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A COMPARATIVE STUDY OF SOME ASPECTS
OF THE BEHAVIOUR OF PEROMYSCUS
MANICULATUS GRACILIS (LE CONTE)
AND PEROMYSCUS LEUCOPUS NOVEBORA-
CENSIS (FISCHER).

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OF SOME ASPECTS OF THE BEHAVIOUR OF
PEROMYSCUS MANICULATUS GRACILIS (LE CONTE)
AND
PEROMYSCUS LEUCOPUS NOVEBORACENSIS (FISCHER)

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A thesis submitted to the Faculty of
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of the requirements for the degree of
Master of Science

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ABSTRACT

Two species of deermice, Peromyscus maniculatus gracilis, and Peromyscus leucopus noveboracensis, are sympatric in southern Ontario and Quebec, and the north-eastern U.S.A., apparently in contravention of Gause's hypothesis. In order to reveal behavioural differences that might be related to their ecology in the field and which might explain this apparent incompatibility with classical ecological theory, laboratory studies of captive individuals of the two species were carried out.

When several mice of each species were caged together for one week, the amount of interspecific association increased over the week and was less than the amount of intraspecific association, and gracilis associated with its own species more than did noveboracensis.

In aggression tests, gracilis was far more aggressive to noveboracensis than vice versa; noveboracensis was fairly aggressive to its own species, in contrast with gracilis' almost complete tolerance of its own species.

These two results suggested that gracilis would tend to form more dense populations than noveboracensis - a disadvantage in times of overpopulation and that noveboracensis would tend to avoid gracilis, inhabiting spatially separate areas.

In tests involving release in a covered runway and in a simple maze, characteristic darting and freezing movements of noveboracensis were demonstrated; gracilis tended to be more exploratory. This was interpreted as

indicating that noveboracensis may possess a valuable escape reaction in times of surprise, possibly giving it an advantage over gracilis when both are subjected to aerial predation, while gracilis, being more exploratory, may be at an advantage in new situations.

In the hand, gracilis was usually aggressive, while noveboracensis was docile; in their cages, gracilis was usually inquisitive, but noveboracensis was typically found 'freezing' motionless in their nesting cans or on the walls of the cage.

In brief preliminary swimming tests, gracilis took up in its fur almost twice as much water as did noveboracensis; if this situation persisted in natural conditions, noveboracensis might be able to swim across larger bodies of water than gracilis, and so colonize certain areas not available to gracilis.

The two species appeared in preliminary tests to be similar in their amounts and times of running activity in revolving cages, and in their weight losses resulting from total deprivation of food.

Each species therefore seems to have peculiar traits which may be advantageous under different circumstances. Gracilis is good at exploring new areas, and is more aggressive to noveboracensis than vice versa. Noveboracensis seems to have a valuable disturbance reaction, forms less dense populations that are less likely to overexploit an area, and may be able to swim greater distances. Thus it is concluded that the two may coexist indefinitely in the same general area in a manner such that Gause's hypothesis is not contravened.

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INTRODUCTION

Mice of the genus Peromyscus are very common over most of the North American continent, and in certain areas pose problems of sympatry. The geographical ranges of Peromyscus maniculatus gracilis (Le Conte), the woodland deer-mouse, and Peromyscus leucopus noveboracensis (Fischer), the white-footed mouse, overlap over a fairly large area. Fig. 1 shows that the area of overlap of the ranges of these two forms extends across southern Ontario, southern Quebec, and the north-eastern and north-central United States. This overlap of range has given rise to some confusion: the two species seem to be considered sympatric in this area by a number of authors, and yet the ecological details of this sympatry have not been fully determined.

By way of contrast, the geographical ranges of P. maniculatus gracilis and P. m. bairdii (Hoy and Kennicott), the prairie deer-mouse, also overlap over northern Michigan and part of New York (Hall and Kelson, 1959). However, it is commonly known (Burt, 1957; Cameron, 1956; Hall and Kelson, 1959; Harris, 1950; Horner, 1954; Johnson, 1926) that P. m. bairdii is found in open country, while P. m. gracilis is a woodland race. Consequently the two can live together in the same general geographical area without competition.

A major complicating factor in this particular problem is the great morphological similarity between P. m. gracilis and P. l. noveboracensis. This causes considerable difficulty

Fig. 1. A map of northeastern United States and eastern Canada, showing the geographical ranges of *Peromyscus leucopus noveboracensis* and *P. maniculatus gracilis*, after Hall and Kelson, (1959).

in distinguishing these species when the two occur together and particularly in identifying individual specimens. This difficulty has led some observers in the past to believe that they were dealing with only one species instead of two. Townsend (1935) reported that he spent the first year of his study of small mammals of central New York believing that he was dealing with only one species of Peromyscus, whereas in fact, as he discovered in subsequent years, he was dealing with the two species being discussed. Hall and Kelson (1959) stated: "In areas where P. maniculatus and P. leucopus occur together, individual specimens are sometimes referred to their correct species only with considerable difficulty, and identification is often a matter for the expert."

Osgood (1909), in his definitive work on Peromyscus, says: "Although living in the same general localities, P. maniculatus gracilis and P. leucopus noveboracensis are nearly always confined to different local habitats, gracilis showing preference for the colder, moister places, or deep, mostly coniferous woods, noveboracensis for the warmer, drier, more open country or deciduous woods". Although these generalizations seem to stand the test of subsequent observations, (e.g., Klein, 1960, and Clark, 1964), they do so only to a limited extent.

Cases of habitat discrimination of a very striking nature over short distances by Peromyscus are fairly common. One example is reported by Ivey (1957) around Albuquerque, New

Mexico. The distance from the city to the adjacent mountain tops is less than 30 miles. While in that short distance one of five Peromyscus species ranges from the shrubby river bottoms, through the foothills, and up to the main mountain range, each of the four other species is restricted to its own separate habitat. This is only partly a case of sympatry; it is also an example of geographical isolation in a sharply changing landscape. Each of the four isolated species occupies its own geographically defined zone, for which it presumably is better adapted than any of the other species. In cases of true sympatry some form of ecological isolation seems necessary.

Volterra (1926) and Gause (1934) formulated what is now known as "Gause's Hypothesis". Stated simply, this proposes that if two species inhabit the same area, if they have the same requirements and if only limited space is available, one will eventually die out. Gilbert et al., (1952), Allee et al., (1949) and most ecology textbooks discuss this hypothesis in detail.

Several examples of sympatry have been worked out. McArthur (1958) found that each of five sympatric species of warblers fed from different parts of trees and were different in behaviour, nesting heights, and times of breeding. Rand (1962) found that each of three sympatric species of lizards most commonly frequented different parts of trees and that this behaviour was correlated with feeding. Wacasey (1962) studied two sympatric species of salamander, and found several important differences in their ecology. McCarley (1954)

worked on the sympatric species Peromyscus leucopus and P. gossypinus. These are fairly closely related and are able to form hybrids in the laboratory, but remain distinct in the field. He found that where the ranges did overlap, only P. leucopus was found in the more upland forest habitat. It was thus demonstrated that they were not truly sympatric, but had minor differences in habitat.

Hamilton (1962) studied five species of the avian genus Vireo, and found them separated by habitat, song, plumage, and behaviour. He proposed that these species, and probably all territorial species, tend to have overlapping territories only when they are far diverged; more closely related species tend to develop territorial separation. The two species of deermice being considered do not seem to be far diverged (Waters, 1961), and they are territorial in behaviour (Burt, 1940). Thus one would not expect to find overlap of their territories. Furthermore, because of the breakdown of territories each winter, and the aggregation of mice in groups of three to six in suitable nesting places (Thomsen, 1945), the two species would be expected to maintain some form of ecological separation wherever they are coincident.

The above accounts indicate that ecological separation of two sympatric species can take place in two ways. The first is by straightforward differences of food habits, precise habitats, times of activity and so on. Alternatively two sympatric species can be separated in a more subtle manner.

The two species of deermice being discussed do not seem to have habitats which are sufficiently accurately defined to explain their sympatry. They also seem to be similar in several other important respects: they eat more or less the same foods - insects, fruits, seeds, nuts, etc., as available (Cahn, 1937; Cogshall, 1928; Hamilton, 1941; Johnson, 1922); they are both nocturnal; they are very similar in appearance; and they both seem to nest in whatever places are available, such as under fallen logs, in old tree roots, in short burrows, and in houses, barns and so on. Consequently it seems that the sympatry of these two species requires a less direct explanation.

There are several ways in which two or more species can remain sympatric without being different in any major respect. First, if each species population inhibits its own expansion more than it does that of the other species, then a state of sympatry may exist. In practice, this can happen by each species being limited by a slightly different factor, or by some density-dependent factor which affects only the population whose density is varying. Steinhaus (1958) considered disease to be an important density dependent factor, and diseases can sometimes be species-specific.

Second, one species could survive by depending on the occasional superabundance of some food supply which is not a food of the other species. Thus, while at other times the population of this species would gradually decline, the periodic increases due to this food supply could maintain a state of equilibrium. McArthur (1958) found this situation

with one of five sympatric warblers.

Third, one species may be more migratory than the other. When conditions become adverse, as they would tend to do annually, this species would move away from the scene of potential competition to a habitat, which although less preferred, would support the population. Caldwell (1960) found this to be the case with sympatric populations of Peromyscus polionotus and Mus musculus. Competition for seeds occurred at certain times, and at these times Mus would migrate, only to return when conditions became favourable once more.

Fourth, territorial animals exhibit the special case of forcing the young out of the parents' territory after a certain time. Errington (1943) considers that this is the time of highest predation on a population. It is possible for the otherwise more successful population to be more heavily preyed upon than the potentially less successful population. A state of equilibrium could thus be maintained.

Fifth, Slobodkin (1961) developed the concept of ecological space. The ecological space in a geographical area is the sum of all the components of that area which might affect any animal or plant living in it. The ecological space therefore includes all parts of the environment, living and non-living. The niche of any animal is the sum of all the aspects of the life of the animal. Animals often manage to survive in places to which they are not completely adapted; under these circumstances, however, the population would not be expected

to develop to the same density as it would under optimal conditions. It is possible for two populations to be living in an area whose ecological space is such that the niches of both species are not fully satisfied; the two populations could not therefore develop to their maximum densities, and the two populations could therefore co-exist.

Sixth, since the environment is changing, with a main annual cycle, if first one species, and then the other were favoured, then neither species would be at a continual advantage. Coexistence is a possible result of such a situation (Slobodkin, 1961).

When the published observations on the habitats of these two species are critically analysed, it becomes evident that no simple explanation of the sympatry of P. maniculatus gracilis and P. leucopus noveboracensis is possible. The situation does not bear such simple experimental analysis as Harris (1950) applied to the habitat discrimination of the prairie deer mouse and the white-footed mouse. Kendeigh (1945) came to a conclusion similar to that of Harris in his study on birds; namely, that the appearance of the foliage acts as a releaser mechanism (Tinbergen, 1948) which causes the animal to remain in that environment.

It is a common supposition that P. l. noveboracensis is a woodland form. Jackson (1953) and Nicholson^{*} (1941) have

^{*}The following survey consists largely of all the information available in the Journal of Mammalogy since Vol. 1 (1919).

both put nest boxes in trees and on the ground, and caught P. l. noveboracensis more commonly in the boxes on the trees. Bailey (1929), Brand (1955), Cahn (1921), Clark (1964), Connor (1953), Dice (1923), Dice and Sherman (1922), Getz (1961), Hamilton (1930), Hayes (1958), Hendrickson and Schlesselman (1937), Jameson (1943, 1949), Johnson (1922), Klein (1960), Lewis (1940), Lindsay (1960), Linsdale (1928), McNair (1931), Schmidt (1931), and Welter and Sollberger (1939) all have found noveboracensis in woods, particularly deciduous ones. Of these workers, however, Bailey, Connor, Dice, Johnson, Klein, Linsdale, and Welter and Sollberger also found the species in open places. Wilson (1945) states that he did not find it to be entirely a woodland species, as he collected it in most habitats, including fields and civilized centres. Hamilton (1950), Howard (1949), and Johnson (1926) found noveboracensis in the same areas as P. maniculatus bairdii, a renowned open field inhabitant; Pruitt (1959) found it to be ubiquitous in Michigan.

These observations should be compared with the statements of Cameron (1956), Goodwin (1929), Green (1925), and Soper (1923) that one way in which P. l. noveboracensis may be distinguished from P. m. gracilis is that gracilis has a longer tail. And yet Horner (1954) reported a definite correlation between length of tail, habitat and habits; the forest-inhabiting and presumably arboreal forms tended to have longer tails. One would therefore expect to find that gracilis is more of a woodland form and perhaps more arboreal than noveboracensis.

Concerning P. m. gracilis, Cahn (1921), Dice and Sherman (1922), Jameson (1949), Klein (1960), Komarek (1932), Manville (1949), and Schmidt (1931) found the species in woodlands. Johnson (1922) found it in fields and in woods in Minnesota.

Where the two species have been found together, the following observations have been made: Cameron (1956) reported that P. m. gracilis prefers open mixed forests where there is plenty of leaf litter and rotten logs, while P. l. noveboracensis prefers forested and bushy areas, especially dry upland mixed woods. Schmidt (1931), in Wisconsin, found gracilis in hemlock-hardwood forest on soil of a poor type with little humic content; noveboracensis he found among hardwood and pine forests where the topsoil is rich. Green (1925), in Michigan, found that noveboracensis preferred pine barrens and coniferous swamps, where he did not find gracilis. Klein (1960) measured the coefficient of interspecific association of the two species with the vegetation in New York; gracilis had an affinity for hemlock - white pine - northern hardwoods forest; noveboracensis did not show any positive association such as gracilis did, but rather a negative association for the gracilis habitat. Jameson (1949) found the two together in a bottomland area in New York with basswood, maple, white ash, and tulip tree. Komarek (1932), in Wisconsin, found noveboracensis generally more numerous, and while he considered the two to live in the same habitats, gracilis may have been more numerous in the deeper woods. Hatfield (1938) caught the two

species in the same general area and decided not to try to distinguish between them. Pruitt (1959), in New York, found the two together, with gracilis much less abundant and more restricted in habitat. Clark (1964), working in south-eastern Ontario, found noveboracensis more frequently along the peripheries than within wooded areas. Gracilis on the other hand was found within the woods, and it was concluded that gracilis preferred the damper coniferous areas while noveboracensis selected a drier warmer microclimate, as found on the edges of woods.

So far the distribution of these two species with respect only to woodland and open land has been considered. There are also a number of observations concerning moisture and altitude preferences. The general opinion is that noveboracensis prefers a dry soil; Cameron (1956), Handley and Patton (1947), Kellogg (1937, 1939), Lewis (1940) and Schmidt (1931) reported this to be the case. However, Green (1925) found noveboracensis in swampy areas.

With regard to altitude, Barbour (1951), in Kentucky; Handley and Patton (1947), in Virginia; and Kellogg (1937, 1939), in Virginia, found that noveboracensis was more common on the lower slopes of mountainous areas. However, Pickens (1928), in S. Carolina, found it in mountainous regions, and Starrett and Starrett (1952), in New Hampshire, found two individuals at 6200 feet, 1000 feet above the tree line. Harper and Harper (1929), Schoonmaker (1929), and Starrett and Starrett agreed

that gracilis is generally found at high altitudes. Klein (1960) suggested that gracilis avoids warmer climates in favour of colder ones. Hart (1953), in experimental work on cold acclimation of these two species, did not however find any real difference between them in this respect.

This survey shows that both species are predominantly woodland forms and that gracilis is generally found in higher, colder and moister places than is noveboracensis, although both are in fact very variable in their habitats. Furthermore, when the two species are found together in the same general geographical area, there is no agreement as to the way in which they are ecologically separated.

Since this study is concerned with the apparent or possible sympatry of these two species of Peromyscus, it seems useful at this stage to consider the concept of sympatry. This word was introduced by Mayr in 1942, and is defined by Cain (1960) as follows: "Sympatric species are those in which some individuals from each in breeding condition come into such spatial proximity that fertilization is possible; in allopatry it is not possible."

It is ~~well~~ known that the home ranges of gracilis and noveboracensis do not overlap (Blair, 1942) when the two species are found together. However, the general spatial relationships of the home ranges are not well known. If the home ranges were found to be randomly mixed, checkerboard style, then most workers would claim that the two were sympatric. But

strictly speaking this need not necessarily be so, according to Cain's definition, for the two may be breeding at different times of the year, or may be aggressive to one another such that contacts are avoided. Nevertheless, if one species is able to exploit the habitat more successfully than the other, or if one species is much more aggressive than the other, then it is quite possible that despite the strict allopatry of the two species, one may be excluded from the environment.

In consequence of this, it does seem reasonable to extend the definition of sympatry as given by Cain, to include all situations in which one species can influence another closely related species to the extent that the two must be different in some respect, as discussed before, if the two species are to remain in this sympatric relationship.

If two closely related species have geographical ranges which overlap, the first step is, by field observation, to determine whether or not a sympatric association exists. If such an association does exist, it is possible that one species is in the process of replacing the other - what may be termed "dynamic sympatry". If in fact "static sympatry" can be demonstrated, then it is clear that some form of separating mechanism is at work.

At the present time the problem is that insufficient details are known of the distribution of home ranges of gracilis and noveboracensis, so that at present no decision can be made as to whether the two species are truly sympatric

or not.

Considering our lack of knowledge of any clear-cut ecological separation, and the theoretical 'necessity' for the existence of some kind of ecological isolating mechanism, it was felt that a laboratory study of certain aspects of the behaviour of captive Peromyscus leucopus noveboracensis and Peromyscus maniculatus gracilis might reveal differences in behaviour which might help to explain the nature of the overlap of geographical ranges exhibited by these forms, and suggest whether the two might be able to be truly sympatric or not.

The following series of experiments was thus devised to establish objective differences and similarities in behaviour between the two species under consideration:

- 1) "Paired Cage Experiment" - in which groups of mice of equal numbers of each species are given the choice of two connected cages and various types of nesting material.
- 2) "Aggression Experiments" - in which aggressive behaviour between individuals and groups of the same species and of the two subspecies was noted during short term (five minutes) and long term (24 hr.) experiments.
- 3) "Large Cage Experiment" - in which pairs of mice, one of each species, were obliged to seek food on the floor of a large cage. Two forms of food were used: natural food from the litter

of a local forest floor, and laboratory animal chow.

- 4) "Starvation Experiment" - in which the response to total deprivation of food by several mice of each species was measured by weight loss.
- 5) "Activity Experiment" - in which the amount and time of activity in revolving drums of single and paired mice of each species was measured.
- 6) "Running and Maze Experiments" - in which the reaction of single mice of both species released in a runway covered with transparent plastic and in a maze was measured.
- 7) "Swimming Experiment" - in which single mice of each species were forced to swim in a tank of water for two minutes and the amount of water taken up in the fur measured.

MATERIALS AND GENERAL METHODS

The subjects of this investigation were members of a laboratory colony containing both P. leucopus noveboracensis and P. maniculatus gracilis. Most of the original mice were live-trapped in southern Ontario, in the area of sympatry, in 1960 and 1961, and a few were added in 1963. Litters were produced by these original stocks in 1961, 1962 and 1963. The mice used in the experiments were from the original stock (of undetermined age), the litters, and the mice added in 1963. About 50 individuals of each species were used for the various experiments. All animals used were at least twelve weeks old.

Each mouse was marked about six weeks after birth with a small numbered metal fingerling tag on the right ear. While these tags did not seem to cause any irritation to the mice, a few tags were torn out of the ear. A new tag was placed in the right ear if possible, or otherwise in the left ear.

The marking of the mice so as to make them easily distinguishable by species and sex during an experiment proved necessary. The system adopted was based on the observation of Finlay (1959) that deermice "seem insensitive to a dull red light". Fur was cut from the back of gracilis only, leaving a dark gray patch in the normal brownish pelage; a V-shaped notch was cut in the left ear of males of both species. It was found that during darkness (when a

photographic darkroom red safelight was used) and during the hours of daylight, the different species and sexes of mice could be distinguished.

The mice were normally housed in standard laboratory cages (either 18 in. x 15 in. x 9 in. high, or 9 in. x 15 in. x 9 in. high), with no more than three mice in each small cage, and no more than five in each larger cage. Possible mating pairs and pairs with litters were housed in the larger cages. While the two species were caged in the same room, they were kept in separate cage-racks to reduce the possibility of individuals of one species becoming accustomed to the presence or proximity of individuals of the other species.

Food was supplied in the form of Purina Laboratory Animal Chow; corn, milkweed seeds and carrots were occasionally used to add variety to the diet. Water was always available, and all cages contained one to two inches of wood shavings and one or more tin cans, for nesting.

When not being used in experiments, the mice were kept in one of two places, depending on the time of year. Until December 7, 1962, the cages were kept in a room 24 ft. x 12 ft. x 8 ft. high, containing other caged laboratory animals. Lighting was by a sky-light and by daylight fluorescent lighting kept on during the normal working day. Ventilation was by an air conditioning system; the temperature varied between 18°C and 25°C over a period of one year. After December 7, and until May 11, 1963, the cages were moved to a

ventilated compartment built at one end of this room. This compartment, 12 ft. x 6 ft. x 8 ft. high was very nearly light-tight. It was illuminated while the main cages were in it by means of a 100-watt lamp at ceiling height giving about 25 lux in the area of the cages. The lighting was turned on and off by a time switch arranged so that the daylength was the same as that normally experienced about six weeks later, (Fig. 2). Whitaker (1940) found that this system should advance the date of the earliest matings. As a result litters were produced earlier than otherwise could be expected, giving more mice for later experiments. The cages were removed from this compartment on May 11, 1963, and returned to the main room.

During the time that the non-experimental cages were in the compartment, and afterwards, various experiments were carried out in it. The advantages of the compartment were that it screened the mice from unnecessary human interference, and that the lighting could be controlled to suit the conditions. After May 11, 1963, the daylength within the compartment was arranged to be the same as that outside, with darkness setting in at 9 p.m., except as described when the various experiments are discussed. The temperatures in the compartment varied between 20° and 25°C. and were 5° C. higher on the average than those in the main animal room.

The maintenance of total darkness during the hours of darkness in the compartment might be criticized as an unnatural condition; however Moody (1929) showed that P. m.

Fig. 2. The daylengths used during the time the mice were subjected to daylengths other than normal (from Dec. 7, 1962 - May 11, 1963).

gracilis moved most freely in total darkness, and less freely as the amount of light increased.

The animals were generally handled directly in the gloved hand.

"PAIRED, CAGE" EXPERIMENT

Harris (1950) tested the habitat selection of Peromyscus maniculatus gracilis and P. m. bairdii by giving the mice a choice of two artificial habitats, one resembling forest and the other grassland, and noting the amounts of time individuals of each species spent in each habitat. An experiment of a similar nature might theoretically help solve the present problem, but the design of such an experiment would be difficult because simple and direct selection between two distinct habitats does not seem to be the mode of ecological separation of these two species. Furthermore, Wirtz and Pearson (1960), in a field study of P. leucopus noveboracensis and Microtus pennsylvanicus, did not find P. l. noveboracensis exhibiting any local habitat selection in an old field environment.

It seemed, however, that if the mice were presented with a series of situations differing in availability of nesting sites, "companions", amount of food and so on, they might exhibit selection which would give some information concerning choice of nesting sites, and intraspecific and interspecific association. These two types of association represent the extent to which individuals associate with other individuals of the same or the other species during the inactive part of the day, and can be of ecological importance.

Methods

The simple apparatus used is shown in Fig. 3. Pairs of intercommunicating large colony cages were arranged in such a way that six or eight mice placed in them in any one test would tend to show definite selection of one cage or the other, and either of the nesting can, or of cotton batting when either or both of these were supplied. A hole 10 cm. wide x 6 cm. high cut in the adjacent sides of two cages could be shut if desired by means of a sliding door.

The mice were handled as little as possible during an experiment, the markings described earlier generally being adequate for the recognition of mice by species and sex. As many different mice as possible were used in random combinations, and as far as possible the mice within any pair of cages had not been exposed to one another before. In each pair of cages there were equal number of males and females of the species present. The cages were always clean at the start of any experiment; this procedure presumably eliminated any attraction for a mouse to the smell of a cage. None of the mice tested had ever been in the paired-cages before the experiment commenced. Presumably their simultaneous introduction to a situation strange to them all helped prevent fighting, as previously observed by Dice (1929). Food was always supplied in measured amounts and water was supplied ad libitum.

Fig. 3. Interior of one cage-pair used in the "Paired-Cage" experiment. The left cage contains a large nest-can and animal chow; the right cage, cotton batting and animal chow.

Experimental Procedure

Six tests were performed consecutively, with two to seven days between each pair of tests. Each test involved one, three or four such pairs of cages, which contained various arrangements of nesting cans, cotton batting, and mice. The arrangements of these in each test are shown in Table I, columns (1) to (6). All except the first test (A) were carried out in the ventilated inner compartment. A total of 18 cage-pairs were used. In each test the mice were introduced into both sides during the day. About four hours after the lights were turned on each morning thereafter, the nesting arrangement of the mice within each pair of cages was recorded on sheets designed for the purpose (see Appendix I). Specifically, the numbers of males and females of each species in the following locations in each cage were noted: within the can; outside the can; under the cotton batting; or not under the cotton batting. Any mouse that died or was killed during early experiments was replaced; this practice, however, was not followed in the later experiments because of a shortage of mice.

Each test lasted from 5 to 14 days; the total number of cage-pair days was 201, where a test involving three cage-pairs lasting eight days is considered to comprise $3 \times 8 = 24$ cage-pair days. A total number of 1343 observations were made, where each record made of the morning position of one mouse is considered as one observation. Column (7) of Table I lists the duration of each test, and columns (8) and (9) the

TABLE I
DETAILS OF THE PAIRED-CAGE
EXPERIMENT

Cage- pr.	Test	Contents of cages		No. of mice		No. of days	No. of obs.	
		left	right	P.m.g.	P.l.n.		P.m.g.	P.l.n.
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
1	A	L	L	6	6	5	44	46
2	B	L	L	6	6	8	38	46
3		L	S	6	6	8	35	35
4		L	L	6	6	8	36	28
5	C	L	L	4	4	10	35	31
6		S	L	4	4	10	35	35
7		-	L	4	4	10	36	35
8	D	L	L	8	0	10	72	--
9		-	-	8	0	10	60	--
10		L	L	0	8	10	--	73
11		-	-	0	8	10	--	72
12	E	L & C	L & C	8	0	14	72	--
13		C	C	8	0	14	54	--
14		L & C	L & C	0	8	14	--	71
15		C	C	0	8	14	--	72
16	F	L	C	8	0	12	81	--
17		L	C	0	8	12	--	66
18		L	C	4	4	12	39	37

Note: in columns (3) and (4) the following abbreviations are used to indicate the type of nest supplied:

L: large nesting can
S: small nesting can
C: cotton batting

numbers of observations recorded therein for each species. These numbers are not always the same because one or more mice sometimes died during a test.

Results

Because the conditions in the 18 cage-pairs were not exactly identical, all the data resulting from this experiment have not been presented herein in one place. Instead, the data for the cage-pairs containing certain combinations of mice and conditions have been grouped to attempt to answer certain questions about the behaviour of the mice.

- a) Did the two species segregate so that one species tended to be found during the inactive period in the left cage and the other species in the right cage?

Table II lists the numbers of times that mice of each species were observed in the left cage and in the right cage respectively of those eight cage-pairs that contained both species of mice. These data are presented as a series of 2 x 2 contingency tables. The significance of the difference between the observed distribution of mice in the two cages and that to be expected if there was no segregation between the species was tested by χ^2 for each cage-pair. The type of table and formula used is as follows (Snedecor, 1959):

	Situation 1	Situation 11	
Species a	a	b	a + b
Species b	c	d	c + d
	a + c	b + d	a+b+c+d = n

TABLE II
 FREQUENCIES OF OBSERVATIONS OF THE TWO SPECIES IN
 LEFT AND RIGHT CAGES OF THE CAGE-PAIRS

Cage-pair	species	Left	Right	χ^2	p
1	<u>P.l.n.</u>	25	21	0.46	0.80
	<u>P.m.g.</u>	28	16		
2	<u>P.l.n.</u>	26	7	1.98	0.16
	<u>P.m.g.</u>	23	15		
3	<u>P.l.n.</u>	28	7	8.69	<0.005
	<u>P.m.g.</u>	15	20		
4	<u>P.l.n.</u>	13	15	-	-
	<u>P.m.g.</u>	15	21		
5	<u>P.l.n.</u>	17	14	-	-
	<u>P.m.g.</u>	17	18		
6	<u>P.l.n.</u>	12	23	-	-
	<u>P.m.g.</u>	10	25		
7	<u>P.l.n.</u>	6	29	-	-
	<u>P.m.g.</u>	4	32		
18	<u>P.l.n.</u>	23	14	0.89	0.25
	<u>P.m.g.</u>	19	20		

$$\chi^2 = \frac{n(ad - cb - \frac{1}{2}n)^2}{(a+b)(c+d)(a+c)(b+d)} \quad \#$$

The term $\frac{1}{2}n$ is known as Yates correction,

and should be used when $n < 200$

The values of χ^2 and the probabilities that the observed distributions varied from the expected by chance alone are also given in Table II. Clearly in only one of the eight cage-pairs (No. 3) was there any significant segregation of the two species.

b) Were there differences between the two species in the frequencies with which they were observed inside and outside the nest cans 1) when equal numbers of mice of the two species were present, and ii) when only a single species was present?

The data for the same eight cage-pairs, which contained both species of mice and at least one nest-can, are presented in Table III. Herein the number of times that mice of each species were observed inside either of the two cans available (or the single can available in cage-pairs 7 and 18), and outside the nest-cans are tabulated for each cage-pair and totalled.

Table III shows that noveboracensis was found within the nest-cans more frequently than outside them, while gracilis was found outside the nest-cans more frequently than within them. When the totals are set up as a 2 x 2 contingency table and tested by χ^2 , these behaviour differences between the two species are shown to be highly significant ($\chi^2 = 78.6$ and $p = < .005$). Table III shows that only in two of the eight cage-pairs (5 and 6) did the behaviour of either species vary from

If $(ad - cb - \frac{1}{2}n)$ is a negative number, the calculation should be terminated.

TABLE III
 FREQUENCIES OF OBSERVATIONS OF THE TWO SPECIES
 INSIDE AND OUTSIDE THE NEST CANS

Cage-pair	noveboracensis		gracilis	
	inside can	outside can	inside can	outside can
1	40	6	8	36
2	28	5	14	24
3	28	7	6	29
4	21	7	14	22
5	14	17	29	6
6	30	5	19	16
7	26	9	15	21
18	20	17	6	33
Totals:	207	73	111	187

the overall trend. In both these cases, gracilis was observed more frequently within the nest-cans than without, but only in cage 5 did the distribution of noveboracensis deviate from the average.

The data for the remaining cage-pairs in which nest-cans were present and in which were mice of only one species are presented in Table IV. Herein are tabulated and totalled the numbers of times mice were observed within either of the two cans available (or the single can available in cage-pairs 16 and 17) or outside the nest cans.

Table IV shows that in the absence of gracilis, noveboracensis was still found inside the nest cans significantly more frequently than outside. Gracilis, however, in the absence of noveboracensis, showed no significant preference.

c) Were there differences between the two species in the frequency with which they were found under or in the cotton batting, when this was made available?

In Table V the numbers of times on which the mice of each species were observed under the cotton or not under the cotton, and in the latter case the number of times on which the mice were found in the can, when available, are tabulated.

Table V shows that noveboracensis was observed out of the cotton much more frequently than in it. The distribution of gracilis, however, was on the average random with respect to the use of cotton for nesting sites in the morning.

TABLE IV
FREQUENCY OF USE OF NEST CANS BY SINGLE SPECIES

Cage-pair	inside can	outside can	
10	68	5	<u>noveboracensis</u>
14	68	3	
17	45	21	
Totals:	181	29	
8	47	25	<u>gracilis</u>
12	34	38	
16	34	46	
Totals:	115	109	

TABLE V
 FREQUENCY OF USE OF COTTON BY THE TWO SPECIES, WHEN ONLY
 ONE SPECIES IS PRESENT

Cage-pair	use of cotton	no use of cotton	inside can [#]	
14	0	71	68	<u>noveboracensis</u>
15	15	57	-	
17	10	56	45	
totals:	25	184	113	
12	37	35	34	<u>gracilis</u>
13	53	1	-	
16	15	64	34	
totals:	105	100	68	

[#]these totals for "inside can" are included
 in "no use of cotton" totals.

Furthermore, when no nest-can was available (as in cage-pairs 13 and 15, gracilis almost invariably nested in cotton, but noveboracensis continued the usual behaviour of its infrequent use.

- d) Is there any sex difference in either species in the degree of use of nest-cans?

Table VI tabulates the total observations of males and of females of each species in each cage pair. The data are set up as a series of 2 x 2 contingency tables, and the significance of the difference between the observed distributions of the mice and that to be expected if there was no segregation by sexes was tested by χ^2 for each species and for each cage-pair. The values of χ^2 and the probabilities that the observed distributions varied from the expected by chance alone are also given in Table VI. Clearly there was segregation by the sexes in only one case: that of gracilis in cage-pair 7. In cage-pair 17, females selected cans while males were randomly distributed inside and outside the cans. The overall tendency in both species, however, was for there to be no significant sex difference with respect to utilization of nest cans during the morning.

- e) Is there any association between the species or within either species?

A measure of the amount of association between species and within species can be obtained from the data already presented. Table II showed that no species permanently established

TABLE VI

FREQUENCIES OF OBSERVATIONS OF MALES AND OF FEMALES
INSIDE AND OUTSIDE THE NEST-CANS IN ALL CAGE-PAIRS

Cage-pr.	inside or outside	<u>noveboracensis</u>				<u>gracilis</u>			
		♂	♀	χ^2	P	♂	♀	χ^2	P
1	Observations on the distribution of mice by sex not made.								
2	in	17	11	1.4	0.29	77	7	-	-
	out	1	4			13	11		
3	in	6	22	-	-	4	2	-	-
	out	1	6			14	15		
4	in	9	12	.76	0.35	8	6	-	-
	out	5	2			11	11		
5	in	8	6	-	-	16	13	-	-
	out	8	9			4	2		
6	in	15	15	-	-	12	7	2.41	0.25
	out	2	3			5	11		
7	in	10	16	2.75	0.09	15	6	7.31	<0.01
	out	7	2			3	12		
8	in					25	22	.25	0.75
	out					11	14		

TABLE VI (cont.)

Cage-pr.	inside or outside	<u>noveboracensis</u>				<u>gracilis</u>			
		♂	♀	χ^2	P	♂	♀	χ^2	P
10	in	35	33	-	-				
	out	3	2						
12	in					18	16	-	-
	out					18	20		
14	in	34	34	-	-				
	out	2	1						
15	in	7	8	-	-				
	out	29	28						
16	in					19	15	.46	0.29
	out					21	25		
17	in	14	31	14.1	0.005				
	out	13	8						
18	in	8	12	.68	0.525	3	3	-	-
	out	10	7			18	15		

itself in any one cage, and suggested that no form of association or intolerance took place. It was felt, however, that if, instead of using the total observations for a cage-pair, a comparison was made between the observations on the first and on the last days for every cage-pair, more meaningful results might be found. In Table VII the interspecific association is measured by taking the numbers of gracilis and noveboracensis in each cage of a pair on the first day of a test, and putting in columns (1) and (2) the figures for the cage with more gracilis, and in columns (3) and (4) the numbers for the cage with fewer gracilis. These four columns are summed and put to a χ^2 analysis; $\chi^2 = 14.2$ and $p < 0.005$. The low probability revealed by this test indicates that there was little association between the two species; or in other words, that there was a highly significant degree of segregation between them at the start of the tests.

Table VIII contains comparable numbers of gracilis and noveboracensis per cage for the last day of each experiment tabulated in a similar manner. Here $\chi^2 = 2.7$ and $p < 0.10$ which indicates that by the end of the tests there was no significant segregation between the two species.

Tables VII and VIII thus suggest that the amount of interspecific association during the inactive part of the day increased a great deal during the tests.

Tables IX and X demonstrate the method of establishing indices of the intraspecific association of each

TABLE VII

DISTRIBUTION OF INDIVIDUALS ON THE FIRST DAY OF EACH
TEST IN CAGE-PAIRS WITH BOTH SPECIES

Cage-pair	number of observations:-			
	in cage with more <u>gracilis</u>		in cage with fewer <u>gracilis</u>	
	(1)	(2)	(3)	(4)
	<u>P.m.g.</u>	<u>P.l.n.</u>	<u>P.m.g.</u>	<u>P.l.n.</u>
1	4	2	2	4
2	5	2	1	4
3	5	0	1	6
4	4	3	1	3
5	2	2	2	1
6	2	1	2	3
7	4	2	0	1
18	3	0	1	4
totals	29	12	10	26

TABLE VIII
DISTRIBUTION OF INDIVIDUALS ON THE LAST DAY OF EACH TEST
IN CAGE-PAIRS WITH BOTH SPECIES

Cage-pair	number of observations:-			
	in cage with more <u>gracilis</u>		in cage with fewer <u>gracilis</u>	
	(1)	(2)	(3)	(4)
	<u>P.m.g.</u>	<u>P.l.n.</u>	<u>P.m.g.</u>	<u>P.l.n.</u>
1	4	4	1	1
2	6	5	0	0
3	6	1	0	5
4	5	4	1	0
5	4	1	0	3
6	4	4	0	0
7	4	4	0	0
18	2	3	2	1
totals:	35	26	4	10

TABLE IX

DISTRIBUTION OF INDIVIDUALS ON THE FIRST DAY OF EACH TEST
IN ALL CAGE-PAIRS, ARRANGED TO GIVE A MEASURE OF
INTRASPECIFIC ASSOCIATION; (See text, page 41)

Cage-pair	no. of P.m.g. found in cage with:		no. of P.l.n. found in cage with:	
	(1) more <u>P.m.g.</u>	(2) fewer <u>P.m.g.</u>	(3) more <u>P.l.n.</u>	(4) fewer <u>P.l.n.</u>
1	4	2	4	2
2	5	1	4	2
3	5	1	6	0
4	4	1	3	3
5	2	2	2	1
6	2	2	3	1
7	5	0	2	1
8	5	3	-	-
9	5	2	-	-
10	-	-	8	3
11	-	-	5	0
12	8	0	-	-
13	6	0	-	-
14	-	-	8	0
15	-	-	6	2
16	6	2	-	-
17	-	-	8	0
18	3	1	4	0
totals:	58	17	63	15

Index of association for P.m.g. = $100 - \left(\frac{17}{58} \times 100 \right) = 70.7\%$

Index of association for P.l.n. = $100 - \left(\frac{15}{63} \times 100 \right) = 76.2\%$

TABLE X

DISTRIBUTION OF INDIVIDUALS ON LAST DAY OF EACH TEST IN
ALL CAGE-PAIRS, ARRANGED TO GIVE A MEASURE OF
INTRASPECIFIC ASSOCIATION; (See text, page 41)

Cage-pair	no. of P.m.g. found in cage with:		no. of P.l.n. found in cage with	
	(1)	(2)	(3)	(4)
	more <u>P.m.g.</u>	fewer <u>P.m.g.</u>	more <u>P.l.n.</u>	fewer <u>P.l.n.</u>
1	4	1	4	1
2	3	3	5	1
3	4	2	4	2
4	4	2	3	1
5	4	0	3	1
6	4	0	4	0
7	4	0	4	0
8	8	0	-	-
9	6	0	-	-
10	-	-	7	1
11	-	-	8	0
12	8	0	-	-
13	6	0	-	-
14	-	-	5	2
15	-	-	6	2
16	8	0	-	-
17	-	-	5	1
18	2	2	3	1
totals:	65	10	61	13

Index of association for P.m.g. = $100 - \left(\frac{10}{65} \times 100 \right) = 84.6\%$

Index of association for P.l.n. = $100 - \left(\frac{13}{61} \times 100 \right) = 78.7\%$

species at the start and at the end of the experiment. The two pairs of columns show the numbers of gracilis and noveboracensis. Columns (1) and (3) list the numbers of individuals found in the cage containing more individuals of gracilis and noveboracensis respectively. Columns (2) and (4) list the numbers found in the other cage. The measure of observed intraspecific association (I) is expressed as a percentage by use of the formula $I = 100 - \frac{r}{n} \times 100$, where r is the number in the less frequented, and n the number in the more frequented cage. The index of intraspecific association (I) then varies from 100% when $r = 0$ to 0% when $r = n$.

Tables IX and X suggest that while the amount of intraspecific association among noveboracensis may be slightly greater than that of gracilis at the start of the tests, during tests this association does not increase appreciably - only from 76.2% to 78.7%. However, the amount of association among gracilis increases a great deal during the tests - from 70.7% to 84.6%.

Discussion

The results of this experiment show, in a general way, certain behavioural tendencies of the two species under these particular conditions. The main trends are that neither of the two species established themselves in either cage of the two available during any test, that noveboracensis is found much more commonly in cans than is gracilis even when cotton batting is available as an alternative nesting material, that the

amount of interspecific association increases during an experiment, and that the intraspecific association is slightly different for each species and increases significantly during a 10-day experiment in gracilis only.

That neither species established itself in any one cage is probably due to the crowded conditions that existed in all the cages. Both species were introduced at the same time, and consequently neither species was in the position of being the dominant occupant. An experiment in which a group of mice of one species was established in a cage, and then a group of mice of the other species introduced to the cage will be described later.

Despite the limitations of the experiment, useful information concerning interspecific association was obtained. At the start of the tests the two species were highly segregated and interspecific association was almost nil. By the end of the tests, however, the segregation was insignificant. In other words, mice of these two species tended to avoid individuals of the other species during their first encounters. However, as these tests show, if the groups of different species are forced to coexist, for as short a period as 5 to 14 days, even though they are given the opportunity to segregate, the amount of association tends to increase by the end of any test.

The amount of intraspecific association was high in both cases. It is interesting to note, however, that while at

the start of the tests the amount of association is more or less similar in both species, by the end of the tests the amount of association among gracilis groups has increased considerably, and that of noveboracensis groups has barely increased.

In attempting to relate these observations to the ecology of the species, care must be exercised; the great difference between the environments existing in the cages and those existing in the field should always be borne in mind. Nevertheless, certain general conclusions can be drawn. It seems from the above results concerning association that individuals of different species tend to avoid one another, even if forced into a small environment. Individuals of the same species do not avoid one another to the same extent provided that no individual had been established first in the environment.

Wild Peromyscus are not established in home ranges at all times of the year (Burt, 1940), least of all in the spring when the setting up of home ranges following the winter is taking place. Later in the year new litters are also seeking out and setting up home ranges. Under these circumstances, the fact that interspecific avoidance is much greater than intraspecific avoidance could be important in determining the outcome when several individuals of the two species attempt to set up home ranges in the same general area. Home ranges, unlike territories, are not defended but, nevertheless, one

might expect less toleration at the interface of the two newly set up home ranges of different species than one would if the two mice were of the same species. Once the mouse has become established in its home range, different behavioural processes are probably at work.

A general, and rather tentative conclusion may be drawn from the above observations. Suppose an area exists which has no deermice but is ecologically suitable for both P. m. gracilis and P. l. noveboracensis. If this area were subjected to immigration by groups of both species, then one would not expect to find the individuals of the two species randomly scattered, but collected in groups. The area would not necessarily be divided into one area harbouring gracilis and one area harbouring noveboracensis, but would probably present a pattern of groups of home ranges of one species alternating with groups of home ranges of the other species. In this way, it would be possible for the two species to be apparently existing in the same general area. However, the home ranges of deermice break down each winter, and consequently, some other factor would have to be in operation to explain the long term coexistence of the two species in the same general area. Klein (1960) suggested that behavioural differences could emphasize slight ecological differences with the result that the two species considered could have similar (but not identical) ecologies and yet be separated.

The fact that noveboracensis showed less intra-specific association at the end of the tests than does

gracilis seems to have little ecological value by itself. Yet, it could explain the observation of Blair (1942) that the home ranges of gracilis overlap while those of noveboracensis do not. Furthermore, if these tendencies showed themselves in the field, the result might be that groups of noveboracensis in suitable nesting places for the winter would be smaller than the groups of gracilis. Coupled with other observations and backed up by field studies, these tendencies might prove to have ecological importance.

Another result emerging from this experiment is that noveboracensis nests in cans more commonly than does gracilis. This suggests that in the field noveboracensis nests more commonly in secluded places, and that gracilis nests more commonly in open spaces. Gracilis individuals were frequently seen burrowing through the wood chips in the cages. Noveboracensis was never seen doing this. It is reasonable to suppose that gracilis is more apt to nest under the leaf litter, under rock piles and so on, while noveboracensis chooses abandoned burrows and hollow logs. On several occasions I have seen a noveboracensis released from a trap run down a small burrow. A small difference in preference for nesting sites could readily explain the overall sympatry of the two species.

AGGRESSION EXPERIMENTS

Introduction

Experiments on aggression between individuals or groups of different species of small mammals have been carried out by Getz (1962), King (1957) and others. Getz studied meadow and prairie voles, and found that the meadow vole was intolerant of others of its own species, while the prairie vole was intolerant of the meadow vole but tolerant of its own species. King worked on Mus and Peromyscus maniculatus and found that when they were together, Mus attacked Peromyscus, Mus attacked its own species less fiercely, and Peromyscus attacked its own species even less fiercely. Dice (1922), in a field study of P. l. noveboracensis and P. m. bairdii did not consider interspecific antagonism to be an important factor in determining the lack of overlap of the home ranges of these two species. Different habitat preferences seemed more important.

My own observations, together with those of others, e.g., Horner (1947), Goodpaster and Hoffmeister (1954), and Thomson (1945), led me to believe that Peromyscus is intolerant of intruders of the same and other species. While deaths in the paired-cage experiments were rare, because all inhabitants of the paired cages were introduced at the same time, the introduction of a mouse or mice to an established group in the mouse colony was found on several occasions to lead to the death or injury of at least some of the visitors. It was felt

that some objective observations should be made on the long-term and short-term effects of placing a mouse with one or several established mice of the same or different species. Two types of experiment were performed.

SHORT-TERM AGGRESSION EXPERIMENTS

Methods

Five male and five female gracilis, and five male and five female noveboracensis were chosen to constitute four groups of mice, as follows:

Group A: 2 ♂ and 3 ♀ gracilis

Group B: 2 ♂ and 3 ♀ noveboracensis

Group C: 3 ♂ and 2 ♀ gracilis

Group D: 3 ♂ and 2 ♀ noveboracensis

No mouse in any group was acquainted with any mouse in any other group, although some of the mice within any one group may have been acquainted. At times when not being used for experiments, the mice were kept in the cages of the colony, with other mice of the same species.

Five identical, large standard cages were used in this experiment; each was provided with wood chips, food, water, and a nest-can. These were kept in the main animal room. On any one day of the experiment, each of the five cages was occupied by one of the five mice of one group, these mice being termed the 'residents'. They remained in

the test cages for 24 hours, at the end of which, in the morning, each mouse was presented with a 'visitor' for five minutes. In this test on the second day, each of the mice of a second group of five acted as visitors, one to each resident, in turn. Observations were made in daylight of attacks, chasings, dominance, and apparent tolerance during each five-minute visit or "meeting" between two mice. It was always possible to distinguish between the resident and the visitor. The gracilis were marked as mentioned earlier, and the mice of groups A and B had additional markings in the form of fur clipped from the rump, and the tail was blackened with waterproof ink. In this way each group of mice was characteristically marked.

Various combinations of visitor and resident were used, the system ensuring that no two mice met more than once during the whole experiment. In this way a total of eighty meetings took place, arranged ^{so} that there were twenty of each of the four possible species arrangements. The exact distribution of meetings is shown in Tables XI and XII in two different forms. Table XI shows the number of times each group met each of the other 3 groups; Table XII shows how many times each sex of each species met each sex of the two species.

Results

There was great variation in the reactions observed, and following the advice of Simpson, et al. (1960) for recording the ordinarily qualitative results of this type of experiment, quantitative data were compiled. Three types of behaviour were

TABLE XI
ARRANGEMENT OF MEETINGS OF THE FOUR GROUPS OF MICE
USED IN THE SHORT-TERM AGGRESSION EXPERIMENT

Group		VISITORS			
		A P.m.g.	B P.l.n.	C P.m.g.	D P.l.n.
RESIDENTS	A P.m.g.	-	1	2	1
	B P.l.n.	1	-	1	2
	C P.m.g.	2	1	-	1
	D P.l.n.	1	2	1	-

Note: Each number indicates the number of times that the mice of a group acted as visitors to the mice of the indicated resident group.

TABLE XII
ARRANGEMENT OF MEETINGS DURING THE SHORT-TERM AGGRESSION
EXPERIMENT, WITH PARTICIPANTS CLASSIFIED BY SPECIES
AND SEX

		VISITORS			
		♂P.m.g.	♀P.m.g.	♂P.l.n.	♀P.l.n.
RESIDENTS	♂P.m.g.	5	5	8	2
	♀P.m.g.	5	5	4	6
	♂P.l.n.	8	4	4	6
	♀P.l.n.	2	6	6	4

considered - attacking, dominance, and apparent tolerance, and the number of observations of each per five minute meeting was recorded.

An attack is defined as a case in which one mouse rushed at the other in such a way as to give the impression that a bite could have been delivered; in practice few actual bites were seen to be delivered, judging by the condition of the skin and fur of the subjugated mouse. The dominant animal showed itself by following or sniffing the subordinate animal; this was generally not attended by much rushing around. Apparent tolerance was considered to have been displayed when the behaviour of the two animals did not seem to be different from what one would have expected, were the animals alone.

The general behaviour of the two species in this experiment, as in other experiments, was entirely different. Gracilis, whether visitor or resident, was usually quite active, while noveboracensis was almost always inactive. In many of the meetings between two noveboracensis, both individuals remained quite still anywhere in the cage for the full five minutes. This would seem to present a limitation, for a record of apparent tolerance because both individuals remained still does not necessarily indicate real long-term tolerance. It was because of this limitation that the long-term aggression experiments were carried out.

Table XIII shows the number of meetings in which attacks took place, the number of attacks that took place at

TABLE XIII
NUMBER OF ATTACKS WITH DIFFERENT COMBINATIONS
OF RESIDENTS AND VISITORS.

		VISITORS			
		♂ P.m.g.	♀ P.m.g.	♂ P.l.n.	♀ P.l.n.
RESIDENTS	♂ P.m.g.	10		5, 13,2	3
	♀ P.m.g.	3,3	23,1	18,2	10
	♂ P.l.n.	4,1	5,20		1
	♀ P.l.n.	5,2	4,4,1	2	

Note; the lower triangle of each smallest rectangle indicates attacks by the resident on the visitor, the upper triangle attacks by the visitor on the resident. Each number represents the number of attacks at one five-minute meeting.

each of those meetings, and whether the resident or the visitor was the attacker. In nine of the 25 meetings that involved attacks, a visiting gracilis attacked a resident noveboracensis. A visiting noveboracensis never attacked any resident of either species. Moreover, a resident noveboracensis only attacked a visitor in four meetings, twice attacking visiting gracilis and twice a visitor of its own species. Resident gracilis on the other hand made 12 series of attacks, seven on visiting noveboracensis and five on its own species. It is also interesting to note that females made a total of ~~86~~ attacks while 48 attacks were made by males; furthermore, females were attacked only 54 times while the males were attacked 90 times.

Table XIV shows some particulars of the meetings during which dominance was displayed. Gracilis was the dominant animal in 21 of 26 meetings in which this behaviour was observed. Noveboracensis was the subordinate animal in 12 of these 21 cases, five times while it was visited and seven times while it was the ~~visitor~~. Gracilis was subordinate to gracilis in nine meetings, including seven in which the resident was dominant. Noveboracensis never dominated over gracilis and on the five occasions in which noveboracensis was dominant over its own species, it was the resident in ~~two~~ and the visitor in ~~three~~.

Table XV A shows the number of occasions on which tolerance was apparently shown, and Table XV B shows the total for each of the four possible interspecific and intraspecific type of meetings. The totals of each quadrant in Table XV B are more or less equal, except that for meetings between two

TABLE XIV
NUMBER OF MEETINGS IN WHICH ONE MOUSE
DOMINATED OVER ANOTHER

	V I S I T O R S				
		♂ <u>P.m.g.</u>	♀ <u>P.m.g.</u>	♂ <u>P.l.n.</u>	♀ <u>P.l.n.</u>
R E S I D E N T S	♂ <u>P.m.g.</u>	3	1	4	
	♀ <u>P.m.g.</u>	2	2		3
	♂ <u>P.l.n.</u>	3	2	1	1
	♀ <u>P.l.n.</u>			2	1

The lower triangle of each smallest rectangle indicates the number of meetings at which the resident was dominant, the upper triangle the number of meetings at which the visitor was dominant.

TABLE XV

THE NUMBER OF MEETINGS IN WHICH APPARENT
TOLERANCE WAS SHOWN
A. TOTALS ARRANGED BY SEX AND SPECIES.

		V I S I T O R S			
		♂ <u>P.m.g.</u>	♀ <u>P.m.g.</u>	♂ <u>P.l.n.</u>	♀ <u>P.l.n.</u>
R E S I D E N T S	♂ <u>P.m.g.</u>	1	4	1	1
	♀ <u>P.m.g.</u>	0	1	1	2
	♂ <u>P.l.n.</u>	1	0	3	4
	♀ <u>P.l.n.</u>	0	3	3	3

B. TOTALS FOR EACH OF THE FOUR POSSIBLE
INTERSPECIFIC AND INTRASPECIFIC TYPE
OF MEETINGS

		V I S I T O R S	
		<u>P.m.g.</u>	<u>P.l.n.</u>
R E S I D E N T S	<u>P.m.g.</u>	6	5
	<u>P.l.n.</u>	4	13

noveboracensis, at many of which apparent tolerance occurred. This apparent tolerance, as mentioned earlier, could be due to the peculiar "freezing" behaviour of this species, and in the next series of experiments this behaviour was studied further.

LONG-TERM AGGRESSION EXPERIMENTS

Because of the tendency for the two P.l. noveboracensis to remain still for the duration of their five-minute meetings, it was felt that the mice should be left together for a longer period of time so that some measure of the aggression of this species could be obtained. Past experience had shown that a resident group of noveboracensis would sometimes attack and kill a visitor of either species.

Methods

The residents in this experiment were 20 different groups of mice in ordinary colony cages. Each resident cage contained two to five mice, and one of 30 different mice was introduced in the morning as a visitor. Three groups of tests were run, each lasting twenty-four hours, and the groups were separated by intervals of three weeks. Each group consisted of ten separate but simultaneous tests of which six were intra-specific and four interspecific. On the day following the introduction of the visitors, all the mice in each cage were inspected for any signs of fighting, such as wounds or loss of fur.

Results

The number of visits by male and female gracilis and noveboracensis to established groups of each species is shown in the first three columns of Table XVI. For the purpose of analysis, the results of each test are classified into three possible types: the visitor remaining unharmed; the visitor being wounded to some extent, but not killed; and the visitor being killed. On no occasion was any resident wounded or killed.

Columns 4 to 6 of Table XVI show the number of meetings in which each of the three possible results took place. Each of the four species combinations had a preponderance of results of one of the three types. When gracilis visited gracilis, most often the visitor was unharmed; however, the total of wounded and killed almost equalled the number of unharmed visitors. When gracilis visited noveboracensis, most often the visitor was unhurt. When noveboracensis visited its own species, most often it was wounded, half as often it was left unharmed, but it was never killed. When noveboracensis visited gracilis, the visitor was most often killed and never left unharmed.

Considering the results in Table XVI by the sex of the visitor, it is interesting to note that, out of ten male visitors, only one was unharmed, six were wounded, and three were killed. Out of twenty female visitors, eleven were unharmed, four were wounded and five were killed.

TABLE XVI
RESULTS OF LONG TERM AGGRESSION EXPERIMENT

Visitor	Residents	No. of Meetings	Visitor unharmed	Visitor wounded	Visitor killed
(1)	(2)	(3)	(4)	(5)	(6)
♂ <u>P.m.g.</u>	<u>P.m.g.</u>	2	0	1	1
♀ <u>P.m.g.</u>	<u>P.m.g.</u>	7	5	1	1
♂ <u>P.m.g.</u>	<u>P.l.n.</u>	2	0	1	1
♀ <u>P.m.g.</u>	<u>P.l.n.</u>	4	4	0	0
♂ <u>P.l.n.</u>	<u>P.l.n.</u>	5	1	4	0
♀ <u>P.l.n.</u>	<u>P.l.n.</u>	4	2	2	0
♂ <u>P.l.n.</u>	<u>P.m.g.</u>	1	0	0	1
♀ <u>P.l.n.</u>	<u>P.m.g.</u>	5	0	1	4
totals:		30	12	10	8

Discussion

The two aggression experiments run - the "short-term" and the "long-term" - give different results, particularly concerning the aggression of noveboracensis. On the basis of the short-term experiments I conclude that gracilis is rather intolerant of noveboracensis, and more tolerant of its own kind, while noveboracensis is even more tolerant of its own species, and almost completely tolerant of gracilis under these conditions.

However, the long-term aggression experiments give rather different results. The greatest intolerance was shown by resident gracilis towards visiting noveboracensis, five deaths and one wounding occurring out of six meetings. P.l. noveboracensis was also aggressive to noveboracensis visitors; for, although no deaths occurred, wounding occurred in six out of nine meetings. P. m. gracilis was less aggressive to visitors of its own species, killing two, wounding two, and leaving five unharmed. P.l. noveboracensis seemed about equally aggressive to gracilis visitors, killing one, wounding one, and leaving four unharmed. Although it is difficult to make a hierarchy of increasing aggressiveness for the four types of meeting, the 'gracilis resident: noveboracensis visitor' meetings caused the highest degree of aggression in both long- and short-term aggression experiments.

The most notable difference between the two experiments lies in the meetings of noveboracensis with its own species.

In the case of the short-term noveboracensis: noveboracensis meetings, both the resident and the visitor frequently remained still for the duration of the test, but in the long-term tests, the residents were frequently seen to attack the visitor almost immediately. In comparison, gracilis residents in both the short-term and the long-term tests in most cases almost immediately showed awareness of the visitor. Thus, it seems possible that noveboracensis takes longer to become established in a cage. To establish whether only groups of mice, as used in the long-term tests, show this more or less immediate activity on the introduction of a visitor, six separate tests were conducted after the main series of aggression experiments. When single noveboracensis visitors were added to a series of long established lone resident noveboracensis, in every case the lone resident was active soon after the introduction of the visitor. Thus it seems that single mice would react to a visitor in much the same way as would groups of mice. It is also interesting to note that in both the long- and the short-term experiments females tended to be dominant over males.

Horner (1947) found gracilis usually tolerant of one another, and Blair (1942) found that, while gracilis home ranges usually overlapped, those of noveboracensis usually did not. These findings are in agreement with the results of the long-term aggression experiment which indicated that gracilis was more tolerant of its own species than was noveboracensis of its own species. There are important ecological implications in the observations made in these experiments.

Christian (1956), Chitty (1952), Clarke (1953), and Louch (1956) have forwarded and tested the theory that the hormonal balance, particularly the adrenopituitary balance, is disturbed in mammals as a result of crowding. Any balanced population is always on the edge of being crowded, crowding being defined as that density of a population which is greater than would exist under conditions of equilibrium. When the hormone balance of the individuals of the crowded population is disturbed, two things happen. First, the fecundity usually drops; second, the individuals are more susceptible to additional stress in the forms of disease, predation, adverse climate, and so on.

Clarke (1953) found that if a vole was introduced to a cage with two established voles for a total of 20 hours spread over ten days, the increase in weight of the adrenals and pituitary was much greater than if the 20 hours were spread over a shorter time. Louch (1956) found that this adrenopituitary response was linked to the amount of fighting that took place. It is reasonable to suppose that those situations which caused more fighting in the aggression experiments would lead to greater adrenopituitary response, and hence to greater susceptibility to additional stress.

This process acts as a controlling mechanism on the population density; as the population increases, so do the forces which tend to reduce it increase. The adrenopituitary response is a density-dependent factor. The present results suggest that for the same response to take place, fewer contacts between noveboracensis individuals would be required than between

gracilis individuals. Furthermore, in a mixed population, the adrenopituitary balance of noveboracensis would probably be upset at a lower density than would the balance of gracilis.

In other words, all other things being equal, it is likely that noveboracensis would not form as dense populations either by itself or in mixed populations as would gracilis under these circumstances.

LARGE CAGE EXPERIMENT

Introduction

In certain areas where the overall ranges of P. m. gracilis and P. l. noveboracensis overlap according to Hall and Kelson's (1959) distribution maps (see Fig. 1), field trapping records show that in fact only one species is found. The vicinity of Ottawa south of the Ottawa River is such an area, for although it is in the zone of overlap of the two species, P. l. noveboracensis is common and widespread, and P. m. gracilis is rare or absent. Carleton University's Rideau River campus and its immediate environs are typical of the Ottawa region in that the considerable amount of trapping carried out by various students since 1959 has resulted in the capture of many noveboracensis and no gracilis.^{*} In a mixed hardwood forest on a slope on the south bank of the Rideau River (Fig. 4) near the campus, trapping was conducted for two nights in January 1963 using a total of 40 live traps. All 15 mice caught were P. l. noveboracensis. These findings suggest that the campus area in general and this wood in particular are more suitable for noveboracensis than for gracilis, and that gracilis cannot effectively compete for the space available.

The reasons for this particular area not being suitable for gracilis are probably numerous. Whereas a few specimens of gracilis were caught in the general area in the early 1950's,^{*} it seems that this species has now been entirely

^{*}Personal communications from D. A. Smith.

Fig. 4. A view of the wood near the Carleton University campus, from which 15 P. l. noveboracensis were trapped and leaf litter collected for the Large Cage experiment.

replaced by noveboracensis. It seems unlikely that the abundance of noveboracensis can be accounted for by such variable factors as temperature, humidity, cover, drainage and so on. The annual variation found with these factors greatly exceeds that between different localities favoured by each species. More constant features of the environment, such as soil type, vegetation or available food, seem more likely to govern this distribution.

Although several authors, for example Hamilton (1941), have found no differences between the natural food habits of the two species, I attempted to determine whether either or both species could locate and eat sufficient food from the leaf litter from the forest in which I believe that ^{only} P. l. noveboracensis lives.

Materials and methods

For this experiment an area larger than that of the ordinary laboratory cages was made available to the animals. A large cage built in the inner compartment of the animal room was 6 ft. long x 4 ft. 9 in. wide x 4 ft. high, and had a door at one end to allow the experimenter to enter. It was constructed by covering an angle-iron frame with $\frac{1}{4}$ " mesh hardware cloth. The cage rested directly on the floor which was covered with about two inches of topsoil from the forest previously mentioned. The large size of the cage was important in that the large floor area allowed a quantity of leaf litter sufficient to supply some food to be given to the animals; furthermore, as Richter (1927) pointed out, animals in large cages are more likely to behave normally than animals in smaller

cages.

The lighting schedule was arranged to give approximately the same daylength as that found outside. The cage was illuminated by three 100-watt lamps about six feet above the floor, giving about 120 lux at ground level. An extractor fan in the upper part of the wall of the compartment operated while the lamps were on so that their heat did not cause an increase in temperature. The lights were normally turned off at 4 p.m., and the activity of the mice observed for an hour or so thereafter, using a 40 watt photographic darkroom red lamp.

The immediate aims of this experiment were to compare the abilities of mice of the two species to survive and the amounts of weight lost when they were subjected to two different systems of food supply. Their weight losses were presumed to be inversely proportional to the amounts of food obtained under each system of feedings. In the first system (tests 1-5), leaf litter from the forest from which P. l. noveboracensis had been trapped was given in measured amounts to the mice; in the second system (tests 6-10) weighed amounts of laboratory chow and seeds of the milkweed (Asclepias syriaca L) were given to them. All mice used in tests 6-10 were accustomed to eating both of these foods.

In each test one P. m. gracilis and one P. l. noveboracensis occupied the large cage simultaneously. In the tests using the leaf litter, the noveboracensis used were individuals trapped in the wood in January 1963, four months before these tests were carried out. Each test was continued

for three or four days, or until one mouse died. Each test involved different mice, and five tests of each feeding system were carried out; in this way a total of twenty different mice, consisting of ten males of each species, was tested.

The mice were weighed before being introduced to the cage and in the morning of most days thereafter. In the first series of tests (1-5) it was not always possible to catch the mice without a great deal of disturbance, so the records are incomplete. Weights were recorded until the end of the test, or until a natural death showing no cannibalism, or until the day before one mouse was eaten by another.

For tests 1 to 5, two rotting logs about three feet long and about nine inches across were placed on the soil on the cage floor. For each test a new sample of leaf litter was collected in a random manner from a total of about ten square feet of forest floor. In one container was put the upper coarse matter of the leaf litter - large twigs, leaves, etc., while in a second container was put the finer material (duff), and the top quarter inch of compact humic material. The floor of the wood was simulated in the cage by spreading the coarse over the fine litter (Figs. 5-8). At the end of each test, the used litter was removed and the cage cleaned. Water was supplied in a bowl at all times.

In each of tests 6 to 10, five grams of laboratory chow broken into lumps about the size of a pea, and five grams of milkweed seeds were put on the soil surface and covered with

Fig. 5. Showing the bare topsoil and rotting logs in the large cage, prior to putting in the leaf litter for tests 1-5 in the Large Cage experiment.

Fig. 6. Showing the layer of fine litter (duff) added to the bare earth floor shown in Fig. 5.

Fig. 7. Showing the layer of coarser leaf litter added to the layer of duff shown in Fig. 6.

Fig. 8. A general view of the cage as set up for tests 1-5 in the Large Cage experiment.

a thin layer of wood chips. Water was supplied in a bowl. Four cans were supplied for nesting purposes. The cage was cleaned after each test.

Apart from the observations made on the weights of the mice, the mice were watched during the first one or two hours of darkness each night for any signs of dominance. An animal was supposed to have dominated over its partner if it chased, attacked, or appeared to prevent it from moving to any part of the cage.

Results

In order to eliminate variations between the original weights of individuals of the same species and thus to obtain comparable figures, the weight of any mouse on day n was expressed in terms of the average weight for its species at the start of the experiment, using the following formula:

$$\text{corrected weight} = \frac{\text{observed wt. on day } n}{\text{observed wt. on day } 0} \times \text{mean wt. for species on day } 0.$$

The observed and corrected weights for all mice are shown in Appendix II. Fig. 9 shows the average corrected weights for each species on successive days. Each point represents the average weight of five mice.

Fig. 9 suggests that the relative rates of loss of weight of each species are very slightly different under the two conditions. When food was supplied in the form of laboratory chow and milkweed seeds in tests 6-10, the two species

Fig. 9. Changes in average body weights of P. m. gracilis and P. l. noveboracensis with two different diets. In tests 1-5 the food was "natural", and in tests 6-10 the food was animal chow and milkweed seeds (see text page 66). Each point represents the average of five individuals tested.

lost weight at slightly different rates over the full three days of the tests. After one day both had lost about the same weight, but after two days gracilis on the average lost less weight than did noveboracensis. On the third day mice of both species again lost weight at similar rates. Over the three days of the tests, the originally slightly heavier noveboracensis lost more weight than did gracilis.

The upper curves in Fig. 9 represent the weights of mice of the two species with leaf litter as a food source (tests 1-5); these two curves are also very slightly different. They are both fairly smooth curves showing a greater loss of weight on the first day than on the last. Although originally the mean weights of the two forms were almost the same, the overall loss of weight of noveboracensis was slightly less than it is for gracilis.

Discussion

Although these data are too few and the apparent interspecific differences too slight for one to do more than to speculate on them, the tentative conclusions emerging are interesting and if supported by further experimental results may be of some ecological importance. The fact that an attempt was made to simulate the natural environment tends to give more weight to the results.

They suggest that gracilis was able to find more food than could noveboracensis when the food was a limited supply of laboratory chow and milkweed seeds. When indivi-

duals of the two species were forced to find natural food in the leaf litter of the forest normally supporting a population of noveboracensis only, however, gracilis appeared to be at a slight disadvantage and lost weight at a greater rate than did noveboracensis.

Some of the other experiments to be described help to shed light on these different reactions by the two species. A simple situation such as was presented to the mice here may well give results that are inapplicable to the field situation, but it is at least reasonable to suggest as a result of these findings that P. m. gracilis cannot compete successfully with P. l. noveboracensis in this particular forest, and that this slight advantage of the one species over the other in food-finding may be responsible for the fact that a single-species population exists there.

STARVATION EXPERIMENT

Introduction and methods

A difference in reaction to lack of food by these two species might possibly provide some key to the problem being considered. At certain times of the year, especially in late winter, food may be scarce, and it is likely that at this time a great many deaths occur. One factor influencing which species can inhabit a given area could possibly be a differential ability to survive this period of food shortage.

To compare the response of mice of the two species to complete absence of food, a series of five consecutive tests was run, each test examining the reaction of one female gracilis and one female noveboracensis to total deprivation of food in isolation. Tests with one individual of each species were run concurrently to reduce the possibility of results being affected by temperature variations. Each mouse was housed in a large standard laboratory cage containing wood chips, a can for nesting, and water. A test lasted three days or until the mouse died. The mice were weighed at the start of each test and daily thereafter at the same time of day.

Results and discussion

The daily weights of each mouse and corrected weights, calculated in the same way as in the "Large Cage Experiment" are shown in Appendix III. The average corrected daily weight

losses for the two species are shown in Fig. 10, which indicates that under conditions of total food deprivation the rates of weight losses of the two species are similar.

Although the data are too few to be conclusive, they suggest that neither species has any advantage over the other at times of great food shortage - most likely to occur in late winter. Nevertheless, even if any significant interspecific difference in reaction to starvation did show up in a laboratory experiment of this sort, it would not follow that this difference would also occur under normal field conditions.

Fig. 10. Average corrected daily weights of five individuals of each of the two species under conditions of total starvation. (On day 3 only one mouse of each species was still being tested).

ACTIVITY EXPERIMENT

Introduction

Many workers (Behney, 1936; Blair, 1951; Dice and Hoslett, 1950; French, 1956; Hatfield, 1938, 1940; Johnson, 1926, 1939; Orr, 1959; Rawson, 1960; Stinson, 1960) have studied various aspects of the locomotor activity of one or several species of Peromyscus under a variety of laboratory and field conditions and using various kinds of apparatus and techniques. The consensus is that as far as is known, all species of Peromyscus are nocturnal. Although a few comparative studies have been made, the activity of P. l. noveboracensis and P. m. gracilis has never been studied on a comparative basis. As the relative temporal patterns and amounts of activity of different species may be important in characterizing them ecologically or at least in reducing competition between them, a preliminary comparative study of these aspects of locomotor activity was initiated.

Methods

Standard Wahmann revolving activity cages (LC - 34) were used throughout the experiment. These have a cage (size 10 in. x 6 in. x $5\frac{1}{2}$ in. high) in direct communication with a revolving drum 14 in. in diameter and $4\frac{1}{2}$ in. wide. This drum rotates freely about its horizontal axis, and each revolution is counted on a crank-operated counter capable of counting up

to 99999 revolutions. In the cage, food was placed in a bowl, water was supplied, and a small can was fixed to one side for nesting purposes. The activity cage unit is shown in Fig. 11.

Two types of experiment were carried out. In the first type a weighed quantity of food and either one or two mice of the same species were placed in each cage for from three to twelve days, and the daily numbers of revolutions per cage were determined from the mechanical counters. So far as possible, tests were run with two cages containing the two species simultaneously so that both species were equally exposed to variations in external factors. The pairs of mice were male and female together, two males, or two females; details are shown in Tables XIX and XX. The tests were started on March 21, and ended on August 20; a total of 41 mice were tested, including 22 noveboracensis and 19 gracilis. Eight noveboracensis and seven gracilis were tested singly, and seven noveboracensis pairs and six gracilis pairs were tested. At the end of each approximately 10-day run, the weight of food left and the weight of droppings deposited were recorded. A plan of the dropping pan recording the locations and weight of droppings and ground-up food was made at the end of each test. Rather discrete areas of droppings and food powder were usually observed and presumably presented a record of the chief feeding areas and zones of defaecation.

Certain criticisms can be levelled against activity tests of this kind. First, certain active individuals may

Fig. 11. Top view of the activity cage unit used in the Activity Experiment. The cage contains a nest-can and animal chow. A water bottle is at the right.

never learn to run in the revolving drum, and it is difficult to distinguish such mice from inactive ones. Second, when a mouse is watched in the cage, it is sometimes observed that a common way of turning the drum is for the mouse to run hard at the bottom of the drum until it is spinning, and then "ride the drum": the mouse merely goes around and around, sometimes for as many as ten or fifteen turns. The mouse has contributed the energy to start the drum spinning, however, and the manner in which this energy is used seems immaterial. Third, it is more difficult for a small mouse to start the drum turning than for a large mouse, and consequently a small mouse may put on fewer turns. On the other hand, a smaller mouse also finds it harder to stop the drum, for it seemed from observation that it was not the habit of mice to start the drum turning and then leave it for the cage, with the drum still turning. Because of this, the number of turns put on by mice of different weights might not be expected to differ greatly. Finally, different drums run with varying degrees of friction at their axles. To counteract this, each cage unit was used equally by each species.

In the second type of experiment, a single mouse was placed in an activity cage connected to a continuously operating activity-recording device. A total of ten tests were run, using six gracilis and four noveboracensis that had at least seven days previous experience in an activity cage.

The apparatus used is shown in Fig. 12. The

Fig. 12. Diagrammatic representation of the apparatus used in obtaining 24-hr. records of activity.

turning motion of the drum is geared down by a ratio of 6:1, and once every six revolutions of the drum a microswitch is actuated. This activates an electromagnetic lever which makes a mark about one inch from the periphery of a smoked paper record sheet, 20 inches in diameter. The record sheet revolves once every 24 hours, so that a circular record is produced with spikes representing periods of activity. The record thus produced does not, however, give an exact indication of the actual amount of activity - only the times when activity is greatest. Thus a mouse putting on, say, 100 turns of the drum in a short time will cause to be made what will seemlike one spike on the record - the same as a mouse putting on only six turns.

Normally each mouse was left in the activity cage for only two days, the record being made on the second day. The number of revolutions during the recording day was determined from readings of the mechanical counter. The record was made permanent by means of a clear lacquer spray from a pressure can.

Results

The results for the first type of activity experiment for single mice will be followed by those for pairs of mice and finally by those of the second type where times of activity were also recorded.

Tables XVII and XVIII contain the daily records of the number of revolutions per single mouse during the long-term activity experiments. As it was not always possible to take daily readings of the counters, average values per day were calculated from the total number of revolutions recorded in the days between readings and these mean values are given in parentheses.

A Wilcoxon two-sample test run on the known daily turns reveals a probability approaching 100% that the daily amounts of activity of the two species are the same (Snedecor, 1959). There are not sufficient data to show any difference between the amounts of activity of males and of females.

Tables XVII and XVIII also show the weights of food consumed and of droppings produced per day. The averages for the two species are nearly the same. There seems to be no relationship between either the amount of food consumed or the amount of droppings produced and the number of revolutions. The numerical index which results when the amount of food consumed is divided by the amount of droppings produced is intended to give a measure of food utilization. Again, no relation seems to exist between this index and the number of revolutions in each test; nor is there any significant difference between the values for the two species.

Dice and Hoslett (1950) found that the number of turns increased daily up to about the sixth day in P. m. bairdii and P. l. noveboracensis. In order to see if the

TABLE XVII
AMOUNT OF ACTIVITY AND FOOD CONSUMPTION OF
SINGLE GRACILIS IN ACTIVITY CAGES

Test	Number of revolutions per 24 hrs.							Mean of all tests
	1	2	3	4	5	6	7	
Sex	♀	♂	♀	♂	♂	♀	♂	
Day 1	3027	1211	2909	688	4351	12552	1183	
2	6538	887	1054	430	2262	13305	1923	
3	1638	761	1031	(271)	10175	28531	583	
4	(11130)	112	1855	(271)	17470	3169		
5	(11130)		1372	(271)	(21014)	32638		
6	18829		(982)	300	(21014)	29419		
7	22987		(982)	102	(21014)(28400)			
8	23663		(982)		(21014)(28400)			
9	24360				(21014)			
10	28451				18434			
11	(21320)							
12	(21320)							
Mean no. of turns per day ± S.E.	16199 ± 2880	743 ± 460	1396 ± 683	333 ± 183	15776 ± 9500	25610 ± 10700	1229 ± 995	11101 ± 10800
Mean wt. in gms. of food consumed/day	3.79	3.33	2.90	3.31	3.75	4.50	6.17	3.96
Mean wt. in gms. of faeces produced/day	1.0	1.22	0.75	0.85	1.05	0.93	1.33	1.01
Food Consumed Faeces produced	3.79	2.73	3.86	3.90	3.57	4.84	4.63	3.99

Note: figures in brackets are average numbers for the period concerned.

TABLE XVIII
AMOUNT OF ACTIVITY AND FOOD CONSUMPTION OF SINGLE
NOVEBORACENSIS IN ACTIVITY CAGES

Number of revolutions per 24 hrs.									
Test	1	2	3	4	5	6	7	8	Mean of all tests
Sex	♀	♂	♂	♂	♀	♀	♂	♂	
Day 1	1356	11769	1334	5318	11309	1033	1033	10051	
2	1065	11746	10278	1200	8362	15343	502	5784	
3	620	12757	13160	(1379)	5327	19619	13586	13437	
4	(471)	13116	13568	(1379)	4488	18895	18911	10120	
5	(471)	12010	13955	(1379)		25041	17860	16835	
6	437	(12133)	(10943)	643		7209	(19050)	(16934)	
7	2094	(12133)	(10943)	708		(18121)	(19050)	(16934)	
8	831		(10943)			(18121)	19875		
9	390								
10	737								
11	(4701)								
12	(4701)								
Mean no. of revs per day ± S.E.	1489 ± 490	12237 ± 410	11529 ± 1730	1146 ± 1030	5873 ± 1630	16700 ± 5480	13850 ± 8250	13460 ± 436	9355 ± 7680
Mean wt. in gms. of food consumed/day	2.83	4.66	4.08	3.64	2.50	3.16	4.75	5.50	3.89
Mean wt. in gms. of faeces produced/day	0.99	1.50	1.13	1.14	1.00	0.75	1.18	1.25	1.11
Food Consumed Faeces produced	2.84	3.12	3.61	3.19	2.50	4.21	4.06	4.40	3.50

Note: Figures in brackets are average numbers for the period concerned.

same pattern were followed in these tests, the figures in Tables XVII and XVIII were analyzed, and the average daily numbers of revolutions were used as well as the known daily numbers of revolutions. The figures for each species were subjected to a standard correlation test, and no valid relationship was found between the day of the test and the number of turns on each day. The lack of correlation was probably due to the high degree of variability of the observations.

Tables XIX and XX show the number of turns per day in each of the seven tests with two mice per activity cage and also the data on food consumption and dropping production per mouse. As in the similar tests with single mice no valid relationships could be shown between the day and the number of revolutions recorded that day.

A Wilcoxon two-sample test run on only the known daily numbers of revolutions revealed a probability of almost 100% that the two species are the same in this respect. No species differences were found regarding food consumption, dropping production, or ratio of food:droppings. Nor does there seem to be any relationship between these data and the amount of activity.

When the data for single mice and pairs of mice are compared, the daily average number of revolutions is rather similar in all cases. The food consumption values per mouse per day are similar as are the numbers of droppings produced and the ratio of food:droppings. It thus seems that the two

TABLE XIX
AMOUNT OF ACTIVITY AND FOOD CONSUMPTION OF PAIRS OF
GRACILIS IN ACTIVITY CAGES

Test Sex	Number of revolutions per 24 hours						Mean of all tests
	1	2	3	4	5	6	
Day: 1	♂ 10072	(8263)	♂ 9803	♀ 4010	♂ 3735	♀ 12483	
2	(15319)	(8263)	14662	3566	1301	5605	
3	(15319)	(8263)	(12725)	5791	1235	14814	
4	13909	6123	(12725)	6309	936	20026	
5	18907	9640	9318	6559	798	20975	
6	24529	9150	14821	(4852)	917	18991	
7	21449	7250	16514	(4852)	1315	16775	
8	(19800)	15269	(13475)	5935			
9	(19800)	(15439)	(13475)	7034			
10	(19800)	(15439)	(13475)	7182			
11	18401	13164	(13475)	9243			
Mean no. of revs. per day $\pm$ S.E.	17144 $\pm$ 3870	10958 $\pm$ 3740	13130 $\pm$ 2070	5890 $\pm$ 1610	1490 $\pm$ 330	15667 $\pm$ 5100	11303 $\pm$ 5190
Mean wt. in gms. of food consumed /day/mouse	4.08	2.13	4.11	2.82	1.93	3.00	3.01
Mean wt. in gms. of faeces produced /day/mouse	-	1.37	1.27	0.95	0.46	0.60	0.93
Food consumed faeces produced	-	1.70	3.54	3.25	4.15	4.90	3.24

Note: figures in brackets are average numbers for the period concerned.

TABLE XX

AMOUNT OF ACTIVITY AND FOOD CONSUMPTION OF PAIRS
OF NOVEBORACENSIS IN ACTIVITY CAGES

Test Sex	Number of revolutions per 24 hrs.							Mean of all tests
	1	2	3	4	5	6	7	
Day: 1	♂	♀	♂	♀	♂	♀	♂	
2	(3702)	(3761)	1241	5076	9472	10493	1513	
3	(3702)	(3761)	(4587)	5945	12250	13668	9149	
4	3229	4842	(4587)	2764	12890	14100	11534	
5	2179	6421	3329	5730	14294	16256	13989	
6	2500	6651	10002	(4877)	12195	13791	11847	
7	2184	9251	13073	(4877)	11937	13531	11782	
8	(2333)	4637	(18224)	2396				
9	(2333)	(8989)	(18224)	3067				
10	(2333)	(8989)	(18224)	6262				
11	1850	4876	(18224)	11992				
Mean no. of revs. per day $\pm$ S.E.	2419 $\pm$ 660	5995 $\pm$ 2190	10528 $\pm$ 6860	5032 $\pm$ 2700	11666 $\pm$ 1900	14334 $\pm$ 1680	9470 $\pm$ 4240	7914 $\pm$ 4470
Mean wt. of food in gms. consumed /day/mouse	4.00	2.49	2.75	3.23	2.60	3.00	3.86	3.13
Mean wt. of faeces in gms. produced /day/mouse	-	-	0.90	1.20	0.71	0.82	1.00	0.92
Food consumed faeces produced	-	-	3.36	2.95	3.70	3.65	3.86	3.40

Note: figures in brackets are average numbers for the period concerned.

forms of Peromyscus are quite similar in most of the respects measured under these conditions.

Three other observations have been made as a result of these experiments. First, the striking difference between the total amount of activity of two noveboracensis and that of two gracilis in the first test (29,021 and 205,739 respectively), coupled with a very similar food consumption (4.0 and 4.08 grams/mouse per day, respectively) led me to wonder whether the two species had different efficiencies of food absorption in the gut. Water-soluble and acetone-soluble components of the droppings of the two species were measured accurately, but no differences could be detected. The droppings of both species contained 1% acetone-soluble material and about 10% water-soluble components.

Second, it was noticed on many occasions that the faeces of noveboracensis were smaller than those of gracilis. The number of individual faecal pellets in two one-gram samples of the droppings of gracilis were 88 and 97, and samples of identical weight from noveboracensis contained 139 and 181 pellets. Apparently this difference has never before been noticed; this information could be very useful in field studies of these forms in areas of sympatry.

Third, it was noted that the average numbers of revolutions per day for single mice and for pairs of mice were not very different. The mice were rarely seen to run "in tandem", and one would have expected almost twice as many

revolutions to be put up by the pair of mice. I can offer no explanation for this apparent anomaly.

The plans of the locations of droppings and ground-up food on the dropping trays showed no distinct trends. However, examination of the food bins showed that the food remained clean in every case with gracilis; out of a total of fourteen observations of noveboracensis, the food bin was dirty in eleven cases --- the food was caked with urine and droppings. Also, the amount of food powder found on the trays showed a distinct difference between the species. P. m. gracilis left no food powder on the tray in five out of 12 occasions, and on the average left 0.6 gm. per test; noveboracensis left no ground-up food on only two out of fourteen occasions, and left an average of 3.8 gm. per test.

Figs. 13 and 14 show diagrammatic representations of the activity patterns over 24 hrs. of 6 gracilis and 4 noveboracensis. These few records show that there is great variation within each species, and suggest that the variation within each species is greater than the variation between the species.

Discussion

The results of the several parts of this preliminary activity experiment suggest that there is no significant difference between the amount of activity of the two species in activity cages. Furthermore, both species seem to be largely

Fig. 13. Showing activity patterns in 24-hour records of running in revolving activity cages by six *P. m. gracilis*. The record revolved in an anticlockwise direction. Each mark at the periphery represents a period of activity and does not record any particular number of revolutions.

Fig. 14. Showing activity patterns in 24-hour records of running in revolving activity cages by four *P. l. noveboracensis*. See paction for Fig. 13 for details.

nocturnal, and they seem to consume food at about the same rate.

These suggested similarities are interesting, but not completely unexpected. Any great differences that might have shown up in the amount or time of activity, or of food consumption could have been most important in explaining the nature of the apparent sympatry of the two species. As it is, with these possibilities at least weakened by these preliminary findings, other aspects of the ecology or behaviour of the two species will have to be considered in trying to explain their apparent sympatry.

The fact that these tests did not show any progressive increase in the daily number of turns such as Dice and Hoslett (1950) found may be explained by the fact that in their tests the nest-cages attached to the drums were much larger than the cages used in the present tests. Their mice would not, presumably, then have been forced to be active in the drums but could have been active in the larger cages until they became accustomed to the drums.

RUNNING AND MAZE EXPERIMENTS

Introduction

After a number of individuals of each species have been handled, it becomes evident that the two species are different in temperament. P.m. gracilis is much easier to handle; they are easier to remove from the cage, and if they escape while being handled are easy to retrieve. In the hand, however, while being held by the tail they are aggressive - that is, they bite and struggle. P. l. noveboracensis, on the other hand, is very difficult to handle. When the door of a cage containing noveboracensis is opened, any mice not in the nesting can will almost invariably leap from the cage. The quick reactions of an escaped individual of this species make it very hard to recapture. Typically, it remains in a corner until the experimenter is almost upon it, then it dashes to another corner where it "freezes" again. While being held by the tail in the hand, however, it is usually quite still and easy to deal with.

Other workers have noticed similar types of behaviour. Cahalane (1954) describes P. l. noveboracensis as a "perpetually irascible species". Hamilton (1928) kept some individuals of noveboracensis on top of a high building, and sometimes one would leap from the edge of the roof and fall 50 feet without being hurt. Layne and Benton (1954) found that over a distance of twenty-five feet, two noveboracensis

ran an average of 8.4 ft/sec, while two gracilis ran at 6.4 ft/sec.

As it would be useful to show, in an objective manner, two different yet related aspects of the behaviour of these two forms - the speed of running away from the observer over a short distance, and the exploratory reaction to a new environment, two experiments, here termed the Running Experiment and the Maze Experiment, were performed.

RUNNING EXPERIMENT

Methods and procedure

A short tube, semi-circular in section, forty-two inches long with a diameter of four and a half inches, and constructed of clear cellulose sheet was put on a table top in a well-lighted room. At one end of it was a modified Sherman live trap (see Fig. 15). The mouse to be tested was released from the hand at the end away from the live trap, and the time taken to enter the trap was recorded on a stopwatch. Each mouse ran three times consecutively, and a total of eleven noveboracensis and sixteen gracilis were run. Roughly equal numbers of males and females were used. The noveboracensis were divided into two groups called 2 and 4, and the gracilis were divided into three groups called 1, 3, and 5. The groups were run in the tube in the order 1 to 5, and the tube was cleaned between runs. Two days later, the whole sequence was repeated giving a total of 162 readings.

Fig. 15. Showing the tube and live-trap used in the Running Experiment.

Results

Almost every noveboracensis ran to the trap without stopping. In contrast, the gracilis rarely did this; instead they generally walked slowly, sniffing at the table top, the tube, the joins in the tube and so on as they went. On five occasions gracilis individuals had not reached the trap after one minute, as they retraced their steps, performed their "face-washing" motions and so on. At this time, these mice were removed from the tube.

Fig. 16 shows the time of each run of each individual. Excluding all times over one minute, the average time for gracilis was 15.7 seconds, and for noveboracensis was 2.58 seconds. The Wilcoxon two-sample (non-parametric) test (Snedecor, 1959) gave a value of $K = 12.48$ ($p = < 0.01$). Thus even when the very slow trips by gracilis were excluded, this form covered the distance very significantly more slowly than did noveboracensis.

MAZE EXPERIMENT

Methods and Procedure

A simple maze was constructed of Ten-test (see Fig. 17). Each of the three compartments in the maze was 12" by 12" with walls 6" high. Each of the three doors was one and a half inches wide and two inches high. The maze was covered with a removable lid of hardware cloth, which

Fig. 16. Time in seconds for each mouse of the two species to enter the trap in the Running Experiment. Each mouse was tested on two different days. The symbol indicates that at one test the mouse had not entered the trap at the end of one minute.

Fig. 16. (cont).

Fig. 17. Diagram of the maze used.

reduced the light level in the maze little below that of the well-lighted room.

As a roughly quantitative measure of the exploratory behaviour of an individual mouse, I recorded how long it took to enter all three compartments completely after it had been put into the maze at door A. The criterion of complete entry was the passing of the whole mouse, including the tip of the tail, through the door. Each mouse was tested only once, and if fewer than three compartments had been entered by the end of five minutes, the experiment was terminated.

Twenty-one gracilis and twenty noveboracensis were tested.

Results

Fig. 18 shows that P.m. gracilis enters all three compartments much more readily than does P. l. noveboracensis. Of the twenty noveboracensis tested, nine did not enter the three compartments within the five minutes; most of these nine remained quite still in one compartment.

The figures were analyzed using the Wilcoxon two-sample test; this gave a value of $K = 4.69$, ($p = < 0.01$). Thus gracilis is significantly more exploratory than is noveboracensis, in a new situation.

Fig. 18. Times of the individuals of both species to enter all three compartments of the maze, arranged in order of increasing time.

Discussion

The results of the Running and Maze experiments show in an objective manner two striking differences in the behaviour of the two species. In fact most individuals can be identified as to species by means of these and related behavioural characteristics. It has been noted above that P. m. gracilis is much easier to handle than P. l. noveboracensis, for noveboracensis is much given to rapid, darting movements which result in leaps from cages and off table tops, and dashes into dark corners. This particular behavioural pattern has been clearly confirmed by the results of the running experiment, and should be contrasted with the more leisurely walk of P. m. gracilis.

If a noveboracensis individual is put into a new cage, it generally "freezes" on the sides of the cage, whereas a gracilis individual generally moves around the cage in a more leisurely manner. If the individuals of an established cage of noveboracensis are put into a large beaker, all the mice huddle tightly in the bottom of it (see Fig. 19); in the same circumstances, the individuals of a group of gracilis would rapidly climb out (see Fig. 20). This points to the same conclusion as that drawn from the maze experiment. These various aspects of behaviour are further shown in Figs. 21 to 24. Fig. 21 shows the typical investigating attitude of P. m. gracilis in a new environmental situation (a table top); Fig. 22 is a high-speed photograph (1/1000 sec.)

Fig. 19. Showing the typical behaviour of P. l. noveboracensis when several individuals are placed together in a beaker; note how they huddle in the bottom of the beaker.

Fig. 20. Showing the typical behaviour of *P. m. gracilis* when several individuals are placed together in a beaker; they immediately start to climb out.

Fig. 21. Showing the typical behaviour of P. m. gracilis when placed on a table top. It walks along poking its nose at every crevice and object.

Fig. 22. Showing the typical behaviour of P. l. noveboracensis when placed on a table top; this photograph, taken at 1/1000 sec., shows a mouse running rapidly along the bench.

showing a P. l. noveboracensis running rapidly in the same situation. Fig. 23 shows the typical inquisitive behaviour of a gracilis when its cage door is opened; Fig. 24 shows the very different, but again typical, behaviour of noveboracensis under the same circumstances. This latter subspecies typically would "freeze" on the walls of its cage.

Because of these different types of behaviour, in practice each species needed to be handled differently. To remove a gracilis individual from a cage was a simple matter of opening a cage door and waiting for one to emerge from the nesting can to investigate. The mice were easily picked up by the tail, and transferred to a gloved hand. P. l. noveboracensis in a cage needed different handling. If the mice were in the can, they would not usually come out, and could be picked out of the can one by one. If, however, the mice were not in the can, care had to be exercised to prevent the mice from leaping out of the cage. No difficulty was experienced if a mouse was approached slowly, and the tail grasped between the fingers.

These behavioural patterns have ecological implications, but the situation is rather confused. The rapid, darting movement of noveboracensis would seem to be suited to an open type of habitat, and indeed the behaviour of noveboracensis in this respect is very similar to that of P. m. bairdii, the prairie deer mouse, as described by Dice and Clarke (1962), Foster (1959), and Horner (1954).

Fig. 23. Showing the typical behaviour of P. m. gracilis when the door of their cage is opened; note how it is peering in an "interested" way out of the nest-can.

Fig. 24. Showing the typical behaviour of P. l. noveboracensis when the door of their cage is opened; note how they "freeze" on the walls of the cage.

Foster and Horner both suggest that the freezing and rapid movements of P. m. bairdii are adaptations to the open type of habitat that this form favours. It would further seem reasonable that more steady movements would be more suitable for a tree-living species, and thus the type of behaviour so characteristic of noveboracensis would render it unsuitable for tree living. Furthermore, Horner (1954) found that deer-mice with shorter tails are generally not so arboreal in habitat as deer-mice with long tails. P. l. noveboracensis tends to have a shorter tail than P. m. gracilis, and thus seems by this criterion to be again less arboreal.

Alongside these observations, other workers have contradictory information. Jackson (1953) and Nicholson (1941) found that noveboracensis nested entirely in boxes on trees, ignoring those put on the ground in woodland and open areas. Furthermore a great number of ~~references~~ fully listed in my Introduction shows that noveboracensis is largely a woodland form.

While a full discussion of the implications of these two experiments must be left until the general discussion, one further piece of work should be mentioned because it gives an indication of the ecological value of the behaviour of noveboracensis. Pearson and Pearson (1947) found noveboracensis to be very common beneath owl roosts; and yet, in a six-week study not one owl pellet was found to contain the bones of this species. This result is not wholly surprising, for the

behaviour of noveboracensis seems to be such that aerial predation would be made difficult. Frequently I followed with the eye a noveboracensis dashing across the floor, and often not finding it where it was expected to be, found it only part of the way to the anticipated point. A rapid movement that stops suddenly is very deceiving to the eye; it constitutes effectual evasive action at least under certain circumstances.

SWIMMING EXPERIMENT

The occupation of certain areas of land subject to spring flooding, and the colonization of islands by mammals could depend to some extent on the ability of these animals to swim. When a test was carried out on the swimming abilities of the two species, it was noticed that the fur of the gracilis seemed to get much wetter than that of the noveboracensis.

Since different water repellancy of the furs of the two species could be important in deciding habitat choice in certain areas, it was decided to carry out an objective study of this. Fifteen P. m. gracilis and sixteen P. l. noveboracensis, more or less equally divided as to sex, were tested individually by leaving each for two minutes in a 2 ft. x 3 ft. tank containing four inches of water at 20°C. Each mouse was weighed before the test. The mouse was removed from the water, and excess water was allowed to drip from it for five seconds; then the mouse was weighed again.

Results

The weights before and after swimming, increase in weight in grams, and the percentage increase in weight for each mouse is recorded in Appendix V. Fig. 25 compares the increase in weight with the pre-swim weight for each individual. The mean increase in weight for gracilis was

Fig. 25. The relationship between the pre-swim weight and the increase in weight after swimming of the two species.

12.9% of its weight before swimming and the corresponding mean for noveboracensis was only 7.8%. Thus gracilis picks up a great deal more water in its fur than does noveboracensis. A covariance test on the weights before swimming and weight increases gave a probability of less than 1% that the individuals tested of the two species took up dissimilar amounts of water in their fur by chance alone.

Discussion

This significant difference in uptake of water by the pelage of these two species could be important in certain areas. The colonization of islands and the crossing of rivers sometimes takes place in the summer; most of the distribution of these species probably takes place in the early summer when the new litters wander away from the home ranges of their parents. The suggested implication of this experiment is that because noveboracensis' fur takes up less water, these mice are more buoyant and thus can survive longer in water and presumably swim further than can gracilis. No data are available for gracilis but marked wild noveboracensis are known to have voluntarily swum up to 200 ft. between islands, or between islands and the mainland in Lake Opinicon, Leeds County, Ontario.* If noveboracensis is able to swim across wider stretches of water than gracilis, it may thus be able to colonize areas that gracilis cannot reach, by such summer migrations.

*Personal communication, W. Sheppe.

Certain areas are subject to spring flooding; at such a time small mammals able to swim well would seem to be able to survive better than animals not so adept at swimming. P. l. noveboracensis would seem more able to swim from one feeding area to another, and hence it would tend to have a higher probability of surviving under those circumstances than would gracilis.

GENERAL DISCUSSION

These various experiments were performed to help elucidate the problem of the apparent sympatry of Peromyscus leucopus noveboracensis and Peromyscus maniculatus gracilis. Some of the experiments, e.g., the Running and Maze Experiments, the Paired Cage Experiment, the Swimming Experiment, and the Aggression Experiment demonstrate great differences between the species. One experiment, the Large Cage Experiment, shows only a possible minor difference, while the remaining experiments - the Activity Experiment and the Starvation Experiment - demonstrate similarities between the two species.

When these results are discussed with relation to the ecology of the two species, it must be kept in mind that the conditions in the laboratory do not resemble very closely those in the field, for in the field a different set of factors is acting on the individuals. The space made available to the animals in the laboratory cages may be such as to interfere with their normal reactions. Calhoun (1952) and Richter (1927) both discuss this possibility. In the field it is the population, rather than the individual, which is the important functional unit; the population interacts with other populations and with all the variables of the environment and their interactions; no one variable acts in isolation. Bendell (1959, 1961) found an example illustrating this principle. He studied the populations of noveboracensis

on two islands of similar size and physical properties in eastern Ontario. One maintained a natural population of mice, and the other did not, nor could the second satisfactorily support an introduced population of mice. The explanation of this phenomenon involves more than a description of the two habitats, for they were similar according to Bendell's account; evidently it involves a study of the whole ecological space.

Verts (1957) working with P. m. bairdii and P. l. noveboracensis in Illinois came to a similar conclusion when trying to explain the distribution of these mice; he found the distribution unrelated to vegetation, type of ground cover and so on. Johnson (1926), working with the same two species, also in Illinois, decided that the distribution of the mice is dependent upon their relation to the whole biotic community.

Because of the complex relationship of the population to the environment, field work should always be carried out to test the validity of laboratory results. Andrewartha (1961) stresses the need for correlating laboratory and field studies.

The problem of the apparent sympatry of gracilis and noveboracensis can only be solved by taking into account all aspects of the behaviour, physiology and natural history of each of the two species as found alone and as found together. The habits of one or both species may change when

the other species is present; one species may be forced out of its preferred habitat and yet still thrive. Naturally, under suboptimal conditions the population density would tend to drop, but in fact these conditions could lead to an improvement in the physical condition of the population through more rigorous selection. Robinson (1962) found that this happened with white-tailed deer fawn populations under artificial conditions.

The Maze and Running Experiments showed that the two species reacted quite differently to strange conditions and to sudden disturbance. Observations of animals in established cages at night showed that noveboracensis individuals were just as active as gracilis individuals. It seems therefore that under familiar conditions noveboracensis does not behave as it did in the maze; it is only under strange conditions that noveboracensis exhibits its freezing attitude. Nevertheless, the darting movements of noveboracensis when suddenly disturbed aways remain.

It was suggested that these differences found in the Maze and Running Experiments might mean that noveboracensis is adapted to a less arboreal, more open type of habitat than gracilis. But in fact noveboracensis is not found commonly in open areas. The Maze experiment showed that gracilis is a more exploratory animal, and it might be supposed that it is more active than noveboracensis. But in the activity experiment the two species show more or less the same amounts of activity: This is in accordance with

the observations on night-time activity noted above.

If these behaviour patterns existed in the field, each species would have different advantages over the other. Because of its exploratory behaviour, gracilis would be likely to find suitable nesting places in a new area more rapidly than would noveboracensis; and yet in an area not fully explored and therefore unfamiliar, gracilis would be more likely prey for predators than would noveboracensis, because of the reaction of the latter to a new situation. The converse applies to noveboracensis: it would not be expected to find suitable nesting places in a new area as rapidly as gracilis, but at the same time it would not present such an easy prey for its predators because of its peculiar darting movements when it is alarmed. However, once noveboracensis has become fully familiar with its home range, it is suggested that it would no longer act as it does in a strange environment, but would appear to act much the same as gracilis. Nevertheless, the peculiar reaction to sudden disturbance would probably remain.

It has been noted that the behaviour of noveboracensis is similar to that of P. m. bairdii, and that this behaviour of noveboracensis which might make it less vulnerable to predators would be particularly effective against aerial predators. However, aerial predators are not normally found hunting in dense woods, and in certain areas other forms of predation are doubtless more important. P. l. noveboracensis would only be expected to have this advantage over

gracilis in areas where aerial predation is important.

One result of the Paired Cage Experiment was that the two species tended not to associate during their first encounters. This, it was suggested, could cause segregation of the species when two migrating populations, one of each species, arrived more or less simultaneously in an area suitable for both species. The Aggression Experiment seems to show that it is gracilis that causes this segregation by being more aggressive to noveboracensis.

This aggression on the part of gracilis suggests that, all other things being equal, gracilis would have an advantage over noveboracensis. However, all other things are not necessarily equal, as the Running, Maze, Large Cage, Paired Cage and Swimming Experiments show. Slobodkin (1961) suggested that if each of two sympatric species was limited by different factors, a state of equilibrium could result. A corollary is that each species has some advantage not possessed by the other species. P. m. gracilis seems to possess the advantage of being more aggressive and exploratory, and probably sometimes is more able to find food in certain areas, while noveboracensis seems to possess the advantage of being more cautious, less susceptible to certain types of predator, and is also possibly more able to find food in certain other areas.

The result of the Paired Cage Experiment which showed that noveboracensis tended to associate less with its own species than gracilis did with its own species, is further

borne out by the Aggression Experiment, which showed that noveboracensis was more aggressive to its own species than was gracilis to its own species. Noveboracensis may not therefore be able to form as dense a population as gracilis could. Having a less dense population may be an advantage to noveboracensis at certain times. When there are food shortages, due perhaps to an overlong winter, or to a drought in the summer, the noveboracensis population is less likely to "crash" than is the gracilis population.

Because of these differences, in certain areas each species may be at an advantage over the other in different respects; consequently the two may be able to coexist indefinitely.

Slobodkin (1961) has also suggested that if the environment is constantly changing, and if the cycle of change is approximately equal to the life cycle of the two species concerned, neither species will be able to dominate over the other. In the case of the two species being considered, many individuals live only one year, dying at the end of the year because of food shortage. Consequently, at the start of each year each species population will not be high enough to cause competition. Because of the greater association within species compared with that between species (discussed in the Paired Cage Experiment), the two species would remain collected in groups, and the two populations would coexist. Sometimes doubtless the population would be

such that competition could occur, but in fact the extra individuals which could cause that competition would be wandering juveniles. As Errington (1943) pointed out, these are far more likely to succumb to predators than those individuals established in home ranges. Thus the overflow would be lost. The two species seem to have similar fecundities (Coventry, 1937; Svihla, 1932), and the Starvation Experiment suggested that they were equally able to survive periods of lack of food. Consequently neither species seems to possess any advantage over the other in these respects, and under certain conditions the two species could coexist indefinitely.

CONCLUSIONS

In the Introduction the problems associated with the possible sympatry of P. m. gracilis and P. l. noveboracensis were discussed. While at the present there is little field evidence to show whether or not the two species are truly sympatric, this laboratory study of the two species has suggested certain ways in which the two species are different.

One way in which two closely related sympatric species may remain in a state of equilibrium is for each species to be controlled by, or to be able to exploit different features of the environment. In this way no one species need remain at a disadvantage with respect to the other for long enough for the second species to force the first out of the environment. Nevertheless, it is still possible for one species to keep another sympatric species at such a low population density that this second species cannot maintain itself.

Despite this restriction, it is suggested that both gracilis and noveboracensis possess advantages under different circumstances, such that a state of static sympatry could exist. Gracilis seems to be at an advantage in new environments and is more aggressive to noveboracensis than vice versa; while noveboracensis seems to have a valuable reaction to disturbance such that it may be more adapted to more heavily preyed regions, forms less dense populations which are less liable to overexploit an area, and may be able to swim greater

distances.

The possibility of the two species tending to collect in groups, as is suggested by the demonstrated greater association within species compared with that between species, could give rise to a situation wherein the two species are not truly sympatric. There would therefore be no need to invoke differences allowing the species to remain sympatric.

As a result of this study, no definite statements can be made as to what is found in the field. But suggestions can be made as to how the two species could remain sympatric, or occupy similar habitats together even if true sympatry does not then exist.

POSTSCRIPT

Whether these experimental observations are applicable in the field can only be confirmed by direct observation. It would be worth studying the behaviour of the mice in the field from a raised observation platform with red lamps illuminating the area. In this way the behaviour of marked individuals, both those accustomed to the area and those recently introduced, could be studied. If such an arrangement was put in an enclosure designed to retain small mammals, such as that described by Stains et al. (1961), the observer could be more certain of seeing the mice. In such an enclosure treadles, gates, runways, smoked paper sheets and so on could be used to determine the activity of the mice enclosed; Dice (1961) gives descriptions of apparatus useful in such a study.

Studies could also be carried out in the field to test the supposition that noveboracensis is more adept at avoiding aerial predation than is gracilis. A field experiment could be performed using captive hawks or owls; these birds could be set upon released individuals of both species, and the degree of their success in catching the two species could be compared.

Welch (1962) found that the weight of the adrenals of white-tailed deer gave an indication of population conditions. A study of this kind could be applied to deermice.

Populations of the two species could be maintained both separately and together in the enclosure described above. The adrenals of the individuals tested could be weighed giving a measure of the stress affecting the individuals. These results could be compared with the results of the Paired Cage and Aggression Experiments, and if the laboratory results were confirmed, noveboracensis would always be expected to have been subjected to greater stress than gracilis.

Either in an enclosure of this kind, or under natural conditions, the habits of the mice could be further elucidated by means of coloured foods and radioactive implants. Coloured foods have been discussed by New (1958, 1959) and by Larthe (1950). They describe dyes suitable for staining the droppings, fat and teeth of small mammals. In this way the type of food eaten, and the places visited could be established. The use of radioactive implants has been discussed by Kaye (1960) and by Johanningsmeier and Goodnight (1962). The mice can be marked and later found again by means of a Geiger-Müller counter. Daytime tracing could be carried out, thereby establishing the nesting sites of the two species.

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APPENDICES

APPENDIX I

Sample record sheet used in the
Paired-Cage Experiment.

Cage no.	In Can		Sum in can		Out of Can		Sum out of can		Sum ♂♂		Sum ♀♀		Sum by Cages
	♂	♀	a	b	♂	♀	a	b	a	b	a	b	
I	G												
II	L												
	G												
III	L												
	G												
IV	L												
	G												
V	L												
	G												
VI	L												
	G												
VII	L												
	G												
VIII	L												
	G												
IX	L												
	G												
X	L												
	G												
Sum over Cages	Σ ♂♂	Σ ♀♀	Σ ♂♂	Σ ♀♀	Σ ♂♂	Σ ♀♀	Σ ♂♂	Σ ♀♀	Σ ♂♂	Σ ♀♀	Σ ♂♂	Σ ♀♀	a: Sum by species b: sum over species
	Σ ♂♂	Σ ♀♀	Σ ♂♂	Σ ♀♀	Σ ♂♂	Σ ♀♀	Σ ♂♂	Σ ♀♀	Σ ♂♂	Σ ♀♀	Σ ♂♂	Σ ♀♀	
	Σ ♂♂	Σ ♀♀	Σ ♂♂	Σ ♀♀	Σ ♂♂	Σ ♀♀	Σ ♂♂	Σ ♀♀	Σ ♂♂	Σ ♀♀	Σ ♂♂	Σ ♀♀	
				Sum in Can				Sum out of Can					

A. BODY WEIGHTS OF 10 MICE DURING TESTS
1-5 OF THE "LARGE CAGE EXPERIMENT"

a) <u>gracilis</u>		Body weight (gm) on					
		Day	0	1	2	3	4
Original weights	Test 1#	26.1			22.7	21.7	
	2	22.8	17.9	17.1	(died)		
	3	23.0		18.3			
	4	22.6	21.5	20.4	19.6		(eaten)
	5#	25.6	23.0	21.1	20.6		20.2
Corrected weights	Test 1	24.0			21.0	20.0	
	2	24.0	18.9	18.0			
	3	24.0		19.1			
	4	24.0	22.9	21.7	20.8		
	5	24.0	21.6	19.8	19.3		18.6
Average			24.0	21.1	19.9	20.0	18.6
b) <u>noveboracensis</u>		Body weight (gm) on					
		Day	0	1	2	3	4
Original weights	Test 1#	27.7			23.0	23.1	
	2	20.1			17.8		
	3	20.4			15.9	(eaten)	
	4	24.1	21.8	21.5	20.7		
	5#	26.6	25.7	24.0	22.6		22.2
Corrected Weights	Test 1	23.8			19.7	19.8	
	2	23.8			21.1		
	3	23.8			18.5		
	4	23.8	21.5	21.2	20.4		
	5	23.8	23.0	21.5	20.2		19.8
Average			23.8	22.3	20.4	20.1	19.8

indicates that the two individuals of that test were found nesting together at some time, usually by the 3rd or 4th day.

B. BODY WEIGHTS OF 10 MICE DURING TESTS 6-10 OF
THE "LARGE CAGE EXPERIMENT"

a) <u>gracilis</u>		Body weight (gm) on				
		Day	0	1	2	3
Original weights	Test 6#	19.0	17.4	17.3	17.7	
	7#	18.3	18.1	17.6		
	8#	18.1	16.9	16.5	15.7	
	9#	22.8	21.5	20.2	19.7	
	10#	17.7	17.4	18.0	15.9	
Corrected weights	Test 6	19.2	17.6	17.5	17.9	
	7	19.2	19.0	18.4		
	8	19.2	17.6	17.5	16.6	
	9	19.2	18.1	17.0	16.6	
	10	19.2	18.9	19.5	17.2	
Average			19.2	18.3	18.0	17.1

b) <u>noveboracensis</u>		Body weight (gm) on				
		Day	0	1	2	3
Original weights	Test 6#	13.9	13.8	12.8	11.9	
	7#	21.5	20.6	19.6		
	8#	15.6	15.0	14.0	12.6	
	9#	21.0	19.2	17.1	16.2	
	10#	26.0	25.0	24.0	22.4	
Corrected weights	Test 6	19.6	19.5	18.1	16.8	
	7	19.6	18.8	17.9		
	8	19.6	18.9	17.6	15.8	
	9	19.6	17.9	16.0	15.1	
	10	19.6	18.8	18.1	16.9	
Average			19.6	18.8	17.6	16.2

indicates that the two individuals of that test were found nesting together at some time, usually by the 3rd or 4th day.

APPENDIX III
RESULTS OF STARVATION EXPERIMENT

Test	Observed wt. in gms.							
	<u>gracilis</u>				<u>noveboracensis</u>			
	Day 0	1	2	3	0	1	2	3
1	23.1	21.0	19.2	17.8	20.2	17.8	16.5	15.3
2	21.8	17.9	15.3		19.1	16.4	14.6	#
3	21.5	17.2	15.8	#	24.3	20.2	18.6	
4	17.0	15.1	14.1	#	18.5	16.6	16.0	#
5	24.3	22.1	21.8	#	19.9	16.6	15.9	#
mean	21.5				20.4			

Test	Corrected weight in gms.							
	<u>gracilis</u>				<u>noveboracensis</u>			
	Day 0	1	2	3	0	1	2	3
1	21.5	19.6	17.9	16.6	20.4	18.0	16.7	15.5
2	21.5	17.7	15.1		20.4	17.5	15.6	
3	21.5	17.2	15.8		20.4	17.0	15.6	
4	21.5	19.1	17.9		20.4	18.3	17.6	
5	21.5	19.6	19.3		20.4	17.0	16.3	
mean	21.5	18.6	17.2	16.6	20.4	17.6	16.4	15.5

indicates that mouse died

APPENDIX IV

TIME IN SECONDS FOR EACH INDIVIDUAL TO ENTER COMPLETELY
ALL THREE COMPARTMENTS OF THE MAZE; ARRANGED BY
SPECIES IN ASCENDING ORDER OF TIME

<u>GRACILIS</u>	<u>NOVEBORACENSIS</u>
8.5	9.2
11.4	32.6
12.8	33.0
16.0	38.2
16.2	39.5
18.6	40.8
26.8	54.2
27.6	54.2
39.5	180
40.0	196
41.2	198
41.5	300
41.6	300
43.0	300
44.0	300
46.0	300
47.0	300
69.0	300
74.0	300
82.0	300

APPENDIX V
WEIGHTS OF MICE BEFORE AND AFTER
THE SWIMMING EXPERIMENT

<u>gracilis</u>					<u>noveboracensis</u>				
sex	wt. dry (gms)	wt. wet (gms)	increase (gms)	increase (%)	sex	wt. dry (gms)	wt. wet (gms)	increase	
								(gms)	(%)
♂	23.8	27.5	3.7	15.5	♀	29.1	31.0	1.9	6.5
♀	20.3	23.8	3.5	12.2	♂	20.0	21.9	1.9	9.5
♀	19.3	22.3	3.0	15.5	♂	23.1	24.0	0.9	3.8
♀	16.2	18.4	2.2	13.5	♀	21.3	22.6	1.3	6.1
♀	25.4	29.2	3.8	14.9	♀	33.7	36.2	2.5	7.4
♂	21.9	24.6	2.7	12.3	♀	24.6	27.3	2.7	10.9
♂	26.1	28.2	2.1	8.0	♂	29.7	32.8	3.1	10.4
♀	18.9	22.0	3.1	16.4	♂	32.5	34.7	2.2	6.7
♀	19.0	22.1	3.1	16.3	♀	21.2	22.9	1.7	4.1
♂	22.5	24.6	2.1	9.3	♂	25.6	27.5	1.9	7.4
♀	24.5	28.0	3.5	14.2	♀	18.9	20.0	1.1	5.8
♀	22.2	24.4	2.2	9.9	♀	23.3	25.5	2.2	9.4
♂	24.5	25.6	1.1	4.4	♀	24.5	26.1	1.6	6.5
♀	20.8	25.0	4.2	20.1	♂	21.6	22.9	1.3	6.0
♀	20.6	23.6	3.0	14.5	♀	21.2	23.1	1.9	8.9
					♀	20.3	21.7	1.4	6.8
mean	21.7	24.6	2.8	12.9		24.4	26.2	1.9	7.78