A Preliminary Analysis of Habitat Orientation in Microtus and Peromyscus[1]

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Introduction

Each species of organism is restricted in distribution by the limits of its tolerances to the physical and biological factors of its geographical range. In addition, each species is seldom found everywhere within the limits fixed by these tolerances, but appears to be further restricted to certain microhabitats within its environment. This paper is concerned with the orientation of the white-footed mouse, *Peromyscus leucopus noveboracensis* (Fisher), and the meadow mouse, *Microtus p. pennsylvanicus* (Ord), to microhabitats in stages of old field succession on the Piedmont of New Jersey.

This secondary succession proceeds from previously cultivated land through several seral stages. The earliest stages are dominated by annual herbs, chiefly *Ambrosia* and *Oenothera*, but they also contain the subsequent herbaceous dominants in small numbers. By the fifth year several species of *Solidago* and *Aster* have become dominant and generally remain prominent for another 15 years. Broomsedge, *Andropogon scoparius*, reaches dominance by the fifteenth year and remains so for about 45 years. The red cedar, *Juniperus virginiana*, seeds early in the succession and remains the dominant arborescent species for over 60 years. The cedars are joined by the dominant species of a mature oak-hickory forest by the fifteenth year. These oaks are well established in the understory by the sixtieth year, and later constitute the climax forest in this region. *Myrica pensylvanica* and *Rubus flagellaris* are the dominant shrubs in the fields until the twentieth or thirtieth year, when *Rhus radicans* becomes prevalent and remains so to the oldest fields observed.

A series of fields in Franklin Township, Somerset County, New Jersey, represents all the seral stages in this succession. These fields are found on soils of the Norton series formed over the Brunswick formation of the Triassic shales comprising a part of the Piedmont Plateau. A study by Bard (1952) determined the major changes in vegetation occurring throughout the succession discussed above. The results of this study provide an accurate description of the plant variation and the habitat changes.

In 1957 a study of the small mammal populations associated with the secondary succession in these fields provided a foundation for the present project (Pearson, 1959). In addition to indicating the species

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present and the relative population levels in the several seral stages, this study established certain patterns of mammal distribution relative to vegetational cover. The results of Pearson's study point out that captures of the white-footed mouse were associated with perennial forbs in the early stages and with shrubs and trees in the late seral stages, and that captures of the meadow mouse and masked shrew, *Sorex c. cinereus* Kerr, were associated with the dense broomsedge cover found in the 7, 11, and 16 year stages.

The present study was conducted in the series of fields studied by Bard (1952) and later by Pearson (1959). The "age" of these fields, as indicated in Bard's study, was the number of years since the land was last cultivated, and the only difference in the habitats used by these three studies was the difference in "age". The "ages" of the fields in this study were 10, 14, 19, and 24 years and each of these was 9 years younger at the time of Bard's study. However, her study included fields approximating the seral stages used in the present study so that reference is still valuable.

This study consisted of four integral parts. The first, running from September 21 to November 7, 1958, was a census to determine the present population levels, to verify the previously determined associations, and to obtain animals for controlled laboratory experiments to be conducted during the winter. The second phase, in the laboratory, was the construction of an artificial habitat in which association could be further tested. The next part was a series of tests to determine the aggressive tendencies of the two species, and the final phase was a release and retrap study carried on from March 8 to March 19, 1959.

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METHODS

Field Study.—Seventy-five traps were set three nights a week during the fall trapping period. Sherman live traps baited with peanut butter were used. Three parallel lines of 8 or 9 traps, approximately 100 feet apart, were placed in each field. Within each line the traps were spaced at approximate intervals of 50 feet. A series of 25 traps remained in a field for the three nights. Traps were run each morning and replenished with bait or dry cotton if disturbed by the weather or a captured animal. During the fall trapping period all of the animals were removed for use in the laboratory. A careful record of the microhabitat immediately surrounding each trap was kept so that the cover most frequently inhabited in these fields by each species could be determined. A record was kept of the date of capture, the sex and species, and the location of capture for each individual. *Peromyscus* and *Microtus* were marked for future identification by the toe-clipping method described by Pearson (1959). All males captured were immediately isolated from each other by an arrangement described later.

During the spring trapping period, in which all animals were released at the point of capture after marking, the traps were set for 10 consecutive nights. They were placed at 50-foot intervals in a grid coverage of the entire field. The traps were again checked early each morning. All the animals held over the winter were released in these fields, and no animals were again removed. Any new individuals captured were marked and immediately released at the point of capture, as were all the recaptures of previously marked individuals.

Habitat Association.—To determine if there was any habitat association exhibited by the two species an artificial habitat measuring four feet on each side was constructed. Its walls were one foot in height and the top was covered with weathered one-half inch hardware mesh. The floor of the whole enclosure was covered with finely sifted sand. This box was divided into two equal compartments with a joining passage. One side simulated the goldenrod-aster habitat and the other the broomsedge. A wooden cubicle approximately one-foot square fit smoothly into the passage, and the animal to be tested was placed within the cubicle. After a one-minute orientation period the cubicle was silently raised, and subsequently removed, allowing the animal unimpeded choice of either simulated habitat, and also free passage between them.

Ordinary drinking straws were used to simulate the upright stems of the goldenrod-aster habitat. They were placed at four-inch intervals in parallel rows four inches apart; the axes of the individual straws being on a diagonal with, rather than perpendicular to, the sides of the enclosure. Additional straws and a small amount of excelsior were scattered on the sand to simulate the litter. Six bunches of excelsior simulated the clumps of *Andropogon,* and a mat of mixed excelsior and straws was spread over the broomsedge habitat to represent the type of cover found in the field.

An opening with a flush door was placed in a corner of each compartment so that the animal, in its natural wanderings along the wall, could wander out of the artificial habitat of its own volition after the timed trial was ended.

The observer sat motionless at one side of the habitat for half of the trials, and moved to the other side for the second half. The lighting was either natural or from a small ceiling bulb in the center of the room. Neither means lighted the habitat directly. The initial choice of habitat, and the time spent in each simulated habitat were recorded for five-minute trials. Notes were kept on the actions of each animal in the habitat during the trial. No animal was tested more than twice in one day.

Aggressive Behavior.—In order to accurately determine the aggressive tendencies of these two species, the males were, as previously mentioned, kept in isolation from the time of capture. No experiments were run for more than a month after capture. Sixteen cages were built into one unit in two rows of eight. The eight pairs were separated by sliding aluminum partitions. Two sides of each compartment (each 6" x 12" x 8") were of wood, the third was the metal partition, and the fourth contained a hardware mesh access door, while the top and bottom were of the same wire mesh. Each compartment was provided with cotton nesting material, a water bottle, and a diet of Purina Laboratory Chow, supplemented by fresh fruit and vegetables. Meadow mice were placed in one side and white-footed mice in the other. All females and extra males were retained in large holding cages on the same diet. Only males kept in isolation were used in the aggression studies.

Five-minute trials were run in these experimental cages with no change other than removal of the nesting material. The cage was illuminated by a single shaded bulb suspended six feet above the cages, and the observer again sat silently at one side for half of the experiments and moved to the other side for the second half. The partition was removed and all actions of the two individuals were recorded for the timed period.

Behavior was divided into the following main classifications: 1) actual fighting, 2) aggressive, 3) recessive, 4) fraternal, 5) sniffing, and 6) no conclusive reaction. It was felt that all actions of the animals would fall into one of these six categories. In actual fighting records were kept on which animal initiated the fighting. Squeaking, chasing, scratching and nipping were classified as aggressive behavior. Recessive behavior included wild leaping, clinging to the roof wire, crouching in the corner with eyes closed, or assuming a defensive position similar to that of a human boxer. Also included as recessive was flight from any act of aggression. Mutual grooming or huddling together were considered fraternal behavior. Those actions grouped as no conclusive reaction generally occurred when the animals passed each other, usually going in opposite directions, and there was opportunity for reaction but none appeared. Each of the males was tested with every other male in a round robin fashion, both within the same

TABLE I.—A summary of total trap-nights and captures with regard to habitats in the fall and spring trapping periods

		Trap-nights	*Peromyscus*	*Microtus*	*Blarina*	*Sorex*	*Mus*
FALL	Andropogon	609	14	12	18	4	..
	Solidago-Aster	198	6	1	..	1	..
	Shrubs	155	5	3	..	..	..
	Misc.	88	4	..	3	1	1
	Total	1050	29	16	21	6	1
SPRING	Andropogon	530	19	..	2	..	1
	Solidago-Aster	140	9	..	..	..	..
	Shrubs	30	3	..	..	..	..
	Misc.	50	..	..	..	..	..
	Total	750	31	..	2	..	1

species and with the other species. No individual had more than two encounters in any four-hour period.

RESULTS

Field Study.—The results of 1050 trap-nights covering the fall trapping period are summarized in Table I. All species recorded by Pearson (1959) except *Pitymys* were captured. Computation of the number of trap-nights necessary for the capture of one individual, as taken from Table I, indicates that although the white-footed mouse was captured in all habitats it was most prevalent in the goldenrod. The meadow mouse and the short-tailed shrew, *Blarina b. brevicauda* (Say), were limited in their range, occurring most frequently in the broomsedge habitat. The catches of the house mouse, *Mus musculus* Linnaeus, and the masked shrew were not large enough to be included in the habitat association analyses. The table also reveals that the white-footed mouse was taken more frequently in all habitats than any other species. Moreover, there was a greater number of captures for all species in the broomsedge.

Statistical examination of the above-mentioned associations may be obtained by submitting the trapping data of Table I to a four-fold chi square test of the association between trap-nights of capture and no-capture versus broomsedge and goldenrod habitat. When this was done for *Peromyscus* no significant association was found ($\chi 2=0.1$, $P=0.7$). Similarly no significant habitat association was found in this test for *Microtus* ($1\chi 2=1.2$, $P=0.3$).

The low trapping success of this study made it readily apparent that there had been a significant decrease in small mammal populations as compared to the earlier work of Pearson (1959). This was

TABLE II.—A measure of relative population levels is given where the figures represent average number of individuals caught per census period per 100 trap-nights. The figures in parentheses are for the same fields as reported by Pearson (1959).

	"Age" of field in years			
	10	14	19	24
Total Trap-Nights	225(622)	225(625)	225(597)	375
Peromyscus	0.15(3.2)	0.29(0.2)	1.78(3.3)	1.47
Microtus	0.15(2.8)	0.45(3.7)	...... (5.5)	0.40
Blarina	1.18(0.6)	1.03(1.3)	0.45(1.0)	0.67
Sorex	0.15(0.6)	0.45(1.3)	...... (0.5)	......
Mus	...... (0.2)	...... (1.6)	0.15(0.1)	......
All species	1.63(8.2)	2.22(8.0)	2.37(10.5)	2.54

specially true for *Microtus* for they had been quite abundant in the earlier study and considerable effort was expended to get the few males needed for the experimental phase of the present project. However, a comparison of trapping success in the two studies is difficult since a mark-and-release procedure was used earlier for all except *Blarina* while all the animals were removed from the field during the fall in this study. It is seen in Table II that there was little change in the *Blarina* population level from the earlier level.

Even though the indices of population size are not directly comparable for the two studies the data in Table II do show what was also concluded while the field work was underway. That is, there was a significant drop in small mammal population levels. For example, no *Microtus* were taken in the 19-year field where they were most abundant two years before, and their populations were only 60 to 70 percent that of the previous study in the other fields.

It should be noted that the population level, or standing crop of small mammals, increases through the early stages of succession as is apparent from the data in this study, as well as that in Pearson's earlier census.

The results of the spring retrap period, after all laboratory animals had been released, are given in Table I. Three meadow mice were released; they were not retaken and there were no new captures. The white-footed mouse was still the most abundant small mammal and, on the basis of trap effort necessary to catch one individual, it appeared to have a higher population level than in the fall. It was captured with less effort in the goldenrod habitat than in broomsedge. The population level of short-tailed shrews was apparently very low as only two individuals were taken.

Table III.—An analysis of the number of changes made from one simulated habitat to the other; an even number of changes indicates that the animal ended in the habitat of original selection.

Number of changes from original habitat selected	*Peromyscus* Initially Selected: Broomsedge	*Peromyscus* Initially Selected: Goldenrod	*Microtus* Initially Selected: Broomsedge	*Microtus* Initially Selected: Goldenrod
0	9	10	30	3
1	5	5	..	2
2	1	5	5	..
3	2	..	1	1
4	2	1	3	1
5	..	3	..	3
6+	3	2	1	..
Total	22	26	40	10

Habitat Orientation.—Of the 50 artificial habitat trials run, the meadow mice moved initially into the simulated broomsedge habitat in 80 percent of the trials (Table III). They spent 206 minutes in this habitat (82% of the total trial time), and 44 minutes in the simulated goldenrod habitat. In initial habitat selection the white-footed mice showed a random orientation (Table III). They also spent nearly equal time in the two habitats, with 106 minutes in the simulated broomsedge and 133 minutes in the simulated goldenrod.

The data given above and in Table III were tested by chi square to determine whether the observed frequencies of habitat selection and time spent in habitats differed significantly from an hypothesis of random orientation. Analysis of the *Microtus* data indicated significant deviation from random selection on the initial direction of habitat choice ($\chi^2=18$, $P<0.001$) as well as for the total time spent in the two simulated habitats ($\chi^2=105$, $P<0.0001$). Both of these tests verify a positive orientation of *Microtus* to the simulated broomsedge habitat. Analysis of the original choice of habitat and time spent in each for *Peromyscus* gives no evidence of other than random orientation ($\chi^2=0.33$ and 0.23). Thus it appears that there was no positive association between *Peromyscus* and a simulated habitat.

An analysis of subsequent changes in habitat occupancy after the initial movement for the two species is instructive. In 30 of the 40 trials where *Microtus* moved initially into simulated broomsedge the animal remained there for the duration of the five-minute trial (Table III). Also, of the 40 that moved initially into broomsedge only one ended the experiment in the simulated goldenrod habitat. Of the 7 *Microtus* trials where the animal initially chose the goldenrod habitat but later went to the simulated broomsedge, only one returned to goldenrod. There was an average of 1.18 changes of habitat per five minutes for *Microtus*. In contrast there was an average of 2.08 habitat changes per trial for *Peromyscus*. The number of *Peromyscus* remaining in the habitat of initial choice was about equal for both simulated habitats. The number that moved and ended in the habitat opposite to the initial choice was equal also.

During these trials individuals of both species moved chiefly along the walls of the enclosure, particularly on the side simulating the goldenrod-aster habitat. There was movement beneath the excelsior mat in the simulated broomsedge habitat, particularly by the meadow mouse. Animals frequently remained motionless in the corner for long periods in the goldenrod-aster habitat, and there was a tendency for the meadow mouse to remain motionless under the excelsior mat in the broomsedge habitat.

The subjects seldom bolted upon removal of the cubicle, and on occasion remained motionless for as long as two minutes, indicating that the initial response was not motivated by fear. No attempts were made to climb the drinking straws, but the white-footed mice did occasionally climb the enclosure walls and also climbed on top of the excelsior mat in the simulated broomsedge habitat. The animals frequently groomed themselves during the trials, and none of them ate during the trials.

Aggressive Behavior.—Ten intraspecies aggression trials were conducted among the male *Microtus* and 19 among the male *Peromyscus*. The *Microtus* trials resulted in a total of 94 contact reactions, for an average of 4.7 contacts per trial. The *Peromyscus* trials resulted in 190 contact reactions for an average of five contacts per trial. Table IV gives the results of analysis of the contact reactions for both species.

The results of the intraspecies contests indicate that there was little aggressiveness between individuals of the same species. Only a negligible amount of fighting, aggressive, or recessive behavior was exhibited in these intraspecies trials. Dominance between two individuals was established primarily through grooming. The dominant individual groomed, and the recessive individual submitted to the grooming. The pair being tested frequently spent a good part of the period huddled together in a corner.

A total of 108 interspecies aggression tests were conducted, giving 1130 contact reactions, for an average of 5.23 contacts per trial. The average number of contacts per test was about the same for both the intraspecies and the interspecies trials. The analysis of contact reactions for these trials is also reported in Table IV. A comparison of the first three columns for both the intra- and interspecies tests immediately reveals a vast difference in the aggressive behavior of these two species. The figures listed in the first column of Table IV for the interspecies aggression study indicate which species started the fight. The *Microtus* appeared far more aggressive in this respect than the *Peromyscus*. The figures for aggressive behavior substantiate this idea, as does the large percentage of recessive behavior attributed to the *Peromyscus*. No difference for the two species can be noted from the last three columns.

The *Peromyscus* presented an over-all picture of recessiveness. They seldom resisted when the *Microtus* moved into their end of the cage, and removed food or nesting material. Their flight from the advance of a *Microtus* frequently took the form of frantic leaps, or cling-

Table IV.—Tabulation of the results of the aggression studies; figures represent the percent of contacts resulting in the categorized behavior for each species.

	Actual Fighting	Aggressive Behavior	Recessive Behavior	Fraternizing	Sniffing	No Reaction
INTRA						
Microtus	3.19	1.06	2.13	20.22	39.40	34.00
Peromyscus	0.00	0.53	1.05	38.42	21.58	38.42
INTER						
Microtus	79.3	84.6	4.1	45.40	53.20	54.50
Peromyscus	20.7	15.4	95.9	54.60	46.80	45.50

ing to the wire roof of the cage. If they did not flee the meadow mouse's advance they generally assumed the defensive stance, or crouched with eyes closed against the wall. They seldom made any noise in resisting attacks.

Aggressive behavior by the meadow mice was most commonly evidenced by charging and squeaking, directed at the white-footed mice. The meadow mice frequently chased the white-footed mice around the cage, squeaking, and nipping at their hind-quarters. Any assault by the white-footed mice was ignored by the meadow mice. No serious physical injury resulted from any of the fights.

DISCUSSION

The results of the artificial habitat study indicate a positive orientation of the meadow mouse to the broomsedge habitat. Pearson (1959) reports this type of orientation in the natural habitat in the same fields from which these animals were removed. The association has also been noted by Eadie (1953), who suggests that it is a response to the amount of vegetational cover.

The data do not, however, support the position of Pearson (1959) that the white-footed mouse is positively associated with the goldenrod-aster habitat. The fall and spring trapping indicate that the white-footed mouse is captured with less effort in the goldenrod-aster habitat, but in the present study there was no significant statistical association of captures with habitat. The studies in the simulated habitat showed that there may be no differential orientation in selection of habitat and there was no positive association in time spent with either of the habitats.

These artificial habitats were designed to emphasize orientation through visual clues provided by the gross form characteristic of the two microhabitats. However, these were only artificial habitats, and different associations might occur if more emphasis were placed on olfactory or tactile senses. It is difficult to ascertain exactly when and where discrimination actually took place. Perhaps the *Microtus* discriminated at the site of introduction to the habitat, and the simulated broomsedge satisfied the cover requirements of the species. In the orientation trials *Peromyscus* changed habitats twice as much as *Microtus*. This may indicate that *Peromyscus* did not discriminate at the time and point of introduction to the habitat, and/or, neither simulated habitat provided a satisfactory stimulus. Existence of either of the above conditions would produce random search behavior.

The conclusion drawn from the aggression studies is that the meadow mouse is definitely the more aggressive species. Meadow mice were responsible for starting 79 percent of all the fights observed, and they exhibited 85 percent of the recorded aggressive tendencies. The white-footed mice, by comparison, exhibited 96 percent of all recorded recessive activity. The recessivity of white-footed mice has been recorded by King (1957), whose study was on conflicts between house mice and deermice, *Peromyscus maniculatus*. A comparison of his results with those of the present study strengthens the conclusion that the white-footed mouse exhibited very few aggressive tendencies under these experimental conditions.

A significant decrease in population level is apparent upon comparison of the census data from Pearson (1959) with those of the present study. The levels in all but one case have shown a decrease of at least 40 percent, using Pearson's record of captures opposed to the record of the present study. In most cases where heavy *Microtus* activity had been observed two years earlier the runways were still present but little activity was noted. The runway maze was trapped, using the same traps and type of bait employed by Pearson, but few meadow mice were captured.

Consideration of the possible reasons for the change in population levels gives some clue as to why the association of white-footed mice to the goldenrod-aster habitat did not hold. The cyclic phenomenon of population fluctuation for small mammals has been studied by Hamilton (1940), Davis (1933), Christian (1950), Godfrey (1955), Jameson (1955), and others. *Microtus* have an approximate three- to four-year cycle, and Christian has advanced the theory that adreno-pituitary breakdown, resulting from stresses caused by overpopulation, plays an important role in the sudden increase in mortality. Only three female meadow mice were taken in the census, and two of them, plus six males, died within two months of capture. The deaths observed were accompanied by symptoms similar to those described by Christian of adreno-pituitary breakdown.

On the basis of these observations it appeared that the *Microtus* population in the area studied had recently passed the height of its cycle and had moved rapidly downward.

Pearson (1959) concluded that the white-footed mouse was associated with the goldenrod habitat, while the results of the present study indicate that the white-footed mouse is randomly oriented. The orientation for this species to habitats other than broomsedge which Pearson reported was probably due to: 1) the high level of the *Microtus* population, 2) the positive orientation of *Microtus* to the broomsedge habitat, and 3) the aggressive tendencies of *Microtus* experimentally suggested by this study. The increased number of captures of *Peromyscus* in the broomsedge habitat can probably be attributed to the low *Microtus* population level, and the subsequent lack of sufficient aggressive response by the meadow mouse to the entrance into the broomsedge of a larger number of white-footed mice.

An examination of the broomsedge habitat and the goldenrod-aster habitat reveals a great difference in the type and amount of cover provided. The former, with its dense mat of short grasses, lichens, and young plants, interspersed with large clumps of broomsedge, provides a continuous cover for runways and feeding activity. This may be another reason for the high utilization of the broomsedge habitat reported by the current census. The goldenrod-aster habitat has a low ground cover of annual and perennial herbs, not forming a continuous cover, and an upper layer of the stems and leaves of the forbs. The broomsedge habitat provides year-round cover while the forb cover is largely destroyed during the winter, beaten down by rain and snow, leaving only underground burrows for shelter.

Additional information on the orientation of these two species will probably be obtained upon further study of their feeding habits. The meadow mouse may be restricted in its habitat association by its utilization of the shoots and leaves of plants. The white-footed mouse appears to feed chiefly upon trees and shrubs. Upon examination of the vegetation of most fields, it is apparent that the production of forbs and grasses is far more regular than the production of mast and fruit. The irregular pattern of tree and shrub growth, as compared to the extensive ground covering in the broomsedge habit makes it possible that the white-footed mouse is, of necessity, more widely oriented with regard to habitat. Hamilton (1937b) gives the meadow mouse a home range the size of a tennis court while Blair (1942) gives the male white-footed mouse a home range of around 2.31 acres. Food preference may, therefore, have an effect upon the habitat orientation in these two species.

SUMMARY

1. Although there was no statistical association between capture of meadow mice and the broomsedge habitat established by the census, the artificial habitat studies indicate that *Microtus* is positively oriented to the broomsedge habitat.

2. The artificial habitat studies indicate that *Peromyscus* is randomly oriented with regard to habitat, and the trapping data reveal that this species was captured in all major habitats. Though it was most prevalent in the goldenrod, there was again no statistical association between capture and goldenrod.

3. Studies of aggressive tendencies point out the fact that the meadow mouse is more aggressive than the white-footed mouse.

4. The occurrence of the white-footed mouse may be affected by the population level of the meadow mouse. The meadow mouse is positively oriented to the broomsedge habitat, it is more aggressive than the white-footed mouse, and when the population level is high for the meadow mouse few white-footed mice are found in the broomsedge habitat.

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