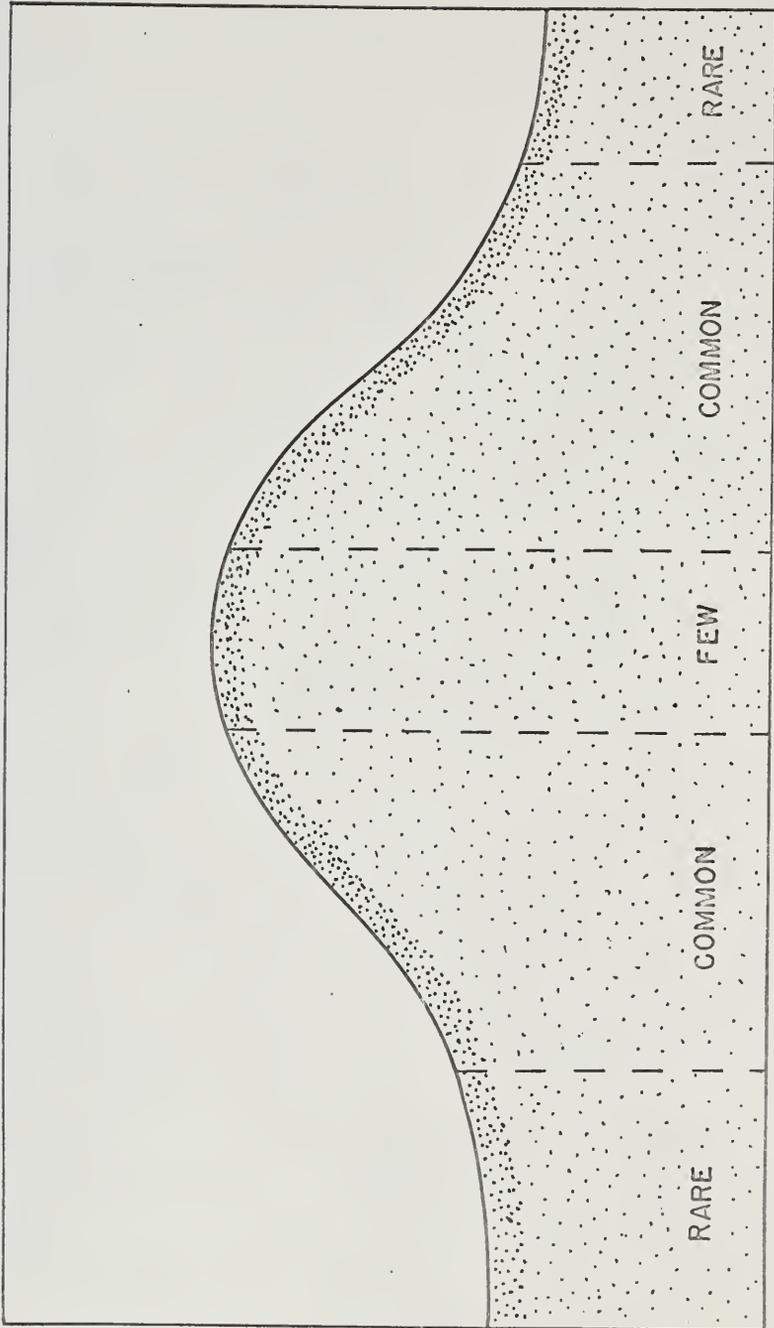


Fig. 2. Relative abundance of burrows on different parts of old sand dunes in the Ocala National Forest.

deposits of fine textured sand were gradually exposed. Their continuity was later destroyed by erosion (Alt and Brooks, 1965). These deposits and their associated vegetation are frequently widely spaced with the intervening habitat unsuitable for the old-field mouse. These interrupted sand deposits are ecological islands for this species.

Description of an average burrow

Over 1,500 occupied burrows were excavated. An average burrow consists of an entrance tube, nest cavity, and escape tube (Fig. 3). The three parts are aligned almost in a single vertical plane with the nest cavity in the center. The entrance tube, closed with a sand plug of 12.8 ± 1.3 cm (range: 2.5 to 61 cm; means are given plus or minus one standard error), levels off horizontally before reaching the nest cavity. The escape tube ends a few centimeters below the surface of the ground under or near a clump of grass. The angle of descent of the entrance tube at a point just behind the sand plug is $38.2^\circ \pm 1.8^\circ$ (range: 24° to 48°) from the horizontal. The escape tube's ascending angle as it leaves the nest cavity is $64.3^\circ \pm 2.1$ (range: 44° to 79°). There is a significant positive correlation between these two angles ($r = .86$, $df = 59$, and P less than .01; statistical methods were adapted from Steel and Torrie, 1960). Mice tend to dig a shallow or a steep escape tube depending upon whether the entrance tube was shallow or steep, respectively.

The volume of each part of the burrow was calculated by assuming it was a cylinder, which shape they did approximate.

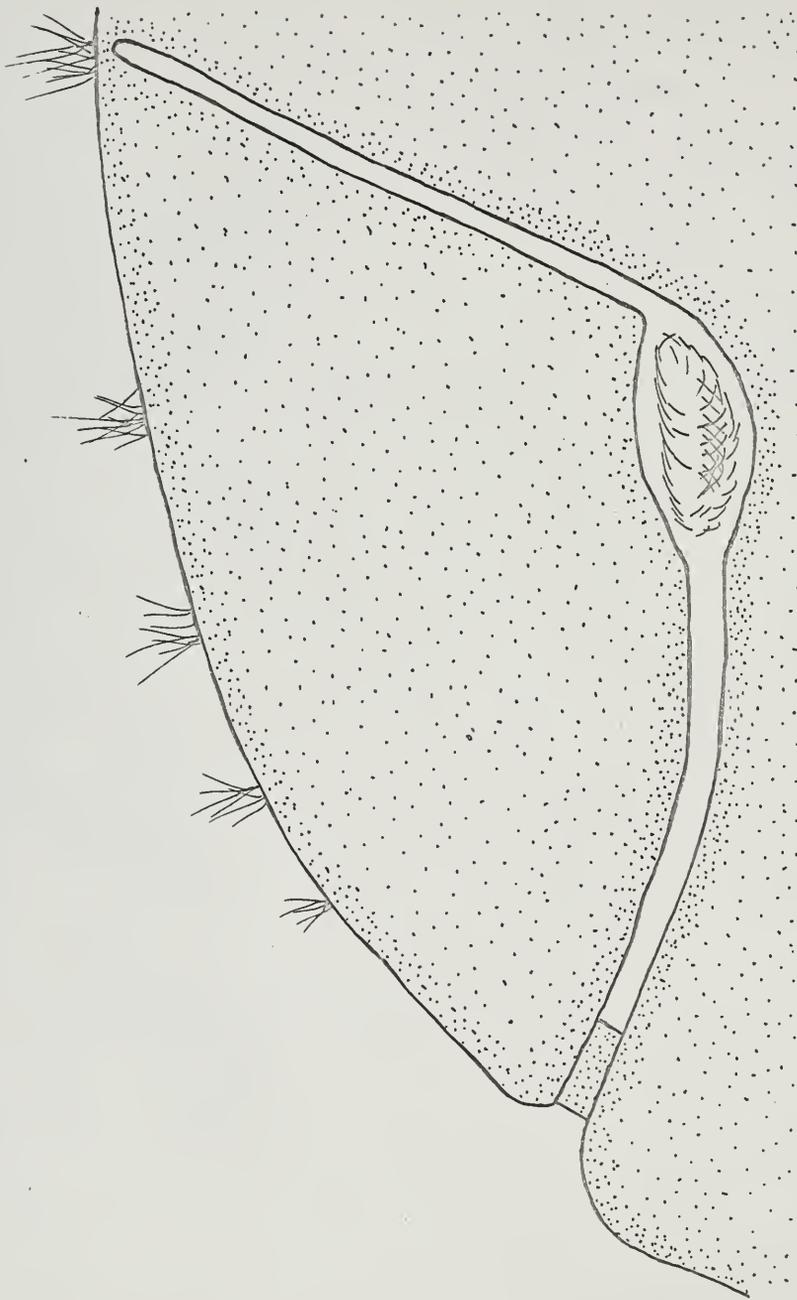


Fig. 3. Lateral view of the burrow of the old-field mouse, Peromyscus polionotus.

The formula was $V = \pi D^2 L / 4$, where V is the volume, D the diameter of the tube, and L its length. The escape tube (102.1 ± 6.8 cm) is almost twice as long as the entrance tube (68.1 ± 3.7 cm) and about ten times the length of the nest cavity ($10.7 \pm .4$ cm). The sum of the three volumes minus the volume of the sand plug is equal to the volume of gas in the burrow which averaged $4,046 \pm 231.8$ cc.

Local variation of burrows

The slope of the ground and the presence of underground obstacles were the primary physical factors which altered the profile of the burrows. Abrupt changes in the course of the burrows were correlated with changes in the slope of the ground. They normally went toward the high ground in the same direction as the slope at the surface of the ground. This variation was common along road shoulders where the direction of slope changed 90° within a few centimeters. Burrows also curved around obstacles, such as roots, and then continued in their previous direction.

Many times adjacent burrows deviated from the average in the same way, e.g., two escape tubes or a very large nest cavity. On three different occasions, several fresh burrows were excavated in a limited area and only one female, molting from the juvenile to the subadult pelage, was captured. No other burrows were found in the immediate vicinity, and each of the excavated burrows had two escape tubes. Once a solitary adult male was captured in one of five fresh burrows in which each of the escape tubes curved back toward the entrance. On

another occasion, an adult female with a litter was found in one of three fresh burrows which all had the escape tube coming off the entrance tube at its junction with the nest cavity. It seemed likely that each captured mouse had constructed all of the burrows in its area, and that each one consistently displayed its own individual peculiarity.

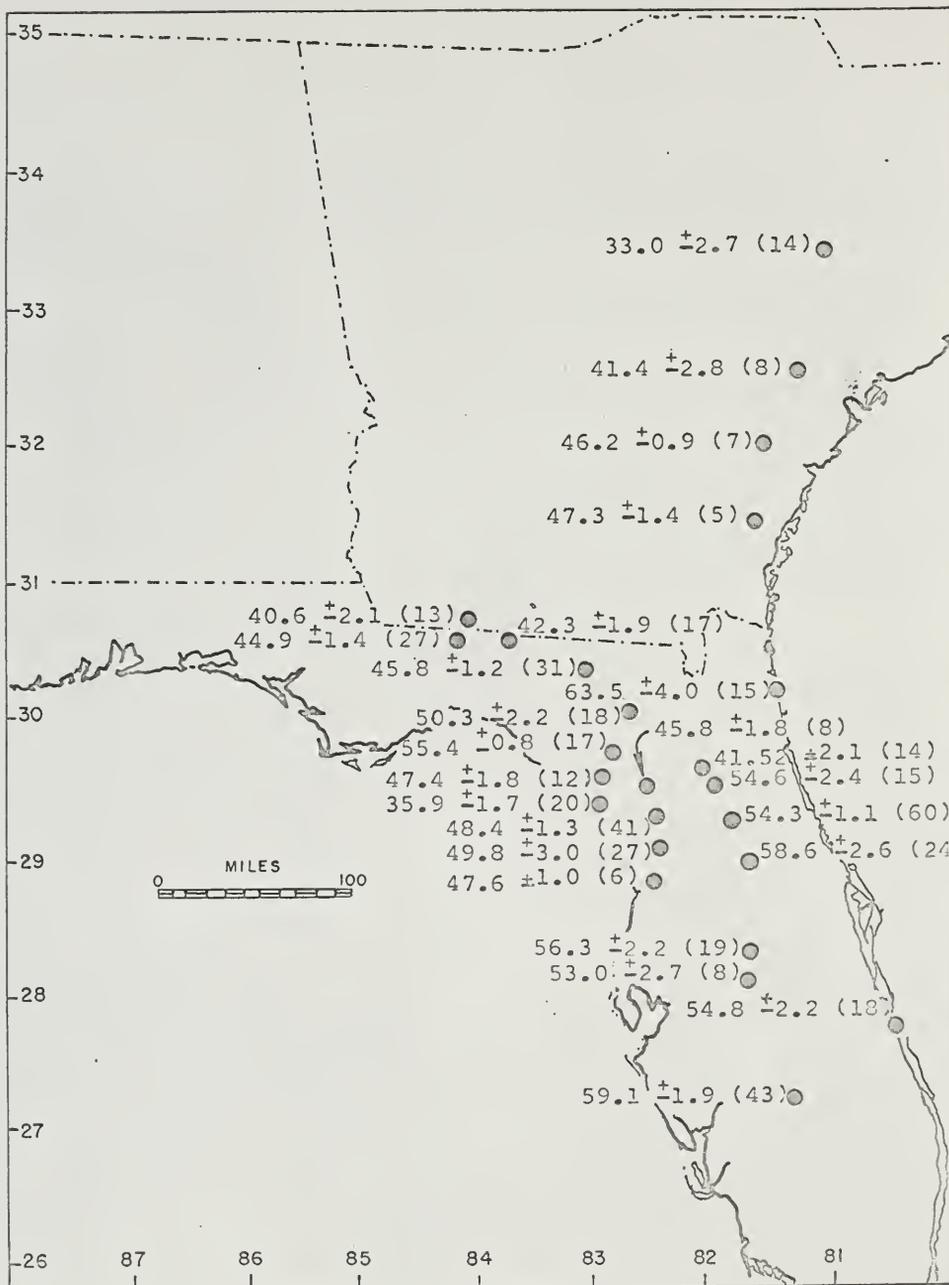
Geographical variation in the depth of the burrow

Only quantitative differences were found between the burrows at the different localities. The depth of the nest cavity is discussed here; it was measured from the bottom of the nest cavity to the closest surface of the ground (Fig. 4). At certain places, e.g., Manatee Springs, Florida, the depth of the nest cavity was limited by the depth of the hardpan, but at most localities, e.g., south of Camden, South Carolina, the hardpan was much deeper than the deepest nest cavity. The shallowness of these burrows may be explained by variation in some other soil characteristics, possibly clay content, which may influence the rate of diffusion of respiratory gases through the soil (Penman, 1940).

Depth of the nest cavity and seasonal temperature fluctuations

With the seasonal variation in soil temperature greater at shallower depths than at deeper ones, the nest cavities were located just deep enough to take advantage of the maximum damping effect of the soil on these seasonal ambient temperature fluctuations (Fig. 5). The difference between the seasonal temperature fluctuations at the average depth of the nest cavity and at a point twice this deep was less than 1°C. Diurnal fluctuations are also negligible at this depth (Vorhies, 1945; Schmidt-Nielsen

Fig. 4. The distance from the bottom of the nest cavity to the surface of the ground at various localities. Mean values are given plus or minus the standard error. The number of burrows at each locality is given in parentheses.



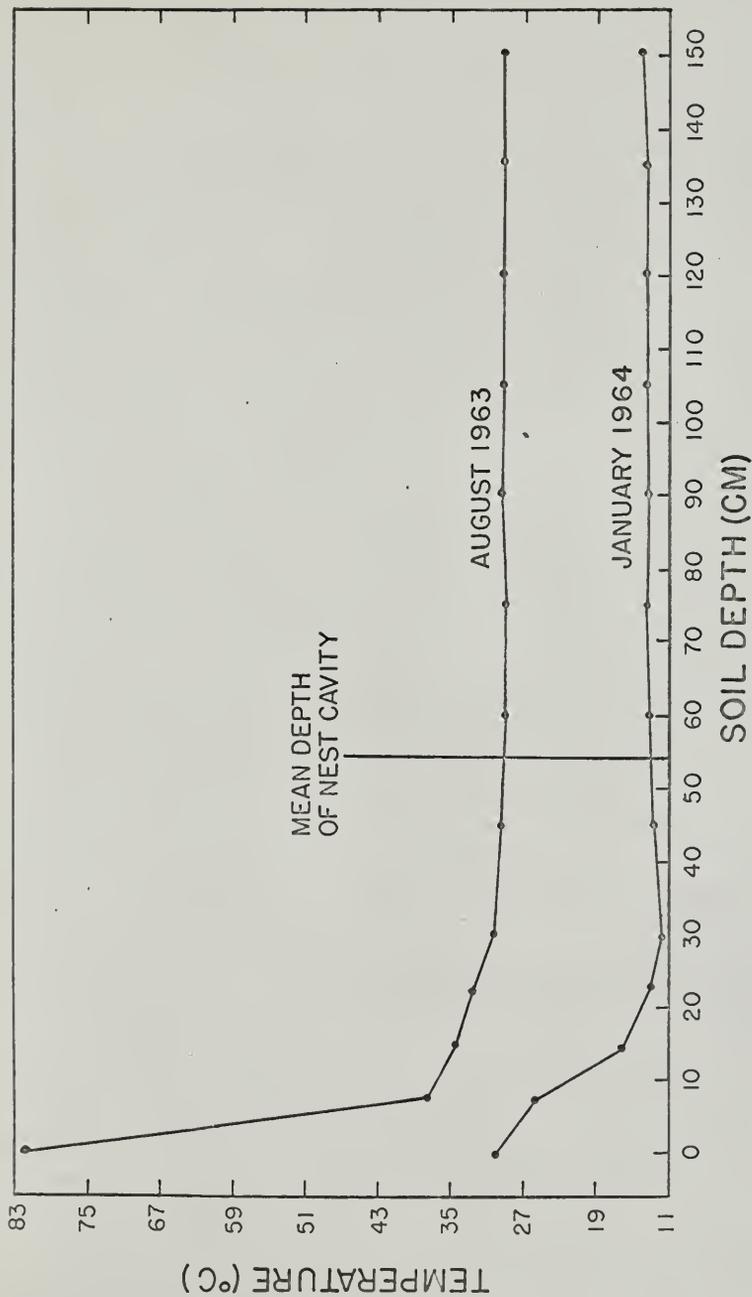


Fig. 5. Temperature at various depths and at two different times of the year. These months were chosen because they show the maximum variation in temperature recorded at the surface of the ground and the typical shape of the winter and summer curves.

and Schmidt-Nielsen, 1950; Petter, 1952; Prakash, et al., 1965). Digging a deeper burrow would not provide the mice with a more constant thermal environment, but this would require them to expend more energy and increase the layer of soil through which the respiratory gases must diffuse.

Ambient temperature and rainfall

The soil temperature at the depth of the nest cavity showed significant positive correlations with the mean monthly air temperature in the nest cavity and above ground at Ocala, Florida ($r = .999$, $df = 11$, and P less than $.01$ and $r = .902$, $df = 28$, and P less than $.01$, respectively; Anonymous, 1962, 1963, 1964, 1965; Fig. 6). The air in the nest cavity ranged from 12° to 34°C , and it averaged 1.0°C higher than the soil temperature at this same depth in both occupied and unoccupied burrows. This indicates that the temperature difference was not due to heat produced by the mice, nor by decay of organic matter. It was approximately the same in the summer when little or no organic matter was found in most of the burrows.

During this study, the air temperature and rainfall at Ocala averaged $.3^{\circ}\text{C}$ lower and $.3$ cm greater, respectively, than expected in an average year (Fig. 7). A significant positive correlation existed between the amount of rainfall (Y) and the mean air temperature (X) for each month ($r = .425$, $df = 30$, and P less than $.05$; Fig. 8); the equation of the regression line was $Y = .78X - 3.6$. The magnitude of the monthly deviations in rainfall and air temperature were not correlated ($r = .203$, $df = 30$, P greater than $.05$), but there was a significant tendency

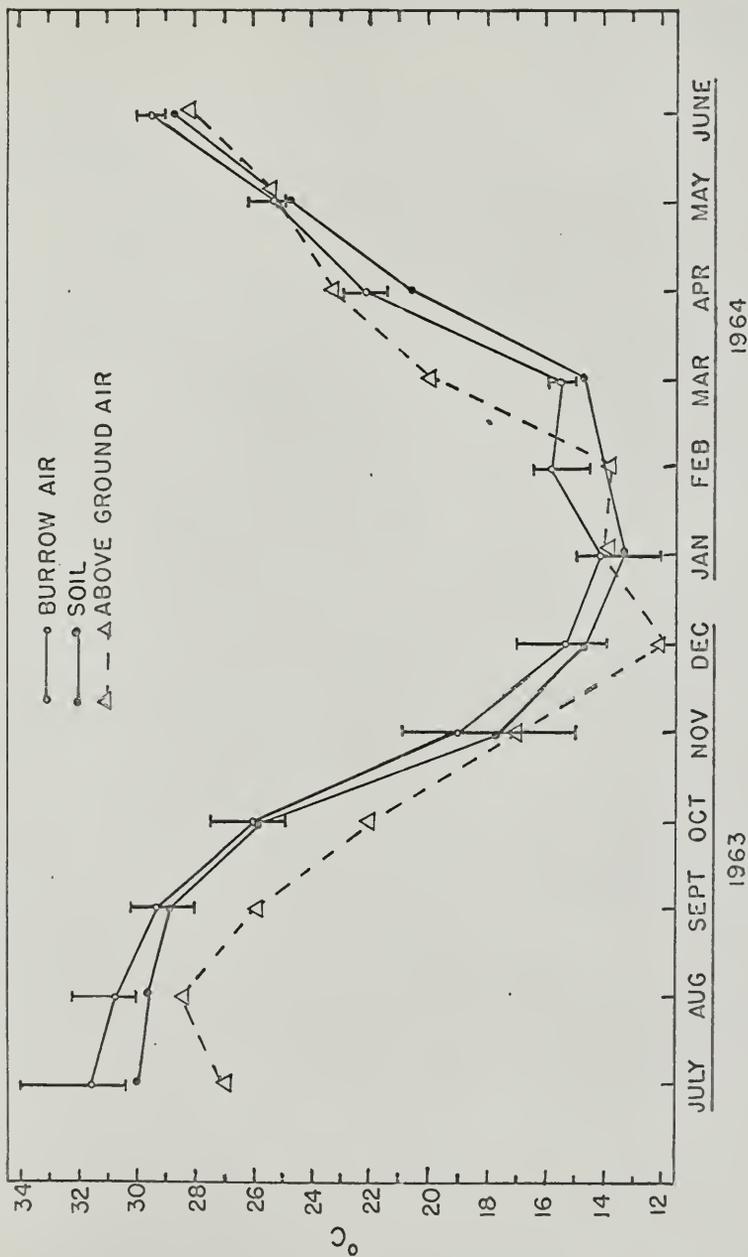
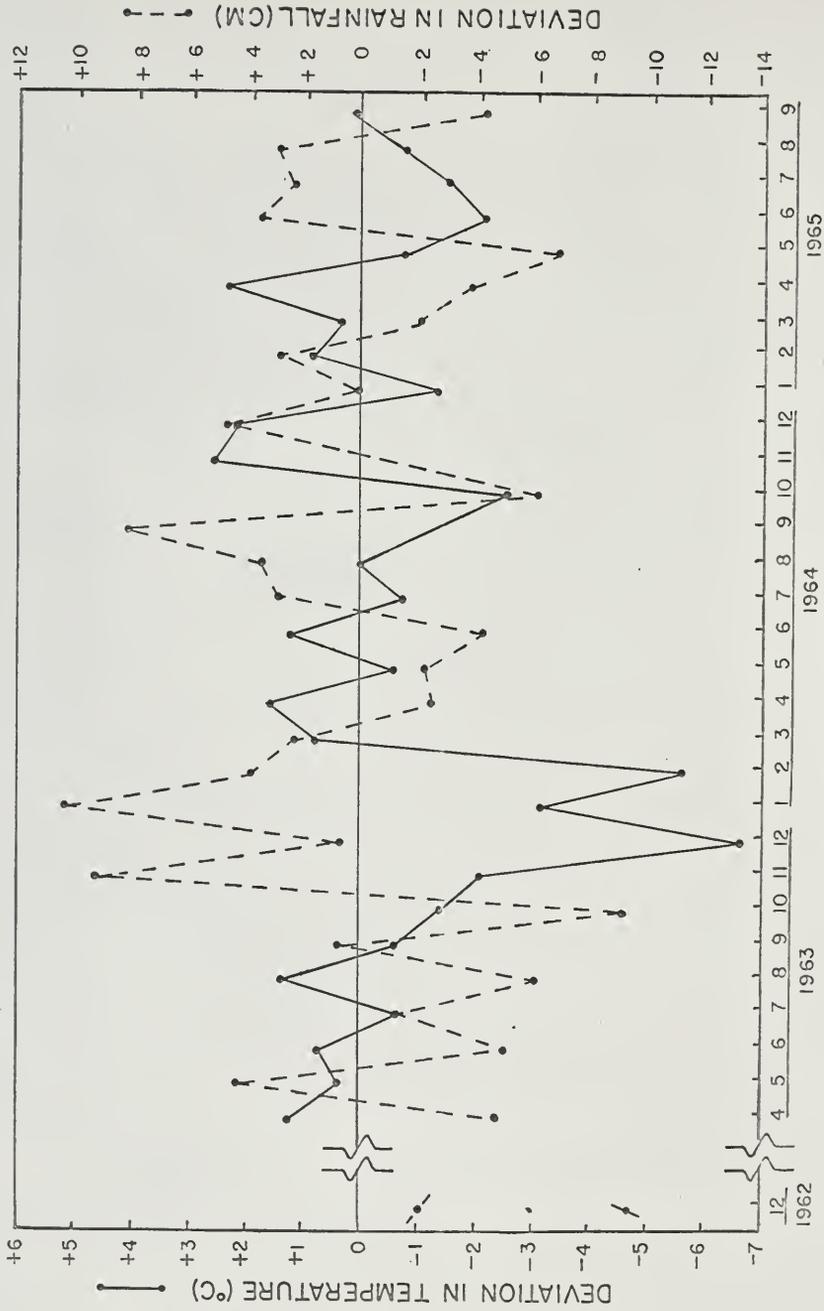


Fig. 6. The range and mean temperature of the air in the nest cavity and the mean temperatures of the soil at the depth of the nest cavity and the air above ground in the Ocala National Forest.



MONTHS AND YEARS

Fig. 7. Air temperature (above ground) and rainfall deviations from the expected values as calculated by the United States Weather Bureau for Ocala, Florida.

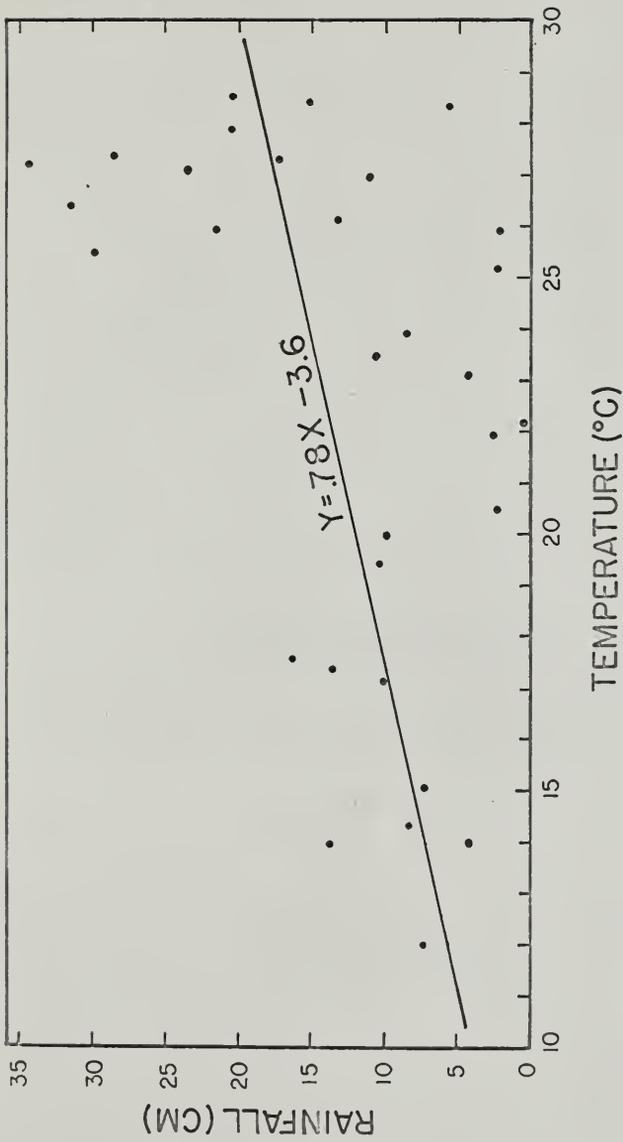


Fig. 8. The regression of the amount of rainfall on the temperature of the air above ground each month in the Ocala National Forest.

for the deviations to occur in opposite directions (Chi square = 3.98, df = 1, and P less than .05; Fig. 7). Seasonal increase in rainfall was associated with higher temperatures but rainfall greater than the monthly average was associated with air temperatures lower than the monthly average, and vice versa.

Other species in burrows

Invertebrates found within occupied burrows or in the entrance tube outside the sand plug, and vertebrates in unoccupied burrows were identified (Table 3). The only animal that was regularly found in burrows with old-field mice was the camel cricket. It builds small lateral tunnels off the sides of the escape tube. The crickets have to avoid the mice since they are readily eaten by them. Two blind cricket-locusts were also found with the mice. Both of these species have also been reported from pocket-gopher burrows (Hubbell, 1936, 1940; Hubbell and Goff, 1939). The commensal relationship between Typhloceuthophilus floridanus and Geomys was thought to be obligatory (Hubbell, 1940). This cannot be true since the collecting sites of the two specimens were both far from the nearest Geomys burrow.

A number of vertebrate species inhabited abandoned burrows. Coachwhips were the most frequently encountered species of snake. All of the snakes found in burrows, except the common hognose and the eastern diamondback rattlesnake, were shedding. Two species of mice, Mus musculus and P. gossypinus, used the unoccupied burrows. The house mice occurred in the burrows only on farmlands. The same was true for the least shrew and the eastern mole. The P. gossypinus were found in one burrow in the sand

Table 3. Animals found in burrows occupied (O) or unoccupied (U) by old-field mice. The invertebrates in unoccupied burrows were not identified

Species	Number of Specimens		Burrow		Part of Burrow Inhabited
	U	O	U	O	
<u>Invertebrates</u>					
Camel Cricket (<u>Ceuthophilus latibuli</u>)		numerous	X	X	escape tube
Blind Cricket-locust (<u>Typhlocyba floridana</u>)		2	-	X	escape tube
Black Widow (<u>Latrodectus mactans</u>)		numerous	X	-	entrance opening
Shore Spider (<u>Pardosa milvina</u>)		1	-	X	nest cavity
Thin-legged Wolf Spider (<u>Pardosa floridana</u>)		1	-	X	nest cavity
Carolina Wolf Spider (<u>Lycosa carolinensis</u>)		numerous	X	X	entrance opening
<u>Vertebrates</u>					
Florida Gopher Frog (<u>Rana arsolata</u>)		numerous	X	-	all parts but mostly entrance tube
Southern Toad (<u>Bufo terrestris</u>)		8	X	-	same as above
Oak Toad (<u>Bufo quercicus</u>)		6	X	-	same as above
Six Lined Racerunner (<u>Cnemidophorus sexlineatus</u>)		numerous	X	X	lateral tunnels off first part of entrance tube
Florida Scrub Lizard (<u>Sceloporus woodi</u>)		5	X	X	entrance tube outside sand plug

Table 3. (continued)

	Number of Specimens	Burrow U	Burrow O	Part of Burrow Inhabited
Fence Lizard (<u>Sceloporus undulatus</u>)	1	X	-	same as above
Coachwhip (<u>Masticophis flagellum</u>)	39	X	-	nest cavity
Red Rat Snake (<u>Elaphe guttata</u>)	21	X	-	nest cavity
Black Racer (<u>Coluber constrictor</u>)	1	X	-	nest cavity
Garter Snake (<u>Thamnophis sirtalis</u>)	1	X	-	nest cavity
Coral Snake (<u>Micrurus fulvius</u>)	1	X	-	nest cavity
Indigo Snake (<u>Drymarchon corais</u>)	1	X	-	nest cavity
Scarlet King Snake (<u>Lampropeltis doliaata</u>)	1	X	-	nest cavity
Eastern Diamondback Rattlesnake (<u>Crotalus adamanteus</u>)	1	X	-	nest cavity
Common Hognose (<u>Heterodon platyrhinos</u>)	2	X	-	nest cavity
Least Shrew (<u>Cryptotis parva</u>)	6	X	-	nest cavity
Eastern Mole (<u>Scalopus aquaticus</u>)	2	X	-	nest cavity
House Mouse (<u>Mus musculus</u>)	numerous	X	-	nest cavity
Cotton Mouse (<u>Peromyscus gossypinus</u>)	2	X	-	nest cavity

pine scrub habitat within the Ocala National Forest.

Food

Peromyscus polionotus is omnivorous like the other species of Peromyscus that have been investigated (Jameson, 1952; Connell, 1959; Williams, 1959). No attempt was made to identify all of the various foods eaten by the mice but the more conspicuous items found in the nest were identified (Table 4). Many different types of organisms were offered to hungry mice in the laboratory (Table 5). They ate all of them except the toads. Live animals, such as cockroaches, were frequently fought over and seemed to be preferred over most seeds. In the field, more fragments of nuts and seeds were found in the nests than animal parts. Most of the plant material consisted of empty shells which do not decay as fast as other materials.

Table 4. List of food items commonly found in nest cavities

Plant MatterAcorns from Myrtle Oak (Quercus myrtifolia)Acorns from Chapmans Oak (Q. chapmani)Acorns from Sand Live Oak (Q. virginiana)Acorns from Turkey Oak (Q. laevis)Seeds from Partridge Pea (Cassia fascioulata)Animal Matter*

Beetles (several types); Carabidae and others unidentified

Beetle Larvae in Acorns; Curculioninae (Balaninus sp.)

Lepidopterans; Danaidae, Pieridae and others unidentified

Eastern Lubber Grasshopper (Romalea microptera)

Grasshoppers (several other types); Locustidae

Dragonflies (several types); Aeschnidae

*the animals were all partly eaten so complete identification was usually impossible.

Table 5. List and number of live animals placed into cages with hungry old-field mice

Species	Number	Fate
<u>Invertebrates</u>		
Black Widow (<u>Latrodectus mactans</u>)	4	eaten
Carolina Wolf Spider (<u>Lycosa carolinensis</u>)	3	"
American Cockroach (<u>Periplaneta americana</u>)	numerous	"
German Cockroach (<u>Blatella germanica</u>)	"	"
Camel Cricket (<u>Ceuthophilus latibuli</u>)	"	"
Blind Cricket-locust (<u>Typhloceuthophilus floridanus</u>)	1	"
Common Field Cricket (<u>Gryllus assimilis</u>)	8	"
Eastern Lubber Grasshopper (<u>Romalea microptera</u>)	3	"
<u>Vertebrates</u>		
Southern Toad (<u>Bufo terrestris</u>)	6	not eaten
Oak Toad (<u>Bufo quercicus</u>)	5	"
Six Lined Racerunner (<u>Cnemidophorus sexlineatus</u>)	3	eaten
Scrub Lizard (<u>Sceloporus woodii</u>)	2	"
Cotton Mice (1 day old) (<u>Peromyscus gossypinus</u>)	4	"
Florida Deer Mice (1 day old) (<u>P. floridanus</u>)	3	"
Old-field Mice (1 day old) (<u>P. polionotus</u>)	4	"

SUBSPECIFIC CROSSES AND ASSORTATIVE MATING

The degree of isolation between various species and subspecies of Peromyscus is highly variable. In some areas, genetic exchange is minimal between different subspecies, while in others, hybridization occurs frequently between recognized species (Howell, 1921; Dice, 1933 and 1940; Dice and Liebe, 1937; Watson, 1942; Blair, 1944; Liu, 1953a and 1953b; Harris, 1954; McCarley, 1954; Barbehenn and New, 1957; Sheppe, 1961; Golley, 1962; Waters, 1963; Dawson, 1965). The results of this interbreeding are important in determining the evolutionary course of the factors influencing genetic exchange at the population and subspecific levels in P. polionotus.

Laboratory colony

During 1962 and 1963, 64 pairs of mice, as they were captured in the field, were used in the laboratory for breeding stock. Occasionally, one escaped or died and had to be replaced; additional pairs were added to the colony. Four Florida subspecies were represented in the laboratory colony, P. polionotus subgriseus from Ocala National Forest, P. p. phasma from Anastasia Island, Saint Johns County, P. p. leucocephalus from Santa Rosa Island, Okaloosa County, and P. p. rhoadsi from Archbold's Biological Station, Highlands County.

The mice were kept in cages similar to those described

by Layne (1958); the sides were made of one-quarter inch hardware cloth and the wood tops were removable. Each cage was placed on a tray covered with sawdust.

The ambient temperature in the laboratory was $24^{\circ} \pm 2^{\circ}\text{C}$ most of the time; occasionally it varied as much as 5°C . Relative humidity was measured with a sling psychrometer at different times during the day and night; it varied from 54 to 84 percent. Overhead fluorescent lights were automatically turned on at 0630 and off at 2030; no outside light entered the room. Purina laboratory chow and water were supplied ad lib.

Laboratory-reared mice gradually replaced the wild stock. Matings of first generation animals were set up with mice from different parental lines but the same subspecies. Litter size and data of birth were recorded for each litter born in the laboratory. After November, 1964, the shelf position of each cage was maintained constant for 11 months to study possible synchronization in reproductive activity.

Subspecific crosses

Crosses were made between P. p. subgriseus and the other three subspecies, P. p. phasma, P. p. rhoadsi, and P. p. leucocephalus. The F_1 from the P. p. subgriseus by P. p. phasma cross were used to produce an F_2 and were backcrossed to P. p. subgriseus (Table 6).

The differences between the various crosses were significant in regards to the number of pairs producing young and the number of young that survived weaning. The interdependence of the treatments was relatively low (Table 6). The initial

Table 6. Analysis of crosses within and between different subspecies of Peromyscus polionotus. The matings included sexually active adults born and reared in the laboratory unless otherwise noted. Wild animals were paired in the laboratory in the same combinations in which they were captured in the field. Only data from pairs that remained together for at least three months during the fall, winter or spring are listed below

Subspecific Crosses	Producing Pairs*		Not Producing Pairs**		Dead Before Weaning		Alive After Weaning	
	Number	Percent	Number	Percent	Number	Percent	Number	Percent
Wild <u>subgriseus</u> (s) X Wild s	44	75.9	14	24.1	14	5.6	236	94.4
s X s	28	53.9	24	46.1	53	15.3	294	84.7
<u>Phasma</u> (p) X p	3	25.0	9	75.0	3	12.5	21	87.5
s X p	3	16.7	15	83.3	25	43.9	32	56.1
s-p X s-p	2	20.0	8	80.0	10	43.5	13	56.5
<u>Rhoadsi</u> (r) X r	9	45.0	11	55.0	10	15.9	53	84.1
s X r	3	16.7	15	83.3	9	18.8	39	81.2
<u>leucocephalus</u> (l) X l	2	40.0	3	60.0	0	0.0	12	100.0
s X l	1	20.0	4	80.0	0	0.0	6	100.0

* Chi square = 40.39, 8 df, P less than .005

** Chi square = 73.29, 8 df, P less than .005

statistics were used as justification for the more detailed analysis presented in Table 7.

More pairs of the same subspecies produced young with a greater chance of surviving weaning than did the pairs formed of different subspecies (Chi squares = 10.20 and 16.37, $df = 1$, and P less than .01, respectively). This was largely due to a decrease in reproductive success in crosses between P. p. subgriseus and P. p. phasma (Chi squares = 5.68 and 32.17, $df = 1$, and P less than .05 and .01, respectively) and partially, to those between P. p. subgriseus and P. p. rhoadsi (Chi squares = 6.96 and .387, $df = 1$, and P less than .05 and greater than .90, respectively). Survival of the young from the latter cross did not show a significant decrease as it did in the former. There were not enough crosses involving P. p. leucocephalus to adequately interpret this subspecies' fertility relationships with P. p. subgriseus. The F_2 from P. p. subgriseus by P. p. phasma also showed a breakdown in reproductive success compared to that of the parental stocks; the decrease in the number of pairs producing young approached significance (Chi square = 3.47, $df = 1$, and P was greater than .05 but less than .10). A significant decrease was observed in the postnatal survival of the young (Chi square = 13.73, $df = 1$, and P less than .01).

The reproductive success of the P. p. subgriseus was higher for wild animals than for those reared in the laboratory (Chi square = 5.32 and 10.70, $df = 1$, and P less than .05 and .01, respectively). Two factors could have accounted for this difference, the degree of antagonism between paired mice and

Table 7. Detailed statistical comparisons of the results from the crosses presented in Table 6. Some of the comparisons are interdependent but the associated increases in the P values were not enough to alter the significance of the Chi square values at the level indicated (.05=* and .01=**)

Crosses Compared	Statistics					
	Number of Pairs Producing Young or Not Producing Young		Number of Young Dead Before Weaning or Alive After Weaning			
	df	Chi Square	df	Chi Square	df	Chi Square
<u>subgriseus</u> (s) X s : <u>phasma</u> (p) X p***	1	3.25	1	2.49		
sXp : s X s and p X p	1	5.68*	1	32.17**		
s-p X s-p : s X s and p X p	1	3.47	1	13.73**		
s X s : <u>rhoadsi</u> (r) X r	1	0.453	1	0.0151		
s X r : s X s and r X r	1	6.96*	1	0.387		
s X s, p X p, r X r and <u>leucocephalus</u> (l) X l: s X p, s X r and s X l	1	10.20**	1	16.37**		
s X s : p X p, l X l and r X r	1	2.22	1	126.3**		
s X s : Wild s X Wild s	1	5.32*	1	10.70**		

***all of the comparison except the last one involve only laboratory-reared mice

their general level of activity or both. The wild mice were paired under natural conditions which allowed them to express individual preferences in selecting a mate. The pair-bonds between some of the laboratory-reared mice may have been weak because they were forced to stay together. This effect probably accounted for at least part of the decrease in reproductive performance.

Laboratory-reared mice were more active than wild mice in captivity. The subspecific hybrids were extremely agile. When their cages were cleaned, they frequently jumped out. Following the birth of a new litter, females normally spend considerable amounts of time in the nest. The laboratory-reared mice spent less time in the nest taking care of their young than did the wild animals, and the same was true for the hybrids in relation to the other laboratory stocks (Table 8). The time spent caring for the young decreases as the females spend more time out of the nest. Neglected young show higher mortality rates during the postnatal period than do those that are adequately cared for. The differences between the reproductive success of the various stocks seem to be correlated with the females' activity pattern; the more active females give less care to their young.

The importance of heredity is pointed out by the differences between the subspecific hybrids and their parental stocks reared in the laboratory. Differences between mice reared in the laboratory and in the field and between field-reared mice that have been in the laboratory for varying lengths of time emphasize the importance of the environment. Wild mice that had lived in the laboratory for a long time are more active than freshly caught animals.

Table 8. The number of times females were observed in or out of their nest on the second, third, and fourth nights following the birth of a litter. All observations were made with the aid of a red light within two hours after the overhead lights went off in the colony room. Chi square = 19.7 and P was less than .01

	Laboratory-reared F_1 from <u>P. P. subgriseus</u> X <u>P. P. phasma</u>	Laboratory-Reared <u>P. P. subgriseus</u>	Wild <u>P. P. subgriseus</u>
Number of Females	3	14	12
Number of Litters	6	17	18
Number of Times in Nest	6	30	45
Percentage of Times in Nest	16.2	47.6	60.8
Number of Times Out of Nest	31	33	29
Percentage of Times Out of Nest	83.8	52.4	39.3

Inheritance of white cheeks

According to Blair (1944), the inheritance of white cheeks in the old-field mouse is controlled by a single gene with the alleles W_C and w_C . The homozygous recessive type has brown cheeks ($w_C w_C$). The description of each phenotype is based on the color of the hair directly under the eye. The percentage of white cheek in the various populations is given in Fig. 9. The Anastasia Island population of *P. p. phasma* is 100 percent white-cheeked, and 8.1 percent of the Ocala population of *P. p. subgriseus* are white-cheeked. Several crosses were made between these two subspecies (Table 9). The lack of a significant difference between the observed and expected number of progeny with each phenotype proves again that this trait is based on one gene with two alleles.

Assortative matings

The effects and interactions of natural selection, differential migration, mutation rate and genetic drift determine gene frequencies. Assortative mating can also influence gene frequency indirectly by altering the phenotypic composition of a population. The occurrence of assortative matings in a natural population would be indicated if the frequencies of the pair bonds between the different phenotypes differed significantly from those expected in a panmictic population. If the phenotype was controlled by a single gene with two alleles, one dominant and the other recessive, the expected frequencies resulting from the pairing of two recessive phenotypes, or a dominant and a recessive one, or two dominant phenotypes should equal the frequency of the recessive phenotype squared (R^2), $2(1-R)(R)$, and $(1-R)^2$, respectively (Li, 1961).

Fig. 9. Geographical variation in the percentage of mice with white cheeks. Only samples of 15 or more mice are included.

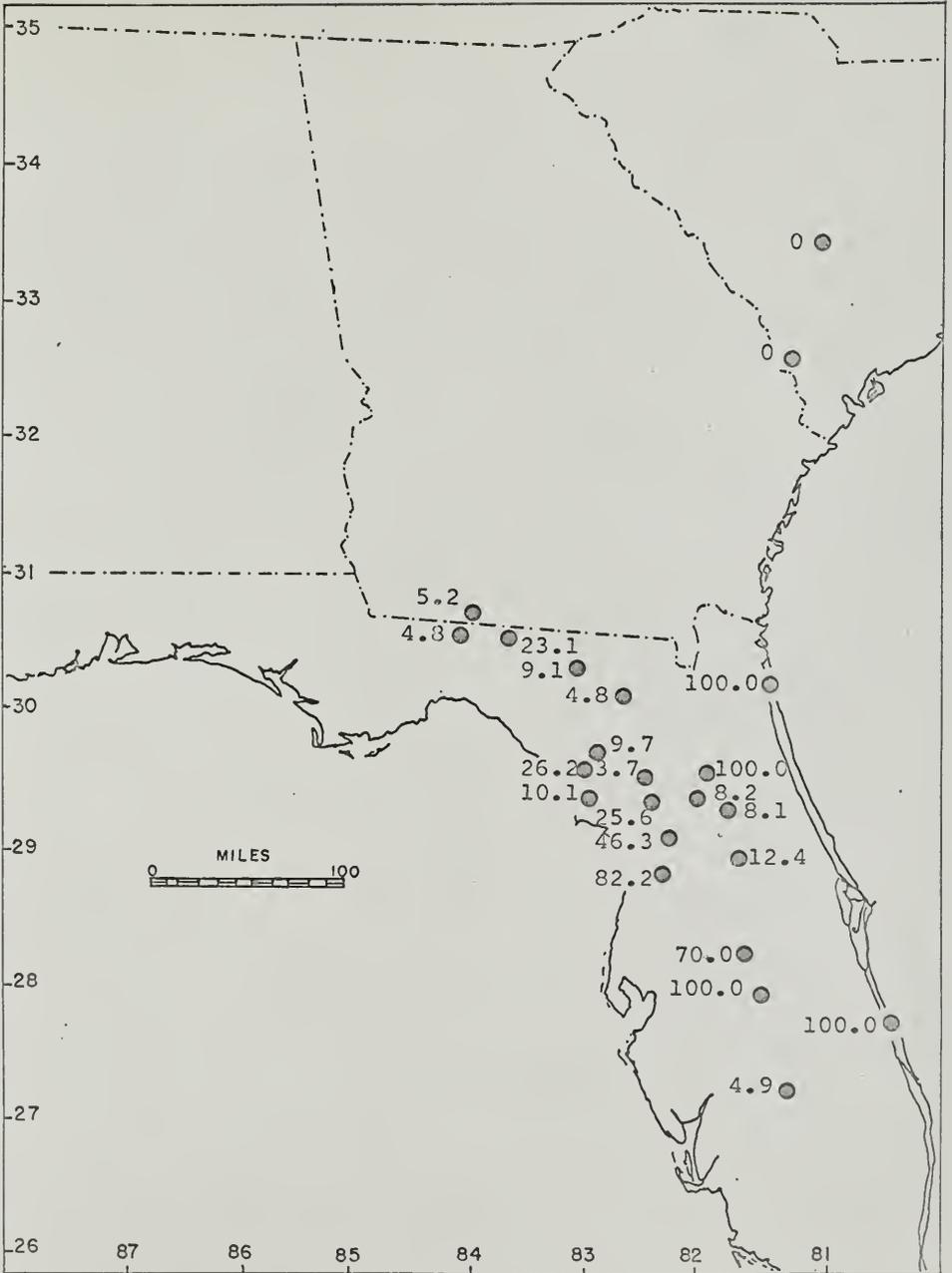


Table 9. Inheritance of white cheeks in Peromyscus polionotus. The expected values for the statistical analysis were calculated by assuming that the inheritance of the trait was due to a single gene with two alleles, w_c and w_C

Cross Phenotype X (Subspecies)	Phenotype (Subspecies)	Number of Litters	Number of Progeny				Chi Square
			Observed White Cheek	Observed Brown Cheek	Expected White Cheek	Expected Brown Cheek	
White (<u>phasma</u>)	X White (<u>phasma</u>)	6	21	0	21	0	0
Brown (<u>subgriseus</u>)	X Brown (<u>subgriseus</u>)	39	0	168	0	168	0
White (<u>phasma</u>)	X Brown (<u>subgriseus</u>)	7	32	0	32	0	0
White F ₁ (<u>phasma</u> X <u>subgriseus</u>)	X White F ₁ (<u>phasma</u> X <u>subgriseus</u>)	4	13	6	9.5	9.5	0.95
White F ₁ (<u>phasma</u> X <u>subgriseus</u>)	X Brown (<u>subgriseus</u>)	5	13	9	11	11	0.40

The "white cheek" trait can be used as a marker to determine the existence and extent of assortative mating in populations in which the frequency of the trait is not 0 or 100 percent. The sample size necessary to test the existence of assortative mating becomes extremely large as the frequency of the trait approaches either 0 or 100 percent. Only two of the populations that were sampled met the requirements of adequate sample size and intermediate phenotypic frequencies. These were P. p. subgriseus from the Ocala National Forest and P. p. rhoadsi from the Highlands County, Florida (Table 10). The same phenotypes paired more often, and unlike phenotypes paired less often than expected if the populations were panmictic. The differences were significant for both populations; the mice did not select their mates at random.

Two factors could account for the assortative mating in these populations. Mice may select their mates on the basis of cheek color or they inbreed within family groups. The following experiment was performed to distinguish between these two alternatives. Females with brown cheeks were housed together either with a brown-cheeked male from the same litter and with a white-cheeked non-sibling male or with a white-cheeked male litter-mate and with a brown-cheeked non-sibling male. None of the mice had bred before, and they were isolated from each other for one month before being placed together. The white-cheeked non-sibling males were assumed to be homozygous dominant ($W_C W_C$). Their parents had white cheeks and were descendants of white-cheeked mice that had produced at least 15 offspring, all of

Table 10. The frequency of mice with white or brown cheeks and the observed and expected number of paired mice with these phenotypes in the Ocala National Forest and at Archbold's Biological Station in Highlands County, Florida. Expected values were calculated from the observed phenotypic frequencies and Yates's correction for continuity was used in the Chi square analysis of the data for the population from Highlands County to compensate for the small sample size of some cells

	Ocala Population		Highlands Population	
	Observed	Expected	Observed	Expected
Frequency of White Cheek	9.1%	-----	4.9%	-----
Frequency of Brown Cheek	91.9%	-----	95.1%	-----
Number of White X White and Brown X Brown	266	243.4	42	38.1
Chi Square		2.10		.40
Number of White X Brown	20	42.6	0	3.9
Chi Square		11.99		2.96
Total	286	286.0	42	42.0
		14.09**		3.36*

* P approximately .07

** P less than .005

which were white-cheeked. The white-cheeked litter mates were heterozygous. The phenotypes of the mice in the first litter produced by each brown-cheeked female were recorded (Table 11).

The preliminary analysis revealed a significant difference among the frequencies of the various matings that occurred (Chi square = 8.63, $df = 3$, and P less than .05). Two additional statistical comparisons were made to determine the factor which contributed most to the difference. Females mated with siblings significantly more often than expected (Chi square = 7.73, $df = 1$, and P less than .05), but they showed no preference for a particular cheek color (Chi square = .64, $df = 1$, and P greater than .50). This supports the hypothesis that assortative mating in the field populations resulted from inbreeding.

Calculation of inbreeding coefficient

Gene frequencies were calculated for the Ocala population. The breeding histories of 38 wild white-cheeked mice from this locality were extensive enough to determine their genotypes. The mice were selected at random from the field population and were crossed to brown-cheeked mice. The occurrence of a single brown-cheeked offspring proved heterozygosity of the white-cheeked parent. The smallest number of offspring used to prove the homozygosity of a white-cheeked mouse was 14. Five of the white-cheeked mice were homozygous dominant and 33 were heterozygous. The expected values calculated from the observed phenotypic frequencies, assuming the population to be panmictic, were .8 homozygous dominant and 37.2 heterozygous. The differences between the observed and expected values were significant (Chi

Table 11. The number of times brown-cheeked females mated with brown-cheeked siblings, white-cheeked non-siblings, white-cheeked siblings and brown-cheeked non-siblings. The choice always involved either the first two possibilities or the latter two and no combinations thereof. Expected values were calculated for the Chi square analysis by assuming the null hypothesis. They had to be adjusted for the choice involving the heterozygous white-cheeked sibling because a certain percentage of the litters sired by this animal would contain all brown-cheeked offspring, and thus, would be counted for the brown-cheeked non-sibling

Mating Choice of Brown-Cheeked Females	Number of Matings		Chi Square
	Observed	Expected	
Brown-Cheeked Sibling ($w_C w_C$)	22	16.5	1.78
White-Cheeked Non-Sibling ($w_C W_C$)	<u>11</u>	<u>16.5</u>	<u>2.75</u>
Sub Total	33	33.0	4.53*
White-Cheeked Sibling ($W_C w_C$)	26	19.4	2.25
Brown-Cheeked Non-Sibling ($w_C W_C$)	<u>17</u>	<u>23.6</u>	<u>1.85</u>
Sub Total	43	43.0	4.10*
Grand Total	76	76.0	8.63*

*significant at the .05 level

square = 17.48 with Yate's correction for continuity applied to the analysis, $df = 1$, and P less than .01). The conclusion drawn from these results is that inbreeding occurred in the field population or that the heterozygotes were at a selective disadvantage or both. There is no evidence to support or contradict the second possibility. The results agree with the earlier conclusion about inbreeding in the field population, and they allow the calculation of F , the inbreeding coefficient (Wright, 1951; Li, 1961).

The number of homozygous dominant mice ($D_{O1} = 5$) divided by the total number of white-cheeked mice in the laboratory (38) equals the relative frequency of this genotype.

$$(1) \frac{D_{O1}}{D_{O1} + H_{O1}} = \frac{5}{38} = .13158.$$

H_{O1} is the number of heterozygotes in the laboratory sample. This frequency should be the same in the field population. The actual frequency of the homozygous dominant genotype (D_{if}) in the inbreeding field population can be calculated by

$$(2) D_{if} = .13158 \times N_{Wc}$$

N_{Wc} is the observed frequency of the white-cheeked mice in the field population. For the Ocala population,

$$(3) N_{Wc} = .081 \text{ (Table 10).}$$

Substituting this value in (2):

$$(4) D_{if} = .13158 \times .081 = .01068.$$

$$(5) D_{if} + H_{if} = N_{Wc} = .081$$

H_{if} is the frequency of heterozygotes in the inbreeding field population. Substituting the calculated value of D_{if} into (5) gives

$$(6) H_{if} = .081 - .01068 = .07034.$$

$$(7) D_{if} + H_{if} + R_{if} = 1 \text{ or}$$

$$(8) R_{if} = 1 - D_{if} - H_{if} = .9190,$$

where R_{if} is the frequency of the homozygous recessive genotype in the inbreeding field population. Gene frequencies are calculated by

$$(9) p = \frac{2D_{if} + H_{if}}{2} = .047 \text{ and}$$

$$(10) q = \frac{2R_{if} + H_{if}}{2} = .953,$$

where p and q are the frequencies of the dominant (w_c) and recessive (w_c) genes, respectively. In addition,

$$(11) p^2 = D_{ofc} = (.046)^2 = .0021,$$

$$(12) q^2 = R_{ofc} = (.954)^2 = .9101 \text{ and}$$

$$(13) 2pq = H_{ofc} = 2(.046)(.954) = .0878.$$

D_{ofc} , R_{ofc} , and H_{ofc} are the expected genotypic frequencies calculated for the field population if it were panmictic (Li, 1961). In the inbreeding field population

$$(14) D_{if} = D_{ofc} + F_{pq},$$

$$(15) H_{if} = H_{ofc} - 2F_{pq} \text{ and}$$

$$(16) R_{if} = R_{ofc} + F_{pq}.$$

Adding (14) and (15) gives

$$(17) D_{if} + H_{if} = D_{ofc} + H_{ofc} - F_{pq}.$$

This reduces to

$$(18) F = \frac{.00888}{.04388} = .202.$$

A large number of parent-offspring matings in addition to many matings between siblings had to occur to account for these

results. The F was very high for a naturally occurring population. A large F means that the selective pressures against certain recessive genes will be much more effective in altering gene frequencies because the recessive lethals and semi-lethals will be expressed more often than if F were smaller. This reduces the amount of hidden genetic variation within the population.

Howard (1949) estimated that up to 10 percent of the matings in *P. maniculatus* involved either a parent and its offspring or siblings. Even a figure twice this minimal estimate could not account for an $F = .202$. The calculated level of inbreeding was also much higher than would have been predicted from the results of the experiments in which the females had a choice of mating with a sibling or a non-sibling male. One factor that may help explain this difference was the high rate of population turnover (p 107). Unless a mouse disperses a long distance, it might have to breed with a related animal or not breed at all during its short life. The laboratory mice were also isolated for one month prior to the mating preference test. Siblings would not ordinarily be separated for long period in the field if they were going to breed with each other.

The magnitude of the error associated with F is not known, but a small change in the number of homozygous dominant mice found in the breeding experiments causes a large fluctuation in F . For example, seven homozygous dominant mice instead of five increases F from .202 to .278, which is a 37.7 percent increase. For this reason, the confidence intervals for F are large.

Greater confidence would require that the genotypes of a larger number of white-cheeked mice be determined. Even though the exact value of F may differ from that calculated, it is clear that a considerable amount of inbreeding occurs in the Ocala National Forest population and probably in the Highland's County population. This may be characteristic of the old-field mouse.

REGULATION OF BODY TEMPERATURE

Ambient temperature is one of the most important factors in the environment of mammals. The energy required for the maintenance of a constant body temperature is increased at low ambient temperatures. Many mammals partially avoid this problem by lowering their temperature during the period of inactivity (e.g., see Morrison, 1962; Morrison and McNab, 1962; Morrison and Ryser, 1962). Greater efficiency in utilizing available energy is important especially when several closely related forms are sympatric.

The lack of a significant difference between the temperature of the air in the nest cavities of occupied and unoccupied burrows (p 22) suggest that P. polionotus reduces its rate of metabolism and body temperature during the day or that the soil absorbs heat rapidly. Mice in the laboratory do show a diel body temperature cycle with a mean maximum value of 38.3°C at 0400 and a mean minimum of 36.2°C at 1600 (Smith and Criss, in press). This small temperature difference does not seem sufficient to account for the lack of heat accumulation in the burrow. The burrow temperatures occasionally went as low as 12°C. It was first thought that these low temperatures might induce the mice to go into daily hypothermia, but the regulation of body temperature in the laboratory was the same at high and

low ambient temperatures (Smith and Criss, in press). The preliminary conclusion is that the mice become torpid in their burrow but are not doing this in response to low ambient temperatures.

Torpidity in the field

Almost all of the attempts to capture and record the body temperature of torpid mice failed for two reasons. First, the mice can raise their body temperature rapidly when their burrow is excavated. Secondly, the mice do not normally drop their body temperature to a level equal to that of their environment. A dry nest was almost a perfect indicator of mice in the escape tube. When it was slightly warmer than the surrounding soil, it was even a better clue. The nest must be slightly warmer than the air in the burrow to stay dry because the relative humidity in the nest cavity is close to 100 percent. Nests in unoccupied burrows were always damp. The mouse was the only source of heat which could account for this difference.

Torpid mice have been found in the field twice. Sixteen adult mice, four groups of four each, were captured on January 29, 1966. Their body temperatures, measured with a small animal probe connected to a Yellow Springs telethermometer, averaged $12.8^{\circ} \pm .3^{\circ}\text{C}$, while the temperature of the soil at the depth of the nest cavity averaged $10.5^{\circ} \pm .1^{\circ}\text{C}$. The probe was lubricated with glycerine and inserted into the anus to a depth of 2 cm. Shortly after their capture, twelve of the mice became active and their body temperatures quickly returned to normal. The four inactive animals were placed singly in jars

with perforated lids in an ice box on top of the ice. At the end of one hour, two of the mice were jumping at the top of their jars trying to escape. The body temperatures of the remaining two animals were 5.3° and 3.6°C . One of them was left in the ice box for three additional hours. At the end of this time, it started moving slowly and its body temperature had gone up to 8.0°C . Half an hour later, the animal jumped around the jar, and its body temperature was 39.2°C . All of the torpid animals were sacrificed one week after their capture. These results show that the mice can go into torpor in the field, but they give no clues as to the causes.

Torpor and availability of food

When food is supplied ad lib. in the laboratory, mice do not drop their body temperature in response to low ambient temperatures (Smith and Criss, in press). The availability of food may be the important factor which determines their response in this situation. This possibility was investigated with 24 wild adult mice from Archer, Florida. Each animal was isolated from the others. Half of them were fed ad lib. during their first night in the laboratory; the other half had no food. Water was supplied ad lib. to both groups. The body temperature of each animal was measured the following morning. Food was then given to all of the animals. None of the mice died.

The groups with food and without food had mean body temperatures of $37.8^{\circ} \pm 1.1^{\circ}\text{C}$ and $29.3^{\circ} \pm 2.8^{\circ}\text{C}$, respectively. Most of the starved animals had body temperatures very close to the ambient temperature. While I was taking the body tempera-

tures of the first few animals, some of the remaining mice seemed disturbed by my presence. This may have caused the difference between the mean body temperature of the starved animals and the ambient temperature (24°C). The mice responded to the lack of food by reducing their body temperature down to or slightly above the ambient temperature.

Peromyscus eremicus also reduces its temperature in the absence of food, but dies when their body temperature falls below 16°C. MacMillen (1965) suggests that they are not subjected to temperatures lower than this during their period of inactivity because they nest at a shallow depth in the soil during the winter. The sun increases the temperature during the day at these depths and the mice are active at night. The old-field mouse is subjected to lower temperatures during the day because they nest deeper in the ground.

Concentration of respiratory gases and torpor

Smith and Criss (in press) suggested that mice in closed burrows reduce their metabolic rate to reduce gas exchange which might become critical were they to continue metabolizing at a high rate. Their observations failed to substantiate this, primarily because the experimental animals were kept in an open room with good ventilation rather than in a confined space like a burrow. The normal concentrations of these gases can be maintained in the nest cavity only by diffusion. Under certain conditions the ratio of oxygen to carbon dioxide in the air of the burrow should be decreased due to the

respiration of the mice. Oxygen concentration of the air in the nest cavities of occupied burrows varied from 15.0 to 20.5 percent and averaged 18.4 percent.

The metabolic rates of 18 wild P. polionotus and 12 P. leucopus were determined at various concentrations of oxygen. The P. leucopus, which were included for comparison with P. polionotus, were laboratory-reared descendants of animals that were originally caught near Chapel Hill, North Carolina. Half of the P. polionotus and all of the P. leucopus were tested in a half quart canning jar (about 100 cc) and the rest of the P. polionotus were tested in a quart canning jar (about 200 cc). The oxygen electrode and the temperature probe were inserted through the lid of a canning jar with their sensitive ends inside the closed jar. The bottle was submerged in a constant temperature water bath after placing an animal inside. The mouse stood on a wire mesh platform two centimeters above the floor of the jar (Fig. 10). Percent oxygen in the bottle and activity of the mouse were recorded every five minutes until the animal stopped breathing or until the oxygen reached 2 percent of the gas in the bottle. Activity was visually recorded as inactive, active, or very active.

The P. leucopus were tested at $24^{\circ} \pm 1^{\circ}\text{C}$. The P. polionotus were tested at $10^{\circ} \pm 1^{\circ}\text{C}$ and $24^{\circ} \pm 1^{\circ}\text{C}$. At 24°C , the metabolic rate of P. polionotus was determined with and without a carbon dioxide absorbent in the jar. Carbon dioxide was absorbed in the other experiments by pellets of soda lime in a screen container placed inside the jar. The rectal

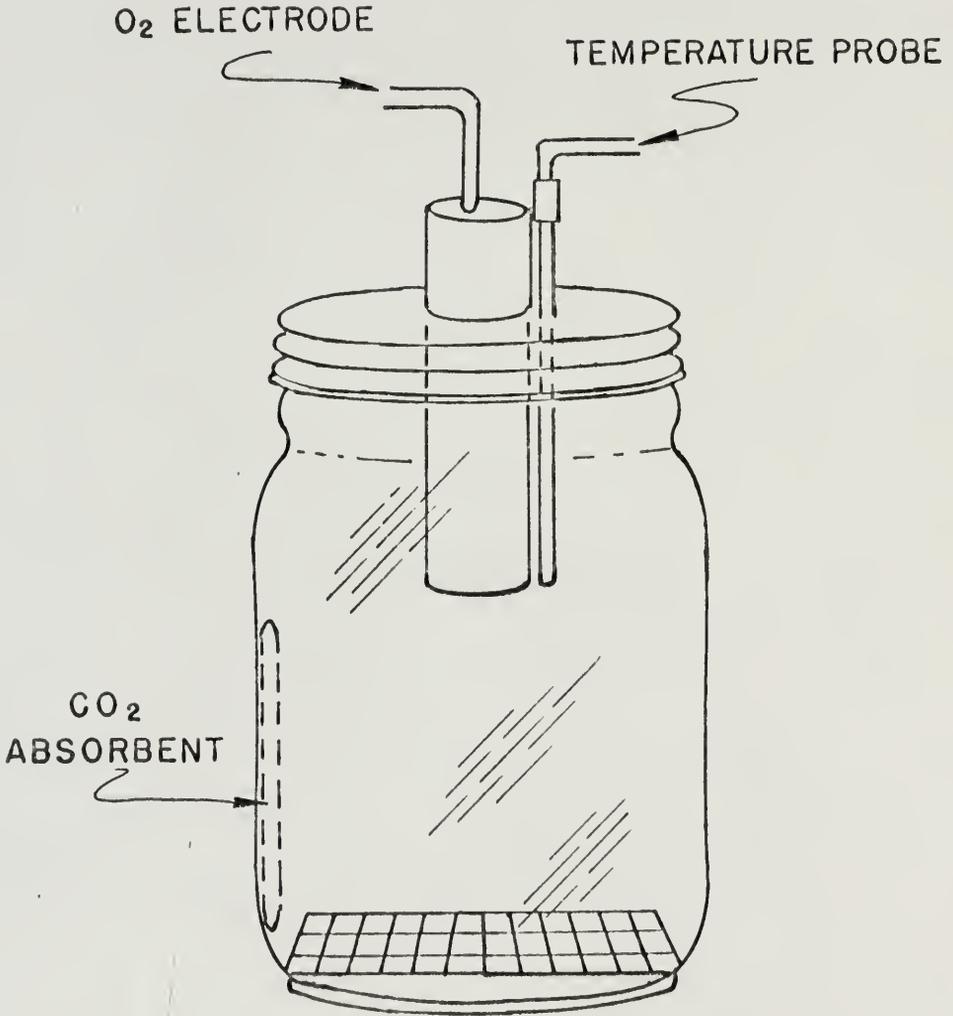


Fig. 10. Metabolism apparatus.

temperature of each mouse was taken at the end of each recording session and was also recorded five times at each ambient temperature for P. polionotus at 14 percent oxygen.

The expected basal rate of metabolism (BMR) was calculated using the equation $BMR = 3.4W^{.25}$ (equation derived from Kleiber, 1961). The metabolic rate was given in cubic centimeters of oxygen per gram per hour. W was the weight of the animal in grams. The percent of the expected BMR of inactive P. polionotus and P. leucopus at the different oxygen concentrations are given in Figs. 11 and 12. The metabolic rates of active or of very active animals are excluded from the data presented in these figures. The only exception to this was that all of the values for P. polionotus below 9 percent oxygen were included. There was still considerable variation in the rate of metabolism and this was probably due to differences in the activity levels of the various animals which were considered to be inactive. There appeared to be no significant differences between the metabolic rates of the P. polionotus tested in the 100 cc or 200 cc jars, or at 24° or 10°C, or with or without a carbon dioxide absorbent.

All of the P. leucopus died when the oxygen had reached 4 to 5 percent. The P. polionotus survived in a 2 percent oxygen atmosphere and appeared normal after this experience. Several of these animals were saved for breeding stock and have since reproduced. The body temperatures of the P. leucopus at 4 to 5 percent oxygen and the P. polionotus at 2 percent oxygen approximated the ambient temperature. At 14 percent oxygen, the P. polionotus had an average body temperature of 26.8°C at an

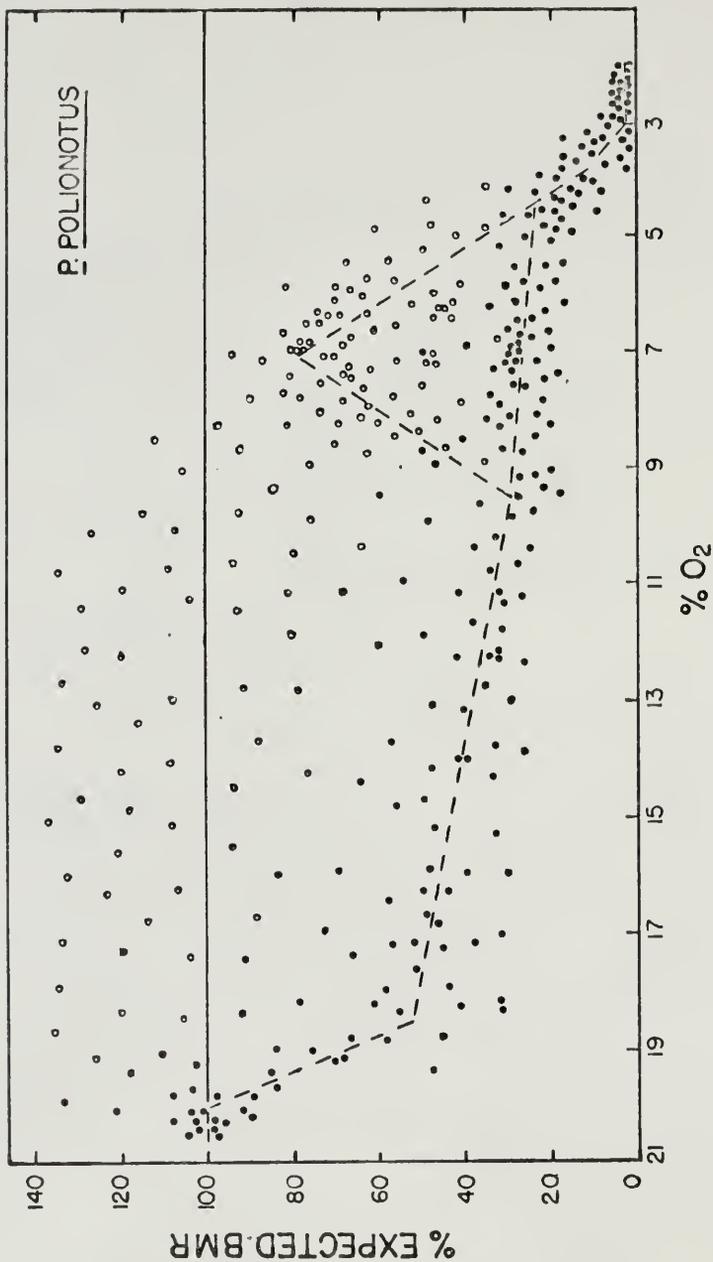


Fig. 11. Metabolic rates of active (open circles) and inactive (solid circles) *Peromyscus polionotus* at various oxygen concentrations. All of the animals survived down to 2 percent oxygen at which time the experiment was terminated. Values higher than those given above were also recorded.

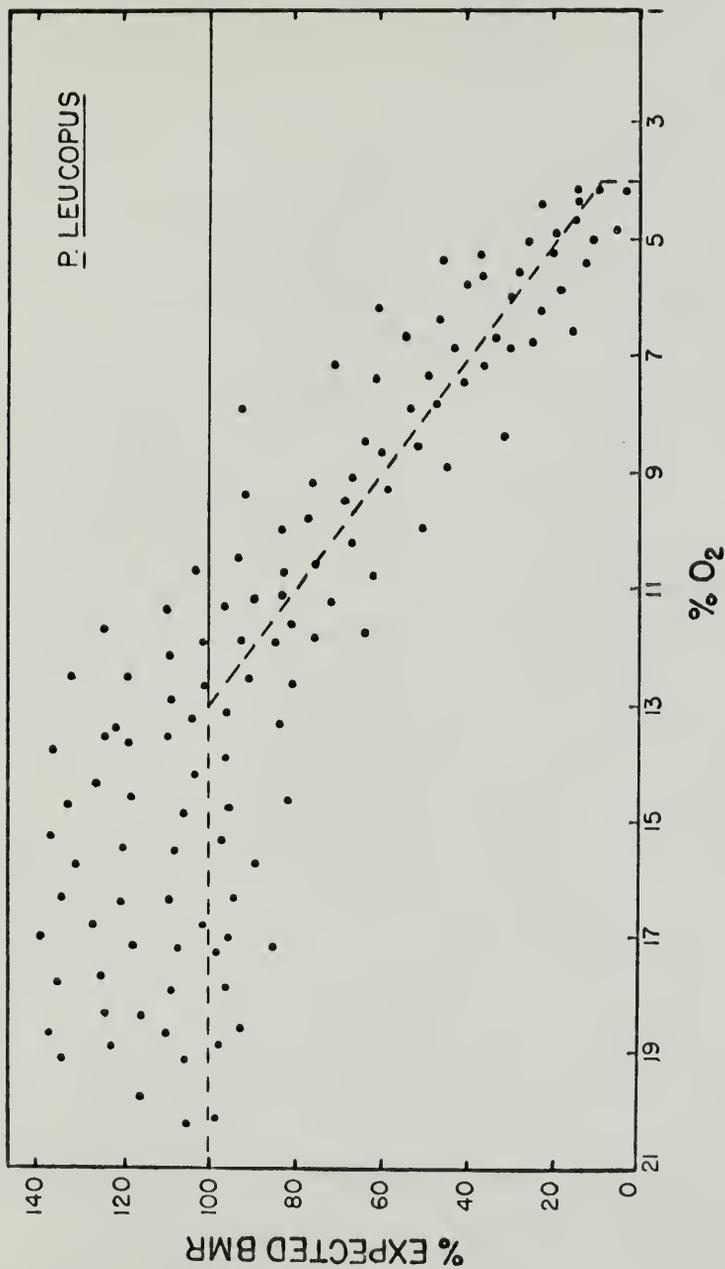


Fig. 12. Metabolic rates of Peromyscus leucopus at different oxygen concentrations. Values higher than those given above were also recorded. None of the mice survived below 4 percent oxygen.

ambient temperature of 24°C and 12.8°C at an ambient temperature of 10°C.

Peromyscus leucopus maintained a metabolic rate of about 100 percent of its expected BMR down to approximately 13 percent oxygen and then was no longer capable of maintaining it. The steady decline in its rate of metabolism below 13 percent oxygen was correlated with the decreases in oxygen concentration. In this range, the mice were probably not able to fully load their hemoglobin with oxygen.

Peromyscus polionotus dropped its rate of metabolism to about 55 percent of the expected BMR between 18 to 19 percent oxygen. Its metabolic rate declined to about 30 percent of the expected BMR at 9 to 10 percent oxygen. At this point, it either continued to decline or showed an abrupt increase. All mice showed decreasing metabolic rates below 7 percent. Between 4 to 5 percent oxygen there was a sharp decrease in the metabolic rate. Very active *P. polionotus* had metabolic rates over 100 percent of the expected BMR between 18 to 10 percent oxygen and chose between activity and inactivity down to about 7 percent oxygen. The sharp increase in metabolic rate around 9 to 10 percent oxygen probably represented an alarm reaction, which could function under adverse conditions by getting the mice to leave their burrow before they became suffocated. Peromyscus polionotus efficiently loaded its hemoglobin down to a concentration of 8 percent, which was much lower than the comparable figure of 13 percent for *P. leucopus*.

Structural variations in the hemoglobins of the two

species may be responsible for the differences in their oxygen loading capacities. Foreman (1960 and 1964) has shown that the electrophoretic patterns of the hemoglobins are exactly the same, but there are differences in the tryptic peptide components. The functional significance of these structural variations is unknown.

The differences between the two species can be understood as adaptive in relation to their respective habitats. The old-field mouse is semi-fossorial; P. leucopus is partly arboreal in some parts of its range, including North Carolina, and does not dig underground burrows (Taylor and McCarley, 1963).

Peromyscus leucopus is not normally exposed to decreased levels of oxygen. The higher tolerance to anoxia, the alarm reaction, and the ability to maintain a high metabolic rate at low oxygen tensions may be interpreted as adaptations of the old-field mouse to its semi-fossorial existence.

The extent to which mice become hypothermic in the field is not known, but the average oxygen concentration of the air in the burrows, 18.4 percent, was low enough to act as a cue for torpor. Some animals showed reduced metabolic rates in the laboratory at this concentration. At 14 percent oxygen their body temperatures were only a few degrees above the ambient temperature at which mice have been found torpid in the field. It seems likely that mice undergo daily hypothermia while in their burrows, and this phenomenon accounts for the lack of a difference between the air temperature in occupied and unoccupied burrows. As many as 14 mice have been found in a

single burrow in which the air temperature did not vary significantly from that of the air in unoccupied burrows.

Torpid mice can be aroused by local disturbances. The sand plug in the entrance of the burrows provides an extra margin of safety by delaying the advance of a potential predator. The mice can come out of torpor before a very efficient predator, e.g., myself with a shovel, can dig them out. While the predator digs down the entrance tube the mice probably elevate their body temperature and are able to leave their nest via the escape tube, which cannot be located from outside until the mice break through the surface.

The lack of a difference between the metabolic rates of P. polionotus with and without a carbon dioxide absorbent was unexpected. Instead of breathing more rapidly as the carbon dioxide concentration increased, most of the mice went to sleep and continued to breath at the same rate or more slowly. This is probably a complementary adaptation which goes along with the reduction in metabolic rate in response to decreased oxygen tension. If an oxygen gradient was established by a respiring animal, a carbon dioxide gradient in the reverse direction should also be established. The higher concentration of carbon dioxide next to the mouse would normally cause an increase in the breathing rate, and thus, stop the mouse from becoming torpid.

Increased concentrations of carbon dioxide in the air that a mammal breathes indirectly change the affinity of hemo-

globin for oxygen by changing the pH of the blood (Bohr effect). The oxygen equilibrium curve shifts in the direction of higher partial pressures of oxygen needed to load the hemoglobin upon addition of acid. The magnitude of the Bohr effect tends to be greater in small, active mammals than in large, sluggish ones (Prosser and Brown, 1961). At lower than normal body temperatures, however, the oxygen dissociation curve shifts in a direction that would partly compensate for the other changes. The way in which the old-field mouse has solved these problems is not known, but it may be expected that the molecular structure of its hemoglobin has been altered and that either the buffering capacity of the blood is high or the mice are not adversely affected by fluctuations in pH.

Significance of torpor

Brower and Cade (1966) state that "species of Peromyscus seem to be characterized physiologically by labile body temperatures." These results support their view. The ability to give up the regulation of body temperature without suffering permanent damage is an adaptation of primary importance. It allows a homeotherm to cut its rate of energy consumption and thus survive for longer periods of time in a harsh environment. The old-field mouse may use this adaptation to cut its daily energy consumption in the field.

Peromyscus polionotus from the Ocala National Forest differs from some of the other species in this genus, in that it does not use ambient temperature as a cue to reduce its body temperature (Morrison and Ryser, 1959; Cade, 1964; Smith

and Criss, 1964 and in press; Smith, 1965c; Brower and Cade, 1966). Low ambient temperatures about 0°C do not occur very often at this locality.

Mathematical models (e.g., McNab, 1963) which attempt to describe the daily energy expenditure of a small rodent in the field must take into account the possibility that its body temperature may be relatively unstable, especially if it is a Peromyscus. The magnitude of the error is compounded when the results of laboratory experiments are extrapolated to the field situation. For these reasons, the estimate of respiratory energy flow of P. polionotus in the old-field ecosystem made by Odum, et al. (1962) is probably too high. Better estimates will require a knowledge of how frequently and to what extent the mice forego homeothermy in the field.

FACTORS AFFECTING REPRODUCTION

Mammals usually have well defined reproductive cycles. Offspring are produced at times when the probability of their survival is high. This implies that there is a relationship between the internal physiological processes and environmental factors which affect survival. The purpose of this chapter is to describe certain aspects of this relationship in the old-field mouse.

Results of field work

The monthly variation in the reproductive characteristics of the females and males are given in Tables 12 and 13. Litter size and mean monthly litter size range from 1 to 7 and 0 to 6.2, respectively. The maximum values were greater than the number of mammae per female (six). Up to 33.3 percent of the females became pregnant while nursing a previous litter. The size of the nursing young and the embryos usually indicated that the pregnancy was the result of a post-partum heat.

The maximum percentage of reproductively active females was 93.3. This figure was a minimal estimate since any female that was imperforate and in the early stages of pregnancy would be excluded from this category. Maturity was determined by the lack of the juvenile pelage or the presence of embryos. Sub-adult females cannot be separated from the adults by pelage

Table 12. Variations in the females' reproductive characteristics. Pregnant or perforate females were considered to be reproductively active

Month and Year	Number of Mature Females	Percentage Pregnant only	Percentage Pregnant and Lactating	Percentage Lactating only	Percentage Reproductively Active	Number of Young per 100 Mature Females	Mean Litter Size	Range in Litter Size
12-62	26	34.6	38.5	11.5	88.5	700.0	6.0	6
4-63	19	31.6	0.0	5.3	36.8	110.5	2.1	2-3
7-63	12	0.0	0.0	0.0	0.0	0.0	0.0	0
8-63	12	0.0	0.0	8.3	25.0	8.3	1.0	1
9-63	15	13.3	6.7	13.3	60.0	83.3	2.5	2-3
10-63	9	44.4	0.0	33.3	66.6	233.3	3.0	3
11-63	14	42.8	14.2	7.1	71.4	271.3	3.7	2-6
12-63	15	40.0	33.3	13.3	93.3	744.0	6.2	6-7
1-64	11	27.3	9.1	9.1	66.3	316.0	5.8	5-6
2-64	21	19.0	14.3	9.5	61.9	240.0	4.2	2-5
3-64	11	27.3	0.0	9.1	45.5	136.4	3.0	3
4-64	10	30.0	0.0	0.0	30.0	30.0	1.0	1
5-64	9	44.4	11.1	11.1	88.9	272.2	3.5	3-4

Table 12. (continued)

Month and Year	Number of Mature Females	Percentage Pregnant only	Percentage Pregnant and Lactating	Percentage Lactating only	Percentage Reproductively Active	Number of Young per 100 Mature Females	Mean Litter Size	Range in Litter Size
6-64	12	16.7	0.0	0.0	25.0	25.0	1.5	1-2
9-64	12	8.3	8.3	0.0	33.0	75.0	3.0	3
10-64	7	0.0	28.6	14.3	57.1	235.7	3.3	3-4
11-64	13	7.7	7.7	30.8	53.9	156.2	2.9	2-4
12-64	20	15.0	20.0	10.0	65.0	221.0	3.4	3-5
1-65	13	15.4	30.8	7.7	61.5	270.8	3.2	2-4
2-65	21	28.6	14.3	9.5	66.7	347.6	3.8	3-4
3-65	13	30.8	0.0	14.4	46.2	130.9	2.9	2-3
4-65	15	13.4	6.7	13.4	40.0	92.0	2.3	2-3
5-65	10	20.0	10.0	20.0	80.0	220.0	3.7	3-4
7-65	16	6.3	13.0	6.3	25.0	56.2	1.5	1-5
8-65	9	22.2	0.0	11.1	33.0	111.1	2.3	2-3
9-65	14	21.4	0.0	7.1	50.0	92.9	3.3	3-4

Table 13. Monthly variation in reproductive characteristics of adult males

Month-Year	Sample Size	Percentage With Sperm	Mean Testicle Size Length X Width	Mean Length of the Seminal Vesicle
12-62	24	83.3	40.1 mm ²	7.5 mm
4-63	20	95.0	38.4	7.2
7-63	8	75.0	34.3	6.9
8-63	8	62.5	33.8	6.8
9-63	12	91.7	36.2	7.1
10-63	10	90.0	35.8	7.5
11-63	16	87.5	34.7	7.4
12-63	15	93.3	39.2	7.6
1-64	12	75.0	32.0	7.8
2-64	23	78.0	37.9	7.2
3-64	9	66.7	35.1	7.3
4-64	7	71.4	34.7	6.8
5-64	7	85.7	38.4	7.0
6-64	7	71.4	34.2	7.1

Table 13. (continued)

Month-Year	Sample Size	Percentage With Sperm	Mean Testicle Size Length X Width	Mean Length of the Seminal Vesicle
9-64	11	90.0	34.3 mm ²	6.7 mm
10-64	13	84.6	31.8	7.2
11-64	12	91.7	36.4	7.5
12-64	16	87.5	39.0	7.4
1-65	13	84.6	36.4	7.7
2-65	20	70.0	39.9	6.9
3-65	12	100.0	38.7	7.6
4-65	13	76.9	32.2	7.1
5-65	8	75.0	36.6	7.3
7-65	14	64.3	31.9	6.9
8-65	5	60.0	32.5	7.2
9-65	13	61.5	33.6	6.8

characteristics, and thus, the percentage of reproductively mature females would be lowered even more during certain times of the year.

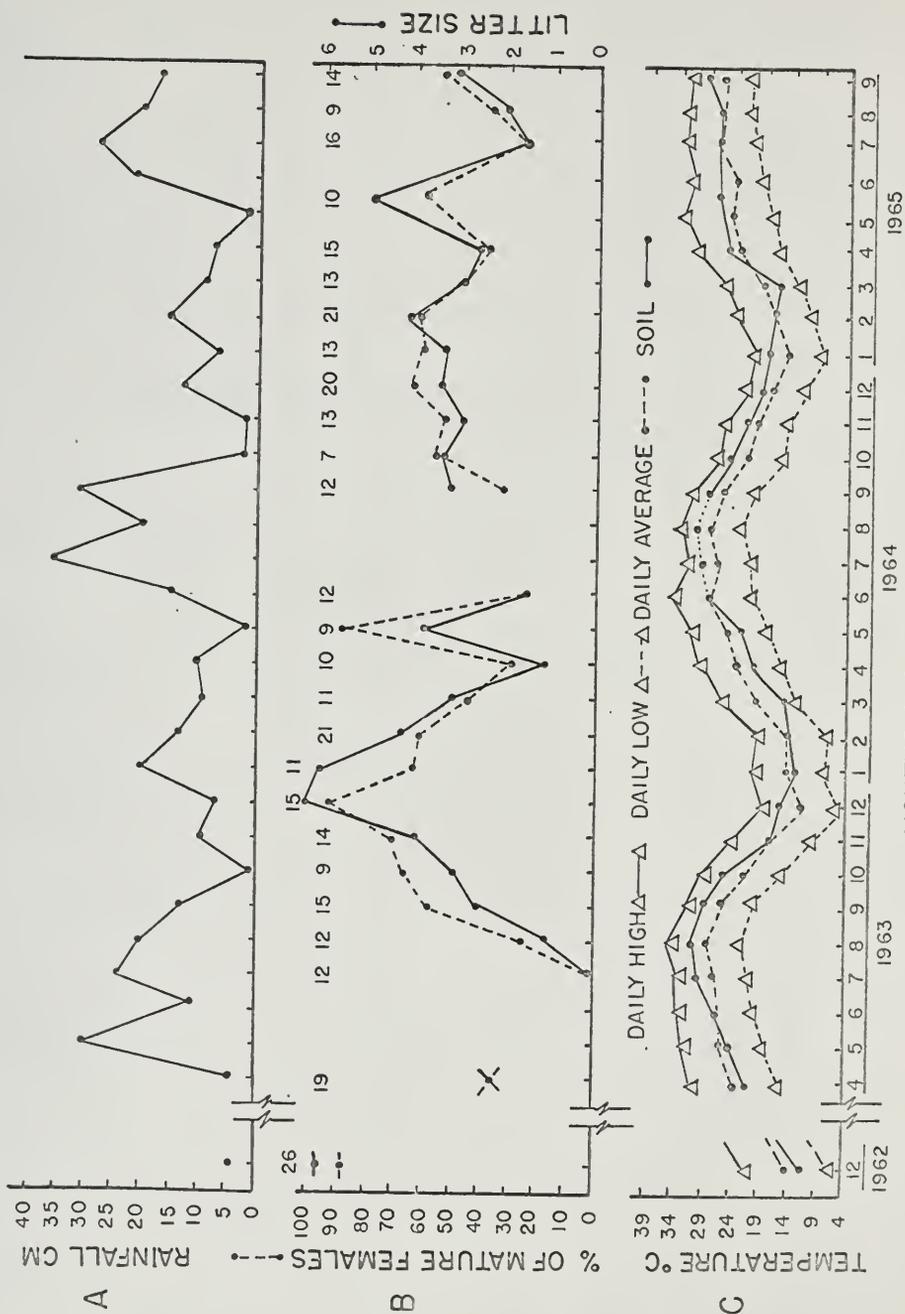
None of the juvenile males was found with sperm. The highest percentage of adult males capable of fertilizing a female was 100. This did not differ much from the maximum percentage of reproductively active females, and these peak values occurred at the same time of the year. The percentage of adult males with sperm never fell to 0 at any time during the study as did the percentage of reproductively active females. There appeared to be a seasonal variation in all of the reproductive parameters of both sexes with the maximum values occurring during the winter and the minimum during the summer. The summer decline may have been due to the sterilizing effect of high temperatures (Cowles, 1965). Another breeding peak occurred during the spring each year.

Correlation between production of young, rainfall, and ambient temperature

The monthly variations in litter size, percentage of reproductively active mature females, amount of rainfall, and various soil and air temperatures in the field are given in Fig. 13. Certain aspects of the relationship between rainfall and ambient temperature have already been pointed out (p 22; Figs. 7 and 8). A multiple correlation analysis was used to separate and determine the magnitude of the effects of temperature and rainfall on reproduction. The dependent variable (P) was the number of young being produced per 100 mature females

Fig. 13. A. Average monthly rainfall at Ocala, Florida

- B. Percentage of mature females that were reproductively active and average litter size per month. The monthly sample sizes are given across the top of the figure. The criterion of maturity was the lack of the juvenile pelage or the presence of embryos.
- C. Mean soil temperature per month at the depth of the nest cavity in the Ocala National Forest and the mean daily temperatures per month of the air above ground at Ocala, Florida.



(Table 12). The independent variables were soil temperature at the depth of the nest cavity (T) and amount of rainfall each month (A). The relationship between these three variables was given by

$$P = 268.7 - 1.02T - 3.82A.$$

$$R_{P.TA} = .626 \text{ (highly significant),}$$

$$r_{PT.A} = -.581 \text{ (significant) and}$$

$$r_{PA.T} = -.105 \text{ (not significant),}$$

where the partial correlation coefficients are $r_{P.TA}$ and $r_{PA.T}$, and the multiple correlation coefficient is $R_{P.TA}$. The probability that the amount of variation in the dependent variable was due to chance rather than to the effects of the independent variables was less than .01 ($F = 7.39$ and $df = 2/23$). The coefficient of determination, which is the percent reduction in the sum of squares of P attributable to the combined effect of T and A, was 39 percent. This was quite high considering that the small sample sizes in some months should have increased the experimental error associated with the sampling technique. Even though the partial correlation coefficient $r_{PA.T}$ was not significant, the amount of information given by A about P which was not given by T was significant ($F = 5.68$, $df = 1/23$, and P less than .01). However, A gave only .39 times as much information about P as did T. This means that variations in both temperature and rainfall are important in predicting the number of offspring, but information concerning temperature is more useful in making these predictions than information about rainfall.

One obvious variation in reproduction, which was not revealed by the above analysis, was the consistent spring breeding peak in the field population (Table 12 and Fig. 13). Both litter size and percentage of reproductively active females showed an increase during this season even though ambient temperatures were increasing. Two external factors, a decrease in rainfall and a change of diet, may be associated with this fluctuation.

Effect of temperature on the male's reproductive system

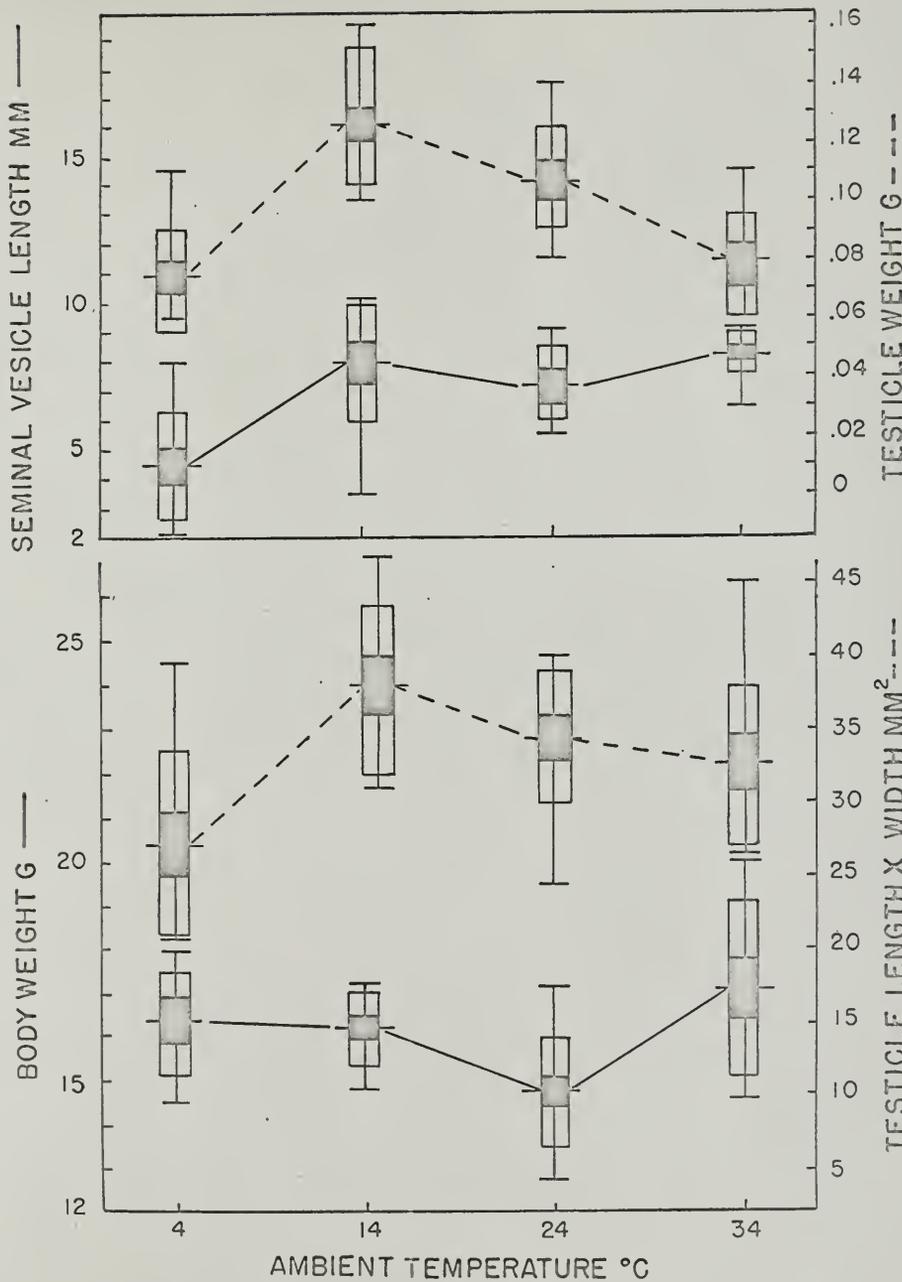
Temperature appeared to have an effect upon the reproductive system of the males. More males were reproductively active and the testes and seminal vesicles were larger during the winter than in the summer (Table 13). An attempt was made to quantify this relationship in the laboratory by keeping males in constant temperature boxes for 60 days at four different ambient temperatures, 4°, 14°, 24°, 34°C with a maximum temperature fluctuation of $\pm 1^\circ\text{C}$. Food and water were supplied ad lib. The males were maintained in groups of three to a cage. Their ages varied from 91 to 108 days at the beginning of the experiment. At this time, their testes were enlarged and in a scrotal position; the males appeared to be reproductively active. The temperature that each mouse was exposed to was randomly selected; nine mice were in each of the four groups. Another group of the same size and approximately the same age were selected at random from the laboratory colony; they were paired with an adult female for at least one month prior to their death. The 45 males were sacrificed on the same day and

the body weight, size and weight of the testes, and length of the seminal vesicles were recorded.

Of all the males, only seven, which were paired with adult females, had their testes in a scrotal position and sperm in their epididymes at the end of the experiment. Males housed only with other males and isolated from sensory cues associated with females became sexually inactive as a result of their treatment at each ambient temperature. Males paired with females had significantly larger ($42.2 \pm 1.1 \text{ mm}^2$, length x width) and heavier testes ($1.30 \pm .005 \text{ g}$) and longer seminal vesicles ($9.0 \pm .21 \text{ mm}$) than the other males (Fig. 14). Either the presence of a female was necessary for the maintenance of the male's sexual activity, or the level of interaction between the males was sufficient to cause the observed effects. In either case, the pair bond may have functional significance in that it enables the field population to achieve a high reproductive rate.

Temperature had a significant effect on body weight ($F = 4.52$, $df = 3/32$, and P less than $.01$), length of the seminal vesicles ($F = 11.4$, $df = 3/32$, and P less than $.01$), and size and weight of the testes ($F = 6.3$ and 16.7 , respectively, $df = 3/32$, and P less than $.01$; Fig. 14). Body weight was lowest at 24°C and from this point increased as the temperature went up or down. This effect of temperature was independent of food since it was supplied in abundance in the laboratory. Similar variation may be characteristic of field populations. Connell (1959) reported that the mean body weight and percentage

Fig. 14. The size of the seminal vesicles and testes, and weight of the testes and body of males housed with other males at four different ambient temperatures. There were nine mice at each temperature. The mean is indicated by the horizontal line through the dark rectangle which represents two standard errors. The range is shown by the other horizontal lines, and the open rectangles indicate one standard deviation on either side of the mean.



of fat were highest during the summer and winter in a northern population of old-field mice. In the Ocala National Forest, acorns and insect parts were usually found during the fall and spring. If food is locally abundant at approximately the same time at the northern location, then the mice are apparently heavier during the time at which food is relatively scarce. This may be an adaptation which helps the mice to survive during the lean periods. Survival during short periods when food becomes scarce would be assured if the mice could rapidly put on fat when food was abundant and use this stored energy when needed. Survival for longer periods could be achieved by torpor (p 63).

Temperature had a different effect upon the males' reproductive system. The high values were recorded at 14°C, and decreases were associated with temperature deviations in either direction from this point, with the only exception being a slight increase in the length of the seminal vesicles from 24° to 34°C. The length of the seminal vesicle is a sensitive indicator of androgen secretion by the testes in other species of Peromyscus (Jameson, 1950; Brown, 1964b). Either this was not the case for P. polionotus or the level of androgen secretion was not related to the weight of the testes in the same way at the different temperatures. For example, the difference between the weight of the testes at 24° and 34°C was not significant, but it was for the length of the seminal vesicles. In the field, there was no correlation between the size of the testes and the length of the seminal vesicles, and most of the

males had sperm when their testes were 30 mm² or more. Shifts in the age composition of the population may account for some of the observed seasonal variation. Sexually active subadults cannot be separated from adults easily; the reported values are pooled means. Treating the data in this way may fail to show some of the more significant effects which contribute to the large variation between the monthly samples, but there is no way at present to adequately subdivide the data for these variables, and the sample size per month is not large enough either. The sensitivity of the seminal vesicles to androgens is not questioned here, but the relationship between testes size or weight, androgen secretion, presence of sperm, and the length of the seminal vesicles cannot be a simple one in this species. Controlled laboratory experiments must be done before we can do more than just describe the seasonal variation in these characters. However, it was clear that the males' reproductive cycle overlapped that of the females and that most of the time there were more sexually active males than females in the population (Tables 12 and 13).

Minimum critical temperature

Sudden short exposures to 4°C stimulated reproduction in the laboratory (p 95), but prolonged exposures resulted in significant decreases in the size and weight of the testes and the length of the seminal vesicles. Reproduction was highest, and the testes and seminal vesicles reached their maximum size in the field, when the soil temperature was slightly below 14°C. The mice never had to endure temperatures below 12°C for any

prolonged period in the field. When the mean daily low temperature dropped below this point the mice could stay in the burrow or limit the amount of time spent above ground. Temperature is an important factor regulating above-ground activity as indicated by decreased trapping success on cold nights (Gentry and Odum, 1957). Prolonged exposure to temperatures below 12° to 14°C has little or no biological meaning for P. p. subgriseus. The lowest temperature that will stimulate reproduction when exposure is prolonged must be slightly below 14°C.

Breeding performance of *Peromyscus polionotus subgriseus* in the laboratory

The breeding performance of the laboratory colony from October 1, 1964 to September 31, 1965 is given for each month in Fig. 15. The mean litter size varied from 3.47 in September to 4.64 in July. The mean annual value was 4.3 for laboratory-reared females while the range was one to nine; this was greater than the range in the field (p 65). The highest percentage of females giving birth was 76.5 in December with a low value of 26.0 in August. Reproductive performance in the laboratory was less variable and always greater than that in the field at the same time. Seasonal variation similar to that shown in the field occurred in the laboratory despite relatively constant environmental conditions.

Onset of sexual activity

Clark (1938) found that juvenile *Peromyscus* females went into their first estrus cycle at as early an age as 23 days, and that the youngest laboratory-reared female that became pregnant

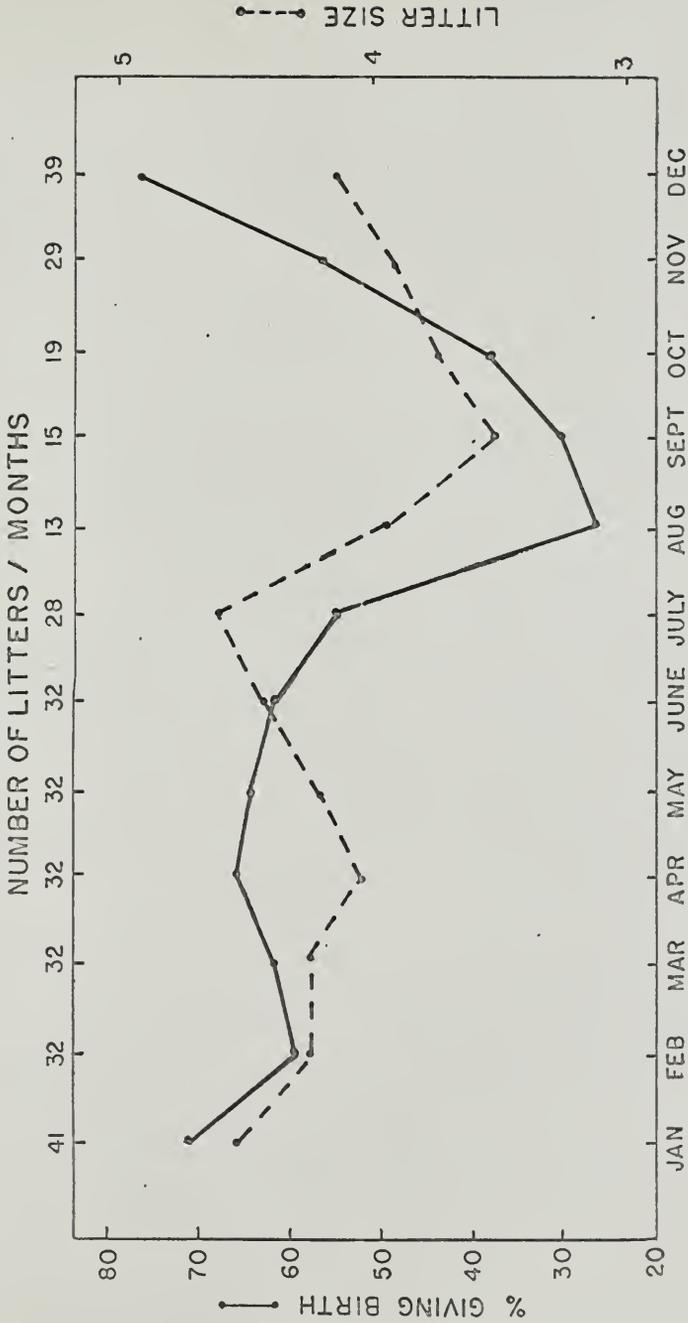


Fig. 15. Breeding performance of laboratory-reared Peromyscus polionotus subgriseus maintained at 24 ± 1°C.

was 102 days old. Rand and Host (1942) recorded the earliest date of reproduction as approximately 48 days in the laboratory and 40 days in the field. They also found one female 26 days old with a perforate vagina. In this study, several females that were less than 26 days old have been found in the laboratory with a perforate vagina; the youngest was 24 days old. Most of the laboratory-reared females first became perforate between 50 to 60 days if they were paired with a male just after weaning. Some females never became perforate in their first year of life when kept in bigger groups, especially in the presence of other adult females. The earliest date at which conception took place in the laboratory was 34 days, assuming a gestation period of 23 days (p 83). Other similar values included 38, 45 and 46-day-old females. All of these had not yet completed the juvenile molt when they first became pregnant. The data for the field population gave similar results. The age of each mouse was estimated using the growth data on the size of the body, tail, hind foot, and ear (Laffodday, 1957). Twelve females between 25 to 30 days old had perforate vaginae when captured. Ten of these were found paired with a sexually active male, one with a sexually inactive juvenile male and one in a group of six mice, some of which were in the juvenile pelage and others were molting for the first time. One of the molting males had its testes descended but had no sperm. Other similar values included 39, 41 and 45-day-old females. While some females bred at an early age, most did not. Over 95 percent of the pregnant

females had completed the post-juvenile molt. The youngest males that sired litters in the laboratory were 45, 47, 61 and 63 days old.

Post-partum estrus and gestation period

The interval between litters in nonlactating females or between copulation involving a nonlactating female and the birth of a new litter was 23 to 24 days; 63 percent on the 23rd day. Smith (1939), Laffoday (1957), and Williams, et al. (1965b) also give 23 to 24 days as the normal gestation period. Nonlactating females have a shorter gestation period than those lactating. For the latter, it ranged from 27 to 33 days and averaged 29.2 ± 1.3 days. The comparable figure reported by Williams, et al. (1965b) is 29.43 ± 3.81 . Larger litters in utero and/or nursing seemed associated with longer gestation periods.

Post-partum heat is characteristic of several species of Peromyscus including P. polionotus (Svihla, 1932; McNair, 1931; Clark, 1936 and 1938; Rand and Host, 1942; Pournelle, 1952; Williams, et al., 1965b). It was of common occurrence in the laboratory colony (Table 14). Female #58 has given birth to 26 consecutive litters with a mean inter-litter interval of less than 30 days. Her first litter was born when she was 118 days old. Her total production thus far has been 139 young, and at this time she shows no signs of stopping. Several other females have also produced over 100 young during the same time. Post-partum heat was also characteristic of the field population, and its occurrence accounts for a considerable portion of the

Table 14. Breeding histories of five typical laboratory-reared females. The size of each litter is indicated in parentheses after the date of birth

Number of Female				
10	15	23	26	58
11-26-64 (4)	11-26-64 (4)	9- 5-64 (4)	10-31-64 (4)	3- 8-64 (1)
12-20-64 (6)	12-24-64 (5)	10- 6-64 (5)	12- 1-64 (2)	4- 4-64 (5)
1-16-65 (6)	1-17-65 (6)	11- 7-64 (5)	12-28-64 (5)	5- 1-64 (6)
2-12-65 (4)	2-15-65 (6)	12-12-64 (5)	1-24-65 (6)	5-31-64 (5)
3- 8-65 (6)	4- 1-65 (4)	1-31-65 (3)	3-16-65 (5)*	6-29-64 (6)
4- 4-65 (6)	5- 1-65 (5)	3- 1-65 (4)	4-11-65 (3)	7-27-64 (4)
5- 1-65 (6)	6- 1-65 (7)	5-11-65 (3)	5- 6-65 (3)	8-25-64 (4)
5-28-65 (6)	7- 1-65 (6)	6- 7-65 (3)	7-18-65 (3)	9-23-64 (3)
6-23-65 (5)	8- 2-65 (5)	7- 2-65 (6)	8-13-65 (4)	10-22-64 (5)
7-17-65 (6)	10-17-65 (5)	10-12-65 (4)	10- 7-65 (5)	11-20-64 (6)
11-19-65 (2)	11-18-65 (4)	11-10-65 (3)	11- 4-65 (4)*	12-18-64 (7)
12-16-65 (5)	12-17-65 (5)	12- 9-65 (4)	11-38-65 (3)	1-15-65 (6)
1-13-66 (6)		1- 6-66 (5)	1- 7-66 (4)	2-14-65 (6)
2-10-66 (5)		2- 3-66 (3)	2- 8-66 (5)	3-14-65 (7)
3- 6-66 (6)				4-12-65 (7)
				5-11-65 (6)
				6- 9-65 (5)
				7- 6-65 (6)
				8- 4-65 (4)
				9- 2-65 (3)
				10- 1-65 (6)
				10-30-65 (6)
				11-28-65 (7)
				12-27-65 (5)
				1-24-66 (7)
				2-22-66 (6)

*young were taken from mother at an early age

total reproductive performance at certain times of the year (Table 12). On two occasions, the laboratory colony increased more than four times its original size in less than a month.

Synchronization of reproductive activity

The distribution of births in the laboratory was not random. They occurred in groups with the inter-group time interval being longer than the average time between individual litters. To investigate this phenomenon, 60 cages on 12 shelves, five to a shelf, were maintained in a set position for one year. The timing and location of each birth was recorded.

There were 363 litters born during this year. Five or more appeared 31 times in non-overlapping periods of three consecutive days. This differs from chance expectation (Chi square = 336.2, $df = 1$, and P less than .01). These results support the preliminary conclusion and give more information about the probable cause. The daily distribution of litters revealed that the clumping was not random in respect to the position of the cages on the shelves (Fig. 16). For example, all of the females on shelf nine reproduced within a three-day period from December 11 to 13. Three days is less than the average duration of the estrus cycle which lasts for about five days (Laffodoy, 1957). Since the gestation period was approximately the same for all females (p 83), they have to go into heat about the same time if they give birth on the same day. The estrus cycle of one female influenced the cycle of females in nearby cages. Once synchronized, the regularity of the post-partum heat and the uniform length of the gestation period in lactating females

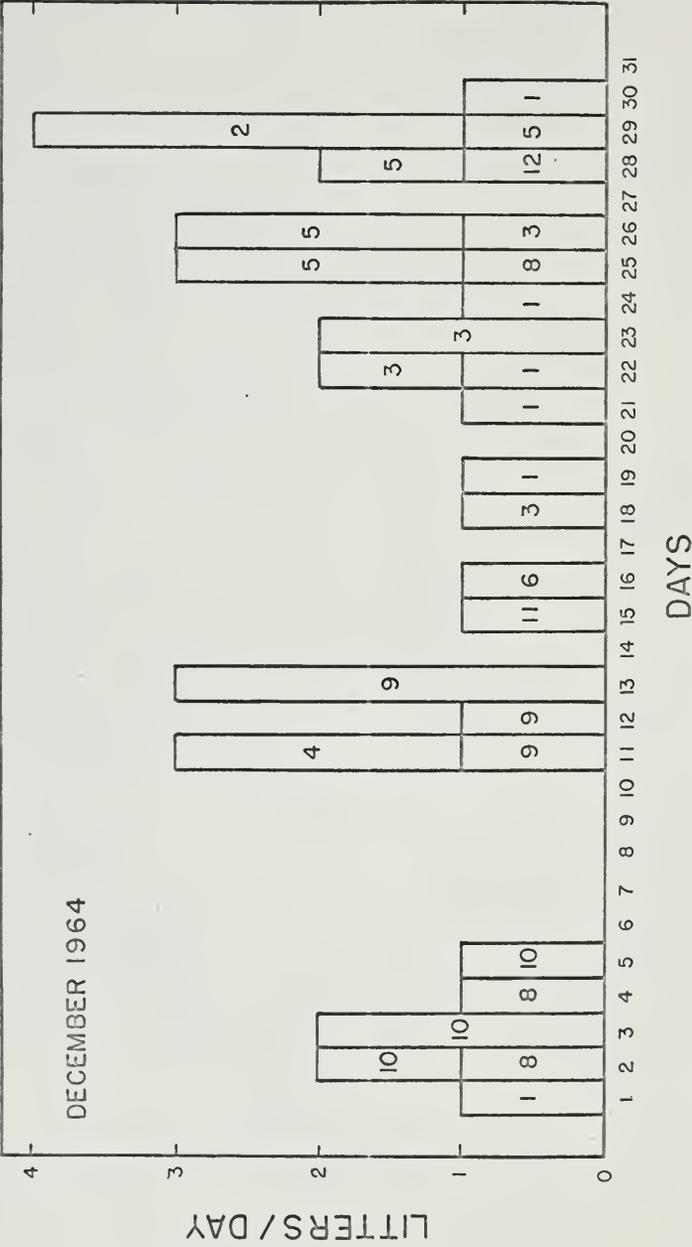


Fig. 16. The number of litters born on each day during December, 1964. The numbers in each block represents the shelf on which the birth occurred. There were five cages on each of 12 shelves.

tended to maintain the synchrony and cyclic reinforcement takes place.

The basis of this behavioral induction is not known. Observations on mating behavior provide some clues. Mice became very active during mating (p 144). This excitement spread to mice in nearby cages and they frequently exhibited as much activity as the breeding pair. This was in contrast to the amount of activity shown by mice in other cages from which they could not see the breeding pair. Physical proximity was also important; mice housed four feet away remained relatively inactive even though they could see and hear the breeding pair. The mice that were about to breed may have produced certain odors which could have influenced the estrus cycle of females and/or stimulated males in nearby cages. The gradient would be more extreme in the vertical direction than in the horizontal because the flow of air in the colony room was approximately parallel to the long axis and the horizontal plane of the shelves. Appropriate olfactory stimulation may have lowered the threshold for mating behavior to a point where the visual stimulation triggered the sequence of behavior patterns which culminated in mating.

Exposure to males or to their urine alters estrus synchrony in grouped virgin female laboratory mice (Marsden and Bronson, 1964); a higher proportion attained estrus earlier than the control groups (Lee and Boot, 1956; Whitten, 1957; Lamond, 1958). The same effect has been observed in rats (Hughes, 1964). Placing females into cages recently soiled

by males also changes the synchrony pattern (Whitten, 1956a and 1958; Lamond, 1959), and removal of the olfactory bulbs causes the ovaries to regress (Whitten, 1956b; Lamond, 1958). These reports stress the importance of olfactory cues in altering patterns of estrus synchrony in the laboratory mouse. Moore (1965) stressed the importance of olfaction in the establishment of pair bonds in the old-field mouse and suggested that sexual excitement and heightened activity was due to the perception of odors "characteristic of estrus." It seems likely that the effect of olfactory stimulation on estrus synchrony is more important than visual stimulation.

Bruce effect

The percentage of recently bred female mice that become pregnant can be reduced by exposure to strange males (Parkes and Bruce, 1961). This is known as the Bruce effect. The following experiment was done to test its possible occurrence in P.

polionotus.

Two pairs of mice were observed mating in different cages at the same time on 20 occasions. A strange, sexually active, adult male was introduced into one of the cages; the other pair served as a control. The resident female and occasionally her mate immediately attacked the intruder so vigorously that he had to run rapidly around and up and down the sides of the cage. The resident male normally continued to chase and attempt to mount the female while she was chasing the intruder. Only once did the female resume mating in the presence of the strange male. After having been chased for several

minutes, he went to the top of one side of the cage and remained motionless. The strange males were removed 15 minutes after their introduction into the cage. In 10 of the 20 pairs mating was not resumed within two hours after the removal of the intruder.

All of the females in the control group gave birth within the normal period. Prior to the experiment the average litter size of this group had been $4.24 \pm .09$, and during the experiment it was $4.31 \pm .38$. Only 55 percent of the females in the experimental group gave birth within the same period of time, and their average litter size was $3.58 \pm .29$. The previous litter size for the experimental group was $4.19 \pm .11$; it decreased significantly, but not in the control group. The incidence of pregnancy decreased in the experimental group as compared to the control group (Chi square = 4.05, df = 1, and P less than .05).

These data confirm the existence of the Bruce effect in the old-field mouse. Its magnitude is variable and can range up to 80 percent (Bruce, 1959, 1960a, 1960b, 1961a, 1961b; Bruce and Parkes, 1960, 1961; Bruce and Parrot, 1960; Parkes, 1961; Parkes and Bruce, 1961; Eleftheriou, et al., 1962). In this study the reduction of pregnancies was small. The sizes of the cages could have influenced these results. Eleftheriou, et al. (1962) showed a 75 percent decline in incidence of pregnancy in small cages but no change in large ones.

Effect of litter sequence upon litter size

In many mammals the size of a litter varies with its position in a sequence of pregnancies (King, 1916; Bittner,

1936; Asdell, et al., 1941; Lush and Molln, 1942; Gruneberg, 1952; Ingram, et al., 1958; Pomeroy, 1960; Negus and Pinter, 1965). This was true for the old-field mice from the Ocala National Forest; their first litter averaged smaller than subsequent ones (Fig. 17). The variability in the size of later litters was probably due to seasonal factors and chance fluctuations. These results contrast with those of Williams et al. (1965a) which showed litter size in P. p. lucubrans increasing by .30 mice per litter up to the fourth litter and at a lesser rate up to the sixth litter. This difference contributes to the higher reproductive rate of P. p. subgriseus compared to P. p. lucubrans (p 97).

Sex ratio at birth

The sex of the offspring from 39 females in the laboratory was determined within one week after birth. There were 636 males and 566 females from 274 litters. The ratio deviates significantly from chance (Chi square = 4.08, df = 1, and P less than .05); certain females contributed more to it than others. For example, #2, #21 and #29 bore 16 males and 2 females, 16 males and 5 females, and 25 males and 6 females, respectively. These results were significantly different from the expected values (Chi squares = 9.40, 5.76 and 10.46, respectively, with Yates correction for continuity applied, df = 1, and P less than .05). Of 21 litters containing one or two young, 15 belonged to these females. There were more males in small litters than females (Chi square = 12.98 with Yates correction for continuity applied, df = 1, and P less than .05).

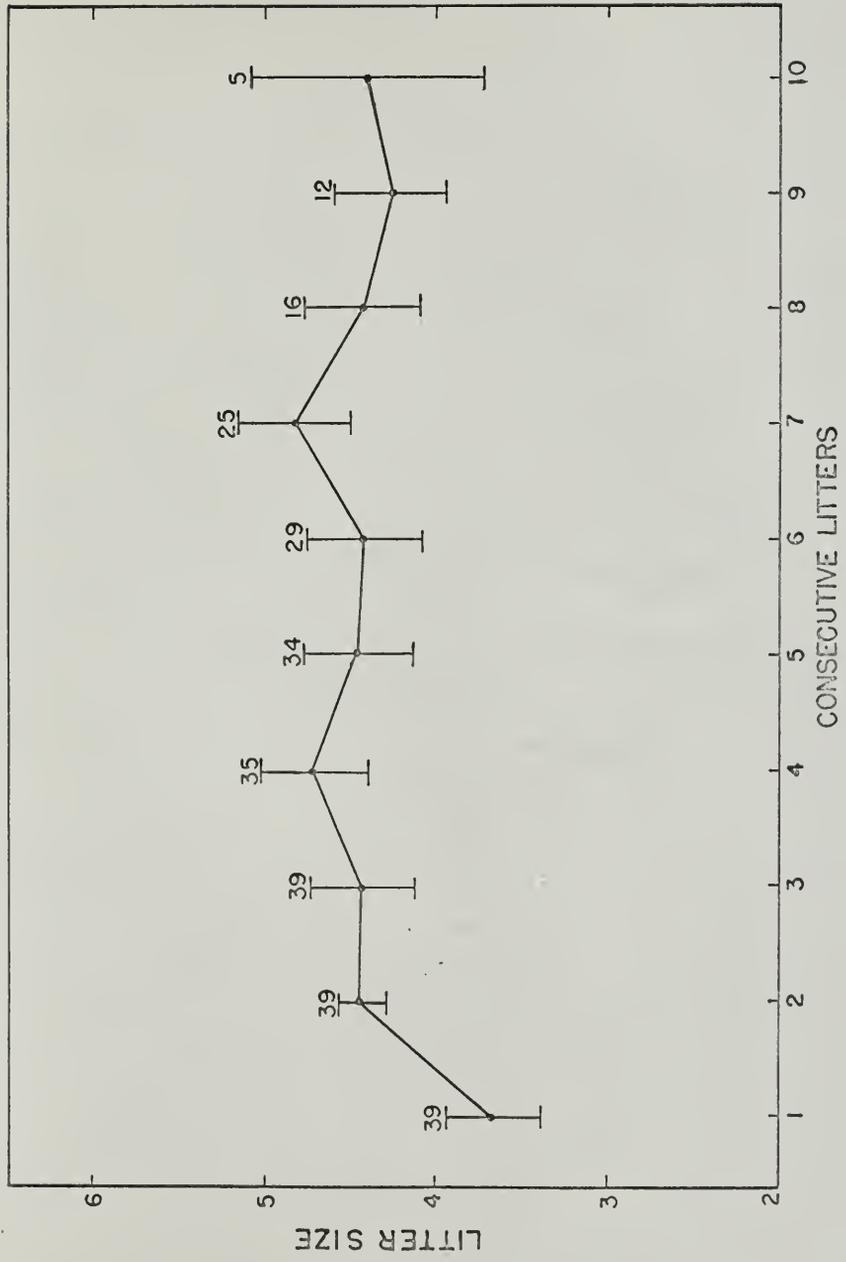


Fig. 17. Average size of sequential litters born to laboratory-reared Peromyscus polionotus subgriseus. Only females which had three or more litters were included. The number of litters is given above each point. The vertical lines indicate two standard errors on either side of the mean.

The ratio of males to females (440:398) in young born in the field and sexed before their eyes opened was insignificantly greater than one (Chi square = 2.12, df = 1, and P greater than .10). The sample included 46 litters of one or two young, whereby the males outnumbered the females by 50 to 31 (Chi square = 4.40, df = 1, and P less than .05). The reason for this sex ratio in small litters is not known. It resulted in the production of more males during the summer when the reproductive activity of the field population was low. Increased production of males efficiently compensates for their higher mortality rate (p 109).

The number of male offspring exceeded females both in the laboratory and in the field. Similar results have been reported for P. p. subgriseus (Laffoday, 1957) and for P. p. lucubrans (Williams, et al., 1965b). Their sex ratios did not differ significantly from one which is probably the result of small samples. The percentage of male offspring varied from 50.8 (Laffoday, 1957) to 53.5 reported here. Williams, et al., (1965b) found 51.7 percent males. Pooling these data gives 1,616 males (52.9 percent) and 1,440 females (47.1 percent), and the difference from the expected was significant (Chi square = 10.41, df = 1, and P less than .01). This is also true in man. In the United States, males constitute 51.5 percent of the births, in Korea 53.2 percent (Russell, 1936; Kang and Cho, 1959a, 1959b).

Seasonal variation in litter size

The mean litter size per month varied in relation to

season, both in the laboratory and in the field. The range in the field, 1.0 to 6.2, was greater than range reported for other mammals (Leslie and Ranson, 1940; Gruneberg, 1952; Beer, et al., 1957; Hoffman, 1958; Beer and MacLeod, 1961; Kott and Robinson, 1963; Caldwell and Gentry, 1965; Goertz, 1965). In many instances, this variation is caused by differences in the age composition of the population; younger females produce smaller litters (Leslie and Ranson, 1940; Gruenberg, 1952; Beer, et al., 1957; Kott and Robinson, 1963). Caldwell and Gentry (1965) estimated that a field population of old-field mice consisting entirely of young mature females produce 12 percent fewer offspring than one composed of older females.

The second litter born in the laboratory averaged 17 percent larger than the first (Fig. 17). Since the two figures are approximately the same, it is reasonable to assume that the effect of age is the same in the laboratory as it is in the field. The age factor accounts for only a small part of the range in production of the Ocala field population (0 to 744.0 young/100 females; Table 12). Seasonal reproductive variation in the laboratory cannot be totally due to differences in the age of the mothers either; none of the females reproduced for the first time during September when the lowest mean litter size was recorded. Other factors must be responsible for seasonal variation.

Effect of light intensity and day length

The importance of light as a controlling factor for mammalian reproduction varies according to species (Bissonette,

1936; Young, 1961). For example, the length of the dark and light periods directly affects reproduction in the racoon (Bissonette and Csech, 1937), the field mice, Microtus agrestis and M. pennsylvanicus (Baker and Ranson, 1933; Hamilton, 1941), and common European hare (Asdell, 1946), but not in the 13-lined ground squirrel (Moore, et al., 1934) or in the cotton mouse, P. gossypinus (Pournelle, 1952). Whitaker (1940) found that in P. leucopus length of daily illumination was of paramount importance. Peromyscus polionotus was similar to P. gossypinus, and they both differed from P. leucopus in this respect. The latter species is primarily confined to more northern locations, while the first two are endemic to the southeastern United States (Hall and Kelson, 1959). Southern species tend to breed throughout the year, while those in the north reproduce during a more limited period of time (Cockrum, 1962).

Light did not directly affect reproduction in the old-field mouse. In the colony room, the distance between the overhead light and each cage varied from .5 m to about 6 m; on certain racks the upper shelves casted their shadows on the cages below. No correlation was found between these variations in light intensity and reproduction.

Short nights are characteristic of the summer season when the mice are reproducing at a low level. The 14-hour day was not effective in reducing the reproductive rate either; the colony produced at a high level.

Effect of food, temperature, and thyroid injections upon production of young

The study of the reproductive cycles of the old-field mice in the laboratory and in the field suggested several experiments. Laboratory-reared and wild caught pairs of P. polionotus, which had produced their last litter in the laboratory more than three months ago, were randomly grouped. One group was kept for three days at 4°C in a constant temperature box and then returned to the laboratory colony. The second group was fed acorns parasitized by beetle larvae (Balaninus sp), while the third group was fed acorns free of beetle larvae. Females in the fourth group were given dl-thyroxine injections of .01 mg per day for three consecutive days, and the fifth group was kept in the laboratory under normal conditions as a control. Groups two to five were maintained at 24°C for a month and a half in the falls of 1963 and 1964. The experiment with thyroxine was conducted during the fall of 1965. The acorns were collected under turkey oaks (Quercus laevis); up to 81 percent were parasitized by beetle larvae. They were induced to leave the acorns when kept warm for several days before feeding them to the mice. For the purpose of this series of experiments, data were discarded when pregnancies occurred within the first 22 days after the start of the experiment because the females had probably become pregnant before the experiment had begun. Resulting pregnancies and mean litter size are given in Table 15.

Cold shock, acorns parasitized by beetle larvae, and

Table 15. Effects of four different treatments upon the reproductive performance of laboratory-reared mice. The group injected with thyroxine had its own control group because this experiment was started after the others had been completed

Treatment	Sample Size	Percent of Sample Giving Birth	Number Giving Birth	Expected Number Giving Birth	Chi Square	Average Litter Size	F
Cold Shock (40C for 3 days)	24	91.7	22	11.1	10.70**	3.82	-----
Acorns with Beetle Larvae	35	78.6	27	16.1	7.37**	3.63	-----
Acorns without Beetle Larvae	24	33.3	8	11.1	0.87	3.50	-----
Control for the Above Experiments	114	29.8	34	52.7	6.64**	3.71	-----
Sub Total	197	-----	91	91.0	25.58**	-----	0.82
Thyroxine. Injections	40	87.5	35	24.9	4.10	4.29	-----
Controls for Thyroxine Injections	42	38.1	16	26.1	3.91	3.81	-----
Sub Total	92	-----	51	51.0	8.01**	-----	0.0013

** significant at the .01 level

thyroxine injections were associated with significant increases in the number of pairs giving birth but not in the average litter size. The group fed acorns without beetle larvae did not differ from their control groups. These results emphasize the importance of environmental factors in the regulation of reproduction in this species.

Geographical variation in litter size

The mean annual litter size of laboratory-reared females was $4.27 \pm .86$ for P. p. subgriseus and $4.79 \pm .42$ for P. p. rhoadsi. Williams, et al. (1965b) gave the comparable value for P. p. lucubrans as $3.25 \pm .93$. A gradient in litter size existed with the lowest value in South Carolina, the intermediate one in north central Florida, and the highest in south Florida.

Data collected during March and April, 1965 showed a similar trend. The average litter size was 4.6 for P. p. rhoadsi from Lake Placid, Florida, 2.9 for P. p. subgriseus from the Ocala National Forest, and 2.2 for P. p. lucubrans from south of Camden, South Carolina, while the percentage of pregnant and/or lactating females was 68.9, 44.4, and 26.3, respectively. Since both seasonal and annual variations occurred within each of the subspecies (Rand and Host, 1942; Davenport, 1964; Table 12 and Fig. 13), direct comparisons of field data should be made only after a considerable amount of data has accumulated and when evidence from other sources suggests that the samples are typical for that particular time of the year. The value

for P. p. lucubrans was approximately the same as that given in a summary of the annual breeding cycles of this subspecies from 1951 to 1955 (Davenport, 1964). The complete annual cycle of P. p. rhoadsi is not known (Rand and Host, 1942), but I have collected comparable samples at Lake Placid on three occasions separated from each other by at least three months. Each time the mean monthly litter size and the percentages of pregnant and/or lactating females were higher than those of P. p. subgriseus from the Ocala National Forest during the same month.

This gradient contradicted that shown for many other non-hibernating prey species of mammals such as rabbits, meadow voles, deer mice, and squirrels (Lord, 1960 and 1961; Moore, 1961; Barkalow, 1962; Jackson, 1965). Lord (1960 and 1961) hypothesized that litter size is directly related to the mortality sustained by the population. No direct data on mortality at different latitudes exist, but adults comprise a larger proportion of northern than of southern populations (Rand and Host, 1942; Caldwell and Gentry, 1965; p 109). It is unlikely that this was due to the differences in the level of reproduction in the different populations. The intensity of natural selection has to be high in populations whose members reproduce rapidly and live short lives. Variation in production of young is related to differences in the mortality sustained by the populations. This is an important bit of evidence supporting Lord's hypothesis, because the direction of the gradient is as predicted but opposite to that normally expected.

DISPERSAL AND PREDATION

Populations are dynamic units adaptable to local environmental variations. The evolutionary course of a population of sexually reproducing organisms is partly determined by the intensity and nature of the natural selection to which it is subjected and also by the amount of genetic exchange with other populations. Dispersal is important in that it increases genetic exchange and maintains the continuity of the species.

Dispersal of the Ocala population

Dispersal distances of the old-field mouse were measured during the winters of 1963, 1964 and 1965. I marked 312 juvenile mice between 13 to 30 days old by clipping their toes their sex and place of capture were recorded, and they were released into adjacent unoccupied burrows within 15 minutes after their capture. I first attempted to recapture them 30 or more days after their release. Only 33 (10.6 percent) were recaptured as adults. The initial sample included 55.4 percent males and 44.6 percent females. The comparable data for the recaptured mice were 42.4 percent males and 57.6 percent females. More females and fewer males were recaptured than expected, the difference was not significant (Chi square = 2.27, df = 1, and $P = .15$). The dispersal distances for each sex are given in Fig. 18.

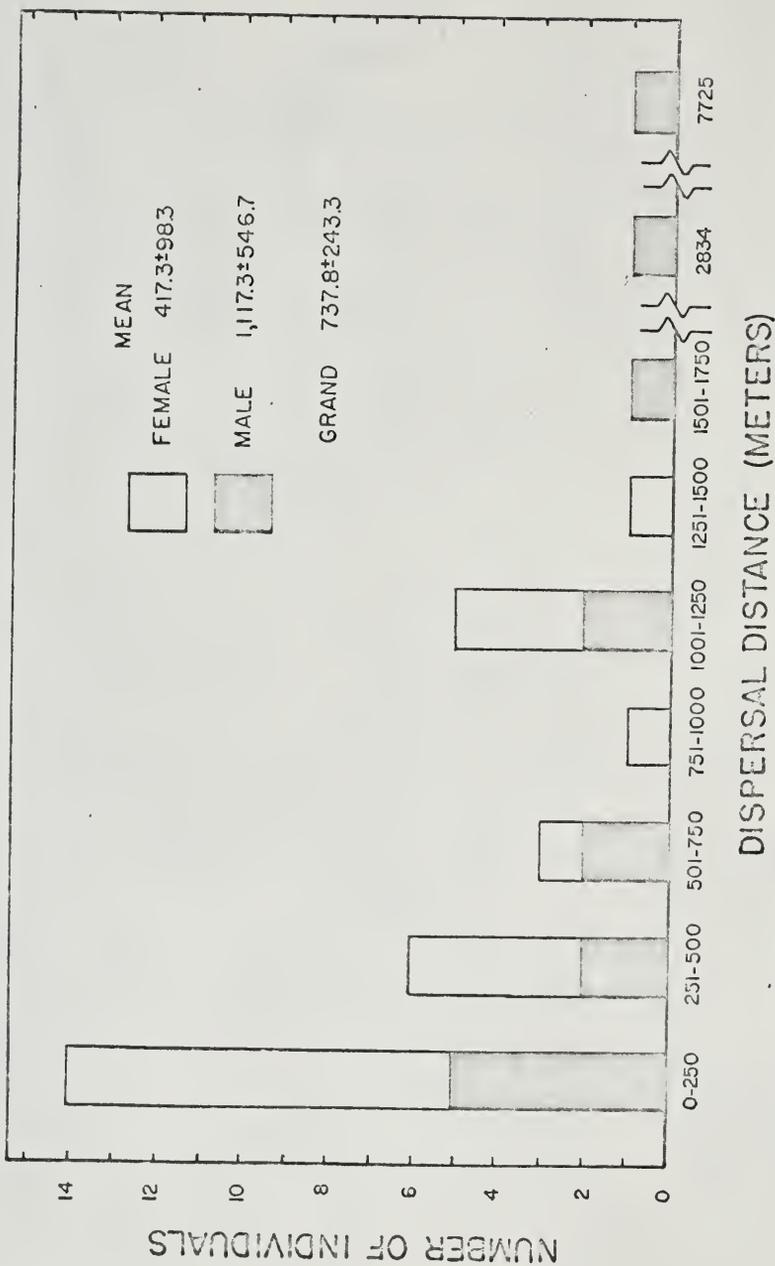


Fig. 18. Dispersal of juvenile males and females (Peromyscus polionotus subgriseus).

The large standard errors of the mean dispersals indicate that the sample size is too small. The means for each sex were not significantly different ($t' = 1.26$, $df = 13$, and P greater than .20), but there was a significant difference between their variances ($F = 30.90$, $df = 13/18$, and P less than .01). The exclusion of the male that moved 7,725 m reduces the mean and standard error of the male sample to 668.7 ± 228.8 m which is not significantly different from the female mean either ($t' = 1.01$, $df = 12$, and P greater than .30); but there remains still a significant difference between the variances ($F = 5.41$, $df = 12/18$, and P less than .01). The males' dispersal distances varied more than those of the females.

To obtain another measure of movement within the forest, all of the burrows were dug out and the occupants removed along one five-mile section of highway 316 between Eureka and Salt Springs. Every new burrow was excavated on subsequent trips. The approximate age and sex were recorded for each captured mouse. A total of 152 males (71.4 percent) and 61 females (28.6 percent), or 138 juveniles (64.8 percent) and 75 adults (35.2 percent), were captured in this area after the initial sample was removed. The deviations from the chance expectations for sex and age were significant (Chi squares = 38.88 and 18.64, respectively, $df = 1$, and P less than .01).

Burt (1940) said of P. leucopus "Dispersal of individuals in this species occurs chiefly while the animals are young and before they have established their homes. Once an animal selects a home site it rarely leaves, but usually remains there

for the rest of its life." A similar conclusion has been reached concerning other species of small mammals (e.g., Howard, 1949; Dice and Howard, 1951; Howard, 1960) and also applies to P. polionotus. Since the interval between samples was about a month, the percentage of juveniles moving into the depleted area must have been higher than 64.8 percent; some of the animals would have completed the post-juvenile molt in this time if they had moved into the study area shortly after the last sample had been taken.

Howard (1960) summarized the literature in regard to the tendency of male vertebrates to disperse farther than females. Males did not range farther than the females in this study, but their average dispersal distance was almost three times that of the females, and the associated standard error was about 2.5 times larger. The standard errors of the dispersal distances of males are usually larger than those of females, and the curves for the individual dispersal distances are strongly skewed in the direction of the lower values (Blair, 1940; Dice and Howard, 1951; Allred and Beck, 1963; Smith, 1965b). Most of the P. polionotus that moved short distances were recaptured on the same sand ridge on which they were born or on the next nearest ridge. Certain individuals moved relatively great distances from their birthplace. The interpretation of these data may be that, if an individual does leave its homesite, it will probably move a longer distance than would be predicted by a normal distribution. These data do not contradict Howard's hypothesis (1960) concerning an innate tendency of certain

individuals to disperse farther than others but they do not necessarily support it. Other interpretations can be given the data (Dice and Howard, 1951; Stickle, 1954).

The average dispersal distance of P. polionotus was much higher than comparable figures for this and other species of small mammals (Blair, 1940 and 1951, Dice and Howard, 1951; Allred and Beck, 1963). In part, different techniques employed in the various studies account for these differences. In most studies, the maximum distance an animal can disperse and still be recaptured is less than the reported average dispersal distance of the P. polionotus males. The exclusion of the longer distances drastically reduces the mean. Theoretically a mouse could have moved over 50 km and still have been recaptured, since collections were made in all parts of the forest. The two males that went farthest were captured unexpectedly when I collected the monthly samples to determine the level of reproduction in the population.

The possibility exists that P. polionotus does disperse farther than other mammals of comparable size. These mice are found characteristically in habitats of early stages of primary or secondary succession (Golley, et al., 1965). For this reason, it is likely that large distances between suitable habitats exist, and with time succession makes the habitat unsuitable for the mice.

The pine forest habitats in which they are found on the mainland are fire subclimaxes (Laessle, 1958a and 1958b). Utilization of available habitat might require certain individuals

to disperse long distances to find recently burned areas. This is mere speculation, however, since these results are not directly comparable with those of other investigators.

Predation in the Ocala National Forest

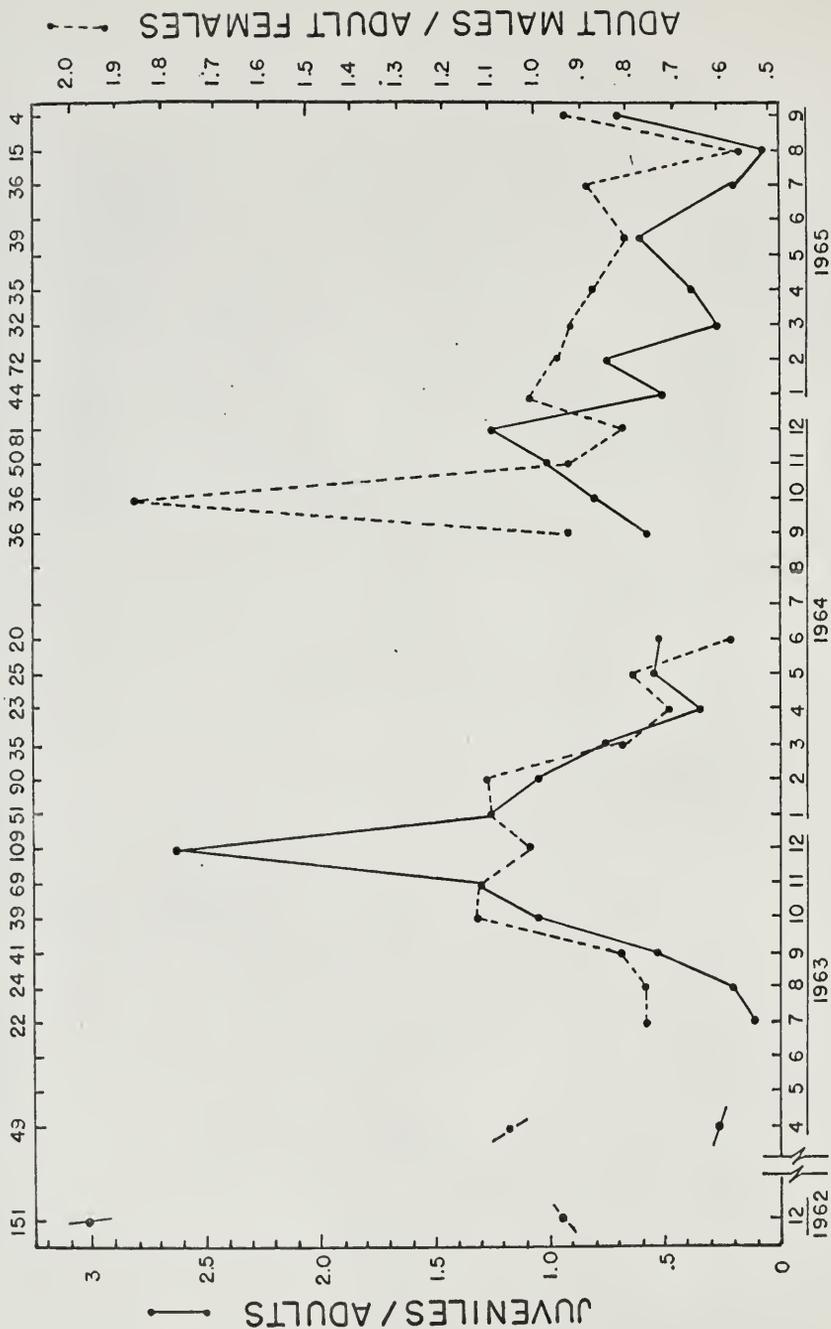
The calculation of the rate of population turnover depends upon a knowledge of the population's size, reproductive rate, and age composition. The size of the Ocala population is not known, but it appeared to show a progressive decline throughout the study. Land management practices in this area exclude the use of fire. This causes the sub-climax sand pine scrub community to undergo further succession. The old-field mouse reaches its highest density in areas with sparse vegetation (Rand and Host, 1942; p 13). Fire is an important environmental factor for this species since it periodically clears the land and creates favorable situations for the expansion of local populations. Continued control of fire will further decrease the population density.

The exact age composition of the population is not known either, but an approximate value is given by the ratio of juveniles to adults. The age composition of the population must have shifted drastically throughout the year since this ratio showed considerable seasonal variation (Fig. 19). The shifts appeared to be cyclic in nature, and the age composition of the population did not show any progressive changes or significant annual deviations.

For the purpose of this discussion, it is assumed that the mean annual population size and age of the mice remained

Fig. 19. The ratio of the number of juveniles to adults and of adult males to adult females in each monthly sample from the Ocala National Forest.

SAMPLE SIZE



approximately the same for each year. Then the average rate of turnover in the population can be calculated by using the data on the production of offspring (Table 12). The calculations can be made in two different ways. If the production were the same as that given in Table 12, the average monthly production equaled 195.3 ± 42.2 young per 100 mature females. This figure is probably too high since it included embryos and excluded juveniles which were not found in a burrow with a mature female. Calculations made by including this latter group and excluding embryos gave 178.6 ± 38.6 young per 100 mature females. Both schemes required the utilization of monthly averages, since some months were represented more than others. Each mature animal in the population was replaced every 1.02 months at the higher reproductive rate or 1.12 months at the lower rate. The actual turnover probably lies between these two values. A more accurate calculation could have been made if the age of the juveniles and embryos had been determined. This did not seem worth the effort; the difference between the two figures was only three days, and the errors associated with the various phases of the study were probably larger than this. If the population became smaller during the study period, as it seems likely, the average time of turnover would have been less than one month.

These results are not comparable to any other study of longevity in small mammals because they are based on individuals trapped and not on the total number born. This means that the mice are 30 or more days old when they become part of the sample.

The average reported life spans for species of Peromyscus include 152 days for P. maniculatus, 190 days for P. truei, 275 days for P. californicus (McCabe and Ranson, 1950), less than 155 days (Blair, 1948) or 122 to 235 days for P. leucopus (Snyder, 1956), and about 207 days for P. boylii (Brown, 1964a). The average life span of P. polionotus was 30 to 33 days. This suggests that the mortality rate was very high for certain animals just after weaning because the population could not sustain itself if all of the animals died at 30 days of age. A large number of juveniles obviously die when they first leave the burrow. Once an animal survives this period, it must have a good chance of surviving to the reproductive age. The values based on trapped mice are probably too high because most of these animals have survived this period of intense selection.

If the survival rate had been the same throughout the year, striking seasonal variations in density should have been noted. No such variations occurred. It seems likely that the average life span was significantly shorter than one month during the winter and longer in the summer. Mortality rates vary seasonally in P. maniculatus (Howard, 1949), P. leucopus (Snyder, 1956) and P. boylii (Brown, 1964a). In P. polionotus, the maximum mortality and reproductive rates probably occurred concurrently.

Adult females outnumbered adult males in 18 of the 26 monthly samples; this differed from the chance expectation (Chi square = 5.02, df = 1, and P less than .05; Fig. 19). The

opposite was true for newly born young (p 92). Males must have been subjected to a higher level of predation than females. The production of a higher percentage of males is probably an adaptation to compensate for their higher mortality rate. The lower recapture rate of marked males in the dispersal study may have been due to their higher mortality rate.

Geographical variation in selection pressure

The rate of evolution is directly related to the level of natural selection. Local populations of the old-field mouse should adapt rapidly to small but consistent differences in their environment because of the high intensity of the natural selection they are being subjected to. Geographical variation in the reproductive performance of the different subspecies is probably an example of this tendency for divergence.

In April, 1965, the ratio of juveniles to adults was lower in P. p. lucubrans (.25) and higher in P. p. rhoadsi (.68) than in P. p. subgriseus (.39; Fig. 19). This was probably a reflection of the higher average age of mice in South Carolina. A mouse that outlives another should have a higher biotic potential, other things being equal. If the life expectancy in the populations and the selection pressures on them were the same at the three localities, then the mice in South Carolina should become extinct because they do not replace themselves at the same rate as the population in the Ocala National Forest. The P. p. rhoadsi should expand at a rapid rate for the same reasons. Neither of these situations appears to be the case. It seems likely that mortality sustained by the populations is

relatively low in the north compared to that at more southern latitudes. Reproductive rates probably reflect the average level of predation that the population has been subjected to in the past. This implies that the most efficient utilization of available energy is achieved by populations which are relatively stable over long periods of time. The reproductive cycle of P. polionotus enables it to live under a range of environmental conditions which vary geographically and seasonally.

Possible predators

The stomach contents of 36 snakes of nine species (Table 3) were examined for the remains of P. polionotus. The results were negative. The only known predator is the barn owl (Trost and Hutchinson, 1963). A list of predators for this species would include snakes, owls, hawks, and carnivorous mammals.

Once I put a gopher frog into a container with some young mice about two days old. Four hours later the gopher frog had eaten one of the mice. While this and other species of amphibians were found in the entrance to burrows (Table 3) and may occasionally have the opportunity to eat young mice, the importance of this type of predation is doubtful. The young mice are normally protected by their parents. The lack of information on predation is unfortunate since the nature of the selective forces operating on the population is very important in determining the direction in which it will evolve.

MORPHOLOGICAL VARIATIONS

The description of new species or subspecies usually depends upon morphological differences between them and other closely related organisms (Mayr, 1963). "External measurements, color, patterns, and character of the pelage, and skeletal characters, principally of the skull, are used in the description and identification of mammals" (Blair, et al., 1957). Subspecific differentiation in P. polionotus depends primarily upon coat color (Schwartz, 1954). This is unfortunate since this is such a variable character. It is correlated with the coloration of the soil (Hayne, 1950) and also shows variation with age. Old P. p. subgriseus can be recognized in the laboratory and probably in the field; younger adults have a darker pelage not quite as red as that of the older mice.

Mice are preyed upon significantly more often when they contrast with their background than when they blend it with it (Dice, 1947). The background color varies with soil type, the presence or absence of vegetation, seasonal fluctuations and successional stages of the local vegetation. The color of the subsurface soil frequently contrasts with that at the surface; this is especially important for the old-field mouse since it spreads this soil around outside the entrance of the burrow and frequently

crosses this area. Considering the variety of backgrounds on which these mice occur, as well as the intense selection pressure they are subjected to, a high degree of local variability should be expected and can be observed. Failure to recognize this has led to considerable difficulty in describing and recognizing subspecies. Convergent evolution has resulted in the same average coat color in non-overlapping populations separated from each other by a great distance. Some of these even belong to different subspecies.

Schwartz (1954) places the subspecies of P. polionotus into two categories: 1) a pale form that occurs exclusively on the beaches and these included P. p. phasma, P. p. decoloratus, and P. p. niveiventris on the east coast of the Florida peninsula, and P. p. leucocephalus, and P. p. peninsularis on the Gulf Coast of Florida; 2) a darker form that usually occurs some distance from the beaches and these included P. p. rhoadsi, P. p. subgriseus, P. p. albifrons, P. p. polionotus, P. p. lucubrans and P. p. colemani. After proposing these categories, Schwartz (1954) points out that P. p. niveiventris, a beach form, most resembles in coloration P. p. rhoadsi, a mainland form. The resemblance is so close that I cannot separate adult specimens from Vero Beach (P. p. niveiventris) from those collected at Lake Placid (P. p. rhoadsi) by using the color of the dorsal pelage. Peromyscus polionotus albifrons also resembles P. p. rhoadsi and P. p. niveiventris. It seems that his classification depends more upon the geographical location of the subspecies than upon their coloration. This type of classification

is good, if numerous samples are taken in the area of intergradation between subspecies. Schwartz's (1954) description of P. p. colemani depended upon his examination of 12 specimens from South Carolina, six from Georgia, and 13 from Alabama. This is insufficient to describe such a wide ranging subspecies, let alone, clearly outline its intergradation with other subspecies it contacts. Measurements were given for only 11 of the 31 P. p. colemani and he based his description of P. p. lucubrans on 23 adult skins. Both of these subspecies described by Schwartz (1954) are questionable at best. The validity of these taxa must rest upon future work since there is considerable interpopulational variation within this species.

Schwartz recognized the wide range of variation but attributed most of it to age differences. He says "The variation in this series of 23 adult skins at hand is noteworthy. The skins may be divided into four groups. These groups are correlated neither with geography nor with season, and seem to be rather dependent upon age of the individual and degree of wear. Group 1 is composed of seven individuals that are grayer than the type in color; these are skins taken in October and November and are presumed to represent the worn pelage. Group 2 is represented by seven specimens that are brown rather than gray, but are not quite so bright as the type; this series grades imperceptibly in Group 3, of which there are seven specimens (including the type). The third group shows more reddish coloration; both Groups 2 and 3 contain specimens in fresh pelage and are here considered to be typical of lucubrans.

Group 4 is composed of two individuals, taken in November; both are extremely pale dorsally. The sides are Avellaneous, but the typical dorsal stripe is very inconspicuous (Wood Brown). The crown and face generally are likewise paler than the remaining specimens. These two individuals have the darker brown pigment much reduced on the dorsum, and black pigment is absent; apparently they represent a very local population of P. p. lucubrans at Talatha, Aiken County, South Carolina. The series of adults in fresh pelage (Groups 2 and 3) varies in coloration from specimens which resemble the type at one extreme to individuals at the other extreme in which the sides are Wood Brown and the dorsal stripe is closed to Buffy Brown. In this entire series the tail is always distinctly bicolor." The description of any wide ranging group must be considered inadequate when it is based upon small samples, especially when there are several confounding variables, such as age and locality. There were many more specimens available in 1954 than Schwartz examined, and additional specimens are easily collected.

General trends in pelage color

The almost continuous range of variation shown by the various subspecies is obscured by placing them into definitive categories. For example, P. p. phasma more closely resembles the mainland form, P. p. rhoadsi, than it does P. p. leucocephalus, the palest subspecies, but P. p. phasma is the palest form on the east coast. Despite all the confusion, certain generalizations concerning coat color appear to be valid. These are based upon

the examination of over 500 specimens, some of which were collected by myself, and the others were part of the collection of the Florida State Museum.

- 1) The palest mice are found on the beaches along the Gulf Coast of Florida. The dark dorsal hairs are limited in extent to the upper back and top of the head. The tail is not distinctly bicolored.
- 2) A gradient runs from north to south on the east coast, with the palest mice found in the north on the beaches south of the mouth of the Saint Johns River and the darkest forms found in the area of Palm Beach and Fort Lauderdale. None of these mice are as pale as the Gulf Coast forms. Their reddish brown dorsal hair extends down their sides including their hips, and the ventral hairs are white to the base.
- 3) The mice on the southern east coast beaches resemble the southern mainland form and those just off the beaches along the Gulf Coast. Their coloration is reddish brown on the dorsum and they generally lack a distinct dorsal stripe of brown hair darker than the rest of the dorsal coloration. The ventral hairs are frequently white to the base but not uniformly so, and the tail is only lightly bicolored if at all. White hairs on the face are limited to patches over and under the eyes, lower nose, upper forehead, and in front of the ears. Any one specimen usually does not have white hair in all of these places.
- 4) Pelage becomes progressively darker in the northern populations. The dorsal hair changes from a reddish brown to dark brown and the ventral hairs are grey at the base. The dorsal stripe of dark brown hair becomes more distinct and patches of

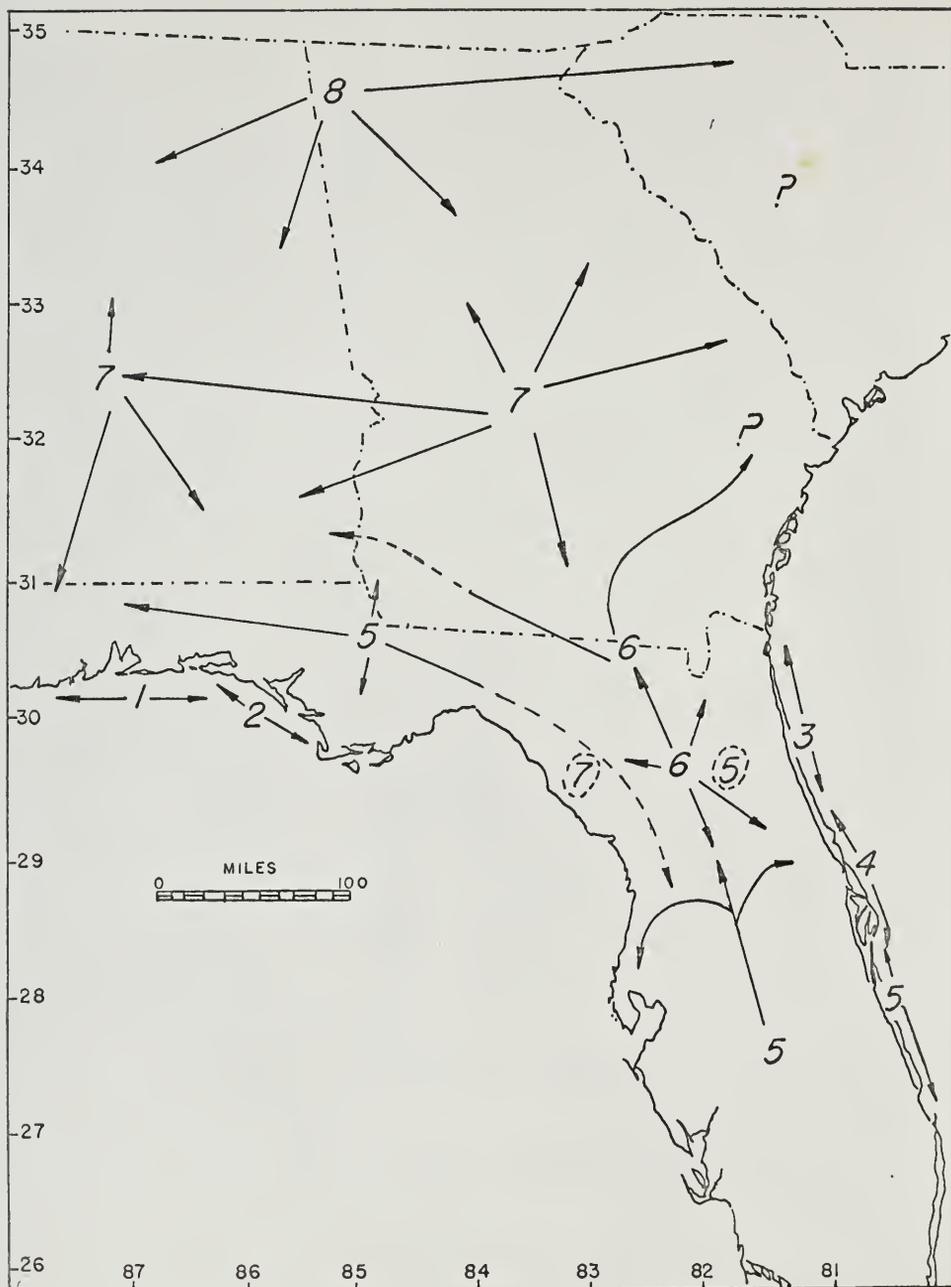
white hair on the face are normally lacking. The tail is distinctly bicolored. These trends in coat color are summarized in Fig. 20.

Interpopulational variability of coat color in north central Florida

The overall darkness of the pelage of P. p. subgriseus is intermediate to that shown by P. rhoadsi, the lighter southern form and that of the darker northern form, P. p. polionotus (Schwartz, 1954). Certain populations in the middle of the range of P. p. subgriseus, however, could be assigned to adjacent subspecies if it were not for their geographic locality. Two examples will be used to illustrate this point. Between 25 to 30 adult mice were examined from each of the populations used as examples.

Mice from Interlachen, Florida, occurred on Lakeland soil in a habitat predominated by sandhill vegetation; they most closely resembled P. p. rhoadsi by their pale reddish dorsal coloration without a distinct dorsal stripe, ventral hairs on the belly white to the base, tail bicolored for less than 10 percent of its length, and numerous patches of white hair on the face. The frequency of white cheek was higher in this population than in any other within the range of P. p. subgriseus (Fig. 9). This was also the only mainland population in which the percentage of animals with tails not bicolored to the tip (100 percent) exceeded 5 percent. This character alone would suffice to differentiate this population as a separate subspecies. The low lying ground around Interlachen apparently

Fig. 20. Geographical variation in coat color of Peromyscus polionotus. The numbers are on an ordinal scale with one being the lightest and eight the darkest.



isolates this population from its next nearest neighbor and may explain how such a high degree of local differentiation can be maintained.

The origin of this population may hold the key to the interpretation of the observed polymorphism in coat color within this species at least in the southern part of its range. Some authors believe that Interlachen is on the 200-250 foot Upper Miocene shore line, near the 90 foot Pliocene shore line (Alt and Brooks, 1965). If so, this area was a part of the east coast shore line for a long period of time. Selection always results in a lighter pelage along the beach in this species. The succession of the vegetation after the water receded gradually changed the background and, thus, also the nature of the selective forces operating on coat color. The pelage of the mice from Interlachen would be expected to be darker if genes were regularly exchanged between this population and the darker northern forms which are characteristic of later successional stages. Other populations, which are not as isolated from the northern element but are on the same shore lines, should be paler than normal but not as extreme as the Interlachen population. The Florida populations at Trenton, Bell, Archer, and Newberry are good examples of this, since they are not as dark as those at Gainesville and Alachua. The first set of localities are close to either the 90 foot Pliocene or 200-250 Miocene shore line, while the last two are on the central ridge of high ground down the center of the Florida peninsula. This ridge is continuous with the higher ground in Georgia.

The correlation between the color of the pelage and the old shore lines was first pointed out to me by Mr. Bowen of the Dartmouth Museum. He is currently preparing a manuscript describing this relationship in detail. The majority of his work was done in the panhandle area of Florida.

My second example, the population at Manatee Springs was the darkest population of P. polionotus east of Tallahassee and south of the Georgia-Florida border. The dorsum was dark brown with a distinct dorsal stripe of dark brown hair. The tail was distinctly bicolored and the ventral hairs are grey at the base. This description resembles that of P. p. polionotus not P. p. subgriseus. The deviation from the general type found in this area cannot be explained on the basis of old shore lines since this population is darker not lighter than expected, and because the proximity of the Suwannee River and the low elevation at this site suggest that the mice are occurring on the river's flood plain. The suitable natural habitat at this site is very limited in extent and is surrounded by broad leafed evergreen climx forest on one side and long leaf pine flatwoods on the other. Soils supporting this vegetation are quite dark in comparison to the soils on which the species normally occurs. Isolation appears to be as important a factor at this locality as in Interlachen, since there seems to be no direct connection between this and adjacent populations. Isolation is important in maintaining local adaptive peaks created by selection of mice on different backgrounds.

These examples illustrate the dynamic nature of the evolutionary process and indicate the difficulties of a classical taxonomic approach. A detailed study of populational variation is needed before new subspecies are named. Small samples from widely spaced locations are not sufficient to distinguish subspecies from widely spaced populations occurring along a cline or on segments of an eroded relict shore line. The logical extension of a work like that of Schwartz's (1954) would be the naming of several dozen subspecies in peninsular Florida alone. This may eventually be needed but at this time it would only add to the confusion and contribute nothing to the understanding of this species. The value of naming individual populations in limited geographical areas is doubtful when carried to an extreme.

Interpopulational variation of external dimensions

What follows is a preliminary attempt to determine quantitatively the extent of interpopulational variation using the length of the ear from the notch, hind foot, body, and tail. The variation in the length of the ear, hind foot, body, and tail are given for 17 populations representing six subspecies in Figs. 21, 22, 23, and 24, respectively. The sample size was 20 adults per population.

The range was 11 to 18 mm for the ear, 13 to 20 mm for the hind foot, 62 to 88 mm for the body, and 32 to 62 mm for the tail of adult animals. Peromyscus polionotus phasma from Anastasia Island, Florida had, on the average, the largest hind foot (15.0 mm), tail (54.1 mm), and body (83.7 mm), while P. subgriseus from Williston, Florida had the smallest hind

Fig. 21. Variation in the size of the ear in 17 populations representing six subspecies (separated by dashed horizontal lines and indicated by the letters inside the open rectangles; L = Peromyscus polionotus lucubrans; P = P. p. polionotus; PH = P. p. phasma; S = P. p. subgriseus; R = P. p. rhoadsi; N = P. p. niveiventris). The number of each population as given on the map corresponds to the number at the right of the histogram representing it. The vertical line denotes the mean, the horizontal line the range, the closed and open rectangles one standard error and one standard deviation on either side of the mean.

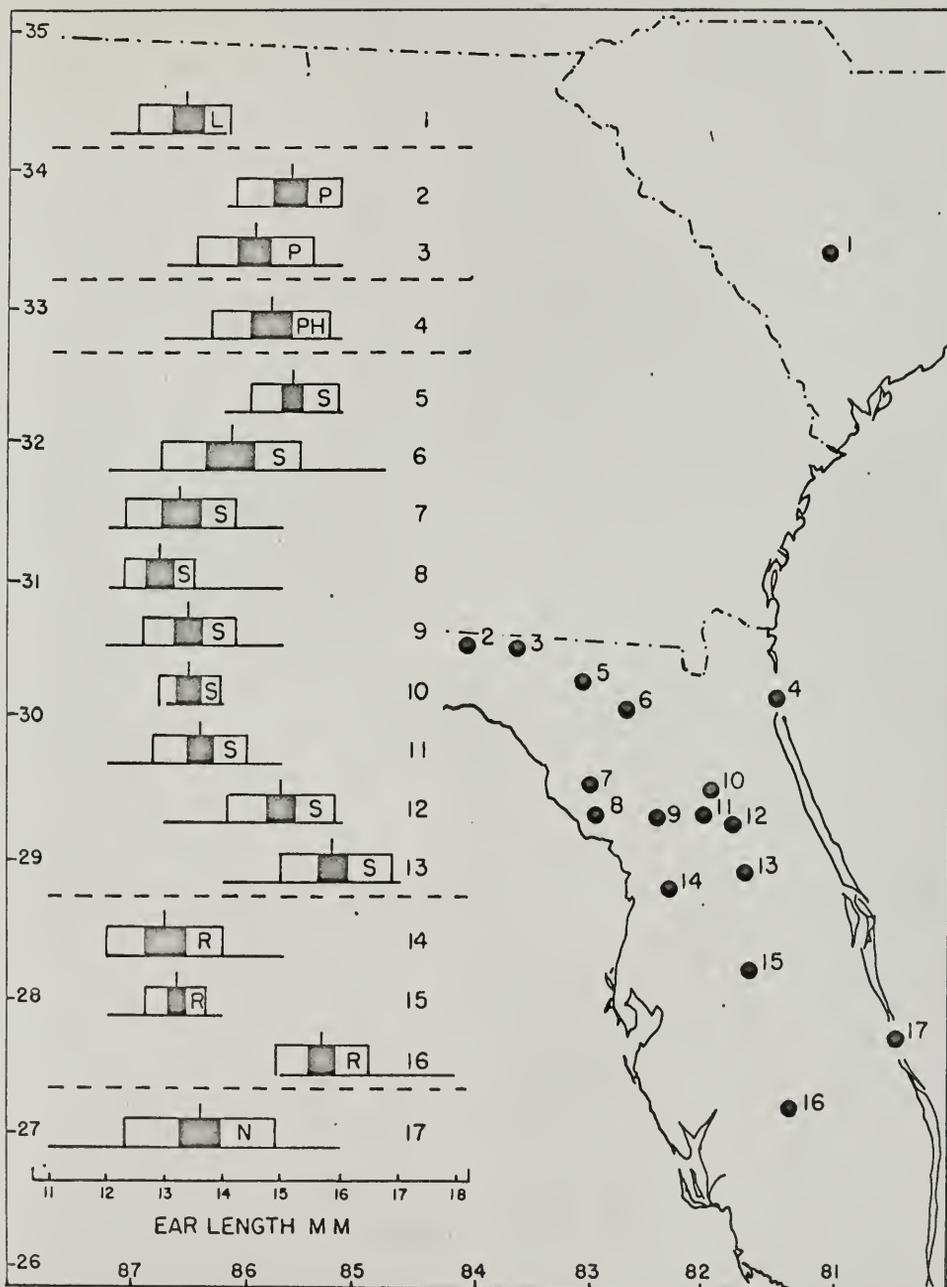


Fig. 22. Variation in the size of the hind foot in 17 populations representing six subspecies (separated by dashed horizontal lines and indicated by the letters inside the open rectangles; L = Peromyscus polionotus lucubrans; P = P. p. polionotus; PH = P. p. phasma; S = P. p. subgriseus; R = P. p. rhoadsi; N = P. p. niveiventris). The number of each population as given on the map corresponds to the number at the right of the histogram representing it. The vertical line denotes the mean, the horizontal line the range, the closed and open rectangles one standard error and one standard deviation on either side of the mean.

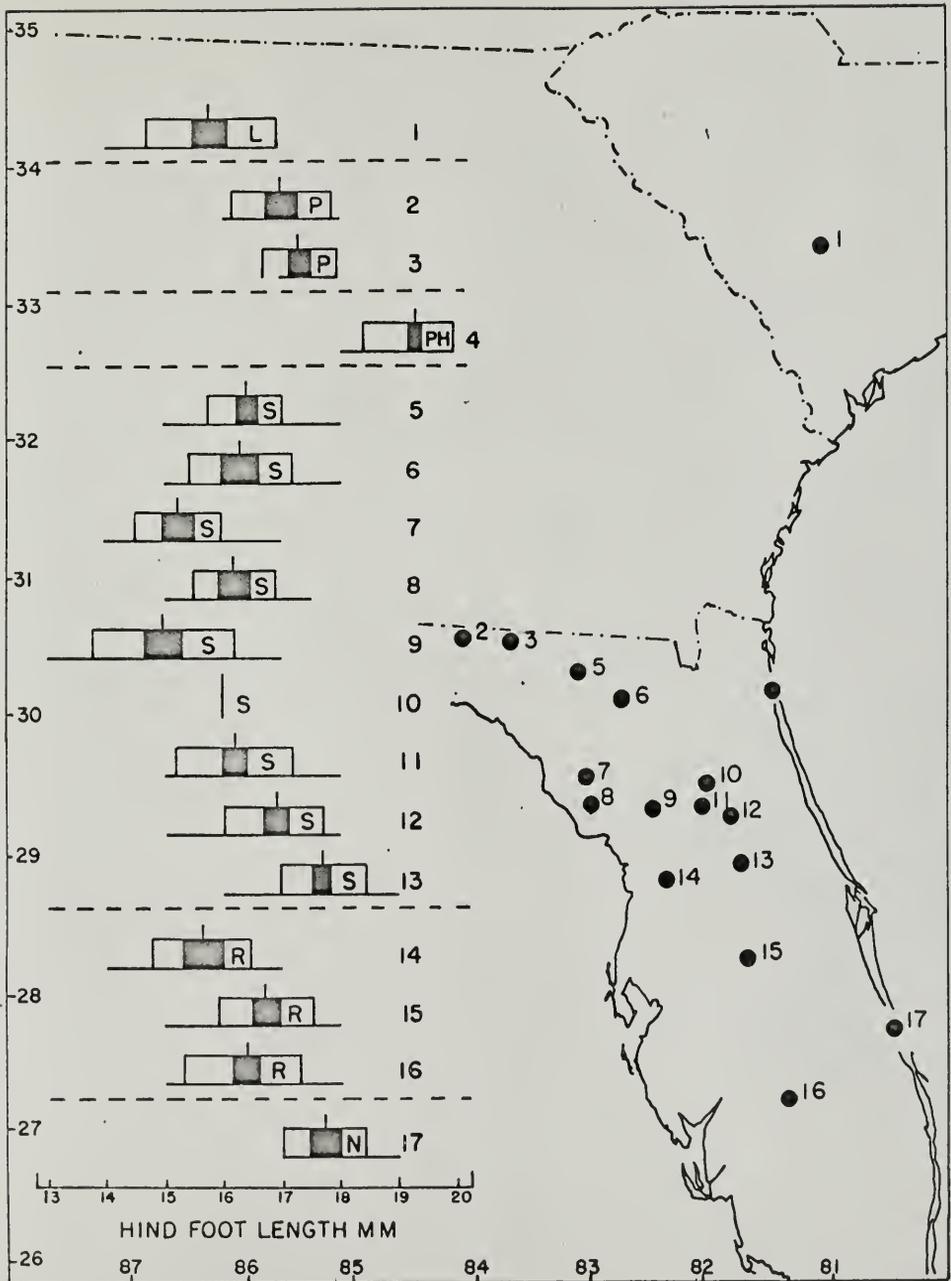


Fig. 23. Variation in the size of the body in 17 populations representing six subspecies (separated by dashed horizontal lines and indicated by the letters inside the open rectangles; L = Peromyscus polionotus lucubrans; P = P. p. polionotus; PH = P. p. phasma; S = P. p. subgriseus; R = P. p. rhoadsi; N = P. p. niveiventris). The number of each population as given on the map corresponds to the number at the right of the histogram representing it. The vertical line denotes the mean, the horizontal line the range, the closed and open rectangles one standard error and one standard deviation on either side of the mean.

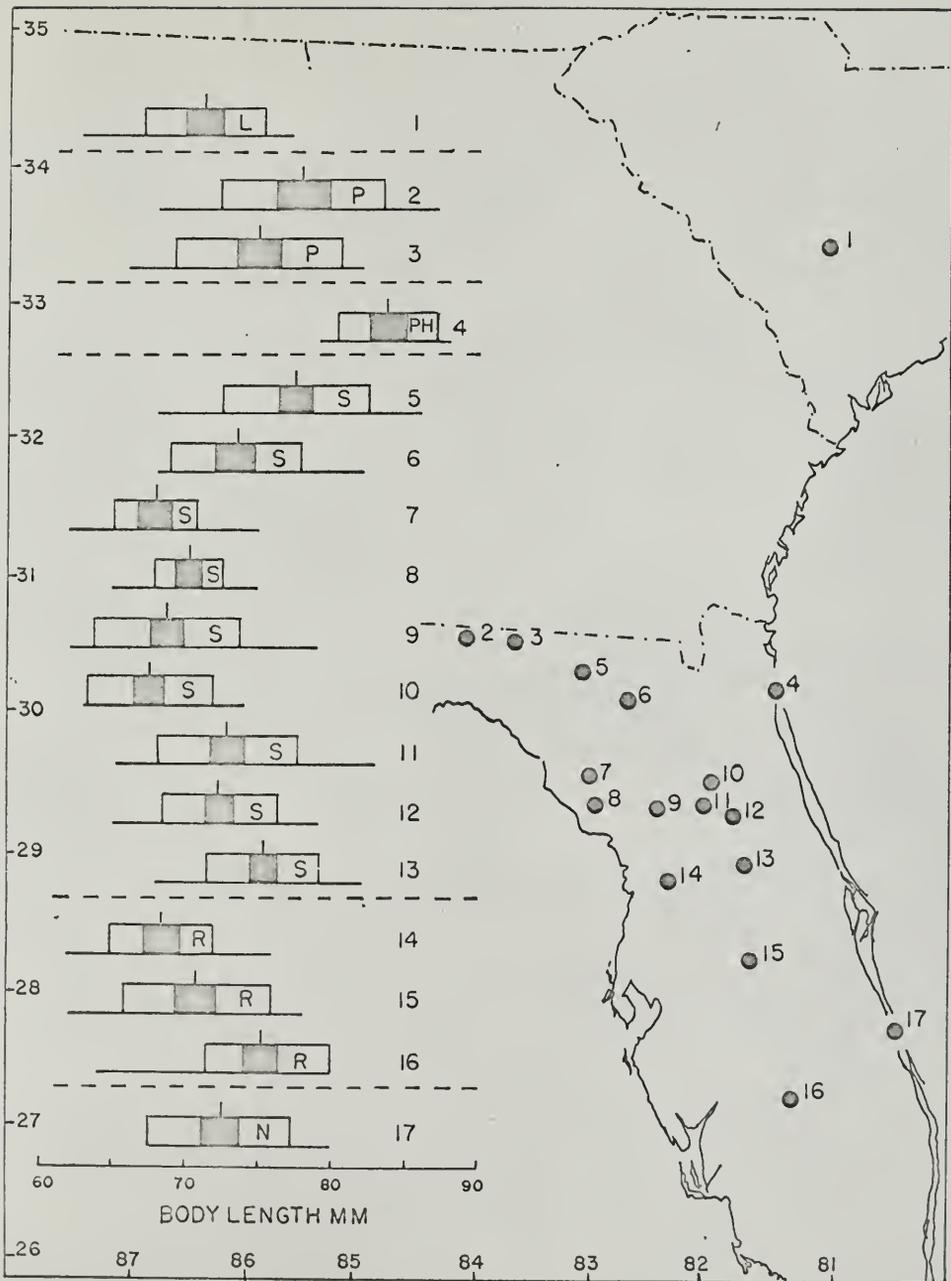
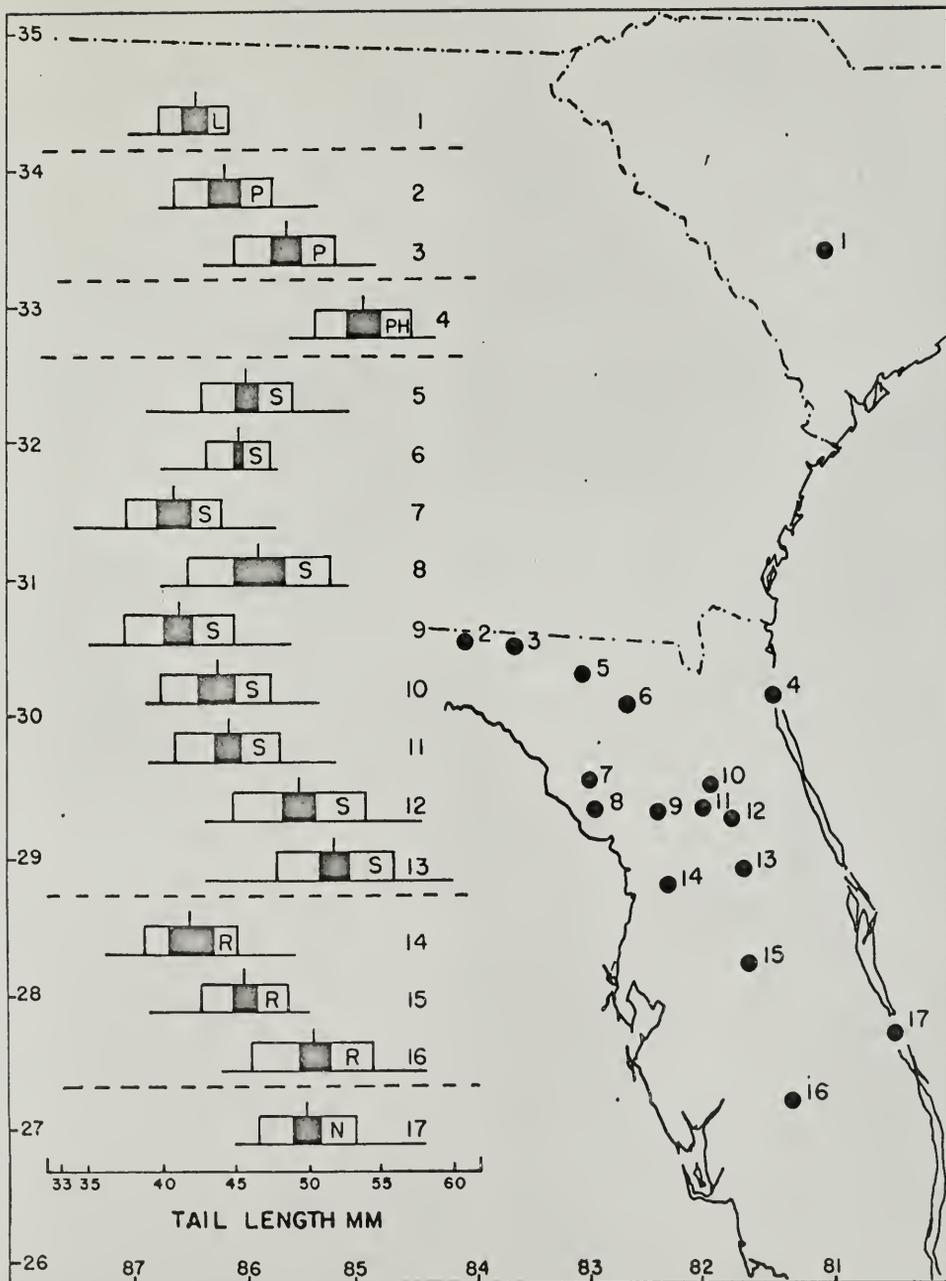


Fig. 24. Variation in the length of the tail in 17 populations representing six subspecies (separated by dashed horizontal lines and indicated by the letters inside the open rectangles; L = Peromyscus polionotus lucubrans; P = P. p. polionotus; PH = P. p. phasma; S = P. p. subgriseus; R = P. p. rhoadsi; N = P. p. niveiventris). The number of each population as given on the map corresponds to the number at the right of the histogram representing it. The vertical line denotes the mean, the horizontal line the range, the closed and open rectangles one standard error and one standard deviation on either side of the mean.



foot (15.0 mm) and tail (41.3 mm). The mice with the largest and smallest average ear were P. p. subgriseus from south of Astor Park, Florida (15.9 mm) and from Manatee State Park, Florida (12.9 mm), respectively. The average body size was smallest in P. p. subgriseus from Interlachen, Florida (67.5 mm).

The ranges of the values and the means of the populations for each external dimension were greater than those reported by Schwartz (1954) for the six mainland subspecies of P. polionotus. The same is true if we consider only the values from populations of P. p. subgriseus. Intrasubspecific variation cannot be greater than intraspecific variation. The number of mice used by Schwartz was insufficient to estimate the various parameters of the populations; his discussion of size trends and tail length should be disregarded.

None of these characteristics are of any use for differentiating between the subspecies, excluding P. p. phasma, with its distinctly larger tail and hind foot. Many significant intrasubspecific differences do exist between populations of P. p. subgriseus and of P. p. rhoadsi, but none of the populations differed significantly from all other populations of P. p. subgriseus.

Hayne (1950) studied the coat color in P. polionotus and found a strong correlation between the color of the pelage and soil color within a large area. Moreover from place to place within limited areas, there were no correlations between these two factors. The divergence of local populations was also

apparent in this study (Figs. 9, 21, 22, 23, and 24). Hayne (1950) thought that natural selection and dispersal were the important factors determining the mean value within local populations and that genetic drift was relatively unimportant in P. polionotus. Predation of the intensity to which this species is subjected (p 107) should play a major role in determining the mean of any character with a survival value other than neutral. The extreme divergence in the isolated populations at Manatee Springs State Park and Interlachen may exemplify the effect of selection without the damping effect of genetic exchange with other populations in slightly different environments. The intra-subspecific evolution of the old-field mouse is probably best interpreted in terms of local variations in the type and intensity of predation and genetic exchange between populations which are highly adapted to their local conditions.

BEHAVIOR PATTERNS OF THE OLD-FIELD MOUSE
IN THE WILD AND IN CAPTIVITY

The study of the action system of a species in the wild under natural conditions is a basic source of information highly necessary for comparative behavior studies. However, this approach may become very difficult when the animal is small in size and lives a nocturnal life, as is the case in the old-field mouse.

Such animals may be better studied in the laboratory than in the wild. An interpretation of their behavior in captivity benefits from a thorough ecological knowledge of the species. The ecology of P. polionotus is well known and contributes directly to our understanding of its behavior.

The terminology used by Eisenberg (1962) in a study of the behavior of two species of Peromyscus is used here to make the direct comparison of the two studies possible.

Individual Behavior

Burrowing

The burrowing habit of P. polionotus distinguishes it from all other species of Peromyscus. Variations between burrows were essentially the result of the mice trying to avoid obstacles in the soil, their response to changes in the slope of the ground, and to the different types of soil. The latter seems

especially important for this species. Digging appears in the same stereotyped way in the several subspecies (Rand and Host, 1942; Ivey, 1949); the mice dig with their forefeet and throw the dirt back between their hind legs. The hind feet kick the sand further back.

The sand plug is so solidly packed in the entrance that it seals the burrow from the air above ground. The mice frequently plug the burrow after they leave it. This plugging behavior of the old-field mouse is unique in the genus Peromyscus.

The number of occupied and unoccupied burrows per unit area was relatively small compared to the number of families in a given area. The reproductive activity and the population turnover were very high at most times of the year. If each animal moved some distance from its birthplace and then dug a new burrow, in a short time there should be more burrows than one finds in the field. Most of the young animals occupy vacated burrows. Some move into burrows with open escape tubes. In this case, they either put a short plug of 7 to 8 cm of compact sand into it or pack the escape tube with sand all the way back to the nest cavity and dig another tunnel approximately at a right angle to the old one. Most of the new escape tubes were directed opposite to the downward slope of the ground in a perpendicular direction to the long axis of the nest cavity. In two burrows, the escape tube lead off the end of the entrance tube just before it entered the nest cavity.

Nest building

Ninety-six percent of the occupied burrows contained a nest. All pregnant and/or lactating females were found with a nest in the burrow. Juveniles and adults of both sexes construct nests. An attempt to identify the nesting materials was abandoned when it became apparent that the mice used anything that was abundant and of soft texture. The materials, that were consistently found in nests from the northern to the southern parts of the range of this species, were Kleenex tissue paper and various types of grasses. The Kleenex were collected from the road shoulders where they had been thrown from passing automobiles. Small leaves (frequently oak of various types), cotton, rags, newspaper, hair from road killed mammals, and shed snake skins were also used.

During the warmer parts of the year, the nests were smaller and open at the top. Bigger nests with roofs were found during the winter. Since most organic matter rapidly decomposes when placed underground, the nesting material must be periodically renewed. Thus nest building behavior occurs at all times of the year.

The laboratory mice were given cotton for nesting after the birth of a new litter. The percentage of nests without roofs on the second day after the birth of a new litter varied seasonally although the ambient temperature was relatively constant (Fig. 25). Laboratory mice had a tendency to remove the

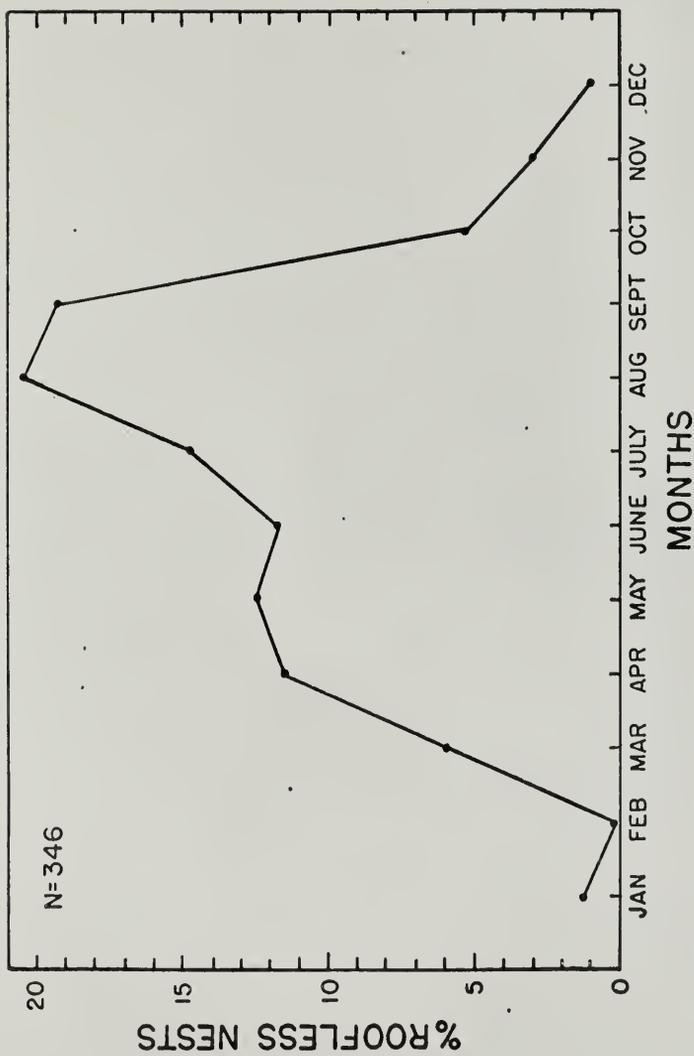


Fig. 25. Seasonal variation in the percentage of nests of laboratory-reared mice without roofs on the second day after the birth of a new litter.

roof of their nest as the young matured (Fig. 26). Most of the roofs were broken apart by the mice several days after the eyes of the young mice opened; this resulted in part from the increased activity of the young mice.

Mice built their globular nests in the laboratory by taking a ball of cotton into their mouth and then raising their head while pushing the cotton downward with their front paws. After separating the fibers, the mice either sat in the middle of the cotton or burrowed into its center and hollowed out a cavity. Most of them sat on the cotton and pulled it up and over themselves to form a roof. The mice usually worked on the nest continuously until they had finished at least its central cavity. Huestis (1933) reports that P. maniculatus sometimes closes the entrance to its nest during the day. This behavior is also characteristic of P. polionotus.

Hoarding of food

Four percent of the occupied burrows in the Ocala National Forest contained uneaten food. The comparable figure for all the localities studied in Florida was 6 percent. Food was found in 46 and 83 percent of the occupied burrows in Georgia and South Carolina, respectively. The largest caches of food were found in Florida in unoccupied burrows. Several adjacent unoccupied burrows were sometimes completely filled with acorns or peanuts. Food was frequently found in the entrance tube between the sand plug and the surface of the ground, but never in the entrance tube of an occupied burrow. There were fewer burrows per family unit at the northern than at the southern

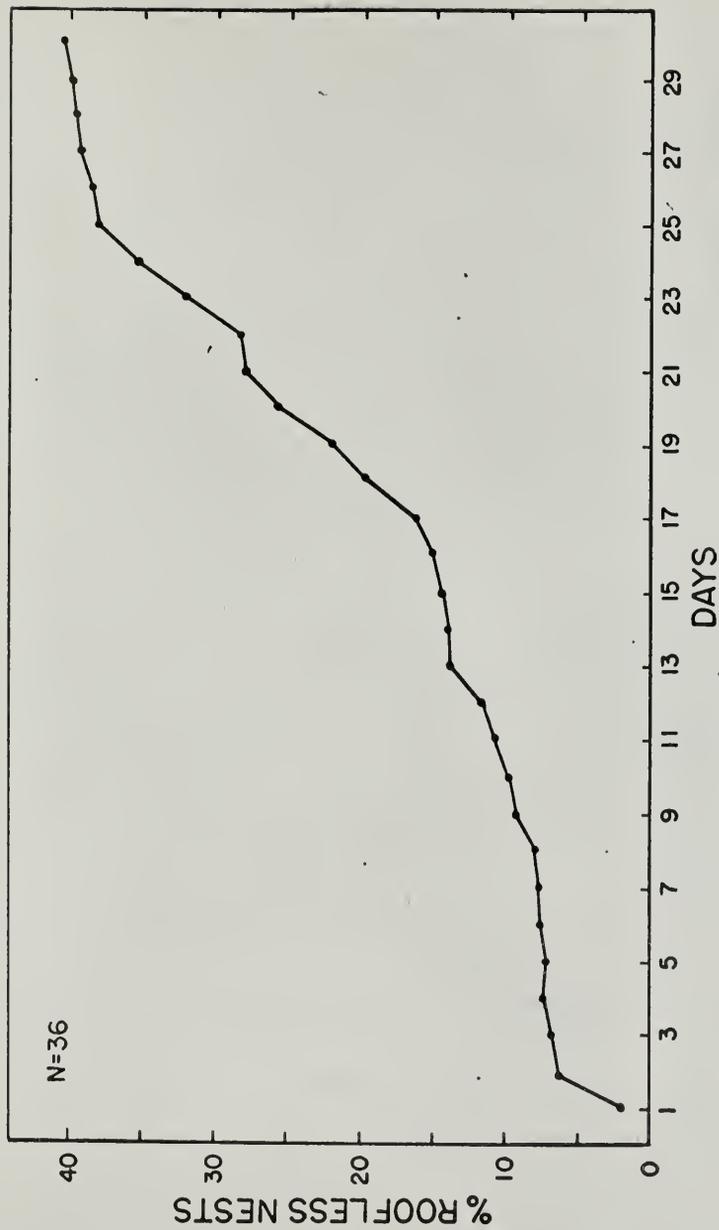


Fig. 26. Percentage of nests without roofs during the month following the birth of a litter to laboratory-reared parents.

localities. Fewer burrows may mean fewer places to store food and, thus, more occupied burrows may be used as storage places in the north than in the south.

Escape behavior

Mice running from one place to the next keep their head and tail low, but do not drag the tail. A startled mouse runs straight back to its nest. Sometimes, the startled animal, after an initial quick movement, will begin digging rapidly in the sawdust as if it were trying to dig a burrow. Mice in cages with snakes, e.g., coachwhip, jump straight up when the snake strikes at them. They also jump vertically when I try to grab them.

In the field, most of the mice were captured in the escape tube. The time required to dig out a burrow varied from three minutes to about 20 minutes or more. If the mice delay their escape until a predator digs in the entrance tube, they may leave without being noticed. On one occasion, mice came scurrying out of their escape tube while I was still about 6 m from the nearest part of the burrow. The extreme case was encountered when the mice used their escape exit before the car doors were opened. Experience may be a major factor contributing to such variation.

When an adult pair of mice use the escape exit of their burrow, the male regularly comes out first (78 percent, $n = 186$). Juveniles, if present, never come out first. Very young mice are usually left in the nest when their mother goes up into the escape tube, but sometimes they are found clinging to her teats

or lying part way up the escape tube.

The escape behavior of mice, which were not caught in their burrow or in its immediate vicinity, varied with the distance from the excavated burrow to the nearest thicket or to the next burrow. If the distance was great, the mice ran to a clump of grass or some other object and tried to hide. When concealment was impossible, they ran to one spot and remained there motionless for a few seconds to five minutes or longer; then they ran to another spot and repeated this behavior. If the distance was short, the mice would run directly into the thicket or the adjacent burrow. Occasionally, five or ten minutes elapsed before the mice which escaped to the adjacent burrows could be pursued. During this time, the mice always attempted to plug the entrance to the burrow with sand. Several times when mice were caught in the open, they started frantic digging.

Adult mice frequently came down the escape tube and stuck their head out of the partly excavated burrow while the digging was still in progress. This happened most frequently when young mice were left in the nest. Some of the adults even tried to escape by running out of the excavated end. In most of these instances, the escape tube ended farther from the surface than usual.

Social Behavior

Communication

Many observations have been made about the importance of olfaction in communication among mammals (Hediger, 1950;

Bourlière, 1954); for Peromyscus see Eisenberg (1962) and Moore (1965). The old-field mouse deposits its urine and feces in a particular place in the cage, and they discriminate between compartments which had been occupied by their species or P. maniculatus (Moore, 1965). This behavior depends upon olfactory cues as did the synchrony in reproduction observed in the laboratory (p 85).

Peromyscus maniculatus marks the boundaries of its territory with urine (Eisenberg, 1962). This type of behavior is absent in P. californicus (Eisenberg, 1962) and P. polionotus. The large preputial glands of P. californicus may provide a means of chemical communication (Eisenberg, 1962); these glands are lacking in P. polionotus. No chemical marking of the limits of their territories has been noticed in the latter species, and may not be needed since this mouse is much more social than other Peromyscus (p 141).

Mice frequently utter squeaks during aggressive interactions. The intensity and duration of these are variable, and both increase as the interaction becomes more intense. This same sound, a "metallic chit," was uttered by females defending their nests, during mating, and by most mice when they were grabbed and held by the scruff of the neck. In all of these vocal responses the mouse shows avoidance reaction. Once a dominance relationship is established between two individuals, the subordinate mouse is the one that squeaks. Squeaks are not uttered by females attacking intruders in the nest.

Peromyscus polionotus adults called more often in the laboratory than P. californicus. P. eremicus, P. boylii, P.

crinitus, P. gossypinus, P. maniculatus, P. truei, P. floridanus, and P. leucopus which were also kept during this study. The beach forms, P. p. phasma and P. p. leucocephalus, were less vocal than the mainland forms, P. p. subgriseus, P. p. rhoadsi, and P. p. polionotus.

Social units

The bisexual pair is the basic unit in this species (Rand and Host, 1942; Blair, 1951; Table 16). The most frequent encountered association was a couple with or without young (59.8 percent). Sexually active adults of the same sex were never found together, but young adults lived in small groups up to six in one burrow, chiefly during the cold months. In P. maniculatus, Howard (1949) interpreted this as an adaptation for survival during cold weather.

Mating behavior

Mating was regularly accompanied by sound and occurred in the evening while the lights were still on in the colony room. Detailed notes were made on 16 different pairs of P. p. subgriseus for a total of 25 matings. One pair was observed at a time. All of these matings occurred during the post-partum heat. The cages were checked in the morning for new-born litters, and if present, observations were begun that night 30 minutes before the overhead lights went off. A reflector lamp with a 100 watt red light located eight to 10 feet from the cage was used after the room became dark.

Sometimes the mice appeared to have no interest in breeding. In a majority of these cases, however, it occurred

Table 16. Social units found in excavated burrows of
Peromyscus polionotus subgriseus

Combinations	Number	Percentage of All Combinations
Couple with Young	296	32.49
Couple without Young	249	27.33
Single Female with Young	89	9.77
Single Male with Young	36	3.95
Single Adult Male	71	7.79
Single Adult Female	46	5.05
Two Adult Males	31	3.40
Two Adult Females	6	0.66
Three or More Adults	24	2.64
Juveniles Alone (Eyes Closed)	2	.22
Juveniles Alone (Eyes Open)	<u>61</u>	<u>6.70</u>
Total	911	100.00

within a few minutes after the mice were given a ball of cotton about 3 cm in diameter. Thirteen of the 25 matings occurred with the previous litter present and 12 without it. Four additional matings were observed in a wooden cage (50 cm high, 45 cm wide, 75 cm long) with a glass front and one-quarter inch hardware cloth on the back. A branch was provided for the mice to climb on. The large cage was used because Tamsitt (1961a) suspected that certain aspects of the breeding behavior might have been caused by the small size of his cages.

All of the phases of mating described by Tamsitt (1961a) for the P. truei species group can be observed in P. polionotus. Mating of the old-field mouse varies from pair to pair and with the number of copulations that have taken place on the same evening (Fig. 27; Table 17). The sequence usually associated with the first few copulations will be presented first and the variation from this sequence will follow.

The female initiates the sequence by positioning herself in front of the male. Her ears are erect, the tail is low, and the body is held high. The white underparts of the side of her body next to the male are displayed, and the eye on the same side is slightly closed. She moved forward displaying one side of her body, and just before making contact, lowers her body and turns her head upward and to the side, thus exposing her white throat. The male has his body relatively high, ears erect, and tail low. Also the male closes his eye on the side of his body closest to the partner just before contact is made.

Fig. 27. Sequence of behavior patterns during mating. Solid lines indicate the usual sequence of behavior leading up to and following the first few copulations. Broken lines indicate alternate sequences used at various times during mating.

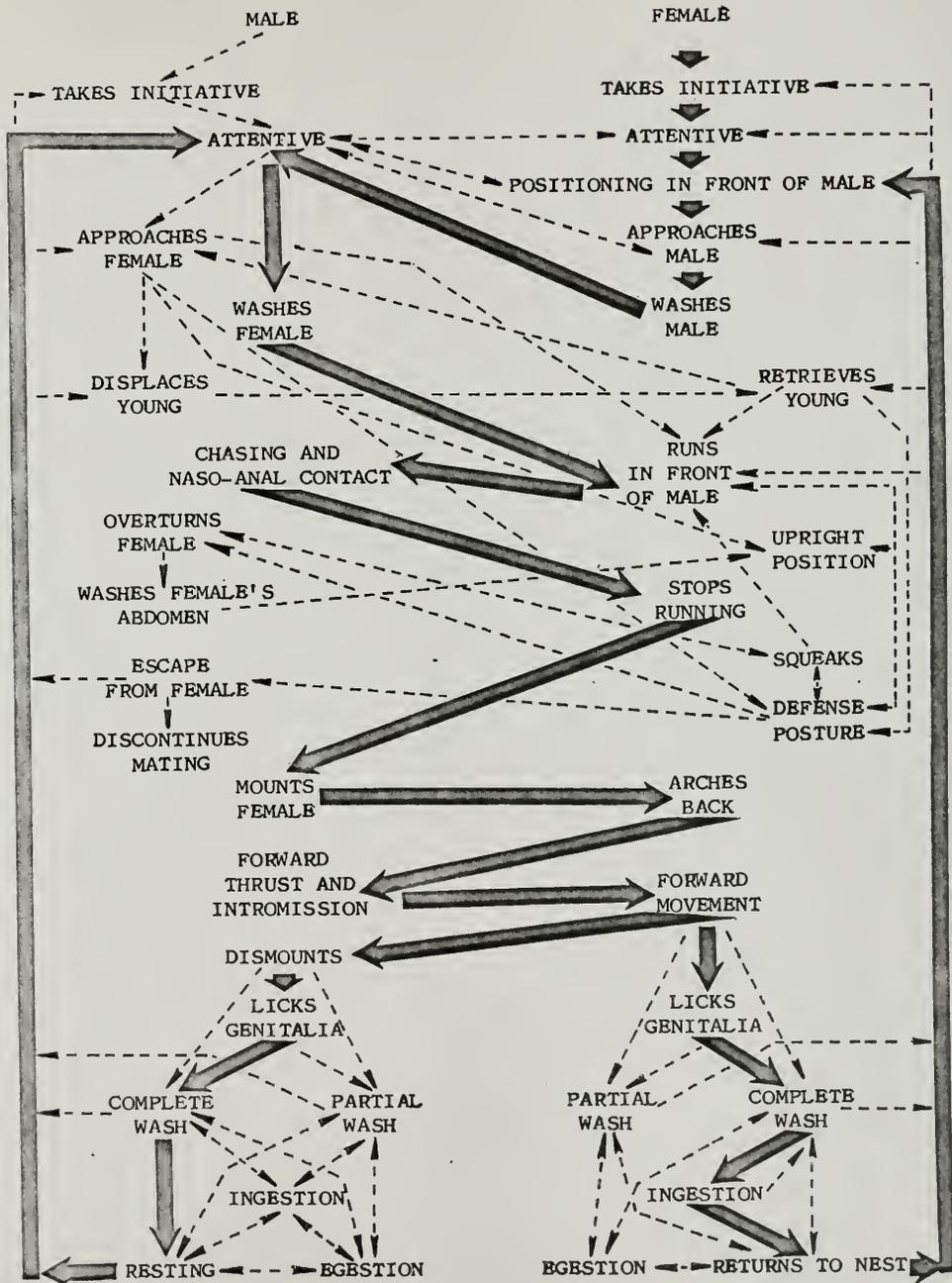


Table 17. Mating data for laboratory-reared
Peromyscus polionotus subgriseus

Number of Pairs Observed	16
Successful Matings	25
Mean Number of Mounts per Mating	49.8
Mean Number of Thrusts per Mating	45.6
Intrusions per Total Mounts	91.6 %
Mean Number of Washing of Penis by Male per Mating	23.1
Mean Observation Time in Minutes per Mating	152.6

Mutual grooming and then smelling of the genital region occur next. The partners occasionally walk in a right circle in naso-anal contact. Grooming is usually confined to the sides and back of the body of the other animal; occasionally the neck and the sides and dorsal part of the head are included. After the female stops smelling the male's genital region, she starts running in a tight circle in front of the male with her head, tail, and body close to the floor. In the large cage, the female runs back and forth in front of the male. If the male does not chase the female, she repositions herself in front of him and repeats the entire sequence.

The naso-anal contact becomes so vigorous in some cases that the female was pushed forward. In other instances, the male repeatedly moved its head upward after placing it under the female's anal region. This movement elevated the posterior half of the female's body 3 to 5 cm exposing her white belly. The male frequently tried to mount the female if she slowed down slightly. Successful mounting occurred only when the female came to a complete stop. At this moment she extended her body forward, angled the tail laterally, arched her back, and thus raised the exposed perineum. The male mounted by extending his body over hers and then grasped her body in the region of the diaphragm with his front legs. Intromission consisted of a single forward thrust of such force that the female was normally pushed forward. The female was never heard squeaking during intromission. After the forward thrust, the male relaxed its grip of the female. The male always lifted one leg as he drove

the penis forward. Occasionally, the other leg was also lifted at the end of the forward thrust, and thus, the male rode on the back of the female. In these cases, the male slowly fell off the female onto his side or back. If one foot remained on the floor, the male dismounted as the female moved forward. The male then sat upright on the hind legs and tail, bent its head toward the floor, pulled the sheath of the penis back with the forepaws, and took the withdrawn penis into the mouth and washed it. At the same time, the female licked her genitalia from a similar position. Both sexes went through a complete "wash" following the cleaning of the genital area. The "wash" of the female was of shorter duration than that of the male. She went back to the nest to check the newborn young and then ate or drank before initiating the next mating. The male was frequently still cleaning his fur when the female repositioned herself in front of him. Mice always copulated many times during the course of an evening (Table 17). No conspicuous marking behavior, such as urination or dragging the genital region on the floor, was observed.

Between a series of copulations the animals rested and showed no sexual behavior for at least three minutes. The male frequently layed facing the nest from the farthest possible point in the cage, keeping his body and tail flat on the floor, ears erect, and limbs extended in a position similar to that used by heat-stressed animals. The female usually stayed in the nest and with the young animals. As the length of the period of mating increased, both mice spent more time drinking,

eating, urinating, and defecating during the rest periods. The number of series of copulations per mating period ranged from six to twelve and averaged 9.2. The mean number of copulations per series decreased and the length of the rest period between each series increased as the number of copulations completed that night increased. The mean number of copulations for the first series was 6.8 and for the last series was 2.6. The average length of the rest period between the first and second series was 3.8 minutes, and it was 15.3 minutes before the last series.

Mating behavior on any one evening gradually changed as the total number of completed copulations increased. The male responded to changes in the female's behavior more quickly than before. Grooming and smelling of the genital region were frequently deleted. The male often started chasing the female without being approached by her. The washing of the penis occurred less frequently, and the partial wash of the head and ears was more common than the complete performance. The female cleaned her genitalia less frequently.

In almost all of the later matings the male took the initiative. He would approach the female head on while she was in the nest. The female would frequently assume the upright posture, and the male would attempt to push the female over on her back and wash her white belly. The female uttered frequent, high-pitched sounds during the initial advances of the male and occasionally while she was on her back. When the female righted herself, she would run out of the nest with the

male chasing after her and the normal sequence of events occurred.

Sometimes, when the female resisted the male's efforts, the male picked up a new-born animal and carried it out of the nest. The female immediately retrieved the young animal and after depositing it in the nest, the female would run from the nest with the male following. The male frequently attempted to mount the female while she was retrieving the young animal but was never successful. Half of the males picked up young animals and moved them out of the nest during their mating behavior. The other males concentrated their efforts on the females. New-born animals were displaced several times from their nest by one male the first time it was observed and not at all during the second period of observation. The general scheme of this male's mating behavior was similar on both occasions except in this one regard.

The female gradually became more aggressive and drove the male and her previous litter from the nest when they were still present. The female frequently lunged at the male and tried to bite him. Eventually, the male left the female alone in the nest and mating ceased. In some cases, the female left her previous litter in the nest although she drove her mate out. The period during which the previous litter and/or the adult male were kept out of the nest varied from several hours to several days.

The young animals from the previous litter were allowed only restricted movements during the mating of their parents. In-

initially, they spent most of their time in the nest but were later found eating and drinking near the water bottle. As the female approached, they would run back to the nest. Except in one case, the young animals played no direct part in the mating behavior. One juvenile male entered into the chasing of the female. The juvenile male never attempted to mount his mother or make any kind of physical contact with her. He ran behind his father and frequently tried to mount him. The adult male payed little attention to the activity of the juvenile, but the female frequently lunged at him and eventually chased him back into the nest to the other young mice.

On four occasions, mating was observed when there was more than one adult male in the cage. Usually only one male bred with the female. The others either remained in one corner of the cage or they attempted to mount the male that chased the female. Once two males alternately tried to mount a female, but one repeatedly failed because the female never stopped and arched her back when he tried to mount.

Parental care

For the first few days after the birth of a litter, the female savagely defends her nest against intruders. Strange mice are killed if they are placed in the cage over night. During the early stages of lactation the females may even drive their mate and previous litter out of the nest. King (1963) described this for other species of Peromyscus, and it can also occur in the field. Of the 36 adult males found with juveniles, 17 were in a burrow adjacent to one occupied by a female with a new

litter. The juveniles with the males were about 30 days old and were probably the females' previous litters. The association of the male with the older juveniles is not interpreted as extended parental care, but it may give the juveniles an opportunity to learn from their experienced father during excursions outside the burrow.

Adult males have been found in the field with litters in P. leucopus (Nicholson, 1941), P. maniculatus (Howard, 1949; Blair, 1958), and most frequently in P. polionotus (Rand and Host, 1942; Table 16); I have observed it in P. gossypinus.

In the laboratory, male old-field mice sometimes attack a forceps placed into their nest and carry their young from place to place. When nursing females were removed from their cage for at least four hours and the young displaced out of the nest, two out of 10 males carried their offspring back to the nest within 15 minutes. Peromyscus polionotus males probably contribute more to the care and protection of their offspring than males of other species of Peromyscus (Dice, 1929; Horner, 1947; King, 1963).

The young mice spend much time with sucking, and if the mother suddenly leaves the nest, they cling to her teats. The female normally carries them, one at a time, between the jaws. When older and larger, they are grabbed by the loose skin on their back. Some females rapidly retrieve their young when they are displaced from the nest, but others leave them out of the nest for several hours. Non-lactating females, some of them virgins, have been observed carrying young and sometimes retrieving them when they were displaced from the nest in the mothers'

absence. Young mice are groomed by their mothers before their eyes open, afterwards the males also participate in this activity.

Discriminatory behavior

In the laboratory mice have no choice of mate. They either breed with an available partner or not at all. In the field, they usually have a choice between females of their own or of a closely related species. In the latter case, the intensity of selection against interspecific genetic exchange can be high (Smith, 1965a).

I tested the possible existence of species-specific discriminatory behavior between P. p. subgriseus and P. gossypinus gossypinus and subspecific discriminatory behavior between the light beachform, P. p. phasma, and the dark mainland form, P. p. subgriseus. The P. gossypinus were captured near San Felasco Hammock northwest of Gainesville in Alachua County, Florida; see p. 33 for the source of the other stocks. Cages with four interconnecting compartments, were used for these experiments during the spring of 1963 (Fig. 28). The cages were located in a room with windows on the west side. Temperature and relative humidity were not controlled. A 40-watt red light was used for illumination at night. Food and water were supplied ad lib. Cotton and a coffee can with a hole in it were placed in each compartment for nesting. An experiment consisted of placing a sexually active adult male and female of each of two types in the cage. Then I recorded the compartment in which they nested each day, their location in the cage every five minutes from 2000 to 0600 for four consecutive nights, their sundry behavior, and the re-

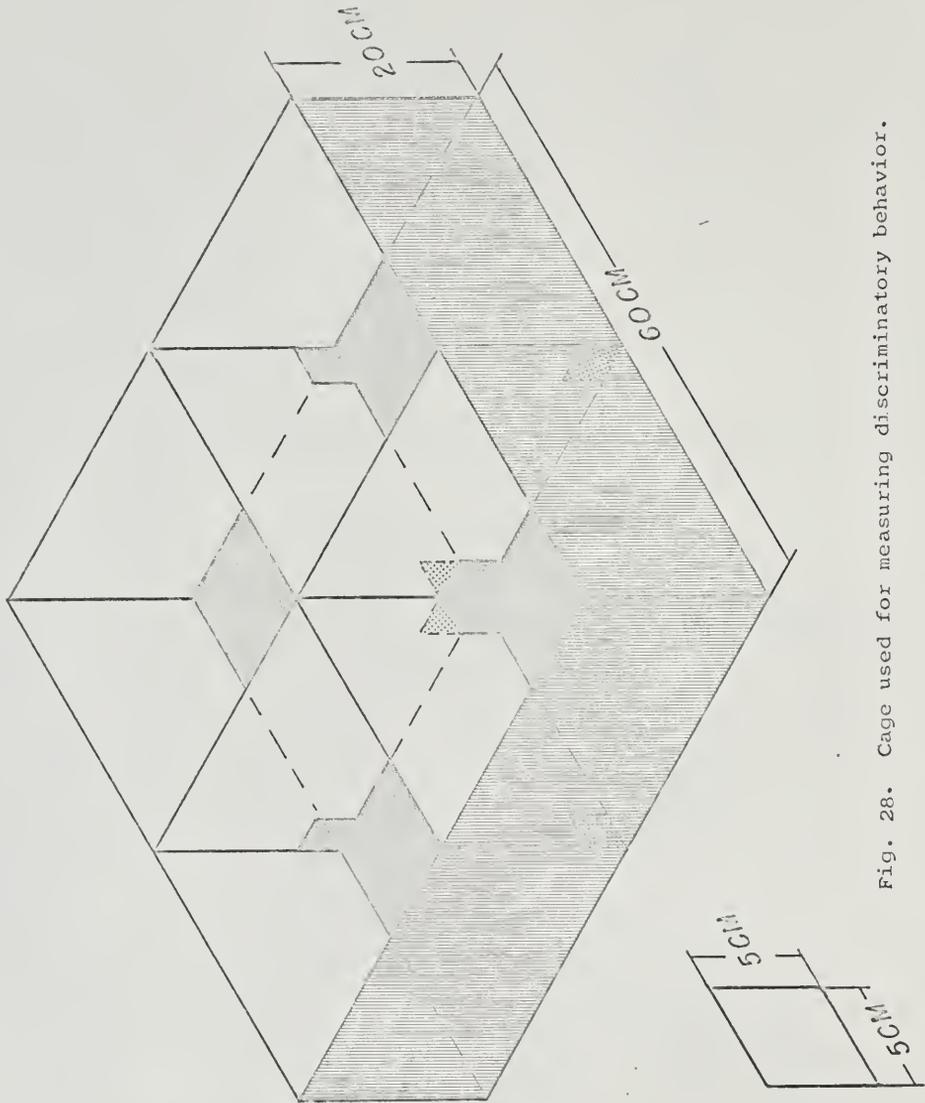


Fig. 28. Cage used for measuring discriminatory behavior.

sulting pregnancies. Each animal was used once and it was unfamiliar with the other animals present in the test cage at the same time. Results of these experiments are summarized in Tables 18, 19, and 20.

The four mice nested in the same compartment 90 and 93 percent of the time in the tests involving the species and subspecies, respectively. This was unexpected since many investigators have shown that under similar conditions mice tend to occur in groups of less than four (Blair and Howard, 1944; Clark, 1952; Blair, 1953a; Harris, 1954; Bradshaw, 1956; Tamsitt, 1961b; McCarley, 1964). In the laboratory, wild old-field mice have a tendency to huddle together even when the group size is twenty or more and they have several nest boxes available. Their possible tendency to establish an oxygen gradient similar to that in a burrow (p 62) may account for their aggregation in one compartment with the P. gossypinus.

Mice were observed together during the night in the same compartment more often than expected. This was partly due to their common occurrence in the compartment in which they nested and stored food. The numbers of all other observed social combinations were reduced because of this tendency. Thus, further discussion will be based on a comparison of the results from the species and subspecific tests rather than on a detailed analysis of each one.

Most of the results can be interpreted in terms of the social units in the cages. The larger P. gossypinus was dominant

Table 18. The nightly distribution of mice of
Peromyscus polionotus and P. gossypinus
 in a cage with four compartments

Resulting Social Groups	Observed	Expected
All together	925	75
<u>polionotus</u> male isolated	214	225
<u>polionotus</u> female isolated	180	225
<u>gossypinus</u> male isolated	586	225
<u>gossypinus</u> female isolated	146	225
Homospecific bisexual pairs	61	225
Heterospecific bisexual pairs	45	225
Heterospecific homosexual pairs	123	225
<u>polionotus</u> paired, <u>gossypinus</u> not paired	726	450
<u>gossypinus</u> paired, <u>polionotus</u> not paired	187	450
Males paired, females not paired	273	450
Females paired, males not paired	459	450
<u>polionotus</u> male <u>gossypinus</u> female paired, others not paired	432	450
<u>gossypinus</u> male <u>polionotus</u> female paired, others not paired	194	450
none paired	244	450
Total	4,800	4,800

Table 19. The nightly distribution of mice of the two subspecies, Peromyscus polionotus subgriseus and P. p. phasma, in a cage with four compartments

Resulting Social Groups	Observed	Expected
All together	1,116	75
<u>subgriseus</u> male isolated	331	225
<u>subgriseus</u> female isolated	196	225
<u>phasma</u> male isolated	290	225
<u>phasma</u> female isolated	220	225
Homosubspecific bisexual pairs	248	225
Heterosubspecific bisexual pairs	146	225
Heterosubspecific homosexual pairs	92	225
<u>subgriseus</u> paired, <u>phasma</u> not paired	653	450
<u>phasma</u> paired, <u>subgriseus</u> not paired	537	450
Males paired, females not paired	328	450
Females paired, males not paired	202	450
<u>subgriseus</u> male <u>phasma</u> female paired, others not paired	143	450
<u>phasma</u> male <u>subgriseus</u> female paired, others not paired	194	450
none paired	<u>244</u>	<u>450</u>
Total	4,800	4,800

Table 20. The nightly distribution of mice in a cage with four compartments. The tests involved two species, Peromyscus polionotus and P. gossypinus, or two subspecies, P. p. subgriseus and P. p. phasma

Social Grouping	Expected	Observed	
		Species	Subspecies
All together	75	925	1,116
Three together, one isolated	900	1,126	1,037
Two pairs	675	229	486
Two not together, one pair	2,700	2,271	2,022
None together	<u>450</u>	<u>244</u>	<u>139</u>
Total	4,800	4,800	4,800

to P. polionotus, and females were usually dominant to males. The level of aggression was higher between males and females of P. gossypinus than of P. polionotus and about equal within and between the two subspecies of P. polionotus. The tendency to associate with another mouse appeared to be indirectly related to the level of aggression between them. This accounts for the higher frequency of social combinations in which the P. gossypinus male was not included, the greater tendency of the P. polionotus to occur together, and the lower number of times P. gossypinus males and females were observed together. It may be erroneous to assume that a male and female will form a close association if they normally live in separate areas and come together only during a short period for breeding. Many species of Peromyscus probably have this type of social system, including P. gossypinus (Burt, 1940 and 1943; Griffo, 1961). In these species, mate preference is something that would be shown only at certain times when the females are receptive. No pregnancies resulted in P. gossypinus, so it is possible that these females were not receptive during the period of observation. Only four of the eight P. polionotus females became pregnant. The forced association of the two species was probably stressful for both and may have accounted for the low level of receptivity in the females.

It is reasonable to expect P. polionotus to express a preference for a particular mate because they normally occur paired in the field. Discrimination between the two subspecies may be indicated by the large number of homosubspecific associations (653 and 537) as compared to the small number of hetero-

subspecific associations (143 and 194; Table 19). This supports other evidence that these two subspecies are partially isolated from each other by more than distance (p 35 and 111).

Discrimination between different forms of one species has been demonstrated by other investigators working with mice. Certain strains of Mus musculus show a mate preference which is specific to strain. (Mainardi, 1963a, 1963b, 1963c, 1964, 1965; Mainardi, et al., 1965a and 1965b). Associative learning and early imprinting are involved in determining the choice that mice make later as adults, and their preference can be artificially altered when the odors of their parents are changed by perfumes (Mainardi, et al., 1965a and 1965b). Different strains and subspecies of mice can be told apart by their characteristic odors (Parkes, 1960). The discriminatory behavior of P. maniculatus and P. polionotus depends partially on olfactory cues (Moore, 1965), and discrimination has been shown between subspecies of P. maniculatus (Harris, 1954).

GENERAL DISCUSSION

The extent to which species can adapt to variations in their environment is inversely related to the amount of genetic exchange between populations living under different conditions. Over a long period of time the interpopulational variation should stabilize if conditions remain relatively constant. The rate at which stabilization is approached is directly related to the intensity of natural selection and the degree to which the populations are isolated from one another. The interpretation of the differences in the old-field mouse depends upon this rate and the length of time the current conditions have prevailed.

According to Blair (1950 and 1953b), P. polionotus evolved from a population of P. maniculatus which was isolated in the southeastern United States during the Pleistocene glaciations. The actual time of their isolation is in doubt since one of the Florida shorelines appears to be of the Upper Miocene (Alt and Brooks, 1965). The species is known only from two localities dated as late Pleistocene and these sites were not part of the Miocene land mass (Sherman, 1952; Ray, 1957; Weigel, 1962; Gut and Ray, 1963). A more recent origin is likely for P. polionotus, but it is possible that it lived in the Southeast since the Miocene.

Peromyscus maniculatus appears in two morphological forms, the short-tailed grassland form and the long-tailed

forest type. Peromyscus polionotus has a tail shorter than its body and is never found in heavily forested habitats. Its parental stock was probably a grassland form. Blair (1953b) cites P. m. pallescens as the ancestral type, but it is difficult to explain how this mouse could get from Texas across the Gulf coast without leaving any intermediate populations in places where the habitat is suitable. If the grassland habitat spread in a southeasterly direction from the central prairie states during the past, the P. m. bairdii is a more probable ancestor. This would explain the absence of both species along the Gulf coast west of Mobile Bay. The mice probably entered the southeastern United States from a northwesterly direction just east of Mobile Bay and spread along the shore lines. After their invasion, the forest of the Appalachian mountains extended its distribution, and eliminated the intervening populations. Grasslands were widespread in the Southeast at various times during the Pleistocene (Neill, 1957; Olsen, 1959). The later extinction of some of the grassland types, such as camels and horses, was associated with a decrease in the area covered by grass. The only major suitable habitat left for P. polionotus was the beach sand dune. The ground cover is especially sparse in this habitat, and selection would not favor a mouse that nested above ground. At this time, the mice probably developed their burrowing behavior.

The sand dunes went through successional stages and, finally, the fire sub-climax community, sand pine scrub became prevalent (Laessle, 1958b). The mice are currently found

abundantly only in four situations, beach sand dunes, road shoulders, old-fields, and sand pine scrub. The latter occurs primarily on old sand dunes (Laessle, 1958b); populations found in this habitat are relict beach forms such as the one found in the Ocala National Forest. This view is consistent with that of White (1958) and Alt and Brooks (1965), but not with that of Cooke (1945) and MacNeill (1949) who think that the Ocala National Forest is located on a Pleistocene island. In either case, the mice probably occurred on the wind-swept sand dunes.

Road shoulders and old-fields both resemble sand dunes by having a sparse cover. Plowing in the old-field loosens the dirt and makes it easier for the mice to dig burrows, it also increases the hydraulic conductivity of the soil. Road shoulders resemble sand dunes in that both have sloping terrain. The mice even dig into the high ground between the furrows in a plowed field.

The interpretation of the present distribution of P. polionotus (Fig. 1) is complicated. The simplest approach equates the present distribution to that in prehistorical times, but several facts indicate that this interpretation may not be true. The species does not seem to have a "natural" habitat in the northern part of its range; they are confined to cleared fields and disturbed adjacent areas. The primitive habitat of the mainland populations, sand pine scrub, is confined to Florida and southern Alabama. The mice are not found on the beaches north of the outlet of the Saint Johns River. Finally, P. polionotus was not reported from South Carolina until 1939 (Coleman).

After colonization of the southeastern United States, men cleared the land for farming and built many roads. The farmland was an ideal habitat with an abundant food supply, and the roads were the dispersal routes by which the mice could rapidly extend their distribution. Even if the old-field mouse had been in South Carolina in the Pleistocene, the activities of man would have served as a factor to promote genetic exchange between populations formerly separated by unfavorable habitat. This is true for the species in most parts of its range. Some populations may still be in a state of flux.

Under these circumstances, one can expect that small differences between adjacent populations should disappear. The long dispersal distances covered by some mice should accelerate the genetic convergence of these populations. Empirically this is not true; interpopulational variation is prevalent in all areas that have been extensively sampled. Genetic exchange between populations is lower than anticipated, and/or other factors may maintain local divergence.

The number of mice that traverse the distance between populations and become parents is not known. Even small distances may not be crossed if the mouse has to go through a habitat that it normally avoids (Golley, et al., 1965). A strange mouse may not be successful in finding a suitable mate in the new population. Behavioral discrimination can occur at the population level if imprinting is important in establishing a mate preference as it is in Mus (Mainardi, et al., 1965b). Old-field mice do discriminate between siblings and non-siblings.

Selection and inbreeding influence evolution. Inbreeding alters the phenotypic frequency. More of the recessive traits are expressed because of increased homozygosity. Selection for or against these genes becomes more effective as the level of inbreeding increases.

Peromyscus polionotus is undergoing extensive inbreeding and is also being subjected to intense predation (p 49 and 107). This should result in the rapid convergence of the population on the phenotype most adapted to local conditions. These conditions vary spatially and temporally and keep the populations in a constant state of flux. In most instances, the adaptive significance of these differences is not known but the majority of the observed interpopulational variation can be accounted for by relatively short-term evolutionary phenomena. In a population that replaces itself about once a month, the frequency of certain genes can change drastically in one year.

Not all of the differences between population can be interpreted as the result of selection. For example, the frequency of white-cheek at Interlachen, Florida was 100 percent which is much higher than any other mainland population in north central Florida. The lack of genetic exchange between it and adjacent populations and its origin on a Pleistocene shore line probably account for this difference. Most of the mainland populations are not now so stringently isolated from one another, whereas beach populations in most areas are clearly isolated from the mainland by inner lagoons and low lying poorly drained soils.

A knowledge of the past history and current distribution of the mice is necessary before such differences can be evaluated. The intensity of selection on these traits must also be known. The assumption that the differences have adaptive significance is usually inherent in the analysis but this may not always be the case. It is at this point that our ignorance is apparent. The contributions which small phenotypic differences make to survival is not known.

Peromyscus polionotus consists of a series of populations which have had relatively independent evolutionary histories. The gross similarity of their environments probably explains their limited local divergence. The populations were isolated from one another until fairly recent times, and barriers other than ecological and geographical ones are involved in the evolution of the subspecies as is indicated by the breakdown in fertility in the various subspecific crosses. The relatively short period of time the species has been in the Southeast was sufficient for it to differentiate from P. maniculatus and to produce significant local trends towards speciation.

However, these trends do not appear to be sufficient to distinguish the taxa at the specific level.

The divergence between P. p. subgriseus and P. p. phasma is especially interesting because it has been associated with the concurrent development of premating isolating mechanisms based on discriminatory behavior. Similar results can be inferred from the test crosses between P. p. rhoadsi and P. p. subgriseus; fewer hetero-subspecific pairs produced offspring than was

expected. Gene exchange in P. p. subgriseus and P. p. phasma is impossible in the field because of the Saint Johns River, but P. p. rhoadsi and P. p. subgriseus do not have any major physical barrier to stop their interbreeding. Schwartz (1954) reports a narrow zone of intergradation between these two subspecies. The description of this zone depends upon the recognition of the subspecific types and their intergrades. This may not be easy since P. p. rhoadsi from Archbold's Biological Station at the southern part of the range of this subspecies more closely resembles P. p. subgriseus than the typical P. p. rhoadsi, e.g., percentage of white-cheek. The old-field mouse possibly consists of a series of mainland populations that are to some degree behaviorally and reproductively isolated from one another. Behavioral discrimination at this level would help maintain the local adaptive peaks. Because of some of the unique characteristics of this species and its history, it offers an ideal opportunity to study the process of speciation.

SUMMARY

The old-field mouse is a small, social, semi-fossorial omnivorous rodent distributed in the southeastern United States. The characteristic burrow, consisting of an entrance tube, nest cavity, and escape tube, is located on well-drained sandy soils. Its habitat is the beach sand dunes and the early stages of primary or secondary succession.

Field work was conducted in the Ocala National Forest from July, 1963 to September, 1966. Burrow temperatures varied seasonally from 12° to 34°C, and there was a significant correlation between rainfall (Y) and ambient temperature (X); $Y = .78X - 3.6$.

Mean litter size and percentage of females reproductively active per month varied in the field population from 1.0 to 6.2 and 0 to 93.3, respectively. Seasonal variation in the production of young (P) was correlated with temperature (T) and rainfall (R). The regression line is given by $P = 268.7 - 1.02T - 3.82R$. The male's reproductive cycle usually overlapped that of the females. The laboratory population reproduced at a higher level than the field population and showed similar seasonal variation. The first litter of a female averaged smaller than later ones, but this factor accounts for only a small part of the seasonal variation in the field or in the laboratory. Genetic and environ-

mental factors are both important in controlling reproduction. The number of pairs reproducing was increased when they were exposed to 4°C for three days, fed acorns parasitized by beetle larvae, or given thyroxine injections. There seemed to be a correlation between the level of reproduction and intensity of selection. The sex ratio at birth differed significantly from one; more males than females were produced but fewer survived to become adults. The level of reproduction was higher, and the ratio of adults to juveniles was lower in southern populations than in northern ones.

Reproduction is also influenced by behavioral factors. In the laboratory, mice synchronized their mating behavior. The introduction of a strange male into a cage during the sequence of mating behavior of the residents affected their reproductive activity which caused a decrease in litter size and percentage of pregnant females (Bruce effect).

Natural populations probably inbred extensively. This is counteracted by the long range dispersal of a small number of animals. In the Ocala National Forest the average dispersal distance was 737.8 m. This same population replaces itself at an average rate of once a month. This accounts for the large degree of populational differentiation in pelage color and external dimensions, ear, hind foot, tail, and body. Inter-populational variation within P. p. subgriseus was almost as large as that between the various subspecies and larger than that previously reported for the entire species (Schwartz, 1954).

Old-field mice are able to decrease their rate of energy

utilization in several ways. Reduced oxygen tension, and lack of food can bring them into a hypothermic state. They also appear to be able to load their hemoglobin at lower oxygen tensions than P. leucopus, and they are therefore more tolerant to anoxia. Carbon dioxide in concentrations of .3 to 19 percent does not influence the metabolic rate of P. polionotus. Under adverse conditions the mice become torpid and thus live longer on their stored energy than would otherwise be possible. Torpid mice with body temperatures as low as 12°C have been found in the field, and once at 3.6°C in the laboratory.

Peromyscus polionotus subgriseus were crossed with several other subspecies with a resultant decrease in reproductive success. These two subspecies also showed behavioral discrimination in respect to each other in the laboratory.

The behavior of P. polionotus is similar to that of other Peromyscus (Balph and Stokes, 1960; Tamsitt, 1961a; Eisenberg, 1962 and 1963). This species is more social than others and the level of aggression between individuals is usually low. The close association of adult males and females in the field maintains reproductive activity throughout the year. Continued predation in the relatively open habitat occupied by this species is counteracted by a high reproductive rate.

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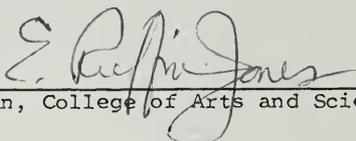
BIOGRAPHICAL SKETCH

Michael Howard Smith was born at San Pedro, California on August 30, 1938. He was awarded a high school diploma from Saint Augustine High School in 1956, a Bachelor of Arts degree from San Diego State College in 1960, and a Master of Arts degree from the same college in 1962. Michael was married to Irma Beatrice Summers in 1958, and they now have a six year old son, Michael William Smith. Graduate study towards the Doctor of Philosophy degree was begun in the fall of 1962 at the University of Florida. While engaged in graduate studies, he has been employed as a graduate teaching assistant, and an interim instructor. He received a fellowship for the summer of 1961 from the San Diego County Heart Association. During the last year his graduate studies were supported by the National Institutes of Health through a predoctoral fellowship. A Sigma Xi Grant-in-Aid was awarded to him in 1963 to support part of his research. The American Museum of Natural History gave him the Theodore Roosevelt Memorial Award in 1964. He received the Annual Award of the American Society of Mammalogists for a paper presented at their 1965 meeting in Canada. During the course of his graduate studies, he has attended and presented papers at more than a dozen state, regional, national, and international scientific meetings in the United States, Mexico, and Canada, and has also given seminars at six different colleges

in the United States. In 1964, he received a National Science Foundation summer fellowship to attend a Summer Institute of Behavioral Genetics at the University of California at Berkeley. He attended a special course in Bio-Medical Telemetry during the spring of 1965 at this same university. He holds honorary memberships in Sigma Xi and Phi Sigma, and has served as president of the University of Florida's Sigma Chapter of Phi Sigma from 1964 to 1966. The national committee of Phi Sigma provided travel funds for his attendance as a delegate at the society's 1964 national convention in Boulder, Colorado. The Mary Goethe Travel Award was given to him for attendance at the 1965 meeting of the Association of Southeastern Biologists at Charlottesville, Virginia. He is currently a member of the American Association for the Advancement of Science, American Institute of Biological Sciences, American Society of Mammalogists, Society for the Study of Evolution, Animal Behavior Society, Ecological Society of America, and the Association of Southeastern Biologists.

This dissertation was prepared under the direction of the chairman of the candidate's supervisory committee and has been approved by all members of that committee. It was submitted to the Dean of the College of Arts and Sciences and to the Graduate Council, and was approved as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

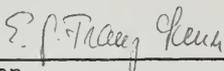
June 21, 1966



Dean, College of Arts and Sciences

Dean, Graduate School

Supervisory Committee:



Chairman

