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NATURAL HISTORY
OF THE SHORT-TAILED SHREW
IN SOUTHEASTERN MICHIGAN

by
John Ewald Lutz

A dissertation submitted in partial fulfillment
of the requirements for the degree of
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Doctoral Committee:

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> . . . I sat watching a Hare in the woods; there was a rustling of leaves. Then I saw the dry brown carpet near me lifting along a crooked line....At one point a sharp nose appeared and worked about in the air, then speedily was withdrawn. The heaving of the leaf-bed continued at the rate of a slow walk; then at a bare place the heaver emerged for a moment. It was a Blarina. He disappeared at once under the next leaf-bed, and so went on burrowing his way....I examined his trail but found no tunnel, all had closed behind him. Free as a mole in the soil, he drove his sub-leaf gangway where he would, and doubtless lived on the country as he went. This, then, was his way of life---this little inter-world betwixt floor and carpet was for him...
>
> Ernest Thompson Seton (1909)

INTRODUCTION

The short-tailed shrew (Blarina brevicauda Say) is an important member of many communities, yet is not as well known as many of its mammalian associates. Various of the small mammals have been studied intensively, either by those interested in learning more about a particular species, or by those who used the animals merely as convenient experimental subjects. The short-tailed shrew, however, has been neglected in comparison with the rest of the common small mammals, partly because of the difficulties attendant with its repeated capture and partly because of the reputed difficulty of maintaining members of the species in captivity.

This shrew, with a range extending over the eastern half of the United States and part-way into the adjacent Canadian provinces, probably outnumbers most, if not all, of the other mammals within its range. In moist woods or in swales, the populations of Blarina may exceed those of the other mammals, but in habitats such as the dry grasslands this shrew often forms but a minor segment of the mammal fauna. Because of its eurytopic nature, however, the short-tailed shrew generally constitutes a considerable portion of the total mammal population even though it might seldom be the most numerous species in any single habitat.

Being less trap-hardy than most small mammals, when continuing studies of populations are conducted, many of the shrews are soon dead and data that might have been gathered are lost. Coupled with this difficulty is the fact that when a population is decimated by the tools of investigation, the remaining members of that group can no longer provide data on the original natural situation. To obviate these problems, an investigator must adapt himself to the primarily nocturnal but continuing activity of his subjects throughout the entire day; most persons studying populations have not done this, with the result that the shrews are commonly killed by live traps, disrupting any previous balance and reducing the numbers available for study. Thus, in spite of relatively large numbers and broad ecological tolerances, Blarina is less well known than its hardier, diurnal, and more easily studied associates.

Although not often recognized as such, this shrew represents an important factor in the control of man's most serious competitors: insects and mice. It has been estimated that with a population density of 25 per acre, the short-tailed shrews in a 20-acre field would eat 3,900 pounds of food, the bulk of which is insects, per year. This estimate is undoubtedly high but, even after allowances have been made for a smaller but more probable population of shrews, seasonal changes in their numbers, and the fact that insects usually constitute closer to 50 per cent of the diet, a figure of 1,000 pounds of insects eaten in a 20-acre field per year is still impressive.

Blarina demonstrates a decided preference for insects in its diet, yet it has been credited with eating large numbers of meadow voles; this shrew is an opportunist regarding its omnivorous diet, and an abnormal abundance of any potential food item would likely result in a concentration on that item with the subsequent control of many pests.

The short-tailed shrew burrows in the soil and digs tunnel systems, assisting in the aeration and mixing of the soil, and its waste products serve as nutrients for the vegetation. The pronounced habit of storage may aid in the dissemination and planting of various seeds. Blarina serves as food for different predators and, although not usually a preferred prey species, may act as a buffer against starvation when other small mammals are scarce.

Blarina deserves more attention than it has received in the past, in part because with its abundance and widespread distribution it constitutes an important segment of the mammal fauna, and in part because of its potential, yet incompletely understood, role as a control agent for human competitors.

My investigation of the natural history of Blarina in southern Michigan was directed primarily toward the ethology of the shrew. During the course of the study certain related problems became evident, and when the opportunities arose these were pursued. Certain previous studies have dealt with various specific aspects of the natural history of Blarina, such as reproduction and diet, many survey-type investigations have included some information on this shrew, and a number of observations have been published as short notes, but few studies have been concerned with the overall natural history of the species. The most recent of the latter type was published in 1931. Considerable, but scattered, information has accumulated in the intervening years and I have attempted to correlate these various studies.

AREAS AND METHODS OF STUDY

This investigation is based upon data from both field work and laboratory study. The field work was conducted between March, 1954, and October, 1956, and involved both live- and kill-trapping; the laboratory phase included both experiments with captive shrews and the detailed analysis of the specimens collected.

Areas of Study

The primary problem of the field work was not how but, rather, where to catch the shrews. In certain relatively small areas an astounding number of individuals were trapped, but such areas were scarce. In other places which were to all appearances favorable Blarina habitat, none were found. In general, more time was spent in locating these pockets of shrew concentration than was consumed in actually trapping the animals. Further, some areas which one year yielded a large number of specimens showed no evidence of shrews the next year.

No extensive single area for study could be located and consequently a number of smaller areas had to be employed. These were selected on the basis of shrew presence, remoteness from young humans, and accessibility. In a highly urbanized region, areas combining the above features

require considerable searching. Accessibility by road was imperative because the traps were, of necessity, visited often both day and night; fewer visits would have resulted in fewer data and the death of many shrews, with the consequent change in the original ecological situation. Areas near occupied houses always chance the danger of raiding by children, and this happened twice during my study, resulting in the loss of over thirty live traps and damage to a number of others.

TABLE 1

LOCATION OF THE AREAS OF STUDY WITHIN WASHTENAW COUNTY, MICHIGAN

Name of Area	Location	Acreage
Huron River	T2S, R6E, Sec. 17, SW 1/4	30
Waterworks Road	T3S, R5E, Sec. 35, SW 1/4	22
Baseball Flats	T4S, R5E, Sec. 1, SW 1/4	18
Crim	T4S, R5E, Sec. 12, E 1/2	14
Greene	T4S, R5E, Sec. 1, NW 1/4	10
Railroad	T3S, R5E, Sec. 36, SE 1/4	9
Maple Road	T3S, R6E, Sec. 31, SW 1/4	8
Loch Alpine	T2S, R5E, Sec. 2, SW 1/4	5
Norden	T3S, R6E, Sec. 28, SE 1/4	4
Hamel	T4S, R5E, Sec. 1, SW 1/4	4
Macon Road	T4S, R5E, Sec. 22, SW 1/4	3

All the areas visited were in Washtenaw County, within either a six-mile radius of Saline or a five-mile radius of Ann Arbor, Michigan. These areas are listed and located in Table 1 in order of decreasing size.

Not all the plots were utilized to the same extent. The Greene, Hamel, Norden, and Railroad Areas were each trapped intensively over a period of several years. The Baseball Flats and Waterworks Road Areas were also studied intensively but only during the final year of the field work. The other sites were used sporadically.

All these areas are briefly described below and the most used plots are covered in greatest detail. In the interest of brevity, the vernacular names of the plants are used; the corresponding scientific names are listed in the Appendix.

Baseball Flats Area:

Several seral stages were represented in this 18-acre area: a dry meadow with scant shrubs, an overgrown field with numerous shrubs and young trees, and a rather densely wooded portion. The Saline River courses along the edge of this area.

The dry meadow, partially shown in Plate I, Figures 1 and 2, had a few scattered patches of gray dogwood, wild grapes, and poison ivy, some seedlings of quaking aspen and box elder, and several apple trees. The majority of the vegetation here was similar to that of dry meadow associations elsewhere in southern Michigan: different golden-

rods, wild carrot, Canada thistle, white melilot, common milkweed, and common chicory grew among the cover of grasses including orchard grass and Canada blue grass.

The overgrown field association (Plate I, Figures 1 and 2) was more brushy than the dry meadow. The trees, mostly young, included sycamore, black cherry, butternut, box elder, American elm, white, black, and red oaks, red and sugar maples, hawthorns, cottonwood, and quaking aspen. The abundant shrubs included many smooth and a few staghorn sumac, elderberry, poison ivy, wild grapes, brambles, and both gray and red osier dogwoods. The actual ground cover consisted of various grasses and sedges, numerous herbaceous plants such as goldenrods, wild carrot, various asters, Joe-Pye-weed, boneset, and melilot; mosses and horsetails were locally abundant. One portion of this association was particularly favorable Blarina habitat and is shown in Plate II, Figure 1.

The wooded portion of this area occurred primarily in the low places and adjacent to the stream. Cottonwood, sycamore, quaking aspen, American elm, butternut, shagbark hickory, and red maple were common, numerous wild grapes and poison ivy vines entangled the trees and ground surface, and many of the shrubs and herbs of the adjacent associations were present here.

The soil was generally a brown sandy loam but in places very clayey. In the low spots with denser vegetation, the ground was moist but most of the plot was rather dry.

The soil here was classified by Veatch et al. (1930) as Griffin loam. Extensive trapping was conducted here and was most successful in the moister places within the overgrown field association. When spring rains were heavy, the lower parts of this area were inundated by overflow from the adjacent stream.

Crim Area:

This 14-acre area, as in the preceding one, contained different associations. Trapping was conducted within the wooded hillsides and down into the lowland bordering the Saline River.

The slopes above the low ground were wooded with moderate- to large-sized trees, the most abundant being black cherry, red and sugar maples, red and black oaks, shagbark hickory, sycamore, and quaking aspen. American elm, red maple, quaking aspen, white ash, box elder, beech, and cottonwood predominated along the base of the slopes. The understory consisted of gray and flowering dogwoods, maple-leaved viburnum, hazelnut, honeysuckles, brambles, wild grapes, clusters of smooth sumac, and an occasional hawthorn. The leaf-litter was rather thin on the slopes and the ground cover consisted primarily of grasses and small sedges and many herbs such as hepatica, early meadow rue, asters, and Joe-Pye-weed. In some places, where moist ravines cut into the hillside, a different association prevailed: flowering dogwood, blue beech, jewelweed, Jack-in-the-pulpit, and skunk cabbage grew here.

The flat land lying between the hillsides and stream was primarily open, with but a few patches of brush and young trees. Much of the lowland vegetation was dense and almost impenetrable, especially in the fall, because of the vigorous growth of the annuals and biennials which included wild carrot, different goldenrods, tall coneflower, common burdock, cocklebur, the common and the abundant giant ragweed. The shrubs, clustered in patches, were elderberry, various willows, and both gray and red osier dogwoods. Along the stream bank both box elder and a few American elm were present. Plate II, Figure 2, shows a general view of this area.

The soil of the ridge and hillside was dry and sandy with underlying clay, the Ottawa loamy fine sand of Veatch et al. The flat land, subjected to flooding during excessive spring rainfall, was described by Veatch et al. as Griffin loam, a friable brown sandy loam. The flat land, especially that with shrubs and dense herbaceous growth, produced the majority of the shrews kill-trapped in the Crim area.

Greene Area:

Within this 10-acre area (Plates III and IV) lay a wooded hillside, several marshes, extremely dense patches of brush, and a meadow in the process of being supplanted by shrubs. A stream and the backwater of an artificial lake bordered two sides of this plot and open farm fields the remainder.

The mixed meadow association, shown in Plate III, Figure 2, included both moist and dry areas and was studied intensively. This plant association had shrubs such as the ubiquitous gray dogwood, red osier dogwood, elderberry, prickly ash, smooth sumac, wild rose, and brambles, and a few young trees including American elm, willows, and hawthorns. Wild grapes, poison ivy, and Virginia creeper vines entangled the shrubs and ground. These plants grew in a matrix of grasses such as Canada blue grass and bluejoint, various medium and tall sedges, and numerous other herbaceous plants including various asters and goldenrods, Joe-Pye-weed, and giant ragweed.

Some work was done in the small adjacent marsh (Plate IV, Figure 1) which was populated mostly with tall sedges, common cattails, and tall scouring rush; in the very dense brush areas dominated by gray and red osier dogwoods, elderberry, various willows, and young American elm; and along the adjacent wooded slopes where various oaks and hickories graded downslope into woods of primarily black cherry, red maple, and American elm.

The shrews were most numerous in the moister portions of the meadow and throughout the small cattail-sedge marsh; both types of preferred habitat here had very dense ground cover. These same areas were subject to flooding by the adjacent waters following heavy spring rains. In March, 1954, one flood completely inundated the lower portions of the area, as is shown in Plate IV, Figure 2.

The soil type of the meadow association was Griffin loam (usually a poorly-drained sandy loam), that in the marsh and dense brushy areas was Ottawa loamy fine sand (a sandy soil with underlying clay), and that of the drier slopes was Miami silt loam (a well-drained clay loam) according to Veatch et al.

Hamel Area:

This rather flat, wooded 4-acre plot bordered the Saline River and was partially flooded during wet springs. The soil was typed as Griffin loam (Veatch et al., 1930), like that of the Baseball Flats Area on the opposite side of the river. The dominant trees, an admixture of red maple, box elder, black cherry, American elm, swamp white oak, sycamore, and cottonwood, had an understory of younger trees and various other woody plants such as serviceberry, hazelnut, brambles, smooth sumac, willows, Virginia creeper, wild grapes, and gray, red willow, and red osier dogwoods. Grasses, other herbaceous plants including wild cucumber, Joe-Pye-weed, jewelweed, hog peanut, and asters, and a thin leaf-litter carpeted the ground. A dry field or meadow association bordered this area of study and interdigitated with the woods. Typical views, both in summer and winter, of this live-trapped area are shown in Plate V, Figures 1 and 2.

Huron River Area:

Lying along the north shore of the Huron River, this rather flat, 30-acre area included woods on the higher

ground and two small cattail marshes at the water's edge. American elm, red and sugar maples, and black cherry predominated in the overstory, while mainly gray and red osier dogwoods, wild grapes, and honeysuckles accounted for most of the woody vegetation nearer the ground. A thin layer of humus overlay the relatively moist soil, listed by Veatch et al. as Griffin loam. Only kill-trapping was done in this area.

Loch Alpine Area:

Adjacent to the Huron River, this 5-acre lowland was trapped only twice and each time with little success. The soil type, according to the Veatch et al. soil survey, was Rifle Peat, a rather deep, granular, little decomposed organic loam. Within the plot was a cattail-sedge portion, a brushy part dominated by willows and both red osier and gray dogwoods, and a wooded portion with red maple, American elm, black cherry, and nannyberry.

Macon Road Area:

This plot, three acres in extent and in a little-used corner of a sheep pasture, was less grazed than the rest of the pasture. The ground was generally low and supported a dense growth of tall grasses and sedges, a few common cattails, burdock, Canada thistle, and goldenrods, scattered clumps of elderberry, red osier dogwood, maple-leaved viburnum, and several isolated red cedar and American elm. Although this low ground, only a few feet above the level of the stream flowing through the pasture, yielded

several specimens of Blarina, the adjacent higher ground dominated by red maple, various oaks, red cedar, and some flowering dogwood produced none. The soil of the low ground was Griffin loam and that of the drier adjacent slopes was Miami silt loam, both previously described.

Maple Road Area:

This 8-acre site was adjacent to railroad tracks and quite similar to the Railroad Area although none of the land here was as low or moist as parts of the latter. The vegetation was primarily tall grasses and herbs tolerant of moderately dry conditions; the woody plants included gray dogwood, elderberry, wild grapes, brambles, and scattered trees such as box elder, black cherry, and various oaks. Kill-trapping was conducted here only a few times.

Norden Area:

Extensively trapped, this small 4-acre area, shown in Plate VI, Figure 1, supported a very high shrew population. A dry, rather sandy hillside sloped to a small, shallow pond which was rapidly becoming filled with vegetation.

The hillside, dominated by smooth and staghorn sumacs and various oaks, produced no shrews, but Blarina were taken in considerable numbers along the pond shore and in the adjacent brush. Figure 2, Plate VI, shows the type of cover where Blarina were taken in greatest numbers. Near the pond, black and pin oaks, pignut hickory, willows, American elm, black cherry, and hawthorns extended above the general shrub level which included mostly gray and some red osier

dogwoods, maple-leaved viburnum, hazelnut, and wild grapes. The dense ground cover of various tall sedges, rushes, and grasses extended to the water's edge.

The organic loam soil of the low ground was the type Veatch et al. termed Rifle Peat, and that of the adjacent slopes was Coloma loamy sand--a dry, yellow, sandy soil.

Railroad Area:

Although relatively few Blarina were caught here, this 9-acre area was trapped often because of its accessibility. The area consisted of the land bordering both sides of a single railroad track. All of the woody vegetation within about 12 feet of the track was usually cut each year by railroad crews, but sprouting and reproduction of the shrubs and trees along this strip assured at least moderate cover. The remainder of the railroad right-of-way was trimmed somewhat at, perhaps, five-year intervals; no large trees were present, but the shrubs flourished and young trees reached a height of about 25 feet. The immediate abutting farmlands had similar, but uncut, vegetation.

About half of the land lay below the track level and in these moist places grew shrubby and spotted St. John's wort, various tall grasses and sedges, some cattails, elderberry, red osier dogwood, quaking aspen, and American elm. This association graded into higher and drier ground with bracken fern, horsetails, shorter grasses, wild carrot, brambles, smooth sumac, gray dogwood, box elder, and bur oak. The soil of the higher ground was Miami silt loam

and in moister low spots was the soil type which Veatch et al. termed Brookston clay loam (a dark organic loam underlain by gray clay).

Waterworks Road Area:

This 22-acre area was actually two adjacent farm woodlots, approximately 200 feet apart and separated by a grazed pasture; one woodlot had been grazed some years earlier and was consequently much more open than the other. Some of the larger trees had been cut in both woods. Black, red, and white oaks, shagbark and pignut hickories, and black cherry were on the higher ground of the gently rolling land, while red and sugar maples, butternut, and American elm were common in the low parts of the woods. Gray, alternate-leaved, and flowering dogwoods, red cedar, wild grapes, maple-leaved viburnum, hazelnut, and the reproduction of the dominant trees formed the understory. Grasses and other herbaceous plants grew throughout the woods but were most abundant in the small clearings. The soil in most of the woods was a well-drained clay loam, while a moist, dark, sandy soil rich in organic matter occurred in the low spots; Veatch et al. (1930) listed the former soil type as Miami silt loam, and the latter as Maumee loam. Because of the prevailing winds from the west and the more rapid decomposition in the moister soil, the leaf-litter was deepest on the higher ground and through the eastern sides of the woods. Both live- and kill-trapping were most successful where the leaf-litter was deepest.

Field Techniques

Live-Trapping Procedure:

Live traps were placed in lines chosen so that a maximum of potentially favorable sites could be used; traps were not organized in a grid pattern, as has been used by so many other workers. The goal here was to catch as many shrews as possible and when using a grid, a trap is often set where there is a low potential of success. Further, in some of the very dense, brushy habitats it would have been exceedingly difficult both to set and to visit traps placed in a grid; it would have been impractical even to establish a grid without considerable destruction of habitat. The absence of a grid precludes the relatively simple calculation of home range and population density, but it seems to me that in the present study this disadvantage is overshadowed by the attendant problems.

The trapping lines were usually established in the form of rough circles in order to end near the starting points. When gathering data on home range, the traps were set, without pre-baiting, at about 50-foot intervals along the line in spots that appeared likely to yield shrews. Whenever a trap contained a live Blarina, four additional traps were usually located in a rough square around the successful trap, with each supplementary trap approximately 30 feet away. Each trap was in operation for a minimum of two days, and if a trap caught the same shrew twice within

a 24-hour period, it was removed and used elsewhere. Once established, each trapline was in operation for a minimum of two days and some, which were particularly successful, were operated over a period of seven days. This system made possible the maximum use of the live traps available and provided considerable flexibility.

The location of the various successful traps was plotted in either of two ways. First, when the vegetation permitted sighting the stakes which were placed temporarily at neighboring traps, a compass direction was read toward at least two nearby stakes and the traps were thus plotted by triangulation. In some instances, prominent fence posts or trees were used as reference points. The second method required both a compass direction and an actual measurement with a 50-foot steel tape from one trap to another. In areas that were trapped over an extended period of time, reference stakes with nails in the tops were driven into the ground approximately 90 feet apart, and by hooking the tip of the tape over the nail, measurements to trap sites were made easily.

Early in this study the live traps were visited each three hours, day and night, while in operation. It rapidly became evident that these visits had to be timed differently to accommodate both the shrews and the investigator. Since some of the traps contained dead Blarina, it was obvious that shorter intervals had to be established during the times that Blarina was most liable to be caught. From early

observations and later accumulated data, it was noted that most captures were made from dusk through the following three hours, and then again within a three-hour period centered about dawn. Consequently, visits at intervals of about two hours were made during these times of high capture probability and less frequent checking was satisfactory between these times, especially during mid-day when few of these shrews were caught. In some instances, traps which were exposed to the late morning or afternoon sun were inactivated during these times to insure that no animals were unnecessarily killed by direct heating of the traps. Those traps in shaded locations were left in operation.

With trap visits timed about every two hours during the evening and early morning, very few shrews were found dead. Occasionally one would enter a trap just after my visit and have to remain there for a full two hours. When this happened, the shrew was usually lethargic, invariably damp, and the hair at least partially matted. In some cases these damp individuals were not recaptured and one was found dead a short distance from its release point on the following visit. Undoubtedly, the population structure was changed to some degree by the shrews removed or weakened in this way, but with the excitable nature of this species I doubt that any existing method of live-trapping can capture these shrews without some accidental deaths.

All the traps were baited with the same mixture: a combination of rolled oats, peanut butter, and bacon grease.

Types of Live Traps Used:

Different traps were built in an attempt to develop a small and simple yet effective trap, but none of the experimental models worked as well as the treadle-type traps which were finally used almost exclusively to capture Blarina. The mechanisms of several experimental models failed to operate properly and these traps were then either modified or discarded; only the traps which were actually used in the field are listed in Table 2.

One experimental multiple-catch trap, listed as model A in Table 2, consisted of a 1/8-inch-thick hardboard shell with outside dimensions of 1.5 x 2 x 6 inches. The plan of this trap is shown in Plate VII. One end was closed by a sheet metal door. Two types of entrance gate were tried with this trap: one was of 1/8-inch-mesh hardware cloth and the second was made from a thin sheet of aluminum. Both entry doors were hinged at the top and sloped back into the trap at about a 45° angle; a 3/8-inch gap was left between the hinge and the top of the trap for ventilation. Both versions of this trap were usually found empty, but from the droppings and odor it was evident that Blarina and Peromyscus had been in the traps. To prevent further escapes, a locking device was designed so that once the door was lifted and then closed, it could not be lifted again by the occupant. The design of this modified model is shown in Plate VII, Figure 1. As the door is lifted by an entering animal,

the locking bar is freed and subsequently drops to secure the door (Plate VII, Figure 3). The trap worked well in principle but very few shrews were caught in known Blarina territory; the great majority of trapped specimens were Peromyscus. When the trap was presented to captive Blarina, the reason for this selectivity was obvious: the shrew investigated the trap but, instead of entering directly, lifted the door part-way, retreated, and then repeated this procedure until the lock was released without the animal having actually entered the trap. Had this study involved Peromyscus, a trap with this selectivity might have been desirable. When it was first designed, no captive Blarina were available and the prototype was tested on a captive least shrew (Cryptotis parva) and worked well. The data come from ten traps built after the test using Cryptotis.

The traps listed as models B, C, and D were all of the treadle type. Model B was built by the investigator, and models C and D were loaned by the University of Michigan Museum of Zoology. All were about equally effective and their only disadvantage was that of being rather bulky and awkward to transport in the field.

The trap constructed entirely of sheet metal, and listed as model E, is known as a Sherman trap. It had a spring-actuated door which was released from the floor of the trap when the occupant's weight depressed an elongated platform having a catch to hold the door in an open position. Both these and the model F traps were loaned by the University

of Michigan Museum of Zoology.

The trap listed as model F, made of both hardware cloth and sheet metal, was a treadle-type trap and quite effective for capturing Peromyscus. Although used in known Blarina territory, relatively few shrews were captured by this trap. Perhaps the open nature of the trap had a deterrent effect on the shrews; Blarina is known to remain under cover much of the time.

The trap made completely of 1/4-inch-mesh hardware cloth, and listed as model G in Table 2, was a very simple multiple-catch type with no lock on the sloping entry gate. The poor performance of this trap was perhaps owing to the fact that the entrance had to be lifted by the potential captive and this gate had the same appearance as the rest of the trap. Since the bait could be approached more closely on the side of the trap than at the entry point, the mammals may have experienced difficulty in locating the entrance.

Effectiveness of Live Traps:

Table 2 shows a comparison of the different traps used and their effectiveness in taking the various species encountered. No attempt was made to insure that the different traps were used equally in the various habitats, and, consequently, legitimate doubt exists regarding an inference that one trap is more effective than another for a particular species. However, since the number of trap-days tallied

for each type of trap is rather high, such an inference is certainly more than a speculative guess.

The traps used varied considerably in both size and construction. Some were made of galvanized sheet metal, others of hardboard or hardware cloth, and a few were a combination of sheet metal and hardware cloth. Some were single- and others of the multiple-catch type. Some closed by a spring mechanism, others by gravity. About half of the traps were loaned by the University of Michigan Museum of Zoology and the rest were of my own construction. The traps ranged in size from those measuring 1.5 x 2 x 6 inches to the largest measuring 3 x 3 x 9 inches. It was hoped that the smaller sizes would prove satisfactory because of their convenience in transportation and setting. Unfortunately, the bulkier traps turned out to be more effective. The very small traps, obviously, did not work as well as the larger ones, but after a critical size was reached further increase in size gave no additional advantage. The trap measuring 3 x 3 x 9, for example, performed no better than the 2.25 x 2.5 x 8-inch size for either Blarina or Peromyscus.

From Table 2, it appears that an open trap made of hardware cloth is less efficient in capturing Blarina than one partly of hardware cloth and partly of sheet metal, and that this, in turn, is less efficient than a trap made completely of sheet metal. It would further seem that a trap constructed of hardboard, such as tempered Masonite, is preferable to one of metal; perhaps either the smoother texture

or the usual cool surface of the metal traps had a slight deterrent effect on shrews encountering them.

The live traps appear to be more efficient, by far, than the snap traps but certain factors undoubtedly distort this inference. When set in nearby locations, both kill and live traps were visited with the same frequency; but when kill traps alone were set, they were visited fewer times per day. The kill traps, once tripped, were thus out of action for longer periods than the live traps and a correction for this would raise the calculated effectiveness of the kill traps. Further, kill traps remove animals from the population and the live traps do not; on successive days the kill traps thus sample continually fewer individuals, whereas the live traps capture a relatively stable population, and a correction for this effect would also increase the calculated effectiveness of the kill traps. The extent of these two corrections is not known and the comparison between live and kill traps is thus tenuous.

Cockrum (1947) wrote that in Wyoming live traps were considerably more efficient than snap traps, whereas Stickle (1946) and Sealander and James (1958) found that snap traps were the more efficient of the two. Gray (1943) claimed that in Washington, kill and live traps were equally effective; and Goodnight and Koestner (1942), working in Illinois, concluded that live and kill traps were equally reliable for estimating populations, but that live traps required six or seven days of trapping whereas kill traps

TABLE 2

EFFECTIVENESS OF VARIOUS TYPES OF TRAPS IN CAPTURING SMALL MAMMALS THROUGHOUT THE YEAR *

Type of trap	Live traps								Kill traps		
	All live traps	Trap A (hard-board)	Trap B (hard-board)	Trap C (hard-board)	Trap D (hard-board)	Trap E (sheet metal)	Trap F (sheet metal and hard-ware cloth)	Trap G (hard-ware cloth)	All kill traps	4-way mouse trap	Mus-eum Spec-ial trap
Dimensions of live traps (inches) (H)		1.5	2.25	2.5	3.0	2.75	2.5	2.0			
(W)		x 2.0	x 2.5	x 2.75	x 3.0	x 2.5	x 2.75	x 2.0			
(L)		x 6.0	x 8.0	x 8.0	x 9.0	x 8.0	x 8.0	x 6.0			
Trap days	4308	400	1498	1908	205	113	84	30	7395	380	7015

TABLE 2- Continued

Numbers captured

All mammals	919	16	340	461	47	29	24	2	633	28	605
Blarina brevicauda	178	2	75	86	8	5	2	0	61	1	60
Peromyscus leucopus	422	11	148	212	21	15	13	2	312	11	301
Peromyscus maniculatus	181	2	66	95	9	5	4	0	120	12	108
Microtus pennsylvanicus	107	0	40	54	7	2	4	0	79	2	77
Sorex cinereus	13	1	5	5	1	1	0	0	42	0	42
Mus musculus	12	0	3	8	0	1	0	0	14	2	12
Tamias striatus	6	0	3	1	1	0	1	0	2	0	2
Synaptomys cooperi	0	0	0	0	0	0	0	0	3	0	3

Effectiveness of traps

(percentage of animals caught per trap day)

All mammals	21.3	4.0	22.7	24.2	22.9	25.6	28.6	6.7	8.6	7.4	8.6
Blarina brevicauda	4.1	0.5	5.0	4.5	3.9	4.4	2.4	-	0.8	0.3	0.9
Peromyscus leucopus	9.8	2.7	9.9	11.1	10.2	13.3	15.5	6.7	4.2	2.9	4.3
Peromyscus maniculatus	4.2	0.5	4.4	5.0	4.4	4.4	4.8	-	1.6	3.2	1.5
Microtus pennsylvanicus	2.5	-	2.7	2.8	3.4	1.7	4.8	-	1.1	0.5	1.1
Sorex cinereus	0.3	0.3	0.3	0.3	0.5	0.9	-	-	0.6	-	0.6
Mus musculus	0.3	-	0.2	0.4	-	0.9	-	-	0.2	0.5	0.2
Tamias striatus	0.1	-	0.2	0.1	0.5	-	1.2	-	0.03	-	0.03
Synaptomys cooperi	-	-	-	-	-	-	-	-	0.04	-	0.04

* No attempt was made to insure that different traps were set in comparable situations and there was no intentional discrimination in trap placement. The live traps were all visited at similar intervals, usually seven times per day, and during each visit an occupant was freed and the trap reset. The kill traps were visited and reset if necessary from two to seven times each day, averaging approximately four. Comparisons of effectiveness between live and kill traps are consequently tenuous but within these two categories, the differences should reflect relative effectiveness. A trap day as used here represents one trap in operation over an approximate 24-hour period without regard to number of visits or time during which the trap was inoperative because an animal had been captured.

required but three.

The number of times within a 24-hour period that the trap is visited has a great deal to do with the apparent efficiency. Had not the live traps been checked quite so often and reset, no trap could have caught more than one specimen per night and the success figures would have been correspondingly lower.

Some traps, for instance, which happened to be in a favorable location, often caught three or four animals between dusk and the following morning.

Table 2 suggests that the different species react differently to different traps, and the conflicting statements by various authors regarding efficiency of the two types of traps may stem from the fact that different species were involved.

Treatment of Live-Trapped Shrews:

Excepting those times when experimental shrews were needed, all live Blarina were released after the following standard treatment. The shrew was first shaken from the trap into a glass quart jar, where it could be examined readily for previous numbering. Both shrew and jar were then weighed on an Ohaus triple beam balance which was fitted into a protective case and carried when I visited the live traps. After releasing the animal,

the empty jar was weighed and the weight of the shrew then obtained by subtraction. Because of the delicate nature of the balance, it was carried in the field only when the probability of shrew capture was moderately high. After the initial weighing, the shrew was examined either in the jar or in my gloved hand for evidence of molt, scarring, obvious ectoparasites, general condition, or any peculiarity, and to determine the sex. If captured for the first time, its toes were clipped with a cuticle scissors for identification.

Numbering systems involving both ear-punching and toe-clipping have been described and used by many authors, such as Burt (1940) and Blair (1941a). These systems use a combination of ear holes or notches for the lower numbers and clipped toes for the higher multiples into the thousands. These investigators were forced to modify their systems for use with Blarina since a prominent ear pinna is absent and, as in the present study, only toe-clipping was used.

Pearson (1945) remarked that clipping of toes is not wholly reliable since it is not unusual to have shrews lose toes naturally. In my study, the only missing toes were apparently those which I had removed. Five digits are available on each foot of Blarina and

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it is possible to number up to 9,999 without clipping more than two digits on any foot.

I assigned numbers one to five to the right manus, ten to fifty to the left manus, and, optimistically, the hundreds and thousands figures to the corresponding right and left pedes.

With few exceptions, only the terminal phalanx was amputated, so as to interfere as little as possible with the survival and usual behavior of the animal.

Bleeding was usually negligible, and commonly stopped before the shrew was released. A few animals bled excessively, but most of these were recaptured and showed no signs of ill effects.

No instances of infection were noted, although no effort was made toward antiseptic technique. It is possible that this absence of care could have transferred diseases and caused eventual death to shrews weakened by their efforts to escape the traps; the low proportion of animals recaptured in the areas of study after an interval of several months might be attributed to this factor, but other investigators claim that toe-clipping produces no serious side effects and it is unlikely that the populations observed here differ markedly in this respect from those studied elsewhere.

Kill-Trapping Procedure:

The live-trapping phase of this study was imperative for information on home range and various other aspects of behavior, but the necessarily short time that the animals were in hand precluded some detailed information that was desired. Relative to the time spent, by far the most information was obtained from kill-trapping because it was possible to study each individual in detail without the time limitations imposed by live animals. Kill-trapping affords an instantaneous yet very complete set of data as compared with the fewer but continuing data from live-trapping.

Each animal caught in a kill trap was placed in a separate polyethylene bag, the type used for packaging frozen foods. The standard data were written on a card and placed inside the bag. This procedure prevented both parasite contamination and loss of existing ectoparasites. Each animal was then either processed soon after leaving the field or frozen in a deep freezer for later examination. The polyethylene bags were superior to other containers tried. They do not permit the toes or other delicate parts to dessicate as will waxed paper, glassine, or cellophane bags, the polyethylene will not stick to the freezer surfaces or to the other bags, the enclosed data cards and any loose parasites can be seen easily through the transparent material,

they can be rolled more compactly than other bags, and can be re-used easily.

A form card was filled out for each specimen captured which included space for the various data on parasites, pelage, fat deposition, habitat, and weather, as well as the usual data on sex, reproductive status, weight, and age. The reverse side of the card had outline drawings of the dorsal and ventral body surfaces, primarily for sketching the extent of any molt. Space was also provided for such data as the time the trap was set and the pick-up time, various factors of the micro-environment near the trap, and so on. Unless circumstances either prohibited or did not warrant collection, the skin, complete skeleton, stomach and intestines, and parasites were saved. Other things were occasionally retained for future investigation, such as the heel organs and the uteri of pregnant females.

Since the time of each visit to a trap was recorded, it was usually possible to determine within one or two hours when each individual entered the trap and these data supplemented those on activity obtained by other means. The dead animals also afforded a population estimate by means of graphing the catch figures.

Both Victor 4-Way and Museum Special kill traps were used, but the Museum Special traps were used most extensively (Table 2). A concerted effort was made to trap only areas where there was a strong probability of catching Blarina, but Table 2 shows that both Peromyscus and Microtus

were taken in larger numbers. The same table indicates that the kill traps were far less effective in capturing small mammals than were the live traps. The reason is not understood. The same bait was used for both kill traps and live traps and essentially the same areas were trapped. Further, since I was interested in activity times, the kill traps were usually visited several times during each night although not as regularly as the live traps. When trapping the same areas in which the live traps were used, a much lower percentage of Blarina was taken in the kill traps than by the live traps; Sorex, for some reason, was more readily taken by the kill traps. All this may indicate simply that because of some innate predilection, individuals of one species are most apt to blunder into or actively investigate a new object which is flat and open, whereas those of another species prefer to examine and search a larger hollow structure. The fact that snap traps remove individuals which cannot be caught again undoubtedly biases any comparison of effectiveness between live-trapping and kill-trapping.

In addition to the species listed in Table 2, the snap traps also yielded the following: leopard frog (Rana pipiens), 3; tiger salamander (Ambystoma tigrinum), 1; common garter snake (Thamnophis sirtalis), 1; Song Sparrow, 2; Towhee, 1; Woodcock, 1; and 2 crayfish. The live traps caught only mammals.

Tracing of Burrow Systems:

Several burrow systems of Blarina were mapped by using a technique which, to my knowledge, has not been used before. The end of a dusting device, commonly employed for spreading insecticide powders on vegetable gardens, was inserted in an opening of a sub-surface burrow system and flour was blown into the opening. This lined the burrow with white flour and, by digging out the burrow a little at a time, the tunnels were followed quite easily. Whenever the white walls became less distinct, more flour was blown into the opening. Side runs, which might easily have been overlooked with the conventional methods, were readily located.

Shull (1907) traced burrows by inserting a rubber tube into the tunnel and digging along its path, and Townsend (1935) diagrammed tunnels by following the course of a string that unwound as the piece of bacon to which it was tied was carried into tunnels. Neither of these methods nor the usual procedure of merely digging along the route of a tunnel assures that all side branches will be noticed. The isolated blind tunnels shown in many published diagrams of burrow systems suggest that at least some connections were missed.

Laboratory Techniques

Collection of Data on Dead Shrews:

Each dead shrew was removed from its plastic bag, measured, weighed, and examined for ectoparasites. Any parasites, either on the animal or loose in the bag, were saved. The animals were skinned, beginning with a midventral incision extending from the chin to the tail base. The skin was removed in one piece after tearing or cutting the skin at the wrists and ankles so as to leave the feet on the body. The tail was opened by a midventral cut.

The skin was washed briefly in a weak detergent solution (Tide), squeezed to remove most of the water, and then shaken in benzene for about 15 seconds. Blotting, brushing, and blowing usually dried the pelt within a half-hour, and it was then pinned out in much the same shape as a commercial beaver pelt--with the hair side down--to dry.

If a female was in hand and in good condition, a vaginal smear was made, usually before skinning the animal. The smear was actually more in the nature of a douche since the usual smear methods proved difficult and yielded scanty material. A dropper, drawn out to a fine tip and containing a drop of physiological saline, was introduced into the vagina, the liquid swished about, and the suspension withdrawn and spread thinly on a glass slide where it dried rapidly.

With males, a smear was made for sperm--partially from the epididymis and partially from a freshly cut testis

surface. Both vaginal and sperm smears were later stained before examination.

The stomach and intestine were removed, with ligatures at the cardiac sphincter and rectum, and saved in 70 per cent alcohol. The sex was verified internally in all cases and whenever the uteri of pregnant females were in acceptable condition, these were removed and saved. Any endoparasites were preserved in 70 per cent alcohol. With most shrews the bulk of the muscle was cut away from the skeleton, the remaining viscera removed, and the skeleton saved.

The diet of the wild animals was determined by examination of the stomach and intestinal contents. Volume of the contents was determined separately for stomach and intestine by immersing the organ in a graduate which was partially filled with water. The rise in water level yielded the volume of organ plus contents. After the contents had been flushed out, the volume of the empty organ was determined in a similar manner and the difference between the two readings gave the volume of the organ contents. This rather time-consuming procedure was done so that the food items could be reported by volume as well as percentage of diet.

The organ contents were flushed into a petri dish and studied under a binocular dissecting scope, and all food items were classified in as much detail as possible, the record including minimum number of each item and the

percentage of total bulk. With most items identification was least difficult in the stomach; Blarina does not chew its food thoroughly and many items were in moderate-sized pieces. In the intestine, food was more dissociated and a greater proportion was included in the unknown category.

Age categories were established, in part, on the basis of tooth wear, using the system developed by Pearson (1945). Pearson admitted that this is not an ideal criterion; he wrote, "The rate of tooth wear in an omnivorous animal such as the shrew would be expected to vary depending upon the type of food available." However, for lack of a better way, tooth wear plus morphological changes were used.

Care of Live Shrews:

A total of 28 shrews was kept in captivity for varying lengths of time until their deaths or loss owing to some other factor. These shrews were kept in glass-sided, 3-25-gallon aquaria, and the majority of the data was secured when using a low-style five-gallon size.

Each aquarium contained dry soil, between one and two inches in depth, and usually a piece of bark for the shrew to hide beneath. Dry grass and leaves were supplied and the shrews usually used these materials to fashion a nest in their hiding places.

Water was supplied in a small, open, jigger glass embedded in a base of concrete so that it could not be tipped over. Dry food such as corn, wheat, or dry dog-food was continually available and frozen horse-meat, hamburger,

or some substitute was usually supplied twice a day.

These aquaria, with hardware cloth covers to prevent escape of the captives, were kept in an unheated garage and away from direct sunlight.

Most of the captives were used as experimental subjects to determine activity periods and for studies on food preferences, sense acuity, and both intra- and interspecific reactions. The experiments performed are described in the sections of this paper on molt, senses, reproduction, diet, and activity.

Equipment Used for Recording Activity

A means of continuously recording the periods of activity was necessary, and various combinations of available apparati were considered, but nothing within a moderate price range appeared to be applicable. As a result, three major pieces of special equipment were designed and constructed: runways (Plate VIII) for detecting movements between nest and feeding area, spring-loaded platforms (Plate IX, Figure 1) for detecting any movement within the supported aquarium, and a recording apparatus (Plates X, XI, XII).

Runway:

The runway consisted of a tunnel extending through a barrier which separated the nest from the feeding area. Centered in the tunnel was a swinging door which, when pushed away from the perpendicular, actuated either of a pair of

Microswitches by means of an off-center cam (Plate VIII, Figure 2). The circuits closed by these Microswitches resulted in a record by pens against the kymograph paper. When the runway was in place, I kept the nest area small so that extensive movement of the shrew was limited to the exercise and feeding area.

The tunnel and barrier were made of 1/8-inch hardboard assembled mostly with waterproof glue. The swinging door and the housing which shielded the Microswitches were of galvanized sheet metal. The door, perforated by 1/4-inch holes so the shrew could see to the other side, was soldered to the hinge wire which was bent on one end to gain leverage against the Microswitch arms. Sand sprinkled in wet varnish provided a slip-proof surface for the tunnel floor. A length of copper tubing 3/8-inch in diameter was soldered to the top of the Microswitch housing to protect the lead wires leaving the aquarium. The Microswitches were set to work with very little pressure so that the subject would experience no difficulty pushing under the gate.

A fair set of data were obtained with this apparatus, but potential objections to inferences from these data became evident. The animal was not free to move within its enclosure without pushing beneath a gate, and this probably modified its behavior somewhat. Certainly the arrangement was an exceedingly unnatural situation.

Spring-loaded Platforms:

An activity detecting device which imposed no physical restrictions on the subject was built to avoid the objections attending the runway. This platform is shown in Plate IX, Figure 1, which also shows the runway mechanism in position.

The wooden platform on which the aquarium rested was suspended from a braced wooden frame by springs on all four corners. To afford more support and prevent excessive side play, a single heavier compression spring was slipped over a vertical rod and positioned centrally beneath the platform. The aquarium was permitted to move very slightly in all directions in response to any movement by the shrew. The sensitivity of the platform was adjusted by raising or lowering the single compression spring.

Set in one corner under the platform was a short length of copper tubing, 3/8-inch in diameter, with an attached electrical lead wire. An adjustable contact (Plate IX, Figure 2) fitted into this tubing from below. The copper tubing and contact formed a switch which would close with any perpendicular or lateral motion of the aquarium. With the switch contacts set close together, even a shift in position during sleep was recorded and occasionally the shrew would carry a piece of meat to one side of the aquarium, shifting the balance enough to cause the switch to close and stay closed. It was necessary to compromise the setting so that more than a slight movement caused circuit closure.

The movement of the aquarium itself was almost imperceptible and probably had little effect on the timing of activity.

Recorder:

The recording kymograph (Plates X, XI, XII) involved a series of rollers which caused a length of paper to move across an opening in the device while a number of pens, actuated by electromagnets, marked the circuit closures. The power source was a constant speed adjustable gear box, Type M, made by Gorrell and Gorrell of Haworth, New Jersey, and offered speeds ranging from one revolution every 56 days to one revolution per second. The inking pens (Model 70-8202, manufactured by Phipps and Bird, Incorporated, Richmond, Virginia) were altered slightly so that they could be applied against a horizontal rather than a vertical drum.

The recorder, shown from the top in Plate X, consisted essentially of three rollers, each four inches long. Paper was loaded on the feed roller (A) and, during operation, was pulled over the master roller (B) which was running at a constant speed; it was then passed to the take-up roller (C). The brass master roller was machined to a circumference of 18 centimeters, which permitted six centimeters of paper to pass under the pens each hour with the gear arrangement used.

As shown in Plate XII, Figure 3, power was applied to the main pulley (D) by belt and this pulley caused a small gear (E) having twenty-four teeth to rotate. This,

in turn, meshed with a larger gear (F) having seventy-two teeth which was attached to the shaft (G) of the master roller. This gear arrangement caused one rotation of the master roller for each three rotations of the main pulley. The feed and take-up rollers were mounted on 3/16-inch shafts, and the master roller on a 1/4-inch shaft; these shafts were held by flanged, porous, bronze bearings.

In order that the revolutions of the constant speed power source would coincide exactly with the revolutions of the recorder, a pulley which was identical with the main pulley of the recorder was machined and substituted for the original pulley on the power source. Adjustment of the gears at the power source permitted different rates of paper flow across the master roller, but most of the records were made with a paper flow of six centimeters per hour.

As can be seen in Plate X, the take-up roller pulley (H) was powered by a loose belt from a larger pulley (I) on the master roller shaft. Slippage of the belt allowed constant yet not excessive tension on the paper as it wound onto the take-up roller.

It was necessary to coat the master roller periodically with a thin layer of rosin applied in alcoholic solution to prevent slippage of paper. The paper was held tight against the master roller by a pair of small pressure rollers (J and K, Plate XI and Plate XII, Figure 5). These pressure rollers were held in place by a pair of springs (L). The pressure rollers were made from small brass tubing which

rotated on a 1/8-inch shaft.

Both feed and take-up rollers (respectively, A and C, Plates X and XI) were made from one-inch-diameter wood dowels which were center-drilled and secured on their shafts. A circular aluminum plate, slightly over two inches in diameter, was glued to the ends of both rollers. The feed roller was equipped with a simple spring-tensioned pressure bar device (M, Plates X and XI) which prevented the paper from becoming loose. This pressure bar (Plate XII, Figure 2) was made of 11-gauge wire and a piece of 3/8-inch-diameter wood dowel which was covered by a length of rubber tubing.

Because the apparatus was operated in an unheated garage, the ink was very slow in drying; to prevent smearing of the records, small Edison base sockets (N, Plate X) and electric bulbs were installed beneath the master roller on either side and a turn-button switch was added to the side of the box. When the humidity was high, both low-wattage bulbs were operating but most of the time the heat from one bulb was sufficient.

The box for this recorder was made from 1/4-inch tempered hardboard and 1/2-inch exterior plywood to assure minimum warpage. The relatively thick hardboard provided an easily worked but rigid base for insetting the flanged, porous, bronze bearings. The hinged top (Plate XII, Figure 1) was made from a piece of sheet metal in which a central rectangular slit was cut to expose the center of the master roller.

MORPHOLOGY OF THE SHREW

Spending much of its time beneath leaf-litter, tangled grasses, and in a system of sub-surface tunnels, the shrew has a structure showing many adaptive features. The general body form, adapted for burrowing through either vegetation or soil, is elongated and rounded in cross-section. The short legs facilitate running through tunnels where elongated limbs would prove a disadvantage; they also permit considerable leverage for the attached muscles, providing the shrews the power necessary to push and dig through the soil. The snout is muscular and tapered, the apical nostrils open laterally rather than anteriorly, the eyes are small and bordered by ventrally-directed lashes, the ear pinna is short and hidden in the fur, and the mouth opens anteroventrally; all these features facilitate burrowing. The structure of the individual hairs with their crinkled bases permits either forward or backward movement in the burrows without disarranging the pelage.

The shape of the shrew's body permits its entry into virtually all mammal burrows within its home range, and no mouse or vole entering a burrow or having an underground nest would be safe from pursuit. For predation and aggression, the shrew is equipped with large, protruding, sharp, recurved incisors, and the highly publicized poisonous

saliva first discovered--or rediscovered--by Pearson (1942).

Some of the structural features are poorly understood. The shrew has a single ventral and paired lateral scent glands which produce a strong-smelling, pungent secretion of uncertain value to the species, and paired heel organs of unknown function, the latter described for the first time here.

Measurements

Body Length and Weight:

Male Blarina were found to average longer and heavier than the females. The differences are shown in Plate XIII, Figures 1 to 4.

The total length of 54 males averaged 120.1 mm. (111.5 - 132.5 mm.) and 57 females averaged 114.3 mm. (100.5 - 123.0 mm.). The frequency distribution of the total lengths is given in Plate XIII, Figures 1 and 2. No attempt was made to distinguish young from adults when computing these averages.

There is little agreement concerning body length in the various published reports. Seton (1909), for example, estimated the Blarina adults to average 127 mm. in length; Anthony (1928) listed the average length as five inches (126 mm.) and stated that both sexes are similar; Goodwin (1935) wrote that in Connecticut the total length averaged 118.6 mm. and, again, that the sexes were of equal length; Townsend (1935) reported of Blarina in New York that males

averaged 119.5 mm. and the females 117.4 mm., whereas Grimm and Roberts (1950) wrote that in Pennsylvania males averaged 117.8 mm. and the females 112.7 mm. From these and other reports it is obvious that as more data were gathered, differences became apparent and the averages more nearly accurate.

Relatively few studies have involved recording weights for large numbers of Blarina. Hamilton (1931) reported that in the vicinity of Ithaca, New York, 53 adult males averaged 20.35 grams, 27 adult females averaged 18.3 grams, and that the heaviest shrew was an adult male weighing 27 grams. He stated that specimens weighing less than 16 grams were never mature. Hamilton wrote later (1943) that 50 adult specimens (no locality given) of both sexes averaged 19.3 grams, while juveniles weighed 12-15 grams. Grimm and Roberts (1950) reported that 169 males in Pennsylvania averaged 18.2 grams (12-24.5 grams), and that 124 females averaged 15.7 grams (11.5-24.5 grams).

As shown in Plate XIII, Figures 3 and 4, the weights of 134 males in the present study averaged 19.1 grams (11.4-25.6 grams), and 150 females averaged 15.6 grams (10.2 - 23.2 grams). In each case, where the weight of a female was above 21 grams, she was either pregnant or lactating. If sexual maturity is used as a criterion of maturity, my data do not support Hamilton's claim that individuals weighing less than 16 grams are never mature.

When large numbers of the short-tailed shrew are considered, the males surpass the females in both total length and weight, but these averages vary from one study to another. The differences are not usually great, however, and might be explained by a combination of factors such as actual differences in the measuring techniques of different authors, varying numbers of young animals included in the calculations, the time of year when the specimens were obtained, and probably actual slight regional differences within the subspecies with the various reports suggestive of a larger body size and greater weight in the more northern populations.

If only individuals considered to be adults were compared, then somewhat higher averages would result. The criteria used for determining adult status, however, is a question which, I am sure, varies considerably among the various authors.

Size alone is a poor criterion for adulthood in Blarina because growth is so rapid; the young reach the size of assumed adults within two months after leaving the nest. Only during a short period of the year would the total length, thus, be valid.

Similarly, weight alone is a poor criterion because it varies considerably both daily and seasonally. One live-trapped male which was caught five times within a span of two days varied from 14.3 to 16.8 grams, a difference of 2.5 grams. This difference was obviously not caused by a

rapid change in body mass, but rather by a difference in the amount of food eaten because the lowest weight was recorded at the second capture within the two-day period. Regarding seasonal variation, most of the non-captive shrews gained weight over a period of months, although one old female lost weight over a 37-day period, dropping from 21.4 to 16.3 grams, and probably then died for she was not retaken. Captive animals usually showed even more spectacular weight changes: an adult male weighing 24.7 grams when captured August 21, dropped to a low of 15.1 grams before death December 19, a range of 9.6 grams; another captive, an adult female which weighed 16.1 grams in late May, increased to 22.9 grams by mid-July and then dropped to 15.6 grams--and shortly thereafter, death--in late July, a range of 6.8 grams.

Writing about Sorex araneus, Middletown (1931) mentioned that a definite weight loss occurred in the autumn. My specimens of Blarina did not exhibit any such loss. The weights of the entire population, if averaged, would have shown a decrease in the fall, but this would not have been due to loss of weight by any individuals; it would have been caused, rather, by the decreased proportion of older and heavier individuals. Contrary to the situation reported by Middleton, Blarina increased in weight during the fall and early winter, but showed a decrease during late winter. By mid-March the individual weights began to show an increase over the low point which occurred in late

February.

The variation in winter weight apparently resulted from the amount of fat deposited in the abdominal cavity and beneath the skin. Individuals caught from October through December usually showed increasing amounts of stored fat, whereas by February the fat deposits were reduced and, in some cases, virtually eliminated. One female, kill-trapped in late December, weighed 18.2 grams; the subcutaneous fat and most of the fat from the abdominal cavity totalled 3.4 grams, and this was the greatest amount of fat found in a wild specimen. One old female which had been in captivity for five months weighed 21.7 grams at death in late August. Three days prior to her death she weighed 24.8 grams, at which time her food was restricted in an effort to reduce her weight; her death was apparently caused by starvation. The fat removed from all parts of her body weighed 5.6 grams, the greatest amount of fat deposition recorded.

Some fat was usually present around the kidneys and in the mesenteries of most individuals. In the late summer and fall, light subcutaneous deposits were noticeable above the shoulders and high along the sides. When large subcutaneous fat deposits existed, they were usually in a continuous mass, the bulk of which overlay the dorsum between and above the shoulders, extending a short distance dorsolaterally onto the neck and dorsolaterally caudad to the approximate posterior limit of the rib cage; these posterior

extensions curved ventrally to cover the ventrolateral thoracic region behind the forelegs. Some isolated subcutaneous fat deposits were occasionally in the throat and midventral thoracic regions, but I have no records of any instances of subcutaneous fat deposits in the pelvic or posterior abdominal regions.

Criteria of Age:

The often implied assumption of adulthood is reproductive maturity, but the reproductive status is difficult to ascertain and the conventional methods used here present difficulties in interpretation. It is common to measure the testes and, if they show enlargement, the individuals are assumed capable of breeding. Scrotal location of the testes is also often presumed to indicate sexual maturity. My data cast doubt on both these criteria.

A number of smears were made from both the epididymis and testis, and if the sum of the length and width of the testis exceeded 10 mm., sperm were always present. If the testis had a sum less than 5 mm., well developed sperm were usually absent. Based on this, it might be assumed that if the sum of these measurements is greater than 10 or less than 5 mm., either adult or juvenile categories could be assigned, but exceptions to this general pattern are too common for any such application. One testis with a sum of 8.8 mm. yielded no sperm, whereas another which was considered to be abdominal in position and having measurements totalling only 3 mm., showed well-developed sperm.

An unsuccessful attempt was made to determine the sexual status of female Blarina by using vaginal smears. Here again, relatively small females yielded smears indicative of sexual maturity. This question will be discussed in greater detail later; the concern here is the fact that apparent juveniles, based on length, weight, or other factors, would fall into the adult category on the basis of sexual criteria; and, conversely, some adults would be placed in the juvenile category.

The entire problem of maturity and what criteria are best for its determination is as confusing in the familiar and much studied human species as it is here.

During the spring to mid-summer period, enough differences can be found to easily distinguish the older shrews or adults from the young, but when year-round collections are made these problems of criteria arise. During the winter, for example, when the females are in anoestrum and the males all have relatively small and non-productive testes by virtue of immaturity or regression, sexual status cannot be used. Tooth wear might be used at this time to distinguish the old from the younger segment of the population, but tooth wear has not been correlated with reproductive ability.

Because of the established use of terms like 'immature,' 'mature,' 'young,', and 'adult,' and the absence of more descriptive terminology, these terms will be used here in the general sense, but with full realization that in

many instances they are misleading.

Differences in Appearance Relative to Age:

A cursory examination of Blarina is usually sufficient to place the individual roughly as either immature, young adult, or older adult. Since the animals age gradually, some specimens are bound to fall between these artificial categories.

The Immature Shrew

The immature specimen shown in Plate XIV, Figure 1, is usually shorter and weighs less than the older individuals. The total length of the male will be less than 115 mm. and the weight less than 15 grams. The female will usually have a total length of 110 mm. or less, and a weight less than 14 grams. The head appears disproportionately large and the whole animal has a rather sleek appearance; the snout tapers rather acutely, but evenly straight back, merging smoothly with the cheeks which show little enlargement. The tail of the immature specimen constitutes about 22.5 per cent of the total length. Without opening the mouth, the central upper incisors appear relatively long and quite curved, with a good deal of the rusty-brown coloration evident. The ventral and lateral scent glands are present, but not well developed. Usually little or no evidence of scars or missing toes is seen here and the pelage is usually slightly darker than that of the older animals.

The Young Adult

Shown in Plate XIV, Figure 2, the young adult is longer and heavier than the immature individual. The males will weigh between approximately 15 and 21 grams, and have a total length between 115 and 126 mm. The non-pregnant females will weigh between 14 and 18 grams, and range between 110 and 120 mm. in total length. The head and body have reached adult proportions. The snout curves posteriorly at a less acute angle than in the immature and rather abruptly meets the more muscular and enlarged cheeks; Palmer (1954) also recognized and mentioned that the older shrews have thicker snouts and broader heads. The tail averages slightly over 21 per cent of the total length. The upper central incisors appear less long and consequently not quite so curved; less rusty coloration is seen than in the younger specimens. The ventral and lateral glands are commonly well developed in both sexes and moderate scarring is often observed.

The Old Adult

Essentially the same length or very slightly longer than the young adult, the old adult shown in Plate XIV, Figure 3, is usually heavier and has a very chunky appearance. The very muscular snout curves posteriorly less acutely than in any younger specimens and merges smoothly with the very muscular cheek area. The head and neck join the trunk without any abrupt demarcation, probably as a result of more highly developed musculature in these regions.

The tail averages here about 20 per cent of the total length, indicating that, since the tail becomes proportionately shorter as the age increases, it must reach maximum development earlier than the rest of the body. The upper central incisors in the old adult are usually quite worn so that they are now shorter, much less decurved, less sharp with less coloring showing, and give the appearance of being heavier than those of the younger animals. The lateral and ventral scent glands showed greatest development in the females which were not sexually active and in old males. Scarring or missing toes are most common in this group.

Tooth wear can be used as a criterion of age because as the age increases the tooth is gradually worn away, decreasing the height of the crown and revealing whitish dentine as the chestnut-colored enamel erodes. Since the teeth are somewhat rounded rather than straight-sided, as they wear down, proportionately more colored enamel is removed than dentine, causing them to appear whiter in old shrews. Pearson (1945) used tooth wear as a measurement of age, correlated roughly with age in months. I did not use Pearson's criteria exclusively because many variables govern the rate of tooth wear and criteria established for one group of shrews may not be applicable to the shrews in other areas. Further, his data included several pregnant shrews which, on the basis of tooth wear, should be considered immature and this apparent discrepancy inhibits use of the teeth to establish sexual maturity.

The pelage provides a rough indication of age with the juvenile or immature shrew being slightly darker than the adult. Other indicators of age, however, such as appearance of the head, length of the tail relative to the body length, the total length, and tooth wear, permit more precise judgments than are possible with the available information on hair color.

Hair and Pelage Structure

Blarina has two pelages per year but the differences are not as conspicuous as might be desirable for their determination. The summer pelage was found on shrews taken from April through November, a span of eight months. The winter pelage was found on specimens taken from September through July, a span of eleven months. Apparently considerable individual variation in time of molting causes this situation; the majority of the shrews had their winter pelage from early September through mid-May, and the summer pelage between late May and mid-August.

Very subtle differences in pelage exist between the summer and winter months. In general, the summer hair is a grayish-brown dorsally blending into a gray-ochre ventrally, and is relatively short. The winter hair is slightly browner above and has a tan wash to the gray hairs on the underside. If light strikes from the proper angle, the pelage has a silvery cast which is more pronounced on the ventral surface.

Length of Hair:

The structure of the pelage was examined in an attempt to learn a method other than gross observation for confirming the seasonal stage. At first, a simple measurement of the hair *in situ* was tried, but found exceedingly difficult of interpretation.

Plate XVII shows measurements made microscopically under 25 power magnification of the longest hairs on tiny excised pieces of skin from prime pelts as these hairs lay naturally and unstraightened on a glass slide. The hair lengths seem to vary erratically, but a general trend is evident with the hair in the summer shorter than that of the cold-weather months. The extreme measurements perhaps can be explained by individual variation in time and speed of pelage change. This graph suggests that the winter male pelage develops more rapidly than that of the female, but the hairs have a shorter maximum length. Little difference is indicated between the male and female summer pelage. The same graph demonstrates that maximum pelage development is not a rapid affair. The new hair of the summer pelage continues to grow for about one and one-half months, while the winter pelage hairs elongate over a two-month or longer period, gradually increasing in length after the pelt is first prime. The winter hairs add approximately a millimeter in the males and two millimeters in the females; the summer pelage of both sexes increases about one-half millimeter in length. The graph also shows that the new winter

pelage is about the same length as the old summer pelage, making a simple measurement an unreliable criterion, especially in the late summer or early fall.

The majority of the hair of Blarina has the structure of exceedingly fine underfur with the zig-zag bends present on all save a very few straight hairs. Individual hairs from representative specimens were measured along their axes to determine whether the crinkled structure could be masking greater differences in length, but such was not the case; the hairs measured in this way yielded only slightly greater measurements than those measured coarsely. This can be seen with a comparison of the data in Table 3 with those in Plate XVII.

A seasonal difference in both pelage and hair structure was found. The underfur of the summer and winter pelts was basically similar, but the shorter summer hair invariably had fewer of the zig-zag bends. The typical summer underfur from the middorsal area usually had five major bends; the comparable winter hair had six or seven major bends. This difference is illustrated in Plate XVIII and Table 3.

Types of Hair:

Several different types of hair occur on a typical Blarina pelt. These are described and the structure of the crinkly underfur is covered in considerable detail below.

Vibrissae

The smooth vibrissae on either side of the rostrum, 2 - 12 mm. in length and 0.04 - 0.07 mm. in greatest diameter, are only sparsely pigmented. The medullary area is scarcely evident except near the base where a few very narrow (about one-twelfth the shaft diameter) and irregular air spaces are periodically seen.

Eyelashes

The straight eyelashes are of two types: a moderately pigmented type without medullary air spaces, most of them 0.8 - 2.0 mm. in length with a rather constant diameter averaging about 0.015 mm., and a more heavily pigmented, longer type 1.7 - 2.4 mm. in length with a diameter of about 0.05 mm. at mid-shaft, tapering to about 0.013 mm. at the skin and to a fine tip distally. This latter type of eyelash is medullated throughout most of its length and is most heavily pigmented at the proximal end, lacking cortical pigment at the proximal end; it appears much like the apical segment of the underfur hair type A_1 described below. The ventrally directed eyelashes are heavier above the eye than below and have interspersed a number of short (about 0.3 mm.), fine, straight, virtually unpigmented hairs. The attitude and arrangement of these hairs probably have functional value in keeping soil out of the eyes.

Guard Hairs

Guard hairs(Plate XVIII, Figure 1) are present but

not common. Most are relatively long--5.5 - 7.5 mm. in length--and are enlarged subapically, the maximum diameter of about 0.036 mm. being approximately one-quarter the distance from the free tip to the base. These guard hairs taper evenly with no abrupt diameter change at any point. The cortical pigment is limited to the distal half and gradually decreases in amount down the shaft from the darkly pigmented tip. The medulla occupies about one-third of the shaft diameter and its pigment, separated by the short, wide air spaces, gradually diminishes toward the base. The guard hairs of the body are most numerous on the back where they comprise about one per cent of the total pelage. The rather sparse guard hairs on the tail are longest at the tip and shortest on the ventral surface; they are 1.2 - 4.5 mm. long, and most have an enlarged portion, nearer the tip than the base, of about 0.035 mm. maximum diameter. These tail hairs are heavily pigmented throughout and have a well-developed medulla occupying about one-third the shaft diameter.

Underfur

The crinkly underfur is made up of several basically similar types of hair. Each has an unpigmented and unmedullated basal portion which is considerably shorter in the summer than in the winter pelage and is 0.4 - 1.0 mm. long. Above this region, the medulla is present containing both air spaces and alternating clusters of pigment which gradually increases in amount distally. The surface cuticular

layer with its easily observed imbricated scale pattern is without pigment. Between the medulla and the cuticle lies the cortex, pigmented only at the distal end of the hair. The medullary air spaces and the sparse medullary pigment within the long proximal portion of the hair yields a silvery-gray color, whereas the apical region with the pigmented cortex produces a brownish-gray hue having a faint silvery or whitish cast.

Varieties of Underfur:

The long proximal portion of each hair of the underfur has alternating, long, relatively wide regions and shorter constricted portions where the medulla is usually still evident but very narrow. At each constriction the hair shaft bends at an obtuse angle, affording the gross crinkly appearance. Usually these angles coincide with those of the neighboring hairs to give the pelage a subsurface wavy pattern when the hairs are parted. Although the total length of various underfur hairs differs, the size of this long proximal portion of the hair remains about the same throughout each pelt.

The different underfur hair lengths result primarily from the type of apical segment on any given hair, and the differences among these tip segments are used here as a basis for categorizing the underfur types.

The two major hair types, here named as type A and type B, are separated on the basis of the size and the curvature of the apical segment. Hair type A, whose apical

segment is longer, wider, and usually recurves slightly with respect to the most distal bend of the hair, is subdivided into two categories, A_1 and A_2, between which there is a virtual absence of intergradation. Hair type B, with a shorter and narrower apical segment that decurves slightly relative to the most distal bend of the hair, is subdivided into types B_1 and B_2; and although the majority of the hairs falls within these two groups, some intergradation exists.

Underfur Type A_1

Type A_1 hair (Plate XVIII, Figures 2 and 3, and Plate XIX, Figure 1) has a very long apical segment averaging about 2.75 mm. long and 0.038 mm. in greatest width, which occurs about one-third the distance from the apical to the proximal end. This segment tapers gradually to a fine point at the free end and narrows to about 0.0067 mm. in diameter at the proximal end. About 60 per cent of the shaft diameter is occupied by the short, wide central medullary air spaces separated by narrower pigment clusters of similar length. The entire medulla appears from the side much like a fossil crinoid stalk. Near the distal end of the segment these air spaces become rounder and less closely packed and occupy progressively less space as they decrease in size. At the proximal end of the segment these spaces are compressed rather abruptly into a narrow solid line in the constricted region at the most distal bend of the hair. The brown pigment in the cortex of these hairs is primarily in the distal two-thirds of the apical segment and it

becomes denser toward the free tip. This type of underfur is the longest, measured along the main axis, to be found generally over the body surface. It averages 5.85 mm. in length in the summer pelage.

Underfur Type A_2

With a few minor exceptions, type A_2 hair (Plate XVIII, Figure 4, and Plate XIX, Figure 2) has a shorter apical segment than, and looks much like a junior version of, type A_1. The segment here averages 1.68 mm. in length and 0.024 mm. in greatest diameter, about two-thirds the average dimensions of the type A_1 underfur. This hair is thickest near the center of the segment and the medulla occupies only about 50 per cent of the shaft diameter. The cortical portion of the segment is pigmented, except at the extreme proximal end, with the pigment, again, most dense near the free tip. This hair type averages 5.62 mm. in length, measured along the hair axis, in the summer pelt.

Underfur Type B_1

Type B_1 hair (Plate XVIII, Figure 5, and Plate XX, Figure 1) has an apical portion averaging 0.9 mm. in length and 0.016 mm. in greatest diameter. The widest part of the segment is the even middle portion which tapers at each end. The medullary air spaces, separated by squarish pigment deposits and making up about one-half the shaft diameter, are rectangular and not as closely packed as in the preceding hair types. The cortical pigment is primarily in the terminal half and most dense at the tip.

Underfur Type B_2

Type B_2 hair (Plate XVIII, Figure 6, and Plate XX, Figure 2) has the shortest apical segment, averaging 0.5 mm. in length and 0.0085 mm. in greatest diameter. It appears to be even in diameter except for the slight taper at the proximal end, where the hair constricts and bends, and at the pointed free tip. The medulla extends only halfway to the free end and consists of elongated pigment clumps irregularly separated by very small air spaces; it occupies barely 30 per cent of the shaft diameter. Cortical pigment is scattered throughout the segment, but is progressively most dense at the free tip. In all other underfur types, the straight segments between the bends of the hair become progressively shorter as the proximal end of the hair is approached. Here, to the contrary, the second segment below the apical portion is always longer than the segment just above it.

Comparison of Pelages:

By referring to Table 3, it can be seen that the winter pelage not only has underfur of greater average length, but also that the structure of those hairs differs. Hair type A_1, for instance, has an apical segment almost 0.4 mm. longer in the winter than in the summer pelage. The apical segments of types A_2 and B_1 hairs are not significantly different between the seasons, but those in hair type B_2 do average about 0.1 mm. longer in the winter. In

all underfur types the maximum diameter of the apical segments averaged greater in the winter than in the summer pelage. Further, the hairs of the winter pelage consistently had a larger number of major bends.

Obviously, the longer and more angled winter hairs would afford a greater degree of insulation than the shorter summer hairs with fewer bends. Of unknown significance is the fact that the winter pelage has about ten per cent more of the hairs with heavier apical segments than does the summer pelage. This may have some adaptive value, but the difference does not seem great enough to afford much increased protection. It is possible that the larger number of coarse tips might stiffen the pelage somewhat, thereby decreasing possible matting and augmenting the effectiveness of insulation. Or, since the coarse tips undoubtedly afford some protection against abrasion, the increase in these may serve as increased protection of the rest of the pelage when the animals are pushing through icy vegetation, snow, or when using frozen runways and burrows. These stiff segments may also protect against wetting which could easily prove fatal during the winter.

Also of unknown value is the fact that the pelage is slightly browner during the winter than in summer. The increased numbers of heavily brown-pigmented underfur hair types A_1 and A_2 are primarily responsible for the slight color difference.

TABLE 3

MEASUREMENTS OF THE UNDERFUR HAIRS OF BLARINA TAKEN FROM TYPICAL MID-SEASON SUMMER AND WINTER PELTS

Type of Hair	Averages Summer Pelts	Winter Pelts
Length of Hairs Measured Along Axis (average of 5 hairs from each of 4 pelts)		
Type A_1	5.85 mm.	7.78 mm.
Type A_2	5.62 mm.	7.32 mm.
Type B_1	5.37 mm.	7.14 mm.
Type B_2	4.99 mm.	6.81 mm.
Length and Width of Apical Segments (average of 10 hairs from each of 5 pelts)		
Type A_1 (length)	2.73 mm.	3.12 mm.
Type A_1 (width)	0.0375 mm.	0.0400 mm.
Type A_2 (length)	1.68 mm.	1.72 mm.
Type A_2 (width)	0.0236 mm.	0.0249 mm.
Type B_1 (length)	0.91 mm.	0.88 mm.
Type B_1 (width)	0.0162 mm.	0.0167 mm.
Type B_2 (length)	0.47 mm.	0.59 mm.
Type B_2 (width)	0.0083 mm.	0.0089 mm.
Number of Major Bends Along Hair Axis (10 hairs each from 5 pelts)		
Type A_1	4-5	6-7
Type A_2	4-5	6-7
Type B_1	5	6
Type B_2	5	6
Percentage of Underfur Hair Types (average of all hairs in small sections of pelts removed from middorsal surface of 4 pelts)		
Type A_1	19.5	24.5
Type A_2	20.5	22.0
Type B_1	18.0	22.0
Type B_2	42.0	31.5

Regional differences occur within the pelage of an individual, not only in vibrissae and eyelashes, but also in the proportion of the types of the underfur. Comparison of various parts of a pelt from one individual in summer pelage yields the following: The rostrum has a much greater proportion of type A_1 hairs than any other part of the pelage, and all hairs here have considerably shortened proximal portions. The chin has a larger number of types A_2 and B_1 hairs than the middorsal back region. On the dorsal head surface, hair types A_1, A_2, and B_1 are proportionately more numerous than on the middorsal back. The hairs of the rump are longer than those of the mid-dorsum, and the apical segments within any type of underfur are longer. On the side, the straight guard hairs are as numerous as in the mid-back and the proportion of B_1 type hairs is increased. On the ventral surface the hairs are shorter and an increased proportion of types A_2 and B_1 are found.

Apparently, wherever abrasion is greatest, the proportion of coarse underfur types increases. The back shows the longest hairs of the pelt and this might be associated with the behavior during sleep; Blarina commonly sleeps curled up so that the most exposed part, the back, would have need of the greatest insulation.

Grooming of the Pelage:

My captives usually kept their pelage well groomed and were frequently seen either scratching, nosing, or

licking their hair. As indicated by Rood (1958), those areas which cannot be reached well with the nose or mouth are groomed with rapid motions of the feet. In the wild, similar care is undoubtedly given the hair.

After some time in captivity, however, the pelage often acquired an oily appearance with individual hairs often matted in clusters, especially on the middorsal rump and over the shoulders. Blarina is apparently unable to keep these two areas as well groomed as the rest of their pelage; ectoparasites were more abundant here than elsewhere in both captive and wild-caught specimens. In the latter, the rump hairs were similarly least well groomed but the pelage never exhibited this oily appearance, and I suspect that when wild shrews travel through their burrows or push through the leaf-litter, the abrasion of the tunnel walls, leaves, or duff aids in conditioning the hairs above the shoulders and, to a lesser extent, of the rump.

It is my impression that the longer an animal is maintained in captivity, the less grooming it performs. Abundant food and considerable storage of fat during captivity may result in excessive secretion by the sebaceous glands in the skin, causing the aforementioned matting. In the wild, the soil and litter undoubtedly absorb oils from the hair; in captivity, such opportunities would be fewer and the hair would become oily even without increased secretion by the sebaceous glands.

Molt and Hair Replacement

The literature accounts of pelage change are somewhat confusing. Townsend (1935) stated that of 742 individuals of Blarina trapped in New York from early June through late August, only one specimen was noted as showing any molt, a male taken July 10. Hamilton (1940b), after having observed over one thousand specimens in the flesh, stated: "...With this large number, it is quite remarkable that only 25 molting individuals have been secured."

Not only do past authors remark on the paucity of molting Blarina, the opinion of Hamilton (1931) that molt is without regard to season has been quoted by a number of others. Hamilton did state (1931) that most change from the winter to the summer pelage occurs in May and June, while most of the change to the winter pelage occurs in October and November. He expressed an opinion (1940b) that since so few specimens exhibit molt, it is probably "...a very rapid affair and must be consummated in a very few days." The fact that captive animals took six weeks to accomplish this process was considered an unnatural situation caused by the influence of captivity.

The data in the present study suggest an entirely different set of conclusions. As mentioned previously, skins were saved whenever the pelt was in acceptable condition. In some cases the hair was slipping badly or ruined by insects, and occasionally a trapped specimen was

spoiled by another animal eating it before the trap was visited. However, no intentional selection was practiced which might result in saving primarily pelts showing molt.

The term molt is used here in a rather broad sense. Strictly, molt involves only the loss of hairs but this loss is accompanied by a simultaneous replacement by new hairs. In the early stages of pelage change in Blarina, the old hair is lost in a salt-and-pepper fashion and the actual loss of the individual hairs is virtually impossible to recognize. One captive shrew whose hair was bleached prior to molting showed new unbleached hairs appearing among the old, but this portion of the pelage appeared no denser than the neighboring areas; thus, the older hairs were being lost but recognition of this early stage of molt could not have been detected by gross examination of an unbleached animal. Because of this difficulty in detecting the actual loss of a few hairs when molt is beginning, indirect evidence was necessary for the recognition of the onset of molt.

Dark pigmentation of the hair follicles, which can be seen only on the undersurface of the skin, indicates the presence of developing new hairs. The new hair, within any single follicle, apparently begins developing in the region of the papilla while the older hair is still held within the upper follicle walls. The old hair is thus not actually lost until the new hair is partially developed within the same follicle. The dark areas which can be seen

on the undersurface of the skin and which mark the growth of new hairs, thus, are indicative of the onset of molt. Although I have little evidence on the actual time sequence between development of pigmentation and the actual loss of the loose hairs, this period cannot exceed two or three days because of the rate at which molt progresses. Since the process of molting or hair loss is so closely associated with the development of new hair and, indeed, the development of new hair is dependent upon the separation of the root of the old hair from the papilla of the follicle, the beginning of molt and the beginning of new hair growth are essentially one and the same. Molt, thus, is considered here as the time between visible pigmentation on the undersurface of the skin and the final loss of the old hair.

Evidence of molt:

Plate XXI shows that the number of pelts in some phase of molt (59) almost equals the number of prime pelts (56). Had only the hair side been available, it is certain that the number of skins classified as molting would have been far fewer. The location of molt evidence is shown on this same graph, i.e., whether the molt showed on the skin side only, the hair side only, or on both pelt surfaces. This is an important consideration because much of the data used here was obtained from the skin surface which is not available on study skins. Of the 59 pelts listed as molting, only 21 had any evidence of that molt showing on the pelage surface and molt in many of these 21 skins was so

obscure that its presence on the pelage surface was found only after examination of the skin side of the pelt indicated where to look.

The difficulty of finding molt on the hair side is shown by the data of Hamilton (1940b). After examining at least 50 individuals from each month of the year, he listed only 25 showing molt distributed by month as follows: March - 5, April - 1, May - 1, June - 9, July - 3, August - 2, October - 1, and December - 1, plus two captives he did not consider as normal.

In most areas, the pelage changes gradually and much of the new hair is present before the remaining old hairs are lost. This, by itself, could account for the low number of molting individuals recorded. Adding to this difficulty is the fact that in the fall molt, the majority of the summer hair is not lost until the interspersed winter hairs have grown to approximately the same length; this assures that no abrupt change in hair length occurs and only color and texture can be used to grossly distinguish a fresh or molting pelt in the fall. These factors could easily account for a failure to notice this molt.

The spring molt is the more obvious; almost all of Hamilton's records (1940b) involve this molt to the summer pelage. During this molt the long winter hairs are lost when the new hairs are still quite short, and the abrupt difference in length is easily noted. The possibility exists, of course, that the shrews Hamilton studied from

New York have a molt pattern unlike that in southern Michigan.

The skin surface shows darkened areas wherever the development of new hairs is in progress; this dark coloration results from the pigment in the developing hair shaft and undoubtedly involves the germinating cells in the outer hair sheath of the follicle. Once the old hair has been lost and the new hair has grown out, the pigmentation disappears. This loss of pigment indicates that it was associated with the cells only early in the hair development and that pigment formation stops, at least in Blarina, well before the hair reaches its maximum development. Enforcing this hypothesis is the fact that the extreme proximal portion of the hair, which continues to elongate until maximum length is reached, is entirely without pigment. Thus, the dark areas of the skin are present only during the time when the pigmented hair segments are produced. On microscopic examination of pelt areas which grossly appear just faintly gray, outlines of the new hairs can be seen embedded in the dried skin; the young hairs show up as speckled images because of the pigment cells present. These pigmented areas are evident long before any molt is noticed on the hair side of the pelt. This new hair grows in almost parallel to the skin surface, which explains why the new hair is difficult to detect until it reaches considerable length. In a number of instances, the new hair was seen only after close examination under magnification; it appeared

dense, fine, and tightly appressed to the skin.

Fall Molt:

The pelts taken in the current study indicate, with few exceptions, that the spring and fall molts are not haphazard processes. The spring molt is apparently basically a reverse of the fall molt, as is also true in various other species. Since the first molt that the adult or young adult shrews experience occurs in the fall, this is described first. Plate XXII, Figures 1-6, and Plate XXIII, Figures 1-4, illustrate selected stages of this fall molt.

The molt begins on the rump (Plate XXII, Figures 1 and 2) in either one or several spots and proceeds caudad on the middorsal surface and craniad dorsolaterally (Plate XXII, Figure 3). The lateral gland either serves as a separate molt center (Plate XXII, Figure 1) or it may be engulfed first by the molt spreading craniad on the dorsum and upper flanks (Plate XXII, Figure 5). A separate center may appear behind each ear or the large dorsal patch may extend forward to that area first. The molt then spreads ventrally around the lateral glands (Plate XXII, Figures 4 and 5) to the belly and onto the hind legs, while on the dorsum it spreads caudad to the tail. A new center now appears on the sides of the rostrum (Plate XXII, Figure 5). Another center develops on the forehead median to the eyes and this rapidly moves laterally and anteriorly, eventually merging with the molt progressing forward on the ventral and dorsal body surfaces. At this stage the entire skin,

except the forelegs and the dorsal aspect of the rostrum (Plate XXII, Figure 6) is molting. The molt then spreads to these last areas (Plate XXIII, Figure 1).

In general, the areas which begin molting first become prime first; compare Plate XXII, Figure 4, and Plate XXIII, Figure 2, noting that the molt began on the dorsal body surface in the lumbar region and that area is prime before the adjacent areas. Some areas molt more or less rapidly than their neighboring regions. For example, note that in Plate XXIII, Figure 1, the forehead has molted much more rapidly than the adjacent area. On the other hand, in Plate XXIII, Figure 3, note that the molt persists on the dorsal tail base, which usually begins molting at about the same time as the neighboring areas.

Within this general framework, considerable variation in speed of molt exists. This occasionally results in a pelt like that in Plate XXIII, Figure 4, in which the back and sides are prime before the molt has even spread to the ventral surfaces. Such variations have undoubtedly contributed to the past confusion regarding a pattern to the molt in Blarina.

It is my opinion that age determines, in part at least, the time of molt, since the skins of young animals appear in molting condition later than do skins of old individuals. Also, pregnant females molt earlier than non-pregnant females of comparable age. Females, in general, appear to molt at an earlier date than do the males of the

species. Lastly, captives do seem to molt more irregularly than wild animals, both pattern-wise and time-wise; captivity apparently delays molting. These inferences are not supported by sufficient data for any conclusion, but from the available evidence they seem justifiable.

Spring Molt:

The spring molt from the winter to the summer pelage is illustrated with selected specimens in Plate XXIV, and is essentially a reverse of the fall molt just described.

This molt begins on the dorsal rostrum (Plate XXIV, Figure 1) and spreads ventrally along the upper lip, but does not spread dorsally. It then extends to the chin and thence caudad on the ventral surface along the sides just below the ears; a separate center begins around each foreleg (Plate XXIV, Figure 2). The molt which previously spread caudad along the sides next merges along the ventral throat surface and extends farther posteriorly along the sides. This same area slowly extends dorsad in front of the ears to meet the separate molt center appearing between the ears on the dorsal head surface (Plate XXIV, Figure 3). The molting side region then extends to the hindlegs, slowly merges ventrally in the thoracic area, and spreads rapidly dorsad where it is met above the forelegs by the molt area on the forehead as it extends caudally. The spreading ventrolateral molt now meets midventrally in the abdominal area, then encircles the tail base and spreads caudally on

the tail (Plate XXIV, Figure 4). The entire animal is now either in the process of molting or has partially completed the change, except for the area on the forehead which slowly proceeds anterolaterally to complete the molt (Plate XXIV, Figures 5 and 6).

The cranial, dorsal lumbo-sacral, and caudal areas usually take longer to complete the molt than the rest of the pelt, and consequently longer hair patches are commonly found in these areas after the remainder of the pelage shows the new hair. Hamilton (1940b) pointed out this situation when relating the molt of captives to that of wild-trapped specimens: "The complete molt in two captives occupied six weeks; but it is noteworthy that in both instances most of the fur was renewed in five days, the old hairs of the rump only persisting for the longer period."

Rate of Molt and Hair Replacement:

Since the appearance of pigmentation on the undersurface is used as a criterion for the initial stages of molt, further information is desirable on the correlation between pigment formation and the loss of the hair previously present in that follicle. The ideal solution would seem to be a surgical operation permitting constant observation of the undersurface of the skin and a subsequent correlation with the loss of marked hairs. This would involve so many variables that the resulting information would have little value. For example, on the pelts of several individuals I found tiny, paired, darkly pigmented

patches on otherwise prime pelts. I suspect that these spots represented healed wounds, perhaps caused by the teeth of other shrews. If this is true, injury or scar tissue may affect normal molt. Intensive histological study of the hair follicles may supply the necessary data, but such has not been done to date for Blarina. Lack of this kind of information handicaps this discussion but some indication of the rate of both molt and hair replacement is afforded by the following observations on a bleached shrew.

One captive male Blarina was painted on several successive days with a ten per cent solution of hydrogen peroxide which was washed off each time after about ten minutes. This successfully bleached the pelage to a peculiar yellowish-tan. The animal was then closely watched for any evidence of molt. Since the new hair, replacing the bleached summer pelage, was a different color than the old, it was possible to detect the molt well before it could have been seen otherwise.

On October 27, approximately one and one-half months after bleaching, the first sign of molt was noticed when new hairs appeared sprinkled among the persistent old hairs of the summer pelage. Each day the animal was anesthetized in order to sketch accurately the extent of the molt. Six days later, approximately one-half of the hair had either been replaced or was at least sprinkled with new hairs. On November 3, about three-quarters of the dorsal surface and a little more than half the ventral surface appeared

prime with new hair. On this date the shrew died, apparently from an overdose of--or degenerative liver changes caused by--the vinyl ether used for anesthesia. After death the skin surface was available and in every region of the pelt which did not yet show any new hairs, the undersurface of the skin indicated the presence of developing hairs. The apparent prime areas of new hair showed no darkening of the skin. Had the animal lived, there is no reason to believe that it would have lost the small patch of old hair on the head and rump any faster than other captives which retained these slowly decreasing patches about three weeks. My specimens were kept in an unheated garage and those which Hamilton (1940b) described as retaining these patches of longer hairs for six weeks were kept in a heated building; the temperature difference might account for the difference in the rate of molt. Another captive Blarina, described by Williams (1962a), retained a line of molt across the mid-back from the second week of September until its death late in November.

The above suggests that visible hair replacement usually lasts for perhaps a month, but this does not imply that the entire process of molting or hair replacement occurs this rapidly. Referring to Plate XXI, approximately one-half the total skins show molt in progress. The inference from all these data is that the entire process--from the initial separation of hair root from the papilla in the hair follicle and the subsequent development of new

pigmented hair to the loss of the last old hairs--may well occupy an exceedingly long period of time, probably close to three months. If one wishes to consider that hair replacement is completed only when the new hair reaches maximum length, then even more time must be added.

Variations in Pelages:

There are differences in pelage which are caused by factors other than molt. Staining of the hairs is quite common and, with my specimens, those tunneling through soil rich in iron content usually had an overall rusty or ochre cast; much of this staining can be removed simply by washing in soap and water. The hair usually has a small amount of oil secreted by the follicular sebaceous glands and the scent glands. After a brief wash in benzene, specimens which previously appeared darker than others usually proved to be basically the same color. In spite of the fact that Blarina spends much of its time protected from bright light, a certain amount of fading does occur, causing specimens taken early during a given pelage to appear slightly darker than those taken late.

Hamilton (1939b) wrote that of over 2,000 Blarina he had handled, one and possibly two were the only albinos he had seen. He mentioned that it was not unusual to encounter specimens with small white or creamy spots on the flanks. Subsequent to Hamilton's paper, many others were prompted to write notes on similar examples. Murray (1939) recorded an albino Indiana specimen; Ulmer (1940a) described

one albino and one spotted specimen from Pennsylvania; Sime (1940) wrote about one and another probable albino from Connecticut; Ulmer (1940b) described an albino from Delaware; Williams (1962b) published a photograph of an albino from Vermont; and Hatt (1930), Hampe (1944), Christian (1947), Gentile (1949), Shapiro (1950), and Werner (1956), all recorded cases of either light-colored pelage or partial albinism. The above instances are far from exhaustive; many other records are scattered throughout the literature following Hamilton's paper. Albinism, light color phases, and white-spotted pelage are apparently thus present but rare throughout the range of Blarina. Further, the occurrence of partial or complete albinism is, from reports, very spotty and apparently some small populations exhibit a tendency for this variation.

Pelage Development in Young Shrews:

I was unable to successfully breed any captive Blarina and did not locate any nests of these shrews which contained young. The pelage of the young shrews is of interest here because this is apparently retained through the summer. The only published description of the pelage of these young animals is that of Hamilton (1929).

He described the early pelage development of a litter of Blarina in captivity as follows: He first mentioned hair when describing young between 36 and 46 hours old; these had vibrissae about one millimeter long and were otherwise pink in body color. On the fourth day he recorded a

lead color developing on the dorsum and this suggests the presence of active, pigmented hair follicles, but there was no hair visible on the surface. The first body hair was recorded on the eighth day; by the tenth day, all the body hair had emerged, and by the thirteenth day the young were described as well-furred. Hamilton wrote that his oldest nestling died at 22 days and fully haired, but that the eyes were not yet open.

Since the young probably leave the nest when they are at most about 30 days old, and none of these small shrews have been recorded as molting by any author, it is unlikely that this pelage, present at 22 days, would be replaced shortly after leaving the nest. According to the available data, this juvenile pelage is thus probably not lost until the fall molt. This molt might also be considered as a post-juvenile or pre-adult molt, but since usually no marked change in sexual condition occurs at this time, I prefer to use the term of fall molt.

Scent Glands and Heel Organs

Both the lateral and ventral scent glands of adult Blarina have been ably described by Pearson (1946). He wrote that, prior to his paper and excepting only two other authors, "...many authors referred to the lateral glands, but curiously, the ventral gland was not mentioned." Curious also is the fact that no author has ever mentioned the paired small structures, having the appearance of glands and here termed heel organs, just above the junction of the

tibia and astralagus on the lateral surface of the hindlegs.

Scent Glands:

The occurrence of the paired lateral and single ventral scent glands of the shrews I observed closely approximated those described by Pearson (1946). These scent glands were visible on all except one of my specimens and that individual had very recently given birth to young. Unlike Pearson, I was unable to correlate the reproductive status of each female shrew with the occasional poorly developed glands; vaginal smears failed to provide the data necessary for such correlations. Poorly developed glands, however, were correlated here with both pregnancy and lactation, and in captive animals these glands were less well developed than those of comparable wild specimens. Pearson disagreed with Eadie (1938) who found no reduction of gland size in sexually active females; my data support Pearson's observations.

The function of these scent glands is not clearly understood. Various authors have speculated that the odor from the glands serves for intraspecific communication, perhaps to bring the sexes together (Eadie, 1938), perhaps to keep them separated (Pearson, 1944). Of no conceivable value offensively, these glands may provide some degree of protection; the general refusal of Blarina as food by most mammalian predators is undoubtedly to the shrew's advantage, but this advantage is tenuous for, although not taken readily for food, the shrews are commonly killed, then abandoned.

Heel Organs:

The heel organs were not recognized until late in this study, and consequently insufficient data are available to formulate any definite correlations between their development and age, sexual condition, season, or other possible factors. It does appear, however, that neither age nor sex can be correlated with the development of these structures: they ranged from being conspicuous to poorly developed in both the young and adult males and females, including females which were lactating and pregnant.

A typical well-developed heel organ (Plate XV, Figure 1) is located on the lateral surface of the hindleg just above the heel, and is bordered by paired, elliptical, swollen ridges. It measures about 3.5 mm. in length and 2.5 mm. in width, and the long axis lies parallel with the tibia and fibula. In the center of the organ, between the swollen lateral ridges, a crusty substance, appearing much like a scab, is usually present. If this scab is removed (Plate XV, Figure 2), an oblong depression is left which contains a viscous, pale yellowish or pink fluid. In some of the depressions, blood was noticed after the scab had been removed. The organ and immediate surrounding region usually had a pinkish or reddish appearance.

In some specimens, such as that shown in Plate XVI, Figure 1, the organs were poorly developed and their locus had the appearance of a dry or slightly shiny, whitish, hair-free area. In Plate XVI, Figure 2, a moderately

developed heel organ is shown.

Grossly, these organs appeared to be glandular structures producing a mucous-type secretion which had dried to form a crust-like surface over the center of the organ. A few of these organs were sectioned, stained, and examined microscopically; no glandular structures were present. Instead, the concave, hair-free, central portion of the organ showed no epidermis and the free surface appeared to consist of rather dense collagenous fibers, continuous with and similar to the contiguous dermis. Having this structure, it is likely that the viscous material filling this depression in life was a mixture of blood and lymph. The tissue adjoining the organ was more highly vascularized than the skin elsewhere.

The histological appearance suggests the possibility that these structures might be infected wounds or areas abraded so severely that the epidermis is missing. The location of the area, on the exposed outer surface of the leg, would facilitate such abrasion but I find it difficult to understand why this area, if it is subjected to periodic or continual wear, has not developed a thick, cornified surface. The resemblance of the so-called poorly developed organs to healed wounds lends support to the hypothesis that the well-developed organs are, in fact, wounds.

If these organs are nothing but wounds, their relatively similar size, consistent shape and locus, and repeated occurrence is puzzling. Of 66 specimens examined

between July 5 and October 22: 12 had poorly developed heel organs resembling that in Plate XVI, Figure 1; 23 had organs which were moderately developed, as in Plate XVI, Figure 2; and 25 specimens showed prominent heel organs such as that in Plate XV, Figure 1.

If, instead, these organs represent some kind of gland, their structure is inconsistent with that of any known type. No odor was apparent, my data indicate their presence from at least early July through October, and they showed no correlation with any of the usual factors. The result is a confusing situation: a heretofore unknown structure of unknown cause and function.

THE SENSES AND COMMUNICATION

Blarina is active primarily in a microhabitat of reduced light and the development of its various senses seems well correlated with its environment. Its eyesight is relatively poor but, perhaps in compensation, the senses of touch and hearing are developed to a comparatively high degree. The sense of smell is apparently less well developed than that in many other mammals and no data are available on its sense of taste. Although most authors would concur with these generalizations, the degree to which some senses have developed is disputed.

Sight

Most authors are in agreement that eyesight of Blarina is relatively poor. Seton (1909) wrote, perhaps more poetically than others, of the Insectivora, "All the eyeless bug-hunters....are creatures that prey where eyes are of little use..." He continued, specifically about Blarina, "It has, indeed, exchanged its sight for better touch, nor has it lost in the bargain." Klugh (1921) suggested that the eyes were used "...only to avoid well-lighted situations." Manville (1949) held the opinion that the eyes could only distinguish light from shadow, and Rood (1958) commented that the eyesight was poor.

After watching Blarina leap directly at a jumping mouse (Zapus), Hamilton (1931) deduced that the shrew could see objects; and Brooks (1908), after noting a shrew jump to capture a cricket, claimed that the eyes are relatively good.

The main basis for disagreement lies in the lack of quantitative data, and my own observations would not contribute to any clarification of these differences in opinion. Assuming that all the reported observations are accurate, the conclusion is that the eyes of Blarina are able to detect at least broad shapes and movement.

Smell

Opinion regarding the sense of smell also varies. Stone and Cram (1905), Klugh (1921), Carter (1936), and Schorger (1947), all wrote that smell was a well-developed sense. Klugh was of the opinion that Blarina depended entirely upon its sense of smell when hunting for food; Schorger described a situation suggesting that a shrew had detected a piece of raw beef when separated from it by seven inches of snow; and Carter wrote of a shrew that climbed the trunk of an oak tree, apparently with the sole purpose of getting to a basket of suet six feet above the ground. Shull (1907) stated that Blarina can distinguish between empty and occupied snail shells by smell alone.

Hamilton (1931) believed that smell is developed to an average degree only and wrote, "Freshly killed mice, placed six inches from the floor of a shrew's enclosure,

apparently baffled the animal." The shrew repeatedly passed beneath the mice but could not locate them.

In agreement with Christian (1950b) who claimed that the nose was "...as much tactile as olfactory.", Rood (1958) observed that Blarina could not find mealworms at a greater distance than three inches, and that frequently they passed within an inch of a mouse without sign of recognition. Rood wrote, "...the sense of smell is not well developed, although shrews constantly twitch their noses and thoroughly sniff any strange object they happen to encounter."

When this shrew is foraging, the continual motion of the snout may be compensatory for its sense of smell rather than--as has been suggested--a reflection of a highly-developed sense. Further, some authors have proposed that the lateral and ventral scent glands produce an odor used primarily for intraspecific recognition rather than for protection; it is difficult to imagine why Blarina would possess such an odor which is strong and pungent, at least to humans, and apparently detected readily by many potential predators, if the sense of smell were keen.

A number of authors have remarked on the inability of a shrew to locate mice at close quarters and then concluded that the shrews have a poor sense of smell. I have witnessed this apparent lack of recognition many times but hesitate to attribute it to generally poor olfaction. First, Blarina may detect a mouse odor but, not associating it with

danger, or perhaps because of preoccupation, may simply ignore the odor. Second, it is not improbable that Blarina may be more sensitive to certain odor stimuli than to others and, based upon my own and published observations, the shrews might well have a higher threshold to the stimuli of mouse or vole odors than to the odors of insects or other of their usual prey.

Detection of Paraffined Mealworms:

To obtain some quantitative data on the ability of a shrew to detect odor, 60 mealworms were killed by freezing and one-half were dipped into hot paraffin to seal the larvae and prevent the release of any usual odor. These dead larvae were then scattered about the enclosure of a shrew which had been feeding on mealworms during the previous two weeks. Two days later the soil was sifted and 21 paraffined and 9 control mealworms were recovered. The shrew was not supplied with any other food during these two days.

Only 30 per cent of the paraffined mealworms were located and eaten in contrast to 73 per cent of the controls; the shrew apparently did not locate the prey as readily when the usual odor was absent. The paraffin may have had an odor of its own, but it is improbable that the shrew would associate any paraffin odor with that of the mealworm; the paraffin did not appear to inhibit feeding because the two paraffined larvae seen eaten were dispatched as readily as the controls. Almost one-quarter of the controls

were uneaten, suggesting that they were not located. This same shrew had, a week before, eaten 20 mealworms within a 24-hour period and had the controls been found, they would likely have been eaten. These figures indicate that both odor and sight are used in the location of prey and that odor is only moderately developed but more important than sight.

Hearing

Sound detection is well developed in this mammal; all authors seem in agreement. Shull (1907) believed this sense to be acute, but wrote that the animals became indifferent to repeated sounds except for that of bird wings which continued to send the shrew running for cover. Similar to Shull's experience with the sound of bird wings, I was able to get a response from my captive shrews, almost without exception, to a squeak from a mouse or another shrew or from human lips. Even when asleep, Blarina usually showed some movement though it seldom awoke. Seton (1909) wrote, "...**Blarina** is possessed of exquisite hearing, associated with which is a fine discrimination that stands between the creature and a world of false alarms."

When shrews are foraging they often emit a soft, barely audible, high-pitched twitter. This may be akin to a happy child whistling as he walks, but the possibility exists that this quiet twitter may have some function like the sonar system of bats and porpoises. If so, sound detection here would be much more sensitive than is currently

thought.

Detection of High-pitched Tones:

Some simple experiments were done to investigate the range of hearing in this animal. When the lowest note on a guitar (sixth or E-string, with approximately 164 vibrations/second) was sounded, the shrews did not react. A definite response, such as turning of the head or a momentary interruption or change of the previous behavior, was not seen until the tones reached a pitch (approximately 1312 vibrations/second) one octave above the pitch of the open first or top E-string. A sudden, sharp note was most effective. These highest tones brought only weak responses and were soon ignored.

A variable-pitch, silent-type dog whistle used at different settings yielded more positive results. At the lowest setting, which I judged to be about one octave above the highest tone of the guitar, a shrew usually responded by some movement. This response was more consistent as the pitch reached and surpassed my ability to detect the noise. The average human ear can detect sounds ranging from about 20 to 20,000 vibrations per second, and the shrew obviously was still receiving stimuli which exceeded my upper limit. I continued to raise the pitch until first my dog ceased to respond and then, at a still higher pitch, the shrew failed to respond further.

I lacked the equipment to measure these highest tones and consequently do not know the exact pitches which served

as stimuli for Blarina. Because some sounds were probably detected without producing any visible response, further work, such as conditioning experiments, is suggested here to determine what sounds are actually perceived.

The present fragmentary data indicate that a wide range of sounds, exceeding that of the human, may be detected by Blarina, and that only certain of these sounds may act as releasers.

Touch

The tactile sense of Blarina is at least as well developed as any other, excepting, perhaps, only hearing. Shull (1907) concluded that this sense was acute, especially about the vibrissae. Only when my captives were asleep did they fail to respond to a gentle poke to the body, but if the vibrissae or tail were touched, the shrews usually awoke.

The Tail as a Tactile Organ:

Hamilton (1939a) described the sensitive tip of a pocket gopher's tail which is used while running backward in a burrow. I suspect that an adaptation of this type, but of lesser degree, is present in Blarina. Captives were occasionally seen moving backward in a burrow against the glass wall of their enclosure, and each time the tail was moved erratically from side to side, usually remaining in contact with either the top or sides of the burrow. More extensive observation on the underground behavior of captives is required for confirmation, but the tail appears to be used as a specialized tactile organ.

Curiosity about the comparative sensitivity of the shrew's tail prompted a series of simple tests involving Blarina, a woodland deer mouse (Peromyscus), and a meadow vole (Microtus). The tips of the tails of these animals were brushed, successively, with a broom straw, a blade of dry grass, and a straight human hair. Each animal responded to the broom straw; the blade of grass drew responses from shrew and vole but usually failed to elicit a response from the mouse; and to the human hair, a response in the shrew was usual, rare in the vole, and absent in the mouse. It is, thus, likely that the tail of the short-tailed shrew is more sensitive, or has a lower threshold of response, to tactile stimuli than either of its usual associates in the wild, supporting the possibility that the tail may serve as a tactile probe within the burrows.

The sense of touch, in addition to its sensory function, has considerable influence on the motor response of the shrew. Blarina is highly thigmotactic. In captivity, a shrew usually appeared to prefer having its sides or back in contact with some surface; its rate of movement was greater when in the open center of the cage than when along the edges, and the shrew usually did not rest until under cover. A piece of clear glass was supplied a shrew in place of the usual piece of bark used for cover, and the shrew spent much of its time with its head near the edge and its body contacting the undersurface of the glass. When given a choice between resting or hiding beneath either the glass

or a dark box which was high enough to prevent contact above, the shrew was usually found beneath the glass.

Communication in Blarina

The Tail:

Both the voice and tail of Blarina can be used as an indication of the individual's reaction toward a situation. The tail is of lesser importance in this respect for it appears to indicate merely the degree of excitement: the greater the excitement, the more sharply arched over the back is the tail. Most of the time when Blarina is awake, its tail is held up with the tip pointing vertically, but under extreme excitement, such as suddenly encountering a strange shrew for the first time, the tail arches more sharply forward and the tip then points anteriorly or even slightly anteroventrally. Although eyesight is considered poor in Blarina, the attitude of the tail may be used as a sign stimulus for communication between individuals.

The Voice:

The voice indicates a wide variety of emotions and only when the shrews sleep are they silent. A possible contradiction to this latter observation was mentioned by Rood (1958) when he discussed a sound like the chatter of teeth, "This sound was also heard from a pile of sleeping shrews and was followed by the breaking up of the pile and sometimes a brief scuffle." His description suggests that

at least one shrew in the pile may not have been asleep. For most calls, the shrew tilts its head up and elevates its snout, drawing the latter back from the teeth, before any sound is produced.

Low-pitched Twitter

One of the most common sounds is that which I associate with interest and contentment; this resembles, according to Hamilton (1931), "...the drowsy twitter of sparrows." In my captives, this was heard when they were foraging, especially when exploring their freshly-cleaned cages. This low-pitched call is extremely soft and barely audible unless the observer is very close. I was unable to detect the sound when farther than three feet from the animals. It did not seem to be uttered often when the shrew was moving about a cage in which it was completely familiar, but if an earthworm or insect were introduced, the sound usually commenced.

High-pitched Squeak

Another common sound, thought by Rood (1958) to be the commonest, was described by him as "...a sharp, high-pitched squeak of annoyance or anger." I believe that this squeak is associated with surprise as much as any other emotion for it is voiced in varying degrees of loudness: very soft when a shrew encountered a beetle, very loud when coming upon another mammal, just prior to battle or retreat. This squeak is sharp, abrupt, and slightly higher-pitched at the start, falling about one and one-half notes before

its curt end. It lasts less than a quarter-second; it was apparently this sound which Seton (1909) described as "... a screech as sharp and fine as a needle." Townsend (1935), describing this call, wrote of the shrew "...throwing its head back and opening its mouth with each call."

Shrill Chatter

When extremely annoyed and apparently not frightened, a prolonged, shrill, scolding chatter was given, the extent of the call apparently proportional to the extent of the annoyance. This usually lasted between one-half and ten seconds. After the call began, it rose quickly to a slightly higher pitch and then, just before stopping, dropped slightly.

Musical Trill and subsequent Slow Chatter

A call, similar to the above, but having a more musical series of notes, seems to be associated with extreme excitement. This call involves high-pitched notes, each following the preceding so rapidly that the net effect is a trill with the middle portion of the call slightly higher than the beginning or ending. As with most other calls, excepting the low-pitched twitter and, perhaps, the unmusical chitter, the shrew throws its head back, curls back its lower lip and snout baring its teeth, and "sings." This call is commonly followed by a slower chatter and the combination was described phonetically by Hamilton (1951) as, "...zeeeee-che-che-che-che." The combination suggests a repetitive series of shrill notes which, before ending,

slows to the point that the individual notes which made the trill are separated from one another, are of lower pitch, and are individually distinct.

Unmusical Trill and subsequent Sharp Chatter

A variation of the preceding call begins as an unmusical, scratchy, grating ca-a-a-a-a-a followed by a high-pitched rapid series of tze-tze-tze-tze sounds. This pattern was usually heard when a shrew was deliberately provoked by my insistent poking with a pencil after removing the piece of bark from the cage so that the animal was without his usual refuge. I associate this call with the utmost annoyance coupled with frustration.

Unmusical Chitter

Another utterance was described by Pearson (1944) as "...a stream of dry, unmusical clicks which might be described as a chitter, similar to the sound made by a twig brushing against a bicycle wheel in which the spokes are loose." Pearson claimed that this is heard only when a sexually excited male is pursuing a female. Rood (1958) wrote that this sound was used by his captives as a warning or challenge, and that it was also heard from a pile of sleeping shrews just before they awoke. I have heard this call used by both antagonistic shrews and by males who were courting females. Its use in different situations indicates a relationship with excitement, sexual or otherwise.

Hamilton (1931) mentioned that the voice is developed at an early age; young voiced a "suckling note" when only

eight days old, and were capable of "juvenile chatter" by the twentieth day. I have not had the opportunity to hear either of these vocalizations.

The various squeaks, chatter, trills, and twitter of Blarina are sufficiently different to distinguish on a rough basis as has been done here, but the nuances are difficult both to detect and to describe. Were an oscillograph used in a study of Blarina voice, I have little doubt that many variations of the above calls could be recognized and correlated with the different probable emotions much more accurately than was possible here.

Odor:

I did not test odor as a method of communication, although some authors have speculated on its possible intraspecific significance. Odor does play an important role in the sexual life of other mammals and, I suspect, based on the behavior of males toward females during courtship, that in Blarina, females in proestrum may produce an odor which is attractive to males.

The ventral and paired lateral scent glands have been correlated with sexual condition in Blarina (Pearson, 1946); they are usually reduced in sexually active females and best developed in sexually active males. The odor emitted from these strong-smelling glands may provide for communication during the breeding season, but, if so, the details are obscure. Pearson pointed out that smaller

glands in sexually active females and the accompanying reduction in odor occurred "...at the very time when according to the theory they should be best developed." He proposed the possibility that scent from these glands functions to keep individual Blarina separated at times other than during the breeding season.

TRAILS AND BURROW SYSTEMS

Evidence for Presence of Blarina

Presence of Blarina in any area is most easily noted during the winter when a thin layer of snow covers the ground. At this time the characteristic tunnels or trails can be seen just beneath the surface and pushing up the snow, occasionally opening onto the surface, or imprinted in the shallow snow. During the rest of the year, sign can be located most quickly by searching for the surface runways just beneath the leaf litter in wooded areas, for tunnels just below or against the underside of logs, boards, or other debris, or by finding the runways coursing through grassy areas.

Sign of the Shrew:

Runways or tunnels alone are not proof of presence of Blarina since other species such as the meadow vole (Microtus) or the white-footed mouse (Peromyscus) are often the residents, and other species often leave more evidence of their presence than does the short-tailed shrew. Microtus will usually leave grass clippings somewhere along its route, and Peromyscus often leaves opened acorns or partially eaten seeds; of course, such signs do not imply the absence of Blarina. Usually, after careful searching, a

runway or burrow used by these shrews will yield such positive evidence as pieces of insects or the characteristic droppings of the species; when the scent glands of Blarina are active, a recently used path will often have the pungent, musky odor.

The diagnostic sign of Blarina is the peculiar type of dropping produced. These typically have a maximum diameter between 2.5 and 3.0 mm, a length of 9.0 to 12.0 mm, and usually they taper irregularly toward each end with a peculiar twisted or rope-like conformation. The other signs noted above are less distinctive; the rodent associates of the short-tailed shrew, although primarily herbivorous, will eat insects and in swampy areas the strong odor of the soil masks that of the shrews.

Description of Trails:

Only once have I identified the tracks of Blarina in any medium other than snow; these were imprinted in soft mud as the animal crossed a dirt road. In this instance, the animal was apparently hurrying across the open mud for no tail mark was seen; when Blarina moves rapidly, the tail is usually elevated.

In a thin substrate such as mud or thin snow, the trail is usually a double line of tracks with the footprints sometimes alternating, sometimes opposite, and occasionally appearing like miniature squirrel tracks if the animal has jumped. A tail mark is usually evident. Most of the trails I have seen suggest a waddling gait with the tail mark

weaving down the center between the rows of alternating footprints, the two rows approximately 7/8-inch apart measured between the centers of the prints.

The trails pictured in Plate XXV, Figures 1 and 2, were made by captives shortly after capture. Figure 1 shows a trail curving back on itself and then disappearing into a tunnel in the snow. Such tunnels often extend for long distances beneath the snow, even when the cover is barely an inch deep; these tunnels periodically open onto the surface where a trail will show for short distances, commonly less than two feet, before it disappears into the same or another subsurface tunnel. Figure 2 illustrates the appearance of a trail in two inches of snow. The path is about 1 1/4 inches wide, the two rows of footprints approximately 7/8-inch apart, and the tail mark is seen in part of the trail. Two of the commonest trails are shown, with both the opposite and alternating footprints. The general erratic pattern of most trails of Blarina is illustrated in Plate XXVI, Figure 1, an example of a trail entirely on the snow surface.

Identification of Trails:

No single feature will serve to identify trails as having been made by Blarina. The structure of the shrew, with its short legs and proportionately long body, is of importance here in that it delimits the type of trail which can be made; most locomotion consists of walking or running,

and seldom does the shrew progress by leaping. The trails made by the short-tailed shrews thus show primarily the double row of footprints separated by a weaving tail mark. The groups of four footprints each, associated with leaping, are seen but seldom. In deep snow a measurement of the width of the grooved path, and in every instance a measurement of the width between the parallel lines of footprints, will prove helpful in attributing the sign to Blarina; most of the mammalian associates would leave paths or trails of larger dimensions. The most useful criterion for trail identification here is the general pattern. Blarina seldom travels very far in any direction before changing course, and the trail usually has an erratic appearance.

Occupancy of Horizontal Strata within Habitat

Vertically, Blarina occupies four fairly distinct strata: 1) the surface of the upper litter, snow, or ground, 2) the litter and true soil interface, 3) a system of tunnels varying from one-half to about eight inches below the soil surface, and 4) a deeper tunnel system, usually ranging in depth between 10 and 20 inches and occasionally still deeper.

Surface Trails:

Evidence of use of the uppermost stratum is confined primarily to winter. When a thin layer of snow exists, it

is not uncommon to find the extensive surface trails randomly crisscrossing one another. I have one record of these trails covering a distance of more than 100 linear feet; the animal was exposed throughout. On a number of occasions I have seen Blarina scurry across a road or other open area during the daytime.

Blarina apparently spends more time than is generally supposed on the surface of the ground, either atop the leaf litter in wooded areas or on the ground surface itself when no leaf litter exists. Proof of this activity is difficult to obtain during most of the year, but during the winter months these trails are automatically recorded in the snow.

The random crisscrossing trails suggest the path of an excited child searching for Easter eggs in a relatively homogeneous park. Figure 2, Plate XXVI, shows such a Blarina trail made in thin, wet snow over a substrate of frozen sandy soil affording no escape burrows. Similar trails have extended over an area of more than 30 by 90 feet, and in many instances there were no signs of connections with underground tunnels. During the larger part of the year, when no such simple trailing method exists, it is likely that--at least to some extent--similar forays occur. Townsend (1935) tabulated figures of Blarina taken in three categories of trap placement: open (usually with two feet of open ground surrounding the trap), cover (with some overhead protection), and burrow (either in a burrow

or at a burrow entrance). Combining his figures for a four-year period, we find that about 10 per cent of the captures were made in the open, 30 per cent under some cover, and 60 per cent either in or at burrow entrances. There is more likelihood of an animal being captured in one of its regularly used travel routes than at some other point where it would encounter the trap primarily by chance; thus, I believe that the 10 per cent figure for captures in the open must represent an absolute minimum for the percentage of time spent by Blarina away from cover. This species is commonly taken by various raptors, and if the shrews spent as much time as is generally suggested hidden beneath the leaves or ground surface, they would seldom be included in the diet of these birds.

Litter-Soil Interface Trails:

Evidence of the time spent by Blarina beneath the leaf litter in the woods and the matted grass in more open areas is difficult to interpret. It is likely that during most of the year, foraging is done primarily between the ground litter and true soil. The only live wild Blarina noted during this study, exclusive of those released from traps or those crossing open areas, were occupied in pushing their way through the leaf litter in wooded areas. Remarkably few signs of their presence were found after they passed. Occasionally fresh shallow diggings suggested an attack on some insect or worm, but usually the shrew

left no visible trail. Thus, even though they are active in a given area, they leave relatively little sign. When the shrew population is high, many incised trenches or paths can often be found by brushing away the ground litter, and in some instances these trenches are as deep as six inches. When the shrews are not present in large numbers, these paths are fewer and more difficult to locate. It seems unlikely that generations of Blarina use the same pathways within the litter-soil interface; the soil floor of these runways is not noticeably compacted and these animals exhibit considerable originality regarding the paths they choose.

The photograph (Plate XXVI, Figure 2) of a second-growth wooded area with the leaf litter mostly removed reveals an incised runway system of Blarina averaging four to six inches deep. The soil was friable on both the floor and sides of the trench. It is apparent that this system resulted from a collapse of near surface burrows; where roots were numerous the supported burrow roofs remained. It may be that many of the shallower paths found beneath the leaf litter originated in the same way. That the shrews use these trenches was demonstrated by setting traps across the trenches; these showed relatively high success in capturing Blarina.

In the litter-soil interface, then, are actually two different types of paths: those used in random foraging which usually leave little or no record, and the incised

paths which are probably used mostly for travel.

Although no quantitative records were kept of the location and abundance of various potential food items for Blarina, it is my impression that the majority of insects and mollusks were present, at least during the non-winter months, within one-half inch of the litter-soil interface. In his study of an Illinois deciduous forest, Blake (1926) found that the greatest numbers of insects and other invertebrates were concentrated within the leaf litter and upper 10 cm. of the soil, between early October and early March. Since a large amount of the shrew's time is spent in feeding, it is logical to assume that most of it would be spent within this portion of the habitat, but because of the transitory record of most of the foraging paths taken by Blarina, the available sign will belie the probable extensive use of the litter-soil interface.

Subsurface Burrows:

Hamilton (1931), Townsend (1935), and Jameson (1949) all remarked on the two-storied systems of the underground burrows of Blarina. In spite of the fact that the upper level systems often connect with the lower tunnels by gradually sloping connectives, many of the connections are rather abrupt and the two systems seem distinct enough to warrant the separation.

Three burrow systems, each in a different habitat, were excavated after dusting flour on the interior walls to mark their courses. The sites were chosen because each had

produced specimens of Blarina. No attempt was made toward an exhaustive study of the tunnels; certain obvious differences among the surface signs present in the three areas generated the question of what subsurface differences, if any, might exist. One system, in the Crim Area, was in a relatively moist loam soil near the base of a ridge and about 200 feet from a nearby creek. Young elm saplings, black cherry, and red osier dogwood predominated. The second system, in the Greene Area, was a rather dry upland woods on somewhat sandy soil with oaks, black cherry, wild grape, and gray dogwood present. The third system was within the Railroad Area in clay soil adjacent to a shallow temporary pond bordered by a few elms, cattails, and sedges; upslope from the pond a grassy area merged abruptly into a ridge with bracken fern and sparse young oaks.

In general, the upper level tunnels were located down to six or eight inches below the soil surface, were approximately the same size in each area, and ranged from about one and one-quarter to slightly over two inches in diameter; most were elliptical in cross-section, wider than they were high, averaging one by one and one-half inches. The lower level tunnels, usually 10 to 20 inches deep, were larger than the upper tunnels and averaged about two inches in diameter. The shape of these lower level tunnels varied: some were rounded, others elliptical, both compressed and depressed. The possibility exists that at least some of these lower tunnels may not have been dug by

Blarina-- their size alone suggests this--even though they appear to be part of the Blarina system.

Underground Travel and Habit:

That shrews use underground tunnel systems has been accepted as fact by all who have studied these animals but, apparently, no author has questioned, "How?" There is little likelihood of light being present in the tunnels except, perhaps, in the immediate vicinity of an entry. The deepest reaches of the burrows would normally never enjoy the dimmest light and the shrews using these tunnels must, in consequence, travel without any assistance from their tiny eyes. No direct evidence is available on the manner in which the shrews navigate while below ground, but laboratory observations suggest an explanation.

Lorenz (1952), describing the behavior of captive Austrian water shrews, mentioned several instances of the unswerving habit displayed in the paths taken by his animals, especially after certain obstacles had been changed. These shrews habitually ran along the edge of their enclosure and, when they came to stones in their pathway, leaped over them and continued on. After this behavior was firmly established, Lorenz removed certain stones. The shrews, running along these usual paths, came to a spot where a stone had been and, although no obstacle still existed at that point, made their usual leap and continued on. In his description of this behavior, Lorenz wrote, "The preponderance of motor habit over present perception is a most

remarkable peculiarity of the water-shrew."

I have noted that when a shrew was moving about its cage and was suddenly startled, it usually ran quickly and directly to its nest beneath a piece of bark. Townsend (1935) reported a similar situation when describing a frightened captive Blarina in relation to the partially concealed opening to its nest: "It did not feel around or seek for the entrance under the stick, but each time ran directly to it without the least hesitation." Either of these examples might easily be explained on the basis of considerable familiarity with the surroundings.

Various shrews, kept in cages (12 by 18 inches) with a soil floor one inch in depth, a water glass, and a piece of bark approximately five inches square at one end, spent most of their time resting or hiding in a hollowed space beneath the bark. After each shrew had become accustomed to its cage over a minimum of one week, the bark was moved or removed, or another piece of bark added or substituted, while the shrew was occupied in feeding at the end of the cage opposite the refuge. The shrew was then frightened, occasionally by poking but usually with an abrupt, loud br-r-r-r-r made by vibrating my tongue in the manner that children mimic a machine-gun burst.

After the bark had been moved, even though closer to the shrew than before, the frightened shrew ran directly to the former position of the bark and began appetitive, or seeking, behavior. After moving about quickly for a few

seconds in the area where the bark had been, the search covered a wider area and, suddenly, the shrew appeared to notice the bark in its new position and scurried beneath it. Complete removal of the bark resulted in the shrew's racing for the refuge site, reaching it, excitedly searching an area a few inches in diameter for several seconds, and then investigating the entire enclosure in much the manner of a shrew newly introduced to a cage.

When an additional piece of bark was added to the cage between the feeding shrew and his usual refuge, the frightened shrew again ran to his usual hiding place. When a different, but roughly similar, piece of bark was substituted for the original and the shrew then frightened, the animal ran directly and without hesitation to the bark with no apparent recognition of any change.

When a shrew had been conditioned by a week's stay in a larger cage (16 by 24 inches), addition of a piece of bark caused a reaction different from that observed in the smaller cages. The usual refuge was at one end of this larger cage, the feeding position at the end opposite, and the new bark was placed about one-third the distance from the shrew to the refuge. When frightened under these conditions, approximately 70 per cent of the shrews raced for the accustomed refuge, the rest ran to the new piece of bark. Although unable to measure it, I have the impression that the more frightened the shrew was, the more likely it was to choose the accustomed refuge.

In the experimental situations described here, the learned travel patterns of Blarina hold precedence over visual stimuli. The presence of such behavior is suggestive of a similar basis for travel through the dark tunnels. The repeated use of the tunnels would permit the learning necessary for the development of motor habit and, while orientation within the tunnels probably involves use of tactile receptors such as vibrissae and the hairs of the body and tail, navigation may depend upon learned travel patterns or habit.

Description of Excavated Burrow Systems

In accord with the data presented below, the more moist the soil, the greater the number and the more intense is the use of the upper level or near-surface tunnel systems. In drier soil the lower system is apparently more highly developed.

Crim Area System:

The tunnel system in the Crim Area (Plate XXVII) proved to be the most complex of the three systems excavated. As was noted by Townsend (1935) in regard to a comparable situation, incised paths two to four inches deep crisscross the area. After brushing away the leaf litter and probing these trenches, I found a series of tunnels immediately beneath and often coinciding with the trenches above. Townsend observed this same feature and remarked, "...some of these passages were found to have a 'double-

decked' arrangement. At first sight they appeared to be mere trenches with a leaf-mold bottom, but occasionally a burrow appeared beneath the leaf-mold layer."

These trenches in the Crim Area were not open throughout. Where roots were dense or in some other fashion afforded support or protection, the line of the trench continued as a near-surface tunnel with no trench above it. This strongly suggests that these trenches resulted from tunnel cave-ins.

The upper level tunnel system, lying one or two inches below the floor of the trenches, had periodic vertical, round, one-inch-diameter holes opening upward into the trenches. The sub-trench tunnels showed many side pockets of about the same size as the tunnels; apparently many of these resulted when unused branches were plugged with loose soil. Other evaginations of the main system had walls of the same texture as the main route, and were perhaps produced when an earthworm was dug out. Apparently some of these side pockets were used as storage chambers for in two of them a few insect legs and elytra were encountered. One small globular side chamber, measuring two and one-half inches high by three and one-half inches in diameter, with a number of coarsely torn leaves and a few pieces of a snail shell on its floor, was at the same level as these sub-trench tunnels. This was apparently a resting nest of Blarina, such as those mentioned by Hamilton (1929) and Rapp (1945).

These upper level tunnels had surface entries which were spaced almost randomly, but closer than those described by Shull (1907) who wrote that these openings were from one to four meters apart. Shull also claimed that the burrows of Blarina led down from the surface at a rather steep angle. In the system described here, as well as the others excavated, I found that most of the burrows opened onto the surface at an angle of about 45°, sometimes less, with the horizontal. The holes which connected directly to a main route often did lead almost straight down, but I believe that these represent check-points through which a shrew can poke its nose to investigate the surroundings. These latter openings, approximately one inch in diameter, are smaller than the openings at the ends of tunnels and from observations on captives, I doubt that they are the usual access points even though their size is large enough to permit a shrew's passage.

The lower tunnel system was not traced to the same extent as the upper, primarily because of the difficulty in excavation. The connecting tunnels between upper and lower systems were rather steep, forming an angle of between 30° and 45° with the vertical. The lower tunnels ranged from 12 to 18 inches below the ground surface, and were not as extensive as the upper system.

Two chambers were found extending off the lower level tunnels, one apparently a breeding nest and the other a resting nest. The breeding nest, a hollow mass of

partially torn but not shredded leaves 6.5 inches in diameter, filled a chamber whose top lay 11 inches below the ground surface. About nine inches from the nest, a midden heap of Blarina feces was found at a wide spot in the adjacent lower level tunnel; because of the dark color of the soil and the flour used in tracing the system, I could not be certain of the extent of the feces. The resting nest was in a chamber 2.75 inches in diameter with its top 12 inches below the ground surface; it was filled with loosely packed, almost entire leaves and a small amount of grass.

Greene Area System:

The tunnel system in the Green Area (Plate XXVIII) was in dry woods and was less extensive than that in the Crim Area. The upper ground surface did not show any surface runways which were distinct enough to be traced. The upper level tunnels were mostly between one and eight inches of the ground surface and had fewer access points than those in the moist woods system. Where the tunnels coursed close to the surface, occasional vertical holes one inch in diameter opened upward, and where tunnel branches sloped upward to the surface, larger openings undoubtedly served as entry and exit points. These latter openings, usually elliptical, 1.25 to slightly over 1.5 inches across and about one inch in height, usually opened near some structure like the base of a tree or shrub, or a piece of bark or a log. These latter observations are similar to those

of Seton (1909) who described the many small one-inch-diameter holes opening from underground galleries onto the surface as well as slightly larger holes with a little fresh soil scratched out; the former went straight down, while the latter sloped.

The lower tunnel system was more extensive here than in the Crim Area and extended deeper, to about 22 inches at one point. Most of these tunnels, approximately two inches in diameter, coursed about 18 inches below the ground surface, were less tortuous than the upper level burrows, had fewer side branches, and showed relatively steep connections with the burrows above. Sixteen inches below the ground surface was an enlarged chamber containing a resting nest; the chamber measured 3.25 inches wide, 3.0 inches high, and 4.5 inches long. Partially torn oak leaves and grass were loosely packed around the perimeter. A few old feces, apparently of Blarina, were against the side of the tunnel adjacent to this chamber.

A rather large tunnel, 2.0 inches high and 2.5 inches wide, crossed beneath the upper level tunnels at a depth of about eight inches. This was probably made by a mole (Scalopus aquaticus), which gave other indication of its presence in the area. A short connection from the tunnel of Blarina above curved sharply down and entered this wider tunnel at the side. It seems obvious that this was a mole tunnel being used by Blarina.

Railroad Area System:

The excavation in the Railroad Area began at the edge of a cattail association and extended upslope into a mixture of sedges and grasses. This system, the simplest of the three investigated, is shown in Plate XXIX. Apparently the high water table precluded any double-storied pattern of the tunnels. Only near-surface tunnels, 0.5 - 3.0 inches in depth, were found and no plunge holes were seen that might have led to a deeper system. After tracing this near-surface system, a number of deeper holes were dug in hopes of finding any existing lower tunnels but none were located. At a depth of approximately ten inches, the ground became very soggy.

The course of the tunnels here resembled the erratic trail left by Blarina in thin snow (Plate XXVI, Figure 1) and indicated quite intensive use of the area. No nests of any kind were uncovered, and this absence may be correlated with the high moisture content of the soil. The shrews which occupied these tunnels undoubtedly had home ranges which extended upslope into the drier bracken fern-grass association, and any nests probably were located in the drier ground.

It is impossible to assure that the three systems described above were made by Blarina in their entirety. It is unlikely, however, that any of the shrew's associates--mammalian or others--were responsible for creating the upper system of tunnels which resembled so closely the

burrows made by my captive shrews. The larger tunnels of the lower systems may well have been made by moles; it is difficult to imagine how the shrews could excavate these large tunnels so far beneath the ground surface. Even if the lower system was not developed by shrews, the connectives provide access to both upper and lower systems and both are undoubtedly used. It would be instructive to excavate the tunnels of Blarina in an area where moles do not exist.

Nests of Blarina

Different authors have described various nests of this species, but generalizations are handicapped by the difficulty in ascribing these nests to the proper categories. Since they are usually located well below the ground surface, it has not been possible to directly study these nests in relation to the behavior of the shrews, and only fortuitous observations have been published. Blarina apparently builds two kinds of nests: one for breeding purposes, and one--usually smaller and simpler--as a resting nest.

Breeding Nests:

The breeding nests are usually rounded subsurface structures ranging from six to eight inches in diameter. Townsend (1935) described nests lying a few inches below the surface of a small mound, but at the same level as the surrounding ground; and Hamilton (1929) wrote of a nest

15 inches below the ground surface. I found a nest of this type with its top 11 inches below the surface of the ground. Thus, the breeding nest can occur, vertically, from a few to 15, or perhaps more, inches below the ground surface. The nests are found in a variety of locations beneath logs, stumps, or stones, or simply deep in the soil as was one in the present study and one described by Shull (1907).

The breeding nest is typically lined with leaves, sometimes with a little grass, and on rare occasions with some mouse hair. Shull (1907) wrote that he found nests composed of grass, sedge, nettle, goldenrod, and ash, and one entirely of meadow vole (Microtus) hair. The leaves in such nests are either entire or torn somewhat, but never shredded or crumbled. The mass of leaves generally has a central cavity about 2.25 inches in diameter.

With few exceptions, the breeding nests have at least two access tunnels; Townsend (1935) recorded four tunnels leading to a nest chamber. Several of the burrow diagrams by different authors show a tunnel partially or completely encircling the breeding nest. The same situation was encountered in the present study. Bourliere (1954), describing the work of Godet (1951), presented a burrow system diagram of the European mole which shows a pair of tunnels circling the nest chamber. These observations suggest the possibility of an interesting correlation of degree within the Insectivora between fossorial habit and nest-encircling tunnels.

Resting Nests:

The resting nests, 2.5 - 6.0 inches in diameter, vary in location. Rapp (1945) recorded a resting nest inside a log; Eadie (1944) described what was probably a resting nest situated in a depression in the ground; Richmond and Rosland (1949) mentioned probable resting nests found against the underside of boards in a field; and others have been reported as occurring beneath the ground surface at various levels, as in the present study. I found this type of nest in chambers off both the upper and lower tunnel systems.

Hamilton (1929) described these nests as about the size of large apples, made of anything handy. The chambers containing these nests are usually not as well filled with leaves as are those of the breeding nests. Rapp (1945) stated that a nest in a log had a little grass in the bottom; those found in my study were sparsely fitted with leaves forming either a bowl-shaped structure or a loose globular nest; and Eadie (1944) described a globular grass-lined nest. These resting nests are apparently merely simplified, smaller versions of the breeding nests.

Jameson (1949) pointed out that since burrows are deeper than necessary for concealment, other factors are undoubtedly responsible for their development. Both Pruitt (1953) and Jameson presented data showing the constancy of the subsurface environment with respect to both temperature and humidity.

Sanitation:

Observations on sanitation in Blarina in the wild are few, most reports dealing with captives. I found one midden heap, mentioned earlier, 17 inches below ground surface against the side wall of a tunnel and approximately nine inches from a breeding nest. I saw no evidence of any feces in the leaf-lined nest and have found no mention, by any other author, of feces in any nests in the wild. From such negative evidence I judge that the sanitary behavior observed in captives applies equally to wild shrews.

Writing of three species of British shrews, Crowcroft (1951a) stated, "These...defaecate almost every minute while awake, but always select a principal lavatory well away from the nest, which is itself kept quite clean." Hamilton (1929) described captive short-tailed shrews that fouled their water and dropped feces about their cages but never in their nests. Describing wild Blarina he wrote, "About the nest, the scats are piled to one side of the runway." and of one captive that had a litter of young, "...[she] rarely ventured from the next box to deposit her feces, but dropped them in the corner of the box, much after the manner carried on in the wild state." Hamilton did not give the size of the next box which is of importance here.

When cages were outfitted for my first captives, a glass dessert dish was used as a water container, but the water was usually soon fouled with dirt and feces and the

dish often overturned as the shrew attempted to crawl beneath it. This was replaced by a jigger glass embedded in mortar which the shrews were unable to upset, and the smaller-sized container discouraged fouling the water. When a shrew had been placed in a fresh cage I sometimes noted feces in the open center portion of the cage but most captives defecated in one corner of their cage, usually that farthest from the nest; on occasion they left feces next to the hardboard or glass sides of their enclosures.

In captivity, Blarina apparently prefers to defecate in close quarters such as a corner, against a wall, or next to some structure like the water container. Scats of wild Blarina were collected by Eadie (1948) on four-inch-square papers which were "...placed in small mammal runways where possible, but otherwise in any likely spot such as at the bases of grass tufts." The placement of these papers afforded Blarina proximity to a surface or structure similar to the situations preferred by captive shrews.

The tendency of captives to deposit feces in a heap, rather than scattering them at random, may reflect the same basic behavior pattern suggested as being present in wild shrews, that of using midden heaps near the nest. Confinement, either in a tunnel system or in a cage, may cause such behavior and, until a shrew has thoroughly investigated a new cage and learned that confinement exists, the feces would be scattered. The captive female that deposited feces

in a corner of her nest box (described by Hamilton, above) may have had a sufficiently large box to permit the deposition of feces, as far as the female was concerned, outside the nest. The apparent preference for close quarters during defecation might be explained as a positive response to thigmotactism.

Blarina does not choose any specific place in which to urinate, this process depending upon wherever and whenever chance dictates. On waking, most of my captives seemed habitually to urinate shortly after leaving the nest and one, when disturbed, often urinated slightly while waking. This latter animal often slept on its back with its posterior third projecting from beneath a piece of bark, facilitating observation.

REPRODUCTION IN THE SHREW

The majority of the information previously available on reproduction in Blarina has been provided primarily by the work of Hamilton (1929) and the detailed study of Pearson (1944). Other data are scattered throughout the literature. I have summarized and added to the previous information and, based on my own data and those of others, have suggested modification of some previous concepts.

Sexual Maturity

The Female and the Estrus Cycle:

Blarina is a seasonally polyestrus species in which the female is obliged to undergo repeated copulations before ovulation begins. If the female is not mated at estrus, she may continue to be receptive to males for a month or perhaps more, but becomes non-receptive a short time following ovulation. Usually, ovulation will occur two or three days after the first mating and, following this, the shrew may experience a rare pseudopregnancy which lasts nine or ten days. A normal pregnancy lasts between 18 and 20 days and Pearson (1944), who determined much of the above information, found no indication that his captive females would breed within two or three days following parturition.

Frequency of mating

Pearson recorded captives which both would and would not breed a second time during a season, and he found that mating will recur following the loss or weaning of a previous litter. He reported one female which became receptive to males--ostensibly indicative of the proestrum period--three times between early April and mid-July; he judged that had pregnancy resulted, this female could have raised three litters before the end of August. The shortest interval, listed by Pearson, between normal parturition followed by nursing and remating was 21 days. The female in this instance was still caring for her litter but apparently not nursing when remating occurred.

There is considerable disagreement regarding the existence of a normal post-partum estrus. Pearson (1944) claimed that since shrews will mate shortly after a litter has been destroyed or lost, the lactating pregnant shrews mentioned by various other authors, "...merely indicate that it is possible for a shrew to produce more than one litter, but they do not prove that there is a true post-partum estrus." Pearson's captive shrews showed no indication of receptivity shortly after normal parturition, but those females that had lost a litter usually remated within four days after the last young died. Pearson wrote, "...true post-partum mating and pregnancy during lactation rarely, if ever, occur in Blarina. Remating depends upon

the loss of the litter."

My data, Plate XXX, Figure 2, show two lactating gravid females, one taken June 27 with five 12 mm. (crown-rump measurement) embryos, and one taken August 25 with five 13 mm. embryos; in both instances, the mammary tissue was well developed and I was able to express milk from the nipples easily. The embryo measurements indicate that parturition in these two females was about a week distant; the mammary development, therefore, was due to a prior pregnancy and the previous litter was either still suckling or had only very recently been weaned.

Five females, of the 207 shrews trapped by New (1959a), were described as pregnant and still nursing previous litters. Hamilton (1949) wrote that his field notes between 1929 and 1941 show numerous instances of lactating gravid females and that, "I have always considered this condition a perfectly natural one in shrews." The evidence favors the existence of a post-partum estrus although a valid conclusion is impossible without further data.

Gestation Period

Most authors list the gestation period of Blarina as 21 days, the figure listed by Hamilton (1929) as a minimum period, and based on the fact that a litter was produced 21 days following the last contact with a male. Pearson (1944) wrote that ovulation occurs between 55 and 71 hours after the copulation stimulus threshold has been reached; the gestation period in Blarina, therefore, is

not simply the number of days between last contact with a male and birth. On the basis of considerable data, Pearson concluded that the gestation period of the short-tailed shrew lies between 18 and 20 days.

Vaginal Smears and the Estrus Cycle

Vaginal smears were collected from a number of kill-trapped specimens in various stages of sexual activity with hopes of correlating the estrus cycle with the smears. I had the same difficulties that Pearson (1944) experienced; he wrote, "The results were not encouraging, however, because cornified smears that seemed to indicate estrus were usually obtained, yet these same individuals habitually refused to mate."

In the initial estrus cycle stages of most mammals, the vaginal epithelium, under the influence of estrogens, proliferates in much the same way as the uterine endometrium. The surface layers of the vagina, when growth is most rapid, become cornified and a smear should contain a mixture of cornified and nucleated cells. At the time of ovulation when the estrogen level is supposedly highest, the vagina reaches maximum cornification. After ovulation, if no fertilization occurs, declining estrogen levels are accompanied by degenerative changes in the vagina and leucocytes become abundant. If the ova are fertilized, cornification is retarded by progesterone levels and the smear should contain primarily nucleated squamous cells and leucocytes.

In general agreement with the above, Pearson (1944) found from vaginal sections that cornified cells were abundant at estrus and for several days following ovulation, during lactation, and following pregnancy. Non-cornified cells usually lined the vagina during pregnancy and anaestrum, and during these times leucocytes were generally abundant.

The smears taken from my specimens varied so much that correlations between stages of the estrus cycle and the actual vaginal epithelium are impractical. Pregnant females, for instance, according to Pearson's vaginal sections, should show primarily non-cornified squamous cells and leucocytes; they yielded instead smears with almost equal numbers of cornified and non-cornified epithelial cells with leucocyte numbers varying from rare to abundant. Cornified cells were always present in the smears expected to show them, but they were usually more abundant than reason dictated. Thus, for reasons unknown, the smears varied considerably and apparently erratically even among individuals ostensibly in the same stage of the estrus cycle. My inability to match the cytological pattern in the vaginal smears with the histological structure in the vaginal sections as determined by Pearson, precluded any use of vaginal smears as indicators of sexual condition.

The Male:

In order to judge the sexual development of the males, the testes of each dead shrew were measured and then

smears were made from both a freshly-cut testis surface and the epididymis. This portion of the study was based upon the assumption that if well-developed sperm were present, especially in the epididymis, the individual was capable of mating; admittedly, this hypothesis will not be valid in all cases, since the shrew might be unable to mate successfully because of inexperience, low sperm count, or psychic barriers, but with dead specimens there is no alternative.

Size of Testes

It is common practice to measure the length of the testes in routine examinations of kill-trapped specimens. This was done in the present study and the distribution of testis sizes during the year is given in Plate XXXI, Figure 2. The testis length varied from 1.6 to 9.3 millimeters.

The testes of a typical adult male Blarina in breeding condition will measure approximately 8.0 mm. in length and 5.0 mm. in greatest width. During the winter when the males are sexually inactive, the testes average 2.5 mm. long and 1.5 mm. wide, due either to youth or regression in size; in summer the young shrews have testes of similar size. These measurements, however, vary considerably within both the young and adults, and relatively small testes cannot be assumed non-productive of sperm; many past authors have made this assumption. Townsend (1935), for example, presented data showing only ten male

Blarina with 'enlarged testes'--and presumably, therefore, only ten sexually active males--of a total catch of 250 male shrews over a period of five summers. Manville (1949), using similar premises, reported only three male Blarina with enlarged testes, indicative of breeding, of the 350 individuals captured.

Occurrence of Sperm

The occurrence of sperm during the year is shown in Plate XXX, Figure 1. It will be noted that fully formed sperm can be found as early as late February (February 21) and as late in the year as late October (October 23). This is in general agreement with Hamilton (1929) and Pearson (1944), with the exception that Pearson did not record any sperm later than October 3. By March, all the males taken yielded sperm and since females captured at the same time showed no enlargement of the reproductive tract, the males apparently enter breeding condition earlier than the females. The young of the year did not appear in my traps until May 24; the juvenile taken on that date had testes measuring 1.8 by 1.4 mm., and showed no sperm.

Correlation of Testis Size and Sperm Presence

When plotting the relationship between testis size and sperm content, it was found that a much better correlation was demonstrated by using the sum of the testis length and greatest width rather than testis length alone. This relationship is shown in Plate XXXI, Figure 1. It

will be noted that when the testis measurements have a sum greater than 10, fully developed sperm were always present. This sum corresponds roughly to a testis length of 6.0 mm. There was no lower limit below which testes did not contain sperm; indeed, the smallest testis, from a young shrew taken in September, had a sum of 3.1 mm. and contained a few fully developed sperm.

The smaller-sized testes, thus, show no absolute correlation between size and sperm content and may not be used, on the basis of small size, to infer reproductive immaturity. In contrast, the larger testes, having sums of length and greatest width exceeding 10 mm., can serve as indications of sexual maturity. Jameson (1950) proposed that the testes and accessory reproductive structures together afforded reliable criteria of sexual condition in many small mammals. Although data were not recorded, I recall no instances in which small or poorly developed testes were associated with enlarged accessory structures; the degree of enlargement of the testes seemed always coupled with the development of the remainder of the system, and I question whether the sizes of testes and accessory structures are any more reliable for inferring sexual condition of Blarina than testis size alone. In view of the simple procedure in making sperm smears, it would seem desirable to include these in any further studies of Blarina reproduction.

Attainment of Sexual Maturity

The age of sexual maturity varies between the sexes although perhaps not as markedly as previously believed.

Maturity of Females

Pearson (1945) wrote, "...females only a few months old are capable of breeding in their first summer, for both pregnant and parous shrews are represented among the young specimens." In an earlier paper (1944) he wrote that young pregnant females "...were probably born in the last half of March and were perhaps 6 to 8 weeks old when they mated for the first time." In the latter paper he mentioned one young female taken in early May that was less than two months old but had sexually mature ovaries and reproductive tract, and another sexually receptive captive female only 47 days old. Although it is, thus, possible for females to breed when approximately 1.5 months old, the vast majority of these young individuals, within the present study and those of Pearson, do not give evidence of successful breeding. Of the eight gravid females I caught in kill traps, the two trapped in September were both young of the year. Pearson (1945) recorded only four females that were parous or lactating in August and September, and three of these were young of the year. These data indicate that the female young of the year which do breed successfully, mate primarily in the late summer; because young pregnant females are not usually taken earlier in the year,

those found pregnant in the fall probably are four- or five-month-old females which were born in the early spring.

Maturity of Males

Male shrews are more difficult to evaluate because they do not show the results of their activity in as concrete a fashion as do the pregnant or lactating females. I was not able to raise any young in captivity, and no captive females gave birth to young even after mating a number of times with one or more males. The finding of well-developed sperm in the epididymis or testis is indicative of, but not necessarily diagnostic of, the ability to mate.

I recorded one young male, not more than two months old, with small testes measuring 4.2 mm. long, having mature sperm in both testis and epididymis. Pearson (1944) observed mating in a young captive male when it was only 83 days old. I have noted young captive males between two and three months of age attempting to mate with both young and older females but, while under observation, none were successful.

With the present information it is impossible to give a definite age at which young wild male Blarina become capable of successful mating. However, since young shrews have been observed both mating and attempting to mate, and since even small testes can produce mature sperm, I believe it likely that sexual maturity is attained between the second and third month of life and that, on the average, young males reach sexual maturity before their female siblings.

Pearson's opinion (1944), that young females reach sexual maturity before the corresponding males, is not in agreement with my hypothesis. These data further indicate that the physiological bases for successful mating are present earlier than the necessary behavioral requirements.

Duration of the Breeding Season

Breeding in the Spring:

Shrews that have overwintered are usually at least five months old when the spring breeding season commences, and consequently all can probably be considered as breeding stock.

Pearson (1945) presented a graph correlating date of capture, degree of tooth wear, and approximate age of a large number of specimens of Blarina; included were data on the breeding condition of a number of the specimens. This graph demonstrated that young individuals were first caught about mid-May. My youngest specimen was taken on May 24, but most young of the year were not caught in any numbers until mid-June. Using the hypotheses developed below, it is estimated that the young shrews captured in mid-May were born approximately 30 days previously, and that their parents had bred about 24 days prior to parturition, a total of 54 days between breeding and appearance of young in the traps.

Relationship between Copulation and Capture of Young Shrews

Figures 1 and 2, Plate XXXII, illustrate composite growth curves of young Blarina compiled from several sources. These will be discussed in detail below; the primary interest here lies in the weight and length of the animals at an age of 30 days. These measurements approximate those of the youngest specimens trapped in the current study and support the contention that the youngest trapped specimens were about one month old.

Pearson (1944) claimed the gestation period of Blarina to be between 18 and 20 days. He also wrote that repeated copulations, usually over a period of several days, are necessary for ovulation, and that ovulation will not take place until some 64 hours after the copulation threshold has been reached. Thus, beginning with parturition and working backward, ovulation took place about 19 days previously, the stimulus for ovulation about 2-1/2 days earlier, and the initial attempts at copulation perhaps 2-1/2 days still earlier, for a total estimate of 24 days between first breeding and parturition.

Calculated Dates of Spring Breeding

By using May 21 as the probable earliest date that any young would appear in traps, it is estimated that parturition occurred 30 days previously, or about April 21, and that copulation probably commenced about 24 days before, or within the last week of March. Supporting this, I

trapped a female which was approximately one week pregnant on April 5. Pearson (1945) showed no pregnant females taken before March 31. The earliest pregnancy in the literature was listed by Richmond and Rosland (1949) as March 4; then three females were captured in northwestern Pennsylvania. This latter record is unique both because of the early date and because it is separated by almost a month from the earliest records of other authors, excepting only Grimm and Roberts (1950) who recorded a female with five 8 mm. embryos as taken on March 5, also in Pennsylvania. Thus, for most populations of Blarina, the breeding season begins in late March or early April and, as is suggested by the records of Pearson (1945), Hamilton (1929), and my own data, all dealing with specimens from approximately the same latitude, reaches a peak before mid-April.

Breeding in the Summer and Fall:

The breeding season extends until mid- or late September. The latest pregnancy in the literature was recorded by Pearson and Pearson (1947) as October 17 when a female with large, apparently resorbing, embryos was taken. Hamilton (1929) wrote that in New York the young were born from mid-April until the end of May, that there was a second litter born in late summer or early autumn, and that there appeared to be no breeding in July and August. Manville (1949) also wrote about the apparent limitation in northern Michigan to two litters per year. Both Hamilton

and Manville suggested inferences in conflict with their own data; both noted an apparent absence of breeding in at least the latter half of July and August, yet refer to a second litter appearing in the fall. Any young appearing in the traplines in September or early October would, of necessity, have been initiated within the period of supposed sexual inactivity. Pearson (1944) conversely claimed that he "...captured pregnant females in every month from April through September..." My own data (Plate XXX, Figure 2) and those of Blair (1940) are less extensive than those of Pearson, but in essential agreement. In these studies, the majority of very young animals trapped in the fall were taken between mid- and late October; allowing for a 54-day period between probable breeding and appearance of the young in traps, the second breeding period apparently centered about late August.

Even though both my own and Pearson's data show a spread of breeding throughout the season, both also show twin maxima of recorded pregnancies or corresponding lactating females centered in early April and in late August or early September. My data suggest a slightly later spring and slightly earlier fall breeding peak than those of Pearson, and this might be attributed to the more southern latitude where many of his data were obtained. It is obvious that although breeding can occur throughout the season, a first March-April peak and a second mid- to late August peak of breeding activity exists. The dearth of

pregnancy records for this species is likely owing, at least partially, to the fact that much of the trapping has been done during the summer months when pregnancies are fewer.

Breeding in Relation to Light:

An intriguing correlation between breeding peaks and season is suggested by the various data. Based on the information above, the first general breeding at this approximate latitude occurs in late March and the breeding season extends until about mid-September. This beginning and cessation of breeding agrees rather closely with the vernal and autumnal equinoxes, spring breeding reaching a peak shortly after the vernal equinox and fall breeding ceasing shortly before the autumnal equinox. These coincidences suggest the inference that without slightly more than 12 hours of daylight, Blarina will not usually breed. A dependence on light would not be unusual, for many other animals as well as plants are known to have their reproductive cycles controlled, at least partially, by photoperiodism.

Breeding Behavior

Courtship:

A form of courtship was observed on a number of occasions and followed about the same pattern as that outlined by Pearson (1944). When a male and female were placed together for the first time, they behaved in much the same manner followed by any two individuals at first encounter.

The shrews faced each other and each, apparently surprised to find another shrew so close, usually emitted one or more squeaks and occasionally the chatter associated with annoyance or anger. The squeaks usually caused the newcomer to the cage to retreat or, if the shrews were in a cage new to both of them, the female usually retreated first. If no retreat occurred within the first few squeaks, at least one shrew began a loud chatter which most times caused the other to run. On one occasion neither shrew retreated after chattering at one another and the male then jumped at the female and began biting her; I separated the pair to prevent a possible killing.

In time, this aggressive behavior usually diminished; when both animals continued being antagonistic they were separated, on the assumption that the female was not favorably disposed toward mating. Because the males did not react to these militant females in the same way as toward those which finally permitted mating, I think that a female in proestrum perhaps produces an odor peculiar to that period although I have found no suggestion of this in the literature. After the male actually began showing interest sexually, as evidenced by his attempts to move closer to the female without demonstrating any hostility, the courtship followed one of two patterns.

If the female was not yet ready to accept the male, she either became hostile or ran off and, if cornered, indicated by her squeaks and chatter a predilection to fight

rather than mate. Once a persistent male was attacked by the female and, had I not separated the pair I suspect one, probably the smaller female, would have been killed. If the female was willing to mate, she either walked away from the male and displayed only mild antagonism or just stood waiting. I did not see any female act as the aggressive partner during courtship. When the female did run off, the male followed, emitting the dry, unmusical 'chitter' described by Pearson (1944), although I suspect that this particular sound is more associated with simple excitement than being limited to a breeding vocalization as Pearson suggested. A female that had recently mated was more readily receptive to either the same or to another male after a relatively short period of acquaintance.

In the majority of the pairing experiments, the shrews did not exhibit this courtship behavior and, after repeated hostile overtures, they were separated.

Copulation:

Twelve different male-female combinations resulted in the male attempting copulation. The male usually approached from the side or from a back corner and tried to grasp the dorsal or dorsolateral neck or shoulder region with his incisors. While the male was holding the female with his teeth, he mounted, usually from the side, and grasped both sides of her lumbar region with his forepaws, at the same time twisting his pelvic region so that it opposed the vulva. This rather rough treatment of the female

did not seem to bother her even when the male renewed his bite, in several cases drawing blood. Burns (1956), without citing his evidence, claimed that a female Blarina is so immune to pain during copulation that she may have a foot torn off without diminishing her sex fervor. She is undoubtedly less aware of pain than usual.

Following a short series of very rapid pelvic thrusts, the male either immediately dismounted or remained coupled for a time. In the majority of these attempts the male failed to copulate successfully.

If the penis had not entered the vagina, the pair separated a few seconds after beginning and the female, to all appearances oblivious of her prior activity, usually began foraging. In three instances, she moved a short distance off from the male and licked her fur or scratched, with her hind foot, the region that the male had bitten. The male, on the other hand, curled his head under his body and, in a sitting position or sometimes rolling over on his side, appeared to lick his penis while he was readjusting it within its sheath. Pearson (1944) and Burns (1956) both remarked on this latter behavior of the male.

With the five pairs in which copulation was successful and entry made by the male, the similar series of rapid pelvic thrusts occurred but, following the final deeper thrust, the male dismounted but remained coupled with the female. On the basis of 14 records, this coupling lasted for an average of slightly over 2.5 minutes and ranged from

25 seconds to 5 minutes and 10 seconds. Pearson (1944) recorded a 4.7 minute average based on 315 timed matings.

While coupled, the male permitted himself to be towed around the cage backwards as the female moved about. Following separation, the male rearranged his penis as described before and the female again appeared quite unaffected by the experience. Two of the pairs were not separated and in both additional matings occurred. One pair mated seven times within 1.5 hours, and the other pair were known to copulate at least four times within a two-day period. None of these females became pregnant.

Fidelity:

Some question exists regarding the constancy of pairing in Blarina and none of the evidence is conclusive. Seton (1909) was of the opinion that "...we are far on the way to proving life-long partnership." Hamilton (1929) wrote, "I believe there can be but little doubt that Blarina pairs, and if not for a life union, it is certain that they are found together in periods other than that of the breeding season." This was supported by the fact that on a number of occasions he caught a male and female on successive nights at the same trap location. He suggested that males may leave the female for a time during, for example, parturition. Some years later (1939a) he generalized, "Deer mice, shrews, moles, and bats are ...promiscuous."

One of my captive females who had already mated once, permitted copulation by another male which was placed

in her cage on the same day. This, although far from a natural situation, is suggestive that fidelity in this species is not particularly strong.

Brooks (1908), Seton (1909), and most other authors, in discussing the social tendencies of Blarina, indicated it was unlikely that these shrews associate much with others of their species. Manville (1949) wrote, "It is difficult to conceive of this voracious creature as being social in its habits." He described two multiple captures in his live traps: the first involved a male and female, both dead, and the second two adults of unknown sex, one having eaten the other. Pearson (1944) advised, "The most important fact to be kept in mind is that shrews are nervous, ill-tempered, unsociable, and frequently blood-thirsty. Two shrews will seldom live amicably in the same cage unless they have been raised together from birth." Rood (1958), to the contrary, on the basis of grouping various captive Blarina, felt that generalizations about social behavior of this species were dangerous because of marked individual differences and he concluded, "...while the short-tailed shrew cannot be considered a particularly social animal, I doubt that it is as solitary as is generally believed."

Inferences from observations on shrews caught in live traps or on captives under highly unnatural conditions, such as crowding, abundant and usually regular food supply, and forced companions, cannot, without danger of error,

be applied to the supposed social behavior of wild individuals. Interpretation of data on wild populations forms a sounder basis for judgment.

Townsend (1935) tabulated, by sex, the number of multiple captures of Blarina within his lines of traps. He wrote, "...there are 32 instances where a male and female were taken together while in 15 instances two males were taken and in 14 instances two females. This is approximately a 2-1-1 ratio. Such a ratio would mean that.... probably companionship is a mere matter of chance. Hence we conclude that there is practically no tendency for the opposite sexes to be together during the summer months." Although most of Townsend's data were collected during the midsummer low in sexual activity, the fall mating period undoubtedly coincided--at least in part--with his trapping and were pairing common, his records should have reflected this.

My own records, like those of Hamilton (1929, indicate a greater frequency of male and female captures in adjacent traps than of two shrews of the same sex. However, as indicated by Townsend, complete random distribution of the sexes would result in similar captures. In the fall when the populations were high, I caught more shrews in adjacent traps than at other seasons, but I suspect this either to be a reflection of the sibling and sibling-mother groups which had not yet dispersed or, perhaps, indicative of a mild tolerance of others without regard to sex.

The evidence points to an absence of life-long pairing and casts serious doubt on the tendency of shrews to pair for other than very short periods.

Birth and Development of Young

Birth:

Description of Birth

Pearson (1944) gives the only description known to me of the actual process of parturition. He wrote, "Much of this time the mother lay on her back with hind feet spread wide and body bent to facilitate frequent licking and nuzzling of the genital region. She appeared quite restless and treated the newborn young roughly, pushing them beneath her with quick sweeps of the front feet." The three young he actually observed being born took ten, five, and five minutes, respectively, between the time the head was first seen and birth was completed.

Birth Dates

The actual or probable birth dates of wild *Blarina* can be inferred from measurements of both embryos in pregnant females and of juveniles caught in traps. The inferred dates must be based upon comparison with a standard, but such has not previously been available. Data from a number of sources, but primarily from Pearson (1944), Hamilton (1929), and this study, were organized into two graphs, Figures 1 and 2 in Plate XXXII. The basis for

these graphs is described later; of immediate interest is the fact that the birthdates given below were determined by comparing the data from various papers with my graphs.

The earliest probable birthdate was March 10 (Richmond and Rosland, 1949), and the latest September 19 (Pearson, 1944). The earliest inferred birth, based on my own data, was April 18, and the latest September 8. The combined records of various authors (Plate XXXIII, Figure 1) indicate a usual birth period commencing on about April 18 and ending about September 10. The four birthdates shown for March come from the data of Richmond and Rosland (1949) and Grimm and Roberts (1950) whose studies, conducted in Pennsylvania, indicate earlier birthdates than those of any other studies and are considered unique.

Size and Number of Litters:

Size of Litters

Almost all authors are roughly in agreement on litter sizes; the average number of young reported lies between five and six, an advantageous number since the mother has but six inguinal nipples. Table 4 lists the figures given by various authors for wild individuals.

The differences which exist in Table 4 could result from a difference in fecundity at different population levels or at different times of the season, although these possibilities cannot be evaluated from the limited data available. Hamilton (1939a) claimed that when Blarina

populations are increasing, reproduction is increased and that embryo counts are lower when the population is low.

As shown in Table 4, the composite average of 5.7 young per litter, based upon embryo counts, is probably not a valid estimate of the number of young remaining at weaning. For the few litters reported, a large number of young were lost. Pearson (1944), for example, wrote that embryo counts averaged 5.7 (21 records) but that young actually present in the nest several days after birth averaged only 4.5 (11 records); only five of the eleven litters which were born survived, and at weaning these five averaged but 2.8 young. Pearson remarked that had the captive mothers and young been disturbed less, more young would have probably survived; he weighed the young periodically and subjected the mothers to males. In the wild, the mothers would also experience problems, although of a different nature, and it is likely that in spite of the average of almost six young born per litter, probably no more than four usually survive to weaning. Johnston and Rudd (1957) reported on Sorex vagrans, "...less than half the salt marsh shrews conceived live to the age of 21 days."

Number of Litters

The number of litters produced by a wild female within any season is not certain. Most authors, such as Hamilton (1929), Asdell (1946), and Manville (1949), claim that but two litters develop, one during the spring and a second in late summer or early fall. Hamilton wrote, "I should

say that two litters are produced annually in central New York, one in the spring and another in late summer. A particularly vigorous female might produce three broods and this may even be the rule in states farther south."

Pearson (1944), basing his opinion primarily on the behavior of one shrew, suggested the possibility that a female was capable of producing five litters within a season; he felt certain that three litters could be raised and wrote, "It seems safe to assume that many wild shrews raise at least two, and probably more litters in one season."

TABLE 4

LITTER SIZES, BASED ON EMBRYO COUNTS, AS REPORTED BY VARIOUS AUTHORS

Reference	Average embryos per female	Range	Number of Records
Hamilton (1929)	6 or 7 (6.5?)	5-10	29
Townsend (1935)	5.6	4-12	13
Richmond and Rosland (1949)	4.8	3-8	15
Grimm and Roberts (1950)	5 most common	5-8	?
Pearson (1944)	5.7	2-8	21
Fowle and Edwards (1955)	5.7	?	40
Present Study	5.5	2-8	12
Average of above (weighted)	5.7	2-12	130

Figures 1 and 2, Plate XXXIII, show the distribution of both calculated dates of birth and occurrence of lactating females; both groups were compiled from a number of different sources and since equal numbers of Blarina were not

collected through the period represented, absolute percentages cannot be calculated.

Most of the trapping records forming the basis for these figures involved work done during the summer months and although fewer data were available for the spring, most of the estimated birthdates are in the spring. During the summer when records are most abundant, no estimated birthdates are shown. In the fall, when the number of records are fewer, estimated births are again shown. This situation suggests that were equal numbers of records available for each season, a much more pronounced difference in the distribution of estimated birthdates would be seen. Figure 1, Plate XXXIII, thus indicates that the majority of shrews which become pregnant do so in the early spring, and that most of these litters would be whelped in late April or in May.

Although the records are sparse, the spring birth period appears to be trimodal although the first peak in March should, perhaps, not be considered here; the data (Richmond and Rosland, 1949, and Grimm and Roberts, 1950) providing the March birthdates did not correspond with either that of Hamilton (1929, 1949) or my own and may, consequently, reflect an atypical situation. Sexually active females that bred early and then, after producing one litter, bred soon again could account for the remaining two spring modes.

The cluster of births estimated to occur in the fall

corresponds to the time when most of the population is young and may, therefore, be associated with females born early in the year. My own data reveal that of nine sexually active females recorded between late August and October, only two had been born the previous year.

Figure 2, Plate XXXIII, shows a large number of lactating females early in the summer, in part a reflection of more concentrated trapping effort at that time, and these females represent the mothers of the spring breeding period. During August the number of lactating females decreases markedly and then increases again somewhat late in August and September, reflecting the late summer or fall breeding period.

A comparison of Figures 1 and 2, discussed above, raises several questions. The latest calculated birthdates in the spring are in mid-May, while lactating females are taken in numbers through late July. One interpretation, based upon the evidence at hand, is to assume that lactation continues over a much longer period than the 26 days claimed by Hamilton (1929). If true, this would demand that pregnant females should be taken in proportionately much smaller numbers than lactating females since for any given litter, the female would be pregnant for about 20 days and lactating for, perhaps, 60 days; the probability of capturing a pregnant shrew would thus be one-third that of capturing a lactating female. In the few studies permitting this comparison, such is not the case. It does not

seem possible that young Blarina would continue to suckle for 60 days, yet the two graphs suggest this. That a mother shrew continues to produce milk for more than a month after weaning her litter, or that the various investigators misjudged lactation, is a remote and unlikely possibility. I cannot resolve this apparent conflict.

To summarize, for this latitude the data indicate that surviving females in the spring usually produce one and probably two litters within the spring breeding period. In the more southern portions of the range of Blarina, breeding is apparently earlier and many may produce three litters by mid-summer. Those old adults which manage to survive through the late summer may mate again and produce a fourth litter in September. I believe that the majority of the fall litters are dropped by females born earlier the same year. For southern Michigan, then, there are probably two and perhaps three litters born during the spring and late summer: the first between early and mid-April, a second about mid-May, and rarely a third between mid-July and late August. In the fall a fourth litter may be produced by the surviving older females, but most likely the young born in September will be dropped by the young females of the year. This hypothesis differs from most in that it suggests that usually two litters, rather than just one, are produced within the so-called spring breeding period.

Development of the Young:

The development of the young has been described in some detail by Hamilton (1929), and Pearson (1944) reported data dealing with the pre-parturition stages as well as the appearance of the young at birth. Since I was unable to successfully breed any females, the data here are restricted to those of others. To date, however, no one has combined the various studies to present an overall view with inferences beyond those of the other authors.

Figures 1 and 2, Plate XXXII, represent an attempt to demonstrate the growth of the young from birth through their fourth month of life at which time they maintain a rather constant size, comparable to that of the assumed adults in late winter. All the available data were plotted to provide as sound a basis as possible, and then the curves were extrapolated to approximate a sigmoid curve so common in biological processes.

Increase in Weight

Figure 1, Plate XXXII, illustrates the range of weights probable in young Blarina; rather than use a single line, a range is shown on the assumption that males will fall within the upper portion of the range and females within the lower. This assumption may not be entirely valid, but on the basis of present information it seems justified. The first part of the curve is based primarily on the data of Hamilton (1929). At birth the young average 0.8 grams

(Pearson, 1944), they gain weight rather slowly the first three days and then grow rapidly between the third and thirtieth day, when it is thought they begin actively foraging for most of their own food and are, in consequence, first taken in the traplines. At this time, when the young are probably using energy more rapidly than they can replace it, their weight should decrease; this accounts for the dip in the curve. Although I know of no data suggesting such a weight loss in Blarina, this phenomenon has been clearly demonstrated in Sorex vagrans halicoetes (Johnston and Rudd, 1957) where the young weigh about 6 grams at one month and then drop to a relatively constant 4-5 grams, the weight of a typical non-breeding adult. These same authors claimed that a similar situation was suggested by a graph dealing with Sorex fumeus, in a paper by Hamilton (1940). Captive young shrews would probably not show a similar weight loss because they are supplied with abundant food.

Shortly after this weight loss the young shrews are able to reverse this downward trend; perhaps they become more efficient in their feeding or, possibly, their metabolism changes. Because very few young are taken at low weights, I assume that weight begins to increase again after about a week. Following this inflection, the curve again rises as the weight increases gradually over a period of months until late winter.

Increase in Length

Figure 2, Plate XXXII, illustrates the probable length curve for young Blarina from conception through the following 80 days. Several measurements used were listed by Pearson (1944), a larger number came from Hamilton (1929), and the rest either from my own or a wide number of other sources. One difficulty was encountered: the pre-parturition measurements were taken on a crown-rump basis, whereas all the data following birth are on a total length basis. This necessitated the initial two curves on the graph, one for each kind of measurement.

Initially, growth is apparently quite slow. The largest embryos recorded by any author were 18 mm. long; Pearson (1944) wrote that a young Blarina, just born, measured 22 mm. long and thus the 18 mm. figure must apply one or at most two days before birth. Pearson (1944) reported the gestation period as between 18 and 20 days; 19 days was used here. The pre-parturition portion of this graph was invaluable for estimating birthdates for wild litters when only embryo measurements were available.

Between birth and the approximate time the young are estimated first to appear in traps, growth in length is rapid. At about the latter time, growth begins to slow down for the shrews are then approaching adult length; it is again assumed that males will fall within the upper and females within the lower portion of the range shown in Figure 2.

Description of Young

Based upon Hamilton's paper (1929), a few major developmental events will give an idea of the sequence and speed of development. At birth the young are dark pink, wrinkled, hairless, and the eyes and ears are closed; by the fourth day the body is a lead gray; by the eighth day short hair is present and the young can crawl; by the tenth day they can emit a weak, squeaky cry; by the thirteenth the ears are open; by the fifteenth they are moving out of the nest; by the nineteenth the upper incisors show; by the twenty-second all the teeth can be seen but the eyes are not yet open, and by the twenty-sixth day they are at least partially weaned and the eyes are likely open. By the thirtieth day the young, although still probably spending most of their time in the company of their siblings, begin to venture afield on foraging trips and are then caught in traps.

These young are usually born in underground nests, well-insulated by coarse, dry leaves and usually without hair of any kind. The supposed breeding nest found during this study and those mentioned by others have been clean and free of feces; apparently the mother shrew cleans the nest by eating the droppings of the young.

SHREW POPULATIONS

The data collected in this study permit comparisons of population densities in different habitats over a span of several years, and the investigation of some factors influencing these populations.

An actual count of all individuals in a delimited area within a stipulated time is the only precise way of determining population density accurately, but with a natural population such precision is virtually unattainable for practical considerations. The majority of the population studies involve, therefore, methods of estimating density and the accuracy of the resulting estimates is seldom free of doubt. With any study of a small and usually secretive mammal, the methods in current use are admittedly less than perfect and errors are unavoidable. Since the natural populations sampled here or elsewhere are inherently temporal, some question exists of the practical necessity of extreme accuracy.

The density of any natural population is more a concept than a definite figure because the population is not static; it is continually fluctuating because of varying rates of immigration, emigration, birth, and death. Any single estimate will, in consequence, fail to mirror the actual situation--that of a pulsating aggregation which

fluctuates from day to day, from one season to the next, and from one year to another. Since different ecological situations permit varying degrees of fluctuation, a pattern laboriously established for one small area will not necessarily obtain in a similar area elsewhere, or even in the same area at a different time. In the present study, determination of population density was incidental to the gathering of other data, but, because so many variables of unknown magnitude attend any estimates of this nature, I suspect that mine are comparable in accuracy to those of most other authors.

The basis of any population is the individual, and it is helpful to understand the temperament of individual Blarina before examining the relationships among members of a population.

Temperament of the Shrew

The opinion of Seton (1909) is typical of that held by many authors who have maligned the short-tailed shrew; he characterized this species as being "...unsociable to the point of ferocity." Brooks (1908), Pearson (1944), and Manville (1949) concluded that Blarina is extremely unsociable; while a few authors, such as Hamilton (1939) and Rood (1958), indicated that the prevalent opinions were not entirely justified. Hamilton claimed that abundant field evidence suggested a moderately sociable disposition. Most of the ill temper attributed to Blarina was observed in the behavior of captives whose small cages would force a much

closer contact with members of their own or other species than is usual in the wild. Such forced proximity should not be the basis for generalizations relative to wild animals.

In spite of the often observed destruction of mice and voles, Blarina is not the fearless aggressor he is usually claimed to be. Admittedly, certain individuals--often the same ones which are aggressive intraspecifically--will attack almost any mouse or vole placed in their cages, but this does not hold true for all short-tailed shrews. Some shrews appear to be cowards; when confronted by another small mammal, three of my captives invariably squeaked and immediately retreated to their nests upon discovering the visitor to their cages. Two of these three shrews were not seen to leave their nests again until the intruder was removed several hours later.

I concur with Rood (1958) who remarked on the great differences in disposition among individual shrews. I found the most antagonistic and irritable captives were usually the older males when in their own cages, and the least likely to fight were young females when placed in cages occupied by other **Blarina**.

When two adult male shrews of similar size were placed together in a small cage (12x18 inches) new to each, the initial squeaks and chatter preceded a short-lived scuffle, lasting no more than a few seconds. One shrew broke loose and retreated to a far corner of the cage and

the two were then separated. When the same two shrews were placed together in a larger enclosure (16x24 inches) four days later, the initial vocalizations occurred but neither shrew attacked and, within several seconds, each went his own way. A similar experiment was done with two females, but they were put into the large cage first; again, fighting occurred in the small but not in the larger cage. In the wild with considerably more space, I would guess that few encounters result in fighting.

Home Range

With the determination of the population size of any wild mammal which is distributed over an area larger than that involved in the census, it is mandatory that information on the home range(s) of the individuals be known. Without such knowledge, the area actually sampled by a series of traps cannot be estimated.

Estimation of home range size entails numerous problems and these have been ably discussed by a number of authors such as Bole (1939), Burt (1940,1943), Hayne (1949, 1950), Stickle (1954,1960), and Calhoun and Casby (1958). Although various authors have proposed solutions to these difficulties, not one method has yet been discovered which is free of either statistical or practical problems. Stickle, for example, wrote in her 1954 article, "Use patterns may change as conditions change, and the 'boundaries' may vary and shift from time to time. In fact, the boundaries of the range must be considered diffuse and general

rather than sharply or definitely outlined. These factors work against an accurate measurement of range size, and too great precision cannot be expected. To these difficulties must be added the interference of trapping." The last sentence is especially pertinent to studies dealing with Blarina because they are prone to die in the traps if not released soon enough.

Two methods of home range determination are applicable to the present study; my trapping methods did not include use of the grid placement of traps preferred by most.

Definition of Home Range:

The home range, as defined by Burt (1940), "...is that area about the established home which is traversed by the animal in its normal activities of food-gathering, mating, and caring for young." It is unlikely that a home range, thus defined, which includes the space often occupied throughout an adult lifetime, can be properly estimated over a short period of time; the actual home range therefore is likely larger than that which would be measured by most current methods, and the bias inherent in my latter method of estimating home range should be in the direction of a true figure. Further, since many of the home ranges in this study are estimated from relatively few captures and, assuming that an animal is much less likely to enter a trap peripheral to, rather than near the center of its usual activity area, any other method of estimating home range would probably yield an inaccurately low figure.

Minimal Home Range:

This estimate involves plotting the capture locations for each individual and then connecting these loci of trap sites with lines to delimit the probable area occupied by that individual within the trapping period. In the present study, each time a Blarina was captured along a trap line, the site of its capture was surrounded by four additional traps, each about 30 feet distant. Since an overall grid pattern of trapping was not used, a miniature grid was established at each capture site. Each point of capture, therefore, became the center of a circle 30 feet in diameter, and in diagramming the probable home range of each individual, a band 15 feet in width was added to the lines extending between diagrammed capture sites. It was necessary to consider, as did Burt (1940), that if adjacent traps were not visited, then the home range did not extend to those surrounding traps. As discussed by Hayne (1950) and Stickle (1954), trap spacing influences these calculations considerably and this influence would be most marked when the animal is captured only a few times. The home range areas were determined by placing the diagram of each home range over a finely ruled grid and then tabulating the number of included squares. The minimal home ranges, determined without an added border of 15 feet, are presented in Table 5, columns 7 and 8; the estimated home ranges, including the added border of 15 feet, are shown in columns 9 and 10.

TABLE 5

CALCULATED HOME RANGES AND RELATED DATA OF SHORT-TAILED SHREWS CAPTURED TWO OR MORE TIMES *

Field number	Sex	Number of captures	Maximum distance between captures (feet)	Circular home range		Minimum home range		Minimum home range plus 15-foot boundary		Maximum time between captures	Area of capture	Estimated age at first capture
				Square feet	Acres	Square feet	Acres	Square feet	Acres			
11	F	8	205	33100	0.77	8050	0.18	15300	0.35	May 24,55-Jun 10,55	Hamel	Ad.
12	F	3	57	2550	0.06	575	0.01	3100	0.07	May 25,55-Jun 14,55	Hamel	Ad.
1	F	3	148	17200	0.40	1650	0.04	7150	0.16	Aug 27,54-Sep 3,54	Hamel	Imm.
2	F	2	58	2660	0.06	-	-	2525	0.06	Aug 27,54-Aug 28,54	Hamel	Ad. ?
9	M	6	312	76200	1.74	20400	0.47	31875	0.73	May 24,55-Jun 10,55	Hamel	Ad.
5	M	5	158	19580	0.45	4000	0.09	9775	0.22	Aug 28,54-Jun 8,55	Hamel	Yng.Ad.
8	M	3	353	98200	2.25	4500	0.10	16050	0.37	Sep 3,54-May 26,55	Hamel	Imm.
13	M	3	197	30500	0.70	675	0.02	7150	0.16	May 28,55-Jun 7,55	Hamel	Ad.
7	M	2	72	4070	0.09	-	-	2850	0.07	Aug 28,54-Sep 5,54	Hamel	Imm.
4	M	2	90	6360	0.15	-	-	3400	0.08	Aug 27,54-Aug 30,54	Hamel	Imm.
55	F	9	178	24900	0.57	6250	0.14	13825	0.30	May 5,55-Oct 4,55	Greene	Ad.
75	F	8	218	37700	0.86	9700	0.22	17825	0.41	Sep 15,55-Oct 2,55	Greene	Yng.Ad.
69	F	6	170	22700	0.52	7000	0.16	13425	0.31	Aug 1,55-Oct 1,55	Greene	Imm.
60	F	6	293	67400	1.54	9500	0.22	19300	0.44	May 20,55-Sep 11,55	Greene	Ad.
59	F	6	118	10900	0.25	3725	0.09	8600	0.20	May 19,55-Jun 8,55	Greene	Ad.
57	F	6	211	34800	0.79	6875	0.16	14700	0.34	May 8,55-July 2,55	Greene	Ad.
66	F	3	102	8170	0.19	1200	0.03	5200	0.12	July 4,55-Aug 3,55	Greene	Imm.
72	F	2	26	530	0.01	-	-	1450	0.03	Sep 15,55-Oct 8,55	Greene	Imm.

TABLE 5-Continued

73	F	2	35	964	0.02	-	-	1800	0.05	Sep 15,55-Sep 16,55	Greene	Imm.
54	M	13	292	66700	1.53	14975	0.34	25150	0.57	Apr 22,55-Jun 28,55	Greene	Ad.
52	M	11	258	52300	1.20	12075	0.28	21250	0.49	Apr 21,55-Jul 4,55	Greene	Ad.
63	M	7	172	23200	0.53	6300	0.14	12925	0.30	Jul 2,55-Sep 15,55	Greene	Imm.
68	M	3	199	30900	0.71	1150	0.03	5100	0.12	Jul 6,55-Sep 14,55	Greene	Yng.Ad.
64	M	2	48	1820	0.04	-	-	2100	0.05	Jul 3,55-Aug 6,55	Greene	Imm.
65	M	2	38	1140	0.03	-	-	1800	0.04	Jul 3,55-Jul 7,55	Greene	Imm.
71	M	2	108	9200	0.21	-	-	4050	0.09	Aug 4,55-Sep 16,55	Greene	Imm.
20	F	5	98	7690	0.17	3275	0.08	7750	0.18	Aug 8,55-Aug 29,55	Norden	Imm.
19	F	4	100	7854	0.18	1625	0.04	4025	0.09	Aug 7,55-Aug 24,55	Norden	Imm.
26	F	3	54	2290	0.05	600	0.01	2450	0.06	Aug 6,55-Sep 21,55	Norden	?
37	F	2	31	754	0.02	-	-	1650	0.04	Sep 5,55-Sep 24,55	Norden	Imm.
29	F	2	21	345	0.01	-	-	1375	0.03	Sep 5,55-Sep 24,55	Norden	Imm.
33	F	2	72	4070	0.09	-	-	2850	0.07	Aug 9,55-Sep 22,55	Norden	Imm.
22	M	11	157	19300	0.44	6275	0.15	12875	0.30	Aug 5,55-Sep 22,55	Norden	Imm.
25	M	3	107	8950	0.20	1050	0.02	5100	0.12	Aug 5,55-Sep 5,55	Norden	Yng.Ad.
36	M	2	45	1600	0.04	-	-	2100	0.05	Sep 4,55-Sep 8,55	Norden	Ad. ?

* The circular home range was computed using the maximum distance between capture points as the diameter. The minimum home range represents the area enclosed within lines connecting the points of capture.

Circular Home Range:

Another method of calculating home range size involves measuring the greatest distance between points of capture. If this linear dimension is considered as the probable diameter of a circular home range, the hypothetical area can easily be calculated. In Table 5, the maximum distances between capture sites of individual Blarina are shown in column 4, and the calculated areas of the corresponding circular home ranges are given in columns 5 and 6. Admittedly, only a rare home range would actually be circular, but perhaps the inherent errors of this method tend to offset one another. Similar calculations using the longest dimension of a well-established irregular home range would always result in a figure greater than the actual; on the other hand, few--if any--home ranges in any study are known in complete detail, and the unrecorded forays beyond the known boundaries may easily compensate for the increased area calculated for a circular home range.

Estimates of Home Range:

Considering individuals caught more than once, and comparing the calculated circular home range areas given in Table 5, column 6, the estimates range from 0.03 to 2.26 acres for males, and from 0.01 to 1.54 acres for female Blarina. By plotting, separately for each sex, all the estimated home range areas against the number of captures used for each estimate (Plate XXXIV, Figures 1 and 2), it can be seen that after the number of captures reaches six

or seven, the home ranges fail to show any further consistent increase in size. Six or seven capture sites apparently provide sufficient information to demonstrate the major spread of a home range of Blarina.

Blair (1951), after working with a mouse population, wrote that estimates based on fewer than ten captures are apt to be incomplete. I doubt that even 13 captures revealed the entire home ranges of Blarina; more captures would certainly have afforded greater accuracy in outlining the borders of the home ranges, if such accuracy is required. Stickle's opinion (1954), quoted above, casts doubt in this regard.

By extrapolation, Figures 1 and 2 in Plate XXXVI suggest that for the areas and dates sampled, the home ranges of male Blarina average about 1.0 acre and those of females extend over about 0.75 acre. Since these estimates were calculated from data collected, in many instances, several months apart, they should approximate the home range as defined by Burt (1940). Had these home ranges been calculated over shorter time intervals, the areas would have been smaller.

Minimal home ranges determined by connecting capture sites with lines, and measuring the included area (Table 5, column 8), also show the home ranges of males (0.02 - 0.47 acre) to be larger than those of females (0.01 - 0.22 acre). When a border 15 feet wide, allowing for one-half the distance to adjacent but unvisited traps, is added to

these minimal home ranges (Table 5, column 10), the areas for males (0.04-0.73 acre) remain approximately double those of female Blarina (0.03-0.44 acre).

No author would claim that the minimal home range represents an accurate description of the area normally covered by an animal, even over a limited time; there are likely to be unrecorded forays beyond its limits. Perhaps a more realistic description of home range is obtained by adding a border equal to one-half the distance to adjacent traps, but the size of this added border is completely dependent upon the spacing of the traps; the calculated home range may thus be influenced more by judgment of the investigator than by the activity of the animal being studied. The calculated area of a circular home range, based on the greatest distance between capture loci, is not subject to increase by the addition of a border of arbitrary size. Obviously, the spacing of traps will have some effect on such a circular home range, but if additional traps are available and judiciously spaced near the sites of previous captures, the influence of trap spacing should be minimized. I believe that the calculated circular home range provides a better estimate of home range size than either of the other two methods employed here.

Other studies are in rough agreement with the home range estimates here, averaging 1.0 acre for males and 0.75 acre for females. Hamilton (1931) estimated the home range of Blarina at about one acre. Burt (1940) gave the figure

of 0.4 acre. Blair (1940) calculated home ranges of between 0.25 and 4.43 acres, and found that males generally ranged more widely than females. Blair (1941c) listed short-tailed shrews which were caught from four to six times: females had home ranges of 0.56, 0.59, 1.00, 1.29, and 1.46 acres, while two males occupied ranges of 1.08 and 1.39 acres; he remarked that some of these ranges may have been larger. New (1958) concluded that his most reliable estimates of the home range of Blarina ranged between 0.12 and 0.8 acre in a wooded plot, and from 0.19 to 1.1 acres in a grassy field.

Factors Affecting Size of Home Range:

Although definite conclusions regarding home ranges would demand more extensive data than are available here, the present study suggests a number of inferences.

First, the males have larger home ranges than the females, as demonstrated by Figures 1 and 2, Plate XXXV. The data of Blair (1941c) neither support nor contradict this finding. In another paper published the same year (1941b), Blair listed the average width of a male's home range as 246 feet and that of the female as 207 feet. Townsend (1935) did not calculate home ranges, but he did state that the 'wandering tendency' of females was usually higher than that of male Blarina. Since Townsend's 'wandering tendency' appears to be related to the current concept of home range, his information contradicts mine.

Second, the home ranges apparently decrease in size as the population density increases. After studying populations of Peromyscus, Stickle (1960) similarly concluded that home range areas are inversely proportional to the population density. If the home ranges presented in Table 5, column 6, are averaged, those averages from the Norden Area (0.28 acre for males and 0.086 acre for females) are markedly less than the comparable figures from the Greene Area (0.6 acre for males and 0.32 acre for females). The Norden Area, which had the highest estimated population density of the three, as shown by Figures 1, 2, and 3 in Plate XXXV, yielded the smallest home ranges. Although I believe this correlation is valid, a number of other factors might also be responsible. The largest home ranges were estimated from data which were in part collected during the spring when the population was relatively low. In the fall when populations were higher, the home ranges were correspondingly smaller. Unfortunately, during the times when the population was low and the home ranges more extensive, the shrews were simultaneously older than the average age of those individuals having smaller home ranges. I am unable to determine whether the differences in home range size are best correlated with population density or age, or perhaps both. A further complication arises when reproductive status is considered, because the older shrews in the spring would have also been reproductively active, in contrast to the many young and probably non-breeding

Blarina later in the year. I cannot resolve this dilemma with the data available.

Third, in addition to the autumnal compression of the home ranges, a greater degree of overlapping is exhibited at that time. This may be caused by family groups which have not yet dispersed, or perhaps there is actually a greater tolerance among all the shrews, a tolerance that might well be correlated with declining reproductive activity.

Lastly, I feel that the type of habitat, its extent, and the habitat immediately surrounding a given area are indirectly responsible for influencing the home range size. The Norden Area, for example, offered only a narrow band of the habitat which was apparently preferred by Blarina, and this was along the edge of a pond; the adjacent land sloped rather abruptly up to the drier hillsides. Thus, the habitat yielding high population densities in the Norden Area was very limited in extent. In contrast, the Greene Area having less dense populations was rather low, flat, extensive, and roughly similar in vegetation throughout; the bordering land was much like the area which was trapped. Although the detailed data required for proof are not available, I believe that the shrews tend to aggregate in the most favorable portions within any area; and if differences between the optimal and adjacent habitats are great, then the population will be markedly compressed within these preferred habitats. On the assumption that compression of the

population influences the home range size of Blarina, the habitat, by affecting the distribution, thus also influences the home range size of the shrews. New (1958) presented data which support this hypothesis that habitat influences the home range size of Blarina and Stickle (1948,1960) reviewed data suggestive of a similar situation for Peromyscus.

Population density, age, sex, reproductive activity, and habitat thus may all influence the size of the home range of Blarina.

Population Density

Many of the animals trapped within a defined area are likely to be residents of adjacent areas as well; therefore, the plot containing traps cannot, by itself, be used as the basis for density calculations. In some studies, such as that by Burt (1940), relatively isolated habitats were surveyed and the area trapped probably coincided with actual source of the trapped animals. This approach eliminated many problems, especially for stenotopic species, but since the young may be reticent to leave a preferred habitat, crowding may cause populations to be more dense than in more extensive habitats. My trapping was done primarily within areas of 3 - 30 acres, and each area was contiguous with land having comparable vegetation. No grids were established for the placement of traps and, therefore, comparison of my results both within this study and with the results of other authors is somewhat handicapped. The

majority of the field work was done over a two-year period in which the population was gradually rising; if a cyclical fluctuation of population exists in Blarina, then most of my data involve the year (1955) just prior to, as well as the year (1956) of, a weak high point.

The estimate of population density applicable to each limited trapping period was, of necessity, calculated on the basis of other estimates; both the number of individuals present and the extent of the area from which they are drawn, neither of which is known precisely, are requisite to any estimate of population density. However, since all the data were treated similarly, the resulting estimates should be biased in the same direction and thus remain comparable within the present study.

Method of Estimating Population Density:

In order that comparisons of population density be as completely documented as possible, data from both live- and kill-trapping are included in the graphs described below. Using methods similar to those employed here when he estimated populations of small mammals in Manitoba, Buchner (1957) wrote that data collected from both types of trapping yielded comparable estimates in late summer, but that in early summer, live-trapping data provided slightly higher estimates.

Since the linear traplines ended near the point of origin, they roughly described a large circle. When the

trapline was not circular, the ends abutted a road or some other unfavorable Blarina habitat such as a pond edge; for practical purposes, the effective trapping areas did not extend beyond the ends of the traplines. To estimate the effective trapping areas, a strip equal to one-half the estimated average diameter of the home range was usually included along both sides of the trapline.

Because the estimated home ranges of males and females differed, the effective trapping areas were usually calculated separately for the two sexes. Males had an estimated average home range of 1.0 acre and since a circular home range with this area has a diameter of 240 feet, a strip 120 feet wide was added along both sides of the trapline when calculating the effective trapping area for males. Similarly, a circle 200 feet in diameter has an area of 0.75 acre and therefore a strip 100 feet wide was added to each side of the trapline when figuring the effective trapping area for female Blarina. In the Norden Area, the trapline coursed near the pond edge and such a strip added to each side of the trapline would have included much open water; here the width of the trapped area was estimated to be 150 feet for both sexes.

Usually, the adult shrews were easily sexed but the young were not and a number of young were tabulated as "sex unknown." Since the home ranges of the young approximate those of the females, the 100-foot strip was used when calculating the effective trapping area relative to

the young. The 1.0- and 0.75-acre home ranges are used here although larger home ranges are shown in Table 6; I believe this is justified because within any short time interval an individual would probably occupy less than its maximum home range as determined over a longer period of time. Manville (1949), in his studies on Blarina, likewise added a 100-foot strip along each side of his traplines and this figure was based on an estimated home range of 0.75 acre for the species. The numbers of Blarina in the trapped areas were estimated by plotting a cumulative curve of the numbers caught each 24-hour period; when this curve reached an approximate level, the corresponding number was considered to be the resident population. Any additional captures were assumed to represent wandering individuals.

The kill traps were set for a minimum of three days; Goodnight and Koestner (1942) claimed that this period was sufficient for a population determination when using kill traps. The live traps were often operative for a longer period because each time an unmarked individual was caught, trapping usually was continued for an additional two days, providing considerable opportunity for catching all the resident shrews which were not trap-shy.

Estimates of Population Density:

The population density figures for Blarina, as presented in Plate XXXV, are based on the estimated number of individuals resident on the estimated effective trapping

area over time intervals ranging from three days to slightly more than a week. I believe that detail greater than that given in Plate XXXV would indicate a degree of accuracy impossible to attain under the circumstances.

Norden Area

The highest population density of Blarina was estimated at 18.3 shrews per acre in late September, 1955; this was obtained with live-trap data from the Norden Area. None of the estimates from the Norden Area are directly comparable to those of other areas because trapping was done primarily along the pond edge and the effective trapping area was based, generously, on a strip 150 feet wide. When estimating the effective trapping area in all the other areas, a narrower boundary was added to both sides of the trapline. This may have resulted in overly conservative population density estimates for the Norden Area, and these figures should thus be considered as minimal. The limited extent of preferred Blarina habitat appears to have resulted in a marked compression of the population and, probably, a figure much higher than would obtain in an identical habitat of greater extent.

Railroad Area

The lowest population estimates were calculated from Railroad Area data, and ranged from zero to 2.2 Blarina per acre; this area was in a narrow strip on each side of the railroad tracks and the adjacent land provided

a continuing source of additional shrews. If all the resident shrews were caught each time the kill traps were set, each subsequent estimate must represent immigration. The numbers taken each time were so low that the capture of one shrew made considerable impact on the estimates.

Greene Area

The Greene Area was studied most intensively and the resulting population density estimates (0 - 9.0 Blarina/acre) are based on both kill- and live-trapping data. Since the kill traps were set in similar habitat adjoining that where the live-trapping was done, I believe that they sampled comparable populations yet did not interfere with the Blarina being live-trapped. No shrews marked in the live-trapping work were taken by the kill traps. The plotted estimates are erratic in a few instances and I judge this to be a function of Blarina behavior rather than actual population fluctuations. Although I have not correlated captures with weather, it is my impression that when the sky was clear and bright, Blarina was less apt to be caught in the kill traps; the live-trap captures seemed less affected. The low estimates of population density for the Greene Area, which seem to contradict the general trend shown in Plate XXXVII, were based on kill-trap data and may be at least partially explained by the influence of weather.

Hamel and Other Areas

The estimates of population density for the Hamel Area (2.2 - 10.6 Blarina/acre) are entirely from live-trap data, excepting the single estimate for 1956. These estimates show a close similarity to those obtained for the Greene Area; both these areas were roughly similar in vegetation, soil, and proximity to the Saline River, and they lie within one mile of each other.

Since the data from live-trapping probably yield slightly higher population estimates than those from kill-trap data, all of the population density estimates for 1956 should perhaps be adjusted upward because these are based solely on snap-trap data. For the same reason, certain of the estimates for 1954 and 1955 should be treated similarly, but no adjustment has been made in these figures because the degree of such a correction is not known. All the estimates which are based on kill-trap data are so indicated in Plate XXXV.

The population densities estimated for the Baseball Flats and the Waterworks Areas are also presented in Plate XXXVII primarily to support the high estimates of density indicated for the other areas in 1956.

Seasonal Factors Affecting Population Density:

Hamilton (1942) wrote that Blarina catches in the fall may be two to five times greater than in the spring. Some of my population estimates suggest an even greater

difference. In the large, rather homogeneous Baseball Flats Area, the population varied from zero and 0.72 to 8.6 Blarina per acre; in the Greene Area, from zero and 0.22 to 9.0 per acre.

Before the young of the year are included in the estimates, the spring populations of ostensibly mature adults ranged from 0.22 to 3.1 Blarina per acre, with the better estimates averaging slightly more than two per acre. This indicated that one pair of Blarina per acre might be the usual situation at the onset of the breeding season. The highest population density within any year appears to occur between mid-September and early October and averages, depending on the year, about four times the spring population. Then, if my estimates are correct, most of the mortality occurs before the year ends, so that the population level in late December is probably only slightly higher than that in early spring. If the latter is true, the winter months are not as hazardous for Blarina as has been previously thought. A number of authors have remarked on an apparent season of mortality in the autumn months, and as evidence point to the carcasses of Blarina found at that time. Hamilton (1931) doubted that any decided autumnal increase in death rate existed, and he felt that the increased number of carcasses found at that season could be attributed to the ease of locating them in the woods after the leaves had fallen. Blair (1948) wrote that survival chances for individual small mammals are roughly equal at all seasons.

According to Pearson (1945), the mortality of shrews is probably no greater than that of other small mammals, but the unpalatability of shrews would result in those killed being left uneaten. The studies of Murie (1936) and Fitch and Packard (1955) support Pearson's contention that certain predators will kill, but do not usually eat, these shrews.

Pearson also wrote that, based on his captives, short-tailed shrews do not die in their nests, and that the bodies are always exposed. In disagreement here, several of my captives died in their nests, and I question whether those found dead and exposed in the wild represent natural deaths. I find difficulty in believing that Blarina, which spends much of its time in underground burrows and beneath the cover of leaf litter, would choose an exposed area for its final natural act.

The shrews would experience the same increased autumnal predation pressure--by virtue of the increased predator population--as other small mammal populations; more shrews would die in the fall simply because more are available at that season even though the rate were not increased. When snow falls, the surviving shrews would be afforded considerable protection and would probably then enjoy a decreased death rate. Such speculation is consistent with the apparent trends shown by my population estimates. Table 6 shows that my population density estimates are closest to those of Burt (1940) and Manville (1949); both worked in Michigan.

Comparison with other Estimates of Population Density:

Various authors have published widely divergent estimates of the population densities of Blarina, ranging from zero to almost 300 per acre. The figures given in most recent books apparently result from attempts to conservatively justify these conflicting estimates. Palmer (1954), for example, when discussing Blarina in his handbook, wrote that "...25 shrews per acre is not unusual." At first glance such a figure does not appear high, but a critical evaluation of the original studies casts doubt on estimates of population density above 25 per acre, and even this figure may be somewhat high.

The differing estimates of populations of Blarina occurring within the geographic range of the subspecies in southern Michigan are listed in Table 6. Much of the variation may be explained by factors such as irruptions, cyclical or other fluctuations, the different habitats and seasons, or a multitude of other variables; indeed, it would seem remarkable if the results of one study did closely approximate those of another done at a different place, at a different time, under different conditions, by a different researcher using different techniques.

The estimates in Table 6 which appear rather low may reflect poor technique in trap placement, ineffective traps, reticence of the shrews to enter the traps, or errors in calculation; but these may also be readily justified since any species can be absent from an area or experience a low

TABLE 6

ESTIMATES OF POPULATION DENSITY FOR BLARINA

Author	Habitat	Estimated density
Williams (1936)	woodland	299.45 per acre
Townsend (1935)	various	5 to 104 per acre
Seton (1909)	woodland	50 per acre
Bole (1939)	various	48 per acre
Burt (1940)	favorable	5 to 25 per acre, maximum
Manville (1949)	various	0 to 11.63 per acre
Hamilton (1931)	favorable	8 per acre, maximum
Shull (1907)	meadow	4 per acre, minimum
Blair (1940)	various	0.8 to 2.2 per acre
Blair (1940)	meadow	0.7 per acre
Blair (1941b)	woodland	0.31 per acre
Present study	various	0 to 18.3 per acre

population level. Certain of the population estimates, however, are so much higher than the rest that they demand closer attention.

The highest estimates appear to be attributable to either faulty experiment design or misinterpretation of the data. Both criticisms seem applicable to the estimate by Williams (1936) of almost 300 Blarina per acre. He based his estimates on quadrats ten meters on a side and, when fortunate enough to locate such a quadrat within the activity area of a family of shrews, caught enough animals per 100 square meters to yield the above figure. Considering the home ranges of Blarina given in both the present and in other publications, the quadrats used by Williams were much too small; he failed to allow for animals whose ranges undoubtedly extended beyond the actual area trapped. Townsend (1935) calculated his estimates of population density (5-104 shrews per acre) using trapping quadrats of 4,356 square feet which measured 33 by 132 feet, and he apparently assumed that the quadrat containing the traps coincided with the area from which the trapped animals were drawn. If I correctly understand his rather complicated trapping procedure, the effective trapping area--after addition of a boundary strip 100 feet in width to adjust the effective trapping area for animals drawn from beyond the quadrat itself--should have been closer to 80,000 square feet. Had this been done, Townsend's estimates would have read 0.4 to 5.1 Blarina per acre. The errors that were made by these

authors are understandable and attributable to the lack of information on population studies such as is available now.

Bole (1939) wrote that he considered the plots of both Townsend and Williams too small, and he consequently employed quadrats 150 feet on a side for his own work, again probably too small considering that a single home range of Blarina would probably be larger than this quadrat. Further, Bole made the same error as the authors whose methods he challenged: he failed to allow for individuals whose home ranges extended beyond his quadrats, thus seriously reducing the effective trapping area used in his calculations and simultaneously increasing the estimated population density.

Seton's figure (1909) of 50 Blarina per acre was probably more in the nature of an educated guess than a population density estimate in the current sense.

Accordingly, each of the estimates shown in Table 6 which is higher than 25 Blarina per acre is open to serious question and, in my opinion, invalid. Unless the conditions border on the remarkable, it is very unlikely that a population estimate based upon secure premises will approach even a figure of 25 individuals per acre in optimum habitat.

If the theoretical changes in a population of Blarina, as outlined by Pearson (1945), are valid, and there is little reason to dispute them, then even at the autumnal population peak, the numbers would not usually exceed a four-fold increase of the number of the initial breeding

stock present in the spring. Thus, if two pairs of short-tailed shrews are present at the start of the breeding season (and, based on my work, I believe this number is generous), then by mid-September the total population should not usually exceed 16 individuals per acre.

In spite of the widespread belief that Blarina is one of the most common small mammals in Michigan and elsewhere throughout its range, only the rather atypical Norden Area of the present study supports this contention. In every other area trapped, Blarina was taken less often than Peromyscus in some places and than Microtus in others. The short-tailed shrew was found in a greater variety of habitats than any of its associates, but its numbers were almost always exceeded at least two-fold by some other species.

In my opinion, the population density estimates of Blarina, both my own and those of others, belie the actual situation. Blarina was not equally distributed over any area which I trapped. Some points along the trapline invariably yielded more specimens than others. Were the extent of the effective trapping areas of these small tracts known, and the populations for them calculated, the results would show much higher population densities than are indicated above. In the various studies, the animals are assumed to be spread evenly throughout the areas of study, an assumption I do not believe is valid. Only where territories are strongly maintained would individuals of a species be forced to distribute themselves rather evenly, and

I doubt that such is the case with Blarina. The home ranges determined in this study showed considerable overlapping in spite of apparently available adjacent space. Townsend (1935) found much this same thing when he indicated a greater intraspecific tolerance for Blarina than for any other small mammal species in the associations he studied. He compared the incidence of captures in adjacent traps in his New York studies, and found that during the summer months Blarina were much more apt to be caught in adjacent traps than were members of other species. Hamilton (1931) also remarked on the apparent tolerance between individuals of this species, and he cited the large numbers caught in the same runway over a short period of time and the fact that when captives were placed in the same cage, they usually just backed away from one another, rather than fought, after coming in contact.

Population Fluctuations:

In both the Greene and Hamel Areas, data were collected periodically over a three-year span; both reveal a yearly population increase extending over the three-year period with the highest estimates occurring in 1956. This pattern is suggestive of a three-year cycle, but without data on the preceding and succeeding years, no definite inference is possible. In this regard, the Norden Area showed a higher population density in 1955 than in 1956 but, as discussed above, the data from these two years in the Norden Area may not be comparable.

A number of authors have remarked on the fluctuations of populations of Blarina elsewhere. Werner (1956) wrote that populations of Blarina in the Thousand Islands area, New York, showed a distinct high in 1953 and that the 1954 population was markedly lower. Working in central New York, Jameson (1949) found that Blarina was much more abundant in 1947 than in 1948. Manville (1949) remarked on the impressive increase in Blarina abundance over a three-year period on the same trapping plots, when the numbers ranged from zero in 1940 to 326 in 1942. Harper (1929) determined that Blarina, in the Adirondack Mountains of New York, was much less common in 1926 than in 1925 and wrote, "No other Adirondack mammal showed such striking fluctuation in numbers between 1925 and 1926 as did Blarina." He continued, that in 1925, "...they filled the traps by day as well as by night." In the following year he did not take a single specimen in the same areas. Describing Blarina as occasionally more numerous than its associates and at other times less numerous, Enders (1930) considered that these differences resulted from minor habitats within larger ones. Fowle and Edwards (1955) reported that in Ontario, Blarina constituted 65 per cent of the small mammal population in 1947 but only five per cent in the previous year.

Blair (1948), on the contrary, wrote that during his study of small mammal populations in southern Michigan, Blarina remained at a "...low, fairly uniform level..." and that there was "...no evidence of cyclic variations in

the numbers of short-tailed shrews on the George Reserve."

That at least many populations of Blarina undergo marked year-to-year fluctuations is well documented, and it may be that unless the population is of moderate size and the conditions favorable, a potential fluctuation will not occur. A question remains, however, regarding the nature of this fluctuation. Blair, quoted above, did not find any evidence of cycles. Bole (1939) wrote that the Blarina populations in Ohio were non-cyclic. After comparing his trapping success with that of others in the same geographic area at the same time, Manville (1949) wrote, "It appears, from these comparisons, that the Blarina population did not undergo the same fluctuations simultaneously throughout the general region; rather this was more a local phenomenon." Jameson (1949), working in central New York, indicated that Blarina was never found to be abundant in one area and scarce in another area simultaneously.

Apparent erratic fluctuations and possible cyclic fluctuations of these populations occur, but without a standardized effort on the part of many investigators over a number of years, it is improbable that these fluctuations can be fitted into a general pattern--if such exists. The potentially cyclic pattern of the populations in both the present study and that of Manville (1949) remains an enigma.

The causes of these fluctuations, either erratic or cyclic, are unknown. They are likely multifaceted and probably interacting to such an extent as to defy broad

generalities. Manville (1949) described this discouraging situation: "I consider that, within broad limits, the breeding potential of a species may remain about the same in one locality over the years... But other factors are not equal; the environment is constantly changing with the resulting fluctuations of the animal populations. The same environmental factors are not necessarily responsible for these fluctuations at all times, although there is a continual interplay of all factors involved. At one period it may be abundant food, at another abundant predators, severe competition, or especially inclement weather, which exerts a predominant effect on the numbers of animals."

At most sites of Blarina capture during this study I often noted and measured soil pH, color, texture, and moisture; amount of cover photometrically; humidity; plant species; abundance of other mammalian associates; snow depth; temperature; wind speed and direction; cloud cover; and humus; but none has shown any obvious correlation with the estimated population densities. I doubt, as did Manville, that any single factor will be found to govern Blarina abundance. Jameson (1949) was unsuccessful in his attempt to find any environmental factor controlling Blarina distribution.

Another explanation of population fluctuations suggests itself. Since no environmental factors have yet been found to govern the variations in populations of small mammals, the answer may lie in the animals themselves. Just

as control of regular daily activity in some species has been attributed to a hypothetical "biological clock" whose nature remains unexplained, control of population cycles or irruptions may depend upon an innate mechanism which, under certain circumstances, cannot express itself. If such be the case, each local population would undergo its own cycles whose periods would not necessarily match those of other local populations.

In partial explanation of these population fluctuations, both Townsend (1935) and Pruitt (1953) suggested that a succession of small mammal populations may terminate with Blarina tending to assume dominance as a climax species until some adverse factor reduces the shrew population and the succession begins again. This hypothesis is weakened by the work of Pearson (1959) who found no correlation between Blarina populations and seral stages, and by the studies of both Beckwith (1954) and Hirth (1959) who found Blarina to be most characteristic of the mid-seral stages of old field succession.

Sex Ratio and Longevity

Sex Ratio:

My study shows that, of 134 sex-verified specimens, 65 (48.5 per cent) were males and 69 (51.5 per cent) were females. Blair (1940) reported equal numbers of both sexes. Pearson (1945) presented a graph based on 173 males and 166 females, almost equal numbers. Manville (1949) reported

equal numbers of males and females on the basis of 22 specimens in one year, and in the following year took 239 specimens of which 56 per cent were females.

Hamilton (1929) reported taking many more males than females (69 per cent of 92 specimens were males); he cited that the collections of Blarina in both the American Museum of Natural History (New York) and the Museum of Comparative Zoology (Cambridge) contained almost twice as many males as females. Townsend (1935) wrote that males were more abundant everywhere except in moist woods and in these habitats the females exceeded the males in some years; of the specimens which Townsend listed as having the sex verified, 240 were males and 198 were females.

Perhaps the sex ratios differ markedly in the different populations sampled, or at certain times one sex is taken more readily than the other, or many investigators misjudge the sex of specimens, or perhaps slight variations in trapping procedure among the different workers result in taking predominantly one sex. Whatever the reason, the data presented by the different authors vary considerably.

Although the difficulty in sexing Blarina has been mentioned repeatedly, it is difficult to imagine that any of the above authors were mistaken in their sex identifications. I doubt, also, that the population structure of Blarina in different localities can vary as much as the data suggest. I suspect that most of the disagreement results from seasonal or year-round differences in behavioral

patterns; if a study were conducted during a period when one sex was markedly less active than the other, unequal captures could easily occur in spite of equal numbers of males and females. The females may range less widely while caring for young and thus be caught less often at that time; or, as Blair (1940) has suggested, since the home ranges of males are greater than those of females, any trapline will intersect the home ranges of more males than females and should, in consequence, produce more male specimens.

Longevity:

Of the 28 shrews maintained in captivity during the present study, one male is noteworthy. It was considered an adult when caught October 11, 1954, and I suspect that it may have been born late the previous year but, conservatively, it must have been a minimum of five months of age at capture. This shrew died November 6, 1956, approximately 13 months after the initial capture; it must have been, at a minimum, 18 months and possibly 24 months old at death. Several of my other captives lived for approximately a year following capture, but their life spans are not nearly so remarkable as those reported by Pearson (1945). He recorded four captives which died at a minimum age of 15 months, and described a female that died when no less than 30 months old, a male that lived 29 months, and another male that lived a minimum of 33 months. Mann (1956) wrote of wild-caught Blarina which were kept in captivity for 16

months.

Longevity in captivity indicates what a maximum life span may be, but this may have little relation to longevity in the wild. In captivity the shrews are not subjected to the necessity of constantly searching for food and existing, I suspect, continually near the edge of starvation. Nor are they subject to the same conflicts and problems of competition, combat, disease, and to the adverse conditions of the physical environment. An important consideration here is that tooth wear will be much slower when the usual soft foods supplied to captives are eaten and, as Flower (1931) has pointed out, when an animal in the wild has very worn and therefore useless teeth, it must die. These factors would all serve to reduce the life span in the wild from what is observed in captivity. However, other conditions associated primarily with captivity, such as lack of exercise and the accumulation of excessive fat deposits, very likely hasten the demise of the captives. Thus, although some conditions undoubtedly prolong the lives of captives in comparison with their wild counterparts, other conditions prevent the potential maximum life spans from being realized.

Only a few studies have dealt with longevity of Blarina in the wild and in the present study, only two individuals are pertinent. Eleven different shrews (five males, four females, and two of undetermined sex) were caught in live traps within two trapping periods in August

and September, 1954, in the Hamel Area; two were recaptured the following year in May and June. One male estimated to be a young adult when first captured on August 28, 1954, was taken last on June 8, 1955, when it was dead in a live trap. This male was born probably early in the spring of 1954; estimating its age conservatively as 107 days at first capture, it was probably 392 days old when it died. Another male, captured first on September 3, 1954, and taken last on May 23, 1955, was immature at first capture and assuming its age then as 75 days, its age at last capture was, conservatively, 340 days.

Pearson (1945) wrote that of 67 shrews trapped, marked, and released one summer, only four (six per cent) were recaptured the following summer. Allowing for the estimated age at the time of initial capture, the oldest shrew was considered to have lived a minimum of 400 days, or slightly over 13 months. With three other shrews the suggested minimum ages were 348, 389, and 389 days. Pearson claimed that the number of Blarina marked, released, and retrapped the subsequent year was lower than the percentage actually surviving in the wild because, in part, many were released in a weakened condition.

Blair (1948) wrote that, "Of thirty shrews recorded alive in the fall twenty-eight were never taken again." One female he marked in September was recaptured almost two years later in July, 22 months after the initial capture. On the assumption that no error was involved and

that the shrew was at least one month old when first captured, it must have been at least 690 days, or 23 months, old at death. Blair recaptured another female in the year following initial capture which was a minimum of ten months old.

Although a total of 350 Blarina were captured in his study, 63 per cent were dead at first capture and Manville (1949) recorded but two individuals taken in successive years and both were about 12 months old when last trapped.

Pearson wrote that his traps were almost always visited at intervals of less than six hours; both Blair and Manville visited their traps just twice a day. With these time intervals, it is not surprising that so few individuals survived the studies. In my work I found that more than two hours in a trap weakened Blarina severely, and that even though an animal may have been alive and released, survival was seriously affected. The surviving shrews described by these authors probably had entered the traps only a short time before they were released.

Obviously, Blarina is able to live far longer than any records on wild populations indicate. This fact emphasizes an unresolved yet important question: Why do the shrews in natural populations fail to realize their potential life span? If mortality were similar in all age groups, then older shrews should be taken in greater numbers late in the year but they are not; an explanation

must consider factors capable of differentially affecting the old more than the young shrews.

Mortality

Based upon his trapping experiences, Manville (1949) wrote that trap confinement was the greatest single cause of death during his study; 63 per cent of the Blarina caught for the first time were dead in his traps. Feebleness or death from fright have been claimed as causes for this by various authors, but Crowcroft (1951b) believed this debility was due merely to a semi-starved and therefore extremely poor condition of the shrews observed. Pearson (1945) wrote that these individuals dying suddenly must be exceptional for he had never seen a similar occurrence.

A cause of death which may or may not exist in wild populations of Blarina is that of shock or hypoglycemia. Christian (1950c) described this shock syndrome as a possible factor in mammalian population cycles. Death of Blarina from shock has been claimed by several authors, such as New (1959b) and Manville (1949), who, for example, described a shrew which, "...after a lively chase,...died within a minute after being caught, apparently from shock." This same thing has been described for other soricids by Manville (1949), Walker (1954), Jackson (1928), and Orr (1949); for squirrels (Allen, 1943); and in snowshoe hares (Green and Larson, 1938). Allen wrote that it seemed

logical that since squirrels showed this shock when pursued by man, they might be subject to similar seizures when suffering from exposure or when pursued by an enemy. The same remarks might apply equally well to Blarina, but I doubt that this would account for many deaths in the wild.

Pearson (1945) listed certain causes of death proposed by various authors regarding both Blarina and other shrews: 1) hunger, 2), thirst, 3) cold, 4) predation, 5) autumnal increase of internal parasites, 6) intraspecific combat, 7) fear, 8) thunder, 9) crossing paths used by man, and 10) old age.

In addition to the above, other causes of death have been proposed. Blair (1948) mentioned disease in general, parasitism, and starvation which are inferred, at least in part, above. He also mentioned accidents and "weather emergencies"; Blair doubted that any of these immediate factors were of great import in Blarina mortality. Both Hamilton (1931) and Klugh (1921) mentioned that the shrews normally avoid bright areas, and Hamilton suggested that exposure to bright light might be fatal. I question the latter since I have photographed Blarina, using bright floodlights, without any ill effects and have seen them abroad on the snow surface in wintertime when the sun was shining brightly. Townsend (1935) suggested that summer droughts may be one cause of death, immediate or later.

Effect of Water:

Water has long been considered an important factor in the life of Blarina. Seton (1909) wrote, "All that I have seen or taken were within 100 yards of a stream or pond, and most of them at the water's very edge." The fact that Blarina spends much of its time in burrows or under the ground litter where humidity is high, and that it is often taken in greatest numbers adjacent to free water, supports the importance of this factor.

In discussing the physical factors affecting Blarina distribution, Pruitt (1953) wrote, "If the environment has no free water, either because it is actually non-existent or is unavailable (in the form of ice), then this factor is indicated as a cause of distributional restriction. Observations on captive specimens of Blarina indicate that comparatively high humidity is important in keeping them alive for any length of time." Chew (1951), after studying the water exchanges of Blarina and other small mammals, found that the shrew had both a higher water intake and a higher water loss than the others under his experimental conditions. Townsend (1935) suggested that death in live traps might be due to thirst rather than hunger. In at least partial disagreement with the above, I made no attempt to maintain high humidity in the open cages of my captives and they showed no ill effects. In fact, these cages had dry soil as a substrate and the only water available was in a small glass container. Pearson (1950)

successfully maintained his captive Blarina in open cages containing a substrate of wood shavings.

Regarding high water intake, my captives were kept in an unheated garage and throughout the winter the only water available was in the glass container and usually frozen solid; the shrews were able to obtain water only by licking the ice and in doing so, wore little grooves in the ice surface with their tongues. Accordingly, I feel that humidity and water will undoubtedly influence distribution but that this is a matter of preference rather than a critical factor in the life of Blarina. It is possible that without high humidity, the olfactory sense would be diminished and this may be the reason that Blarina appears to prefer moist and humid areas.

I doubt that free water is any more critical for Blarina than for many other small mammals; even in very dry places--and these shrews are present in many such areas--the food and dew provide some water, and various physiological adaptations such as lowered sweat production and decreased urine volume would help conserve body fluids. Behavioral adaptations, however, may well control the balance between survival and death. If the majority of the activity were below the ground surface in the cool, humid burrows, water loss would be minimal and the need for high intake of water would not exist.

I do not dispute Chew's (1951) data; with their high metabolic rate, shrews undoubtedly lose considerable amounts

of water, especially in warm, usually dry laboratories. The intake of free water would be correspondingly high. However, this problem for the shrew can be solved either by drinking more water, or by reducing the loss and, in the wild, I suspect the latter alternative is often followed.

If given the opportunity, shrews apparently drink more than is required for survival. Their method of drinking, incidentally, is quite interesting: the typical captive curled back its lower lip and, with the snout turned up sharply, barely touched the water with its vibrating tongue.

Other species of shrew are able to subsist with a low intake of water: Hamilton (1940a) considered that Sorex fumeus obtained sufficient water from its food because his captives drank only limited amounts; no free water was given to captive Sorex cinereus by Blossom (1932) over a three-month period; and Wahlstrom (1928) claimed that his captive Sorex vulgaris never drank.

Effect of Predation:

Predation undoubtedly accounts for a large share of Blarina deaths and it may be the most important factor. Blair (1948) claimed predation as the most logical explanation of the short life span of Blarina.

When these shrews are abundant, they may form a significant part of the diet of various predators. During a year when Blarina was abundant in Ontario, Fowle and

Edwards (1955) found that Barred Owls and red foxes ate them in large numbers; some shrews were found in the stomachs of lake trout. Schueler (1951), who studied red foxes in New York during the same year, wrote that Blarina was often the most common food item.

In contrast, during periods when the populations of these shrews are not notably high, they are rarely eaten by their omnivorous and carnivorous mammalian associates. Investigations have shown that Blarina is seldom included in the diet of coyotes (Fitch and Packard, 1955), red foxes (Dearborn, 1932; Hamilton, 1935; Murie, 1936; Hatfield, 1939; Seagers, 1945; and Scott, 1947), bobcats (Dearborn, 1932; Pollack, 1951), domestic cats (Nader and Martin, 1962), raccoons (Hamilton, 1943), opossums (Hamilton, 1951), mink (Korschgen, 1958), skunks (Seton, 1909; Dearborn, 1932), and weasels (Dearborn, 1932; Kirk, 1921). Blarina might be considered as a predator upon its own species but such cannibalism is rare. I found only one instance of this during the present study: two shrews had entered the same trap and the younger was dead and partially eaten. Shrew hairs were commonly found in the digestive tracts of Blarina but I am convinced that these were ingested accidentally when licking their fur.

Many predators will kill, but not eat, Blarina and these deaths may have a considerable impact upon the shrew populations. The apparent reticence of mammalian predators to eat shrews has been mentioned by many authors and is

best documented for the red fox (Marie, 1936; Scott, 1947) and the domestic cat (Van Hyning, 1931; Nader and Martin, 1962).

Raptors may well be the most important group preying on shrews, and owls undoubtedly capture more Blarina than do hawks. Pearson and Pearson (1947) found that the diet of Barn Owls contained considerably more Blarina (13.8 per cent) than the diet of Long-eared Owls (3.0 per cent) and that Short-eared Owls ate none. After examining over 2,500 Barn Owl pellets, Richmond and Rosland (1949) found that short-tailed shrews represented over 20 per cent of the mammals eaten. Hamerstrom and Hamerstrom (1951) wrote that young Cooper's Hawks and a young Red-tailed Hawk were fed no Blarina by their parents and that a young Barred Owl was given only a few. Owl pellets found both within and near the areas I trapped were examined and those known to be from Long-eared and Great Horned Owls contained no shrew remains; other pellets from an unknown species yielded only an occasional Blarina skull. Obviously some raptors, such as the Barn Owl, represent a more serious threat to Blarina than others, yet even a family of Barn Owls would, according to Pearson and Pearson, remove less than one shrew per acre per year.

From the above, I think it apparent that the short-tailed shrew is not a preferred species to any predator, and is not eaten in numbers except under quite unusual circumstances when the loss of even large numbers would not

decrease the breeding population to a critically low level.

Most of the predators which might kill Blarina range over wide areas, and the influence of any single predator within any part of its home range would probably be slight. The sum total of all predation, however, could easily cause the populations of Blarina to decline when replacements are not available. Blair (1948) believed this to be true when he wrote, "The winter decrease in numbers....results principally from the lack of breeding during the winter months." Predation, thus, may explain a decline in total population yet the apparent higher mortality of the older shrews is still unexplained.

Intraspecific combat, even if severe, cannot imply the death of the vanquished. Based upon the behavior of my captives, I believe that aggression usually ends abruptly with one shrew retreating. Hamilton (1931) mentioned a similar observation. A shrew in its own burrow system would probably be able to frighten another shrew away merely by feigning aggression; this behavior was noticed repeatedly when a resident shrew encountered a visitor to his cage. Occasional scarred animals, sometimes with missing toes, indicate that the shrews do fight, perhaps with one another, perhaps with prey species. Based upon those I have seen, so few shrews have these scars that the fights are probably not a common occurrence and, I would judge, certainly not a major cause of death.

Differential Mortality:

Although most of the suggested causes of mortality undoubtedly contribute to the net result, predation seems to be the most logical immediate cause for the majority of deaths. The older shrews, apparently being removed from the population at a greater rate than the young, may suffer from a combination of factors. During the summer months, the death rates for both old and young shrews may be similar but since the young are continually entering the population, the older animals will represent a continually smaller percentage of the total population. The relatively few adults surviving to the fall might then be affected differently than the young by factors impinging on the entire population. I suspect that as shrews age, their worn teeth and perhaps less vigorous approach to life makes them less efficient competitors than their younger associates. A reduced vitality could easily cause a more marked susceptibility of the older shrews to any autumnal endoparasitic increase (Hamilton, 1931) or other disease, to cold (Soper, 1942), parturition, temporary lack of food, or to predators.

FOOD ACCEPTANCE AND DIET

Both stomachs and intestinal contents from 83 wild-caught Blarina, trapped throughout the year, formed the basis for studying the diet of these shrews. The analyses of these contents are compiled in Plate XXXVI and Tables 8 and 9. In Plate XXXVI, the data are grouped by season and all months except January are represented.

Before the analyses of diet in the wild are discussed, the reactions of captive shrews to various foods must be considered for these bear upon the interpretation of the digestive tract contents.

Acceptance of Food by Captive Shrews

Both known and potential constituents of the wild diet were offered to captives to learn something of food acceptance and preferences that might be exhibited.

Acceptance of Mammals:

Three species of live mammals were offered my captives: meadow vole, white-footed mouse, and house mouse. These were chosen because they were the most common associates of Blarina in this study and all were represented in the shrew stomachs examined. I was unable to capture a live masked shrew and therefore the reaction of Blarina to this smaller species of shrew was not observed, although

its remains were noted in one stomach. Eastern cottontail remains were found in the stomach of one shrew but reactions to a live cottontail were not tested; a partially eaten dead cottontail was discovered close to the trap which caught this shrew and the stomach contents no doubt represented carrion.

Meadow Vole

Three voles, weighing 15.6, 19.0, and 28.6 grams, were offered to various of my captive shrews but only the smallest was killed and eaten, this by a shrew weighing 17.5 grams after a short but energetic chase.

When the 15.6-gram, male meadow vole was placed in the cage of a 17.5-gram, female shrew, the shrew appeared more alert and active than usual but no recognition of the vole's exact position was evident until the shrew was within about three inches of its prey. At first contact, the shrew squeaked, both animals retreated, and the vole, breathing rapidly and appearing nervous, rested in a corner while the shrew, its nose in continual motion, scurried about the cage in apparent search of the intruder. The shrew then cautiously approached the vole a second time and when the vole retreated, Blarina leaped forward and nipped the vole's hind leg. Following this, the shrew continued in active pursuit and the vole continually retreated. Within three minutes, the shrew had bitten the hind quarters of the vole several more times and the vole's only reaction was attempted escape. Only after the shrew managed

to bite the vole's flank and maintain its hold momentarily, did the vole turn on its attacker and both engaged in a tumbling scuffle. Although ineffectually attempting to bite the shrew, the vole seemed preoccupied with its efforts to push the shrew away. Blarina, likewise, used its feet considerably and battled much of the time while lying on its back, pushing, twisting, and biting the vole primarily about its head. When the shrew finally succeeded in gripping the vole securely below the eye, it did not completely release its hold again until the vole had quieted. Blarina renewed its grasp several times while tugging and dragging the struggling vole about the cage. Each time the vole renewed its struggle, the shrew appeared to clamp its teeth more firmly and tug with more insistence. Eight minutes after the active pursuit began, the vole was quiet, yet breathing, and the shrew immediately began to chew the braincase in the parietal region. Death appeared to occur while the shrew was chewing on the vole's skull; the vole suddenly went limp. Throughout this episode the vole made no audible sound and the shrew voiced its soft chitter of excitement only during the pursuit. The vole was removed after the brain and part of the shoulder were eaten.

The two heavier voles each survived two days in the cages of their respective hosts, a 19.0-gram male and a 21.5-gram male Blarina. Each vole was subsequently placed in the cages of other shrews for short periods but neither was attacked. The day following the death described above,

the vole weighing 19.0 grams was placed in the cage and with the same shrew that killed the small vole, but no attack occurred; the shrew met the vole, squeaked, retreated, and although it encountered the vole several times again, I noted no signs of aggression.

The majority of the shrews actually seemed afraid of the larger voles. In one instance, the 28.6-gram vole was placed in the cage of a 19.0-gram male Blarina while the latter was hidden beneath a board. The shrew became excited, poked its head out from under the board, nervously sniffed the air, and cautiously emerged from its resting nest. The vole attacked and, using its forepaws, batted the shrew which retreated beneath the board. A similar encounter was repeated about two minutes later and, although I did not watch the cage continuously, I did not observe the shrew again until the vole was removed about 14 hours later. The vole evidenced no sign of fear or concern after the shrew had been chased out of sight.

A large number of voles, which had been killed in snap traps and which ranged in size from young to large adults, were given to my captive shrews from time to time. All the voles were invariably eaten. The shrews, with minor variations, all followed the same pattern of feeding. They usually began by chewing through the back of the skull and eating the brain. Then, feeding through this opening in the skin, they proceeded to devour the rest of the vole. The result was usually an almost empty skin with just a

few internal parts remaining. These remnants usually consisted of skull (minus brain and the dermal roof bones of the cranium), the distal leg bones, the tail, and occasionally a major portion of a rear leg. The skin was usually intact except for the enlarged opening where the brain was eaten; few additional tears were made.

White-footed Mouse

Four live mice, weighing 11.8, 14.0, 14.8, and 18.4 grams, were placed in the respective cages of a 16.5-gram female, an 18.8-gram male, a 20.7-gram female, and a 22.0-gram male shrew. Two of these mice (weighing 14.0 and 18.4 grams) were killed but the death of the smaller was not witnessed.

Soon after the 18.4-gram mouse was placed in the cage of the 20.7-gram female Blarina, the shrew emerged from under a board, excitedly sniffing the air. The shrew began searching about the cage, continually sniffing and moving its head from side to side, until it came within about 3 1/2 inches of the mouse. The shrew squeaked, retreated a few inches, approached to within two inches, squeaked again, jumped backward about an inch and then attacked. Blarina managed to momentarily bite the hind foot of the mouse as it leaped over the shrew and out of the corner of the cage. During the next half-hour the shrew spent about half its time in the nest under the board and about half its time sniffing around the cage, apparently searching for the mouse. Periodically the shrew came within

a few inches of the mouse, recognized its presence, and attacked; the mouse received occasional quick bites on the tail, foot, or rump as it leaped or ran away. Near the end of this half-hour period, the mouse began appearing sluggish and it quivered slightly as it rested. The shrew finally managed to bite the shoulder region of the mouse solidly and both animals locked in combat, the shrew fighting mostly while lying on its back. The mouse was bitten a number of times about the lips, ears, and ventral body surface and although it appeared to bite the shrew, the latter showed no signs of breaks in the skin. The fight ended when Blarina bit through the mouse's skull several times in quick succession just behind the eyes. The mouse went limp 43 minutes after the initial attack and the shrew immediately began eating the back part of the mouse's head.

The 14.0-gram mouse whose death was not observed was placed in the cage of an 18.8-gram male, hidden beneath a board. The shrew emerged from his nest, sniffed about the cage and, when about 2 1/2 inches from the mouse, squeaked and retreated to the board. This behavior was repeated several times within the next hour but the shrew did not attack. Twelve hours later, the following morning, the mouse was dead and partially eaten.

The 14.8-gram mouse remained in the cage of a 20.7-gram female shrew over a 24-hour period without visible damage and was then removed. The shrew came from its nest

shortly after the mouse was introduced to the cage. After locating the mouse the shrew gave the usual squeak, retreated and approached again. When the shrew was about two inches from the mouse the latter attacked with its paws and batted the shrew which rapidly retreated to its hiding place beneath a board. The shrew was subsequently seen to scurry about the cage but each time it came within about three inches of the mouse she gave a short jump backward and moved away. This shrew obviously avoided the mouse which, though not physically harmed, evidenced a lowered threshold to various stimuli, being startled by the slightest sound or movement.

The smallest mouse (11.8 grams), placed in the cage of a 16.5-gram female shrew, was not attacked while under observation and, four hours after initial introduction to the cage, showed no sign of physical damage when removed. The shrew, although periodically investigating the mouse, limited its reaction to an occasional squeak and sniffing, a few times actually brushing its snout against the mouse. The mouse showed no evidence of aggression and usually just sat shivering when the shrew came close; it moved slowly to different places within the cage only when the shrew was out of sight or at the opposite end of the cage. Most of the time the mouse sat in a corner, hunched up and quivering, and when removed after four hours of apparent terror, it huddled in the corner of its own cage, still shivering. The following morning the mouse was dead, perhaps from shock.

As with the dead voles, every dead white-footed mouse which was given to any shrew was eaten, although not so thoroughly as were the voles. The mouse brains were usually eaten first but in a few instances the shrews ate the abdominal contents or a thigh without touching the rest of the mouse. A rather small opening was invariably torn in the skin and the mouse was simply devoured--bone and all--through that tear. The only parts usually not eaten were skin and hair, unless by accident, the anterior portion of the head, the terminal two-thirds of the tail, and the feet; the lower jaw and anterior half of the skull were eaten only rarely.

House Mouse

One live house mouse (16.0 grams) was offered to three different adult shrews but none was able to capture it within a two-hour period and one shrew avoided the mouse.

Only two dead house mice were offered to my captive shrews, one to a 17.9-gram female and one to a 18.8-gram male. Both mice were eaten in a similar manner with the brains eaten first; the remnants consisted of an almost empty skin having just a few tears, the front part of the skull, the tail, the lower leg bones and the feet.

Hamilton (1930) wrote that his captive Blarina had killed Microtus, Peromyscus, Clethrionomys, Pitymys, and Mus. Christian (1950b) and Phillips (1956) described the deaths of Microtus and Rood (1958) of Peromyscus. My

descriptions, above, corroborate those of these authors and, although basically similar, differ enough in details to warrant their inclusion here.

In discussing British shrews, Crowcroft (1951a) remarked that only if alternative food is unavailable will shrews become cannibals. Rood (1958) stated that his captive Blarina showed a great deal of individuality in their food preferences, and that most readily ate dead shrews that were placed in their cages although one male refused to turn cannibal as long as other food was provided. In the present study, when attempts were made to breed Blarina, fights occasionally began and had the individuals not been separated, I judge one might have died. When dead Blarina and masked shrews were offered my captives, each was at least partially eaten when other foods were withheld; in the presence of other dead small mammals (voles or mice) the dead shrews were usually bypassed.

Preferences and Feeding Behavior

Several generalizations can be made regarding the behavior of Blarina to its mammalian prey. First, the shrews differed widely in their apparent motivation toward this kind of potential food; some shrews energetically chased but failed to capture, others sought, attacked, and killed, others appeared to ignore, others avoided, and some seemed to fear the voles and mice. When hunting their prey, the shrews experienced difficulty in pin-pointing its location until they were within two or three inches

and it is my impression that a moving vole or mouse was detected at a greater distance than one which was still; the turned-up attitude and constant side-to-side movement of the nose and head suggest that odor, and perhaps sound, are used for detection more than eyesight. The shrews were typically rather quiet during pursuit of prey, emitting usually only the chitter which I associate with excitement.

All of the live mammals were offered to shrews living in cages with floor dimensions of 12 by 18 inches. Had the prey not been so confined, I doubt that Blarina would have been as successful in catching those attacked. Even with the handicap of little space, several of these mammals were able to avoid capture. In the wild it is unlikely that Blarina could locate, catch, and kill many small mammals unless they were trapped in tight quarters.

Blarina is able to subdue other mammals almost twice its own size and in large part this ability is attributed to the narcotizing effect of the saliva from the submaxillary and retrolingual glands. The effect of this saliva was investigated first by Pearson (1942) but was either suspected or known about many years before. Cresswell's (1891) translation of Aristotle's classic work refers to some shrew species: "The bite of the shrew mouse is injurious to other animals also; it causes sores, which are more severe if the creature is pregnant when it bites, for the sores then break." After being bitten several times

by Blarina, the opponent becomes groggy and unable to effectively resist the attack. This debility of the prey has been reported by several authors and such an effect was noted with both amphibian and mammalian prey supplied my captives. According to Lawrence (1945), the saliva from the submaxillary gland has an effect virtually identical to the neurotoxic venom of elapine snakes. She remarked that Blarina's habit of biting prey near the brain would inject this saliva close to the site where its action would have quick effect. Although his results were inconclusive, DeMeulas (1954) suggested that the saliva may have an anti-adrenalin effect and that it is a lachrymator; both these effects would inhibit efficient defense by the prey.

A pattern of feeding on small mammals is evident. Blarina almost always begins by chewing through the back of the skull and eating the brain. Then, using the same opening in the skin and, on occasion, tearing an additional entry, the skeletal muscle, bones, and viscera are eaten, leaving a skin which is empty save for the tail, feet, and anterior portion of the skull. This method of eating results in little ingestion of hair and, although none of my shrews were sacrificed to test the belief, I doubt that absence of hair in a stomach can be used as evidence that these shrews have not eaten any mammal associates.

Three separate shrews were supplied both a dead meadow vole and a dead white-footed mouse simultaneously. In each instance the brain of the vole was eaten first.

One shrew then ate the mouse's brain but the other two continued eating the vole until, apparently, they had satiated their appetites; they slept before beginning on the mouse's skull. After this initial selection the shrews ate various parts of either carcass, apparently at random.

In addition to the live and dead small mammals offered to my captives, other food of mammalian origin included raw and cooked horse-meat, hamburg, calve's liver, pieces of frankfurters, pork, lamb, veal, smoked and fresh ham, bacon, lard, beef heart, bologna, and salami. All were eaten readily and, when supplied with any food of non-mammalian origin, were always eaten first. Only when a particular item was fed to a shrew on each of several successive days did that shrew evidence any diminution of preference.

Acceptance of Birds:

No live birds were offered to my captives but several dead English Sparrows and one Slate-colored Junco were given them and these were eaten, except for the skins and feathers, the intact skulls including brains, the forearms and lower leg bones, and portions of the synsacrum and tail; for some reason the sternum and pectoral muscles of the junco remained intact. The failure of Blarina to eat the brains of birds was also noted by Hamilton (1930) and Rood (1958).

The Slate-colored Junco was found dead and without any superficial damage. The shrew began eating this bird at the cloacal aperture and, after enlarging the opening

somewhat, ate most of the musculature, skeleton, and viscera through the same torn spot. The English Sparrows were shot with an air rifle and the shrews which were given these birds began eating at the wound sites. Rood stated that his captive Blarina always began eating at the anal opening and progressed toward the neck. Hamilton wrote that one of his captive short-tailed shrews ate a nestling House (English) Sparrow and Phillips (1956) fed his captive shrews adult English Sparrows.

I did not offer any entire eggs to my captives although they readily ate cooked bits of the yolk and albumen of chicken eggs. Brooks (1908) believed, as will be described later, that Blarina probably ate eggs of ground-nesting birds. Various pieces of chicken organs and flesh were readily eaten by my captives. When two shrews were supplied, simultaneously, with a dead white-footed mouse and a dead English Sparrow, each shrew fed on the mouse until it was finished before they began on the bird.

Acceptance of Reptiles:

A small garter snake that Hamilton (1930) supplied to his captive shrews remained untouched but other authors (Cope, 1873; and O'Reilly, 1949) wrote of such predation in the wild. I placed a 14-inch garter snake (Thamnophis sirtalis) in a cage with an adult female Blarina, but little attention was paid the snake until food was withheld for 12 hours. Finally the shrew attacked the snake, first biting it randomly about the body and then attacking

the head where many rapid bites were inflicted. During this time the snake was twisting violently but could not shake the shrew loose. After about ten minutes, the snake began to calm and the shrew continued to bite the head area while tugging the snake about the cage. When the snake was subdued but still moving feebly, Blarina chewed through the base of the skull but did not eat the brains. The body wall of the snake was then torn in several places but little, if any, flesh was eaten. The snake was removed from the cage three days later in essentially the same condition as it was shortly after death. During this three-day period the shrew was eating wheat, corn, and dried commercial dog food, apparently in preference to the snake.

No turtles or lizards were offered to the shrews.

Acceptance of Amphibians:

Captive shrews described by Hamilton (1930) ate tadpoles of the green frog (Rana clamitans), red-backed salamanders (Plethodon cinereus), only the lips and toes of the spotted salamander (Ambystoma maculatum) and this only after a ten-day exposure. He wrote also that frogs (species not reported) were killed after an interval but only the lips and toes were eaten, and that toads (species not reported) were not touched. Because amphibians are usually present in the humid habitats frequented by Blarina, representatives of several species were offered my captive shrews.

Frogs

Several average-sized specimens each of bullfrog (Rana catesbeiana), green frog (Rana clamitans), and leopard frog (Rana pipiens) were introduced into the cages of both male and female shrews but none of the shrews showed any inclination to attack the frogs. Usually when a shrew approached the intruder to investigate, the frog hopped away and the shrew squeaked and retreated. Even after food had been withheld from the shrews for 12 hours they showed no interest in the frogs.

Toads

American toads (Bufo americanus) of different sizes were placed with both male and female shrews; one was not molested for a period of five days, while others were killed within an hour. The smallest toads, about one-half adult size, were killed more readily than the larger ones. The way in which a toad was attacked is rather interesting and I quote my edited notes on an encounter between a 42-gram toad and a 20.8-gram male shrew (the numbers on the left represent time):

1105- toad placed in shrew's cage; shrew twittering, approaches, smells toad, neither shows fear.

1107- shrew, tail erect, badgering toad and vocalizing: churring with occasional squeaks; approaches toad, bites arm, bites parotoid gland and rubs nose violently in soil.

1108- shrew noses toad several places, rubs nose in soil, shrew sounds angry; toad assumes weak defense posture several times (the inflated toad bends its head sharply ventrad, the forearms extend straight

out from the body and the hindlegs are extended posteriorly lifting the pelvic region up and pressing the head into the soil; the toad is thus almost standing on its head and the parotoid glands are presented toward a head-on attack.)

1113- toad hopping about cage, shrew cautiously searching; toad hopping at glass attempting to escape; shrew's attention not on toad; shrew finds toad, bites its shoulder, rubs nose in soil, retreats.

1115- several more bites, toad assuming defense posture, shrew scrapes snout in soil.

1117- same thing again, then shrew ignores toad.

1125- shrew bites toad's hind legs, tries to bite side.

1130- shrew trying to attack toad from below, apparently doesn't experience any annoying secretion from belly surface; toad keeps side toward shrew down against soil--is in defense posture.

1137- shrew chewing on toad's left arm and underside of hind leg, seems more persistent, less nose rubbing.

1145- shrew continues to bite toad--all over--toad's left arm appears useless and chewed, toad remains in defense posture while being bitten--just presses head into soil.

1148- toad appears groggy, uncoordinated; shrew can roll it over on its back now; toad removed from cage, immobile.

1217- replaced toad, quiet but breathing, could not find any obvious breaks in skin; shrew drags toad into corner of cage and begins chewing on belly in pectoral region.

1220- shrew chewing toad's lower jaw below eye.

1224- toad deflated, shrew eating anterior portion of skull about snout; lower jaw broken at midline; toad still alive but motionless.

1230- shrew continues eating on head, ate tongue and top of head back to level of eyes.

1244- shrew began eating toad's ventral surface, base of hind leg.

1300- shrew still eating muscle and bone of pelvis and hind leg.

When the toad remains were examined the following day only the empty skin, torn through in several places, plus attached feet were left. All the shrews that killed toads showed the same behavior of rubbing their snouts in the soil flooring the cage. The smallest toad given a shrew weighed 5.6 grams and that shrew exhibited only mild irritation. One shrew, which eventually killed the toad, gave a parotoid gland several very energetic bites in quick succession and immediately started violently scrubbing his nose in the soil and, in addition, chewed on small pieces of clay. The poison secretions of the toads are not as effective against shrews as might be desirable but although eaten, these toads were obviously not preferred food items.

Salamanders

Three species of salamanders were offered the captive shrews: red-backed salamander, spotted salamander, and tiger salamander (Ambystoma tigrinum). All three were eaten but not readily. The secretions of these species have an irritating effect on Blarina resulting in much the same nose-rubbing as was caused by the toad; the red-backed salamander caused less irritation than either of the other species. All were killed and eaten in much the same manner and a description of Blarina killing the red-backed salamander differs from its attacks on the others only in that the red-backed salamander practiced autotomy of its tail while the other species did not. The shrews did not attack these salamanders at any particular part of the body; some

began their attack at the tail, others at the body, and others at the head. The head and occasionally parts of the appendages were seldom eaten.

One adult-sized red-backed salamander was attacked and eaten in the following manner. A 17.8-gram female shrew did not evidence recognition of the salamander in her cage until she came within about 1 1/2 inches. She turned sharply toward the salamander without making any audible sound and immediately bit at its thoracic region. The shrew showed slight but obvious irritation and brushed her snout against the ground. The shrew then nibbled on the pelvic area and the tail base and, as the salamander twisted in apparent escape attempts, the terminal half of the salamander's tail broke loose and wriggled violently. The shrew was still chewing on the pelvis when the tail attracted her attention and was eaten. She returned immediately to the tail remaining, began chewing, most of that came off and was eaten. The shrew then ignored the salamander whose posterior half was paralyzed. About five minutes later the shrew went back to the salamander and ate more of the pelvic area (the salamander had died meanwhile). Five hours after the initial encounter only the head and forelegs remained and these were still uneaten 24 hours later when removed.

Acceptance of Fish:

Both Hamilton (1930) and Edgren (1948) reported that fish were readily eaten by Blarina. I fed captives

pieces of perch (Perca flavescens), frozen filets of cod (Gadus morrhua) and halibut (Hippoglossus hippoglossus) and herring (Clupea harengus). Edgren fed his captives both pike and some species of minnow. Admittedly, acceptance of fish has little bearing on usual foods eaten in the wild, but fish are occasionally stranded or left on a stream bank or the edge of a pond. This demonstrates, further, a willingness of shrews to eat things to which they are not accustomed and a readiness to eat almost any kind of flesh.

Acceptance of Insects:

Without exception, no insect, either adult, pupa, or larva, which was offered my captives was refused. Hamilton (1930) reached the same conclusion but claimed that ants were never eaten and he noted but one stomach, of all he had examined, that contained an ant. My captives did accept ants but ate the larvae and pupae more readily than the adults. Virtually every author that has written of Blarina food habits has mentioned their wide acceptance of insects and most relate instances to support their contentions.

My captives received various species representing the following orders: Orthoptera, Dermaptera, Isoptera, Hemiptera, Ephemeroptera, Odonata, Neuroptera, Trichoptera, Lepidoptera, Coleoptera, Hymenoptera, and Diptera. When afforded a choice, they apparently preferred the moderate to larger-sized, soft-bodied insects such as crickets,

grasshoppers, larval stages of butterflies and moths, and beetle larvae. Many of the larger forms were bitten about the head and thorax and then carried to a cache near the nest and a large number of these were still alive when cached but unable to move away.

Small insects that were eaten completely entered the mouth entire and were but slightly chewed; larger insects were torn or chewed apart and the pieces chewed slightly. The legs and wings of the larger insects were usually left and apparently eaten only if they happened to adhere to the thorax when it was ingested. Butterfly wings and the elytra of large beetles were eaten only rarely.

Acceptance of Arthropods other than Insects:

Spiders were always eaten but they were not supplied to my captives in sufficient numbers to judge preference. The spiders were members of three different groups: Harvestmen, Orb Weavers, and Hunting Spiders. The legs were not usually eaten, especially those of the Harvestmen.

Three crustaceans of undetermined species were supplied to the shrews. Sowbugs and pillbugs were eaten entire. Crayfish collected both from streams and a moist streamside area where their 'chimneys' were common, were given to different shrews and seemed to be eaten eagerly. In killing the crayfish, Blarina bit through the exoskeleton in a number of places but seemed to concentrate on the abdomen. The shrew's movements were quick and all managed

to avoid being pinched by the chelae. Although the crayfish moved rapidly when the abdomen was flexed, each shrew appeared cautious but not frightened. Blarina finished by alternately chewing on the abdomen or some other part of the crayfish and, gripping the abdomen, dragging the prey until it was quiet. The crayfish was then eaten slowly. Only two crayfish were seen killed but all ended in about the same condition--a scattered pile of exoskeletal pieces and the smaller appendages. Edgren (1948) wrote that crayfish were readily eaten and Hamilton (1930) stated that sowbugs were liked by his Blarina.

My captives were given several centipedes and one millipede and all were eaten with enthusiasm. Hamilton (1930) claimed that centipedes were eaten readily but that millipedes were not relished.

Acceptance of Annelids:

Nightcrawlers (Lumbricus terrestris) and a variety of smaller earthworms of unknown species were eaten by my shrews. As Hamilton (1930) learned, the smaller worms are apparently preferred over the larger nightcrawlers.

These worms were usually bitten along the body in a number of different places but most of the bites were within the anterior half. The shrew usually began by eating some part of the anterior half and then proceeded caudad. The largest worms, after being bitten a number of times, were carried off and stored more often than were the smaller ones.

Acceptance of Mollusks:

Both snails and slugs were given to the captive shrews; some were eaten readily, others almost neglected. To determine preference for these mollusks, a number were scattered, live, on the surface of freshly screened soil. After permitting four adult shrews to feed on these local mollusks, each for an hour, the soil was again screened and all the missing mollusks, as well as those obviously opened, were assumed eaten. Table 7 presents the results of this experiment.

TABLE 7

ACCEPTANCE OF VARIOUS SNAILS AND SLUGS BY BLARINA

Species	Number available to shrews	Number eaten by shrews	Per cent eaten (Acceptability)
Snails			
Triodopsis(Polygyra)albolabris	6	2	33
Polygyra fraudulenta	8	5	62
Polygyra tridentata	5	2	40
Anguispira kochi	14	11	79
Anguispira alternata	12	10	84
Ventrindens sp.	11	11	100
Succinea sp.	21	17	81
Vallonia pulchella	16	14	87
Slugs			
Droceras (Agriolimax) sp.	4	4	100
Philomycus carolinianus	7	7	100

Different authors have remarked on the readiness of Blarina to eat various snails, especially those of the genus Polygyra. Hamilton (1930) described his captives as readily eating Polygyra sp. as well as the water snail Limnea sp. He continued that his captives liked the slug Agriolimax (now Droceras) campestris but did not like the larger slug Limax maximus. The two slugs offered to my shrews (Table 7) were both eaten readily.

A distinct preference was shown by my captives for the smaller and thinner-shelled snails such as Ventrindens, Succinea, and the tiny Vallonia; as long as these were available, Polygyra and Triodopsis were virtually ignored. Rather than exhibiting any standardized pattern of eating these snails, Blarina simply chewed up the smaller ones, usually leaving a few small pieces of broken shell. Some of the larger snails were eaten through the apex, some were eaten after the aperture was enlarged by chewing away pieces of the shell, and a few shells were completely broken up.

Acceptance of Plant Material:

Although not usually considered as popular for food as animal tissue, plants--and their products--are eaten and often in considerable amounts. Babcock (1914) fed his Blarina nothing but rolled oats for 52 hours and claimed they thrived. Phillips (1956) fed his captives on chicken scratch feed. Reed (1958) wrote that walnuts and Ritz crackers were favored over all other foods, including meat. Contrarily, Townsend (1935) stated that his captive shrew

would not accept vegetable matter but ate other things; Merriam (1884) claimed that corn and oats were eaten when other things were not available, and 21 different vegetables that Babcock placed before his Blarina were untouched for 11 hours.

Hamilton's (1930,1944) captives ate sunflower seeds, raisins, apples (all except the skin and core), peanut butter, English walnuts, cattail (Typha sp.) roots, and both soft and hard corn. Beechnuts were liked, according to Merriam (1884) and Brooks (1908); Seton (1909) stated that dried corn was eaten; and Fitch (1954) wrote that longleaf pine seeds were eaten by Blarina. Townsend and Rood both commented that peanuts were eaten; Rood fed his captives whole wheat bread also. The foregoing emphasizes the variety of plant food which Blarina has been observed to eat. Like most mammals, this shrew is actually omnivorous in the strictest sense of the term.

My shrews ate apples and rarely pieces of potato, Spanish and Virginia peanuts, cashews, almonds, and Brazil and filbert nuts, pecans, English and black walnuts (all the foregoing with the shell or husk removed), potato chips, whole and cracked corn (usually the embryo was eaten and the remainder left), oats, wheat, and beechnuts (the seed coat was seldom eaten). Black and white oak acorns were eaten only after I had removed the husk; none of my captives were known to have eaten an intact acorn. Usually chicken scratch feed was available at all times in the

cages but it was ignored unless animal food was withheld. Grass and sedge leaves were offered the shrews but were not eaten.

No mushrooms or other fungi were given my captives; Hamilton (1930) stated that Coprinus sp. was eaten sparingly.

Acceptance of Other Items:

Some of the prepared foods fed to the shrews cannot be properly placed in any of the foregoing categories. My animals received both dry and canned dog food at irregular intervals; the following brands were provided: Daily, Ken-L-Ration, Gravy Train, and Friskies. The canned food was eaten more readily than the dried. Pearson (1950) fed his shrews a mixture containing prepared dog food; he mentioned, as examples, Gaines, Purina, and Friskies. A Canadian-canned dog food, Dr. Ballard's Health Food for Dogs, was fed to captive shrews by Mann (1956).

Rate of Food Travel in the Gut

The large quantity of food that Blarina is able to consume within short periods of time suggested that the food may not remain long in the gut. To investigate this, calve's liver and carmine stain were ground together and this mixture was fed to shrews along with various foods. The time was measured between ingestion of the carmine mixture and appearance of reddish feces.

The times for travel of food through the gut varied from approximately 1.5 to five hours. When fresh horse-

meat was fed with the carmine mixture to a shrew which had previously been eating dry dog food, the meat was eaten rather steadily over an extended time and the reddish feces appeared after about 1.5 hours. When the shrew was fed chicken scratch feed with the stain mixture the shrew ate less food and the carmine-stained feces did not appear for approximately five hours.

Several things may have governed the speed of the carmine through the digestive tract. The carmine, since its vehicle was in the form of a paste, may have by-passed the solid food eaten with it. In humans, for instance, liquid foods are known to pass through the stomach within a five-minute period, whereas solids may remain there for up to four hours. Assuming the carmine remained with the food taken simultaneously, both large amount of food and meat are correlated with fast passage of food while lesser quantities and dry seeds are correlated with the slower rate.

Although these times for food passage appear suspiciously short, comparable data exist for the rate of food travel through a least shrew, Cryptotis parva. Describing an experiment with this smaller shrew, Hamilton (1944) stated that mealworms passed through the digestive system in 95 minutes, whereas hair embedded in meat took three to four hours.

Digestive Tract Analyses and the Diet

Foods are not all ingested in the same manner; some food items are eaten almost entire or in large pieces, and others sometimes chewed to an unrecognizable mass. By the time certain foods reach the intestine they are reduced, by chewing, enzyme action and churning, to an amorphous condition and even the stomach contents occasionally defy identification. Although no digestive tracts contained 100 per cent unknown material, several approached this degree of uncertainty. Radulae of mollusks, mammalian hairs, earthworm setae, pieces of elytra, antennae, legs, or other exoskeletal structures of insects, pieces of snail shells or hairs were often the only clues to the origin of the gut contents.

In many instances it was not possible and in others impractical to identify materials further than to a major taxonomic category; such was the case with the remains of amphibians, oligochaetes, mollusks, and many insects. Greater detail might have been provided in at least two of these groups because the molluscan radulae are often diagnostic to the specific level, and additional attention to the earthworm setae might have provided more precise identification of the oligochaetes. The potential value here of such additional detail was considered insufficient to justify the expenditure of the additional necessary time.

Close study of the material often permitted relatively precise identification. Hairs were compared with known

standards using some of the criteria of Mathiak (1938). Arthropod remains were keyed to order and often to family on the basis of diagnostic characteristics of the mouth parts, antennae, tarsi and legs, and portions of the bodies which were not excessively mutilated.

Precision in estimation of the volume of various foods was unattainable. In any study of this type the investigator must repeatedly judge, rather than measure, the percentage of the total organ contents to be ascribed to each food item identified as being present. Such judgments are more difficult with intestinal than with stomach contents owing to the advanced stage of digestion in the former. In spite of the inherent lack of precision, these estimates are included because without them it would be impossible to determine the relative importance of the various foods. I was conservative in estimating the percentage of volume attributable to each of the food items; in consequence, 28.1 per cent of the digestive tract contents were listed as unknown.

Year-round Diet of the Shrew:

The food items identified in the analysis of the 83 digestive tracts, collected throughout the year, are tabulated in Table 8 under three headings: 1) frequency of occurrence (number of tracts in which each item occurred), 2) per cent frequency of occurrence (percentage of the tracts showing each item), and 3) per cent of identified volume (percentage of only that volume judged to represent

TABLE 8

ANALYSIS OF THE FOOD EATEN BY BLARINA THROUGHOUT THE YEAR IN SOUTHERN MICHIGAN BASED ON EXAMINATION OF 83 DIGESTIVE TRACTS *

Type of food	Frequency of occurrence	Per cent frequency of occurrence	Per cent of identified volume
MAMMALS	8	9.7	5.2
Microtus	3	3.6	2.2
Peromyscus	2	2.4	1.3
Sorex	1	1.2	0.1
Blarina	1	1.2	0.2
Sylvilagus	1	1.2	1.1
Unidentified	1	1.2	0.3
AMPHIBIANS	3	3.6	3.1
INSECTS	75	90.0	48.9
Orthoptera	14	16.9	9.6
Locustidae	4	4.8	2.5
Gryllidae	10	12.1	7.1
Isoptera	2	2.4	0.7
Hemiptera	5	6.0	1.9
Lepidoptera	8	9.7	2.7
Coleoptera	59	71.3	18.7
Elateridae	14	16.8	5.3
Tenebrionidae	3	3.6	0.2
Carabidae	12	14.5	4.4
Lampyridae	1	1.2	T
Silphidae	5	6.0	0.05
Buprestidae	2	2.4	T
Cerambycidae	1	1.2	T
Scarabidae	7	8.4	1.1
Mecoptera	1	1.2	T
Anoplura	2	2.4	T
Hymenoptera	25	30.0	5.4
Formicidae	21	25.3	4.6
Diptera	8	9.7	0.8

TABLE 8-Continued

ARTHROPODS, exclusive of insects	17	20.5	11.7
Crustacea (Isopoda)	11	13.2	8.6
Arachnoidea	4	4.8	0.4
Araneae and Phalangida	1	1.2	0.4
Acarina	3	3.6	T
Chilopoda	8	9.7	1.8
Diplopoda	3	3.6	0.5
ANNELIDS (Oligochaeta)	53	64.0	16.4
MOLLUSKS (Gastropoda)	11	13.3	9.3
VEGETABLE MATERIAL	37	44.6	5.4
Leaves of grass or sedge	21	25.3	T
Leaves other than above	4	4.8	T
Seeds or Nuts	3	3.6	2.4
Roots	5	6.0	T
Unknown	13	15.6	3.0
MISCELLANEA (Accidentals ?)			
Blarina hairs	38	46.8	T
Sand	69	83.0	T plus

* The volume of food assigned to categories represents 71.9 per cent of the total gut contents.

the identified food items).

Although a common manner of presenting analyses in studies of food habits, the per cent frequency of occurrence merely indicates how extensively the various foods are eaten without providing information on their importance as energy sources. With no allowance for amount, a tiny mite, representing only a small fraction of the ingested total, may be equated with several large earthworms which formed the bulk of an individual's food. Percentage of the total volume of the various foods is another common method of presentation but, should several full stomachs fortuitously contain large volumes of an unusual item, erroneous implications are similarly possible. Both presentations are used here in the belief that together they provide an adequate description of the diet, and that each will preclude misrepresentation by the other.

The volume of each food item is reported as a percentage of the volume of identified foods rather than as a percentage of the total volume. Only 71.9 per cent of the total volume was attributed to specific food categories, and the remaining 28.1 per cent was of such an amorphous nature that I was unable to judge its origin. It is probable that some, and perhaps most, of this unknown material was of the same origin as that judged to represent identified food items and it seems undesirable to compare estimated volumes of identified foods with a total volume probably including more of the same foods. The presentation used here results in a comparison of only known volumes of foods and

consequently does not imply a lesser importance of the various foods, as would be the case if they were compared with the total volume.

Table 8 shows that throughout the year insects, occurring in 90.0 per cent of the digestive tracts and providing an estimated 48.9 per cent of the bulk of the identifiable foods, were more important than any other category of food. If the corresponding figures for the other recorded arthropods are added to these, the phylum Arthropoda emerges as the most important contributor to the shrew's diet. The annelids, found in 64.0 per cent of tracts and forming 16.4 per cent of the volume of identified food, represented the second most important food item. Arthropods exclusive of insects and mollusks both represented similar contributions to the diet bulk (respectively 11.7 and 9.3 per cent of the identified volume), but the former were found in approximately one-third more of the digestive tracts than the latter. The remaining three major categories of food items (vegetable material, mammals, and amphibians) all contributed roughly similar volumes to the diet (respectively, 5.4, 5.2, and 3.1 per cent), but the plant remains were found in almost half the digestive tracts (44.6 per cent), whereas the mammals and amphibians had frequencies of occurrence of 9.7 and 3.6 per cent.

TABLE 9

COMPARISON OF FOOD HABITS STUDIES

	Present study (year-round) % frequency	Hamilton 1941 (year-round) % frequency	Present study (winter) % frequency	Eadie 1944 (winter) % frequency	Present study (year-round) % volume (identified)	Hamilton 1930 (year-round) % volume (Total)
ased on ____ Records	83	460	9	200	83	244
ype of Material	Entire Gut	Stomachs	Entire Gut	Scats	Entire Gut	Stomachs
ategories of Food						
Mammals	9.7	5.2	22.0	60.5	5.2	4.1
Amphibians	3.6		0	0	3.1	
Insects	90.0	77.6	89.0	95.5	48.9	47.8
Arthropods exclusive of insects	20.5	17.2	11.0	53.0	11.7	14.2
Annelids	64.0	41.8	22.0	40.0	16.4	7.2
Mollusks	13.3	5.4	11.0	1.0	9.3	5.4
Vegetable material	44.6	17.1	56.0	8.0	5.4	11.4

Table 9 provides a comparison of my results with those of other authors regarding the food habits of Blarina.

Initially, it was hoped that by grouping the analyses in weekly or 10-day periods, gradual trends in food habits could be followed, but the analyses varied considerably among individuals and the data were sparse in many of these short intervals; any trends were obscure. Monthly groupings were not used because some of the colder months were represented by only a few specimens. To obtain categories, each of which included enough data to be meaningful, the data were grouped by seasons: winter (December 21-March 20), spring (March 21-June 20), summer (June 21-September 20), and fall (September 21-December 20). The 83 digestive tracts studied were distributed as follows: winter - 9, spring - 9, summer - 45, and fall - 20. These data are presented in Plate XXXVI.

Mammals in the Diet:

Based on observation of captive Blarina which ate mammals, the skin and hair are ingested but seldom, and then in only small quantities; this would cause difficulty in determining both presence and identity of the prey. If certain shrews were to eat only the internal portions of victims and simultaneously ingest no hair, predation on mammals could be easily overlooked. Eadie (1944), however, wrote that some winter scats of Blarina resembled miniature fox droppings--comprised essentially of bones and hair; he indicated that in most scats the hair of the prey is easily

seen and relatively common. When my captives fed on small mammals, their scats contained very little hair, and those judged to correspond with the time when the shrew was completing ingestion of the carcass sometimes had no hair. A considerable difference in feeding behavior is indicated here between different populations of Blarina and the conflicting data warrant further study.

Ability of Shrews to Capture Mammalian Prey

Most captive short-tailed shrews exhibited difficulty in capturing mice and voles even though the animals were in forced proximity within small cages. Some shrews, because of apparent fear reactions, avoided contact with their potential prey and other shrews, without evidencing fear or aggression, ignored the potential prey.

The shrews, thus, show considerable variation in their behavior toward potential prey and not all shrews will attack a small mammal although the opportunity exists. Of those captives attempting to capture mice or voles, few are successful within the first few minutes even in a limited space. In the wild, shrews are probably seldom successful when pursuing prey above ground.

Some authors, such as Townsend (1935), believed Blarina to be capable of moving rapidly while others, such as Seton (1909), have claimed the shrew was unable to run fast. To my knowledge only Layne and Benton (1954) have compared the speed of Blarina with the speeds of various

other small mammals; running along a wall, Blarina averaged 2.7 feet per second, about half as fast as the second-slowest mammal tested. Carter (1936) recorded, for the first and I believe only time, an instance of the short-tailed shrew climbing a tree; he described an individual that climbed an oak tree, ostensibly to feed on a basket of suet six feet above the ground. Slow and not usually exercising its ability to climb, the short-tailed shrew is less well adapted for mammal predation on the ground surface than below ground, and most predation on mammals probably involves trapping the prey in a confined space below ground.

Meadow Vole

On the basis of scat analyses in which vole remains were present in 56 per cent of 200 scats, Eadie (1944) suggested that each Blarina may, conservatively, eat four or five meadow voles during a single winter when the vole population is high; his data are suggestive of an actual predation even greater than this. The year following this study, Eadie (1948) repeated his investigation and found vole remains in only 14 per cent of 255 scats, and he estimated the vole population during this period to be about half that of the preceding year. In 1952, Eadie authored an additional paper presenting more extensive data which indicated that in most years, voles usually appeared in 14 to 18 per cent of Blarina feces and that the figure published in his original study (1944) was rather higher than usual.

As shown in Table 8, meadow vole remains (flesh, bone, and hair) were found in three of the 83 digestive tracts (3.6 per cent frequency), representing 2.2 per cent of the volume of identified food; one stomach containing vole remains was collected in late June and two were taken in late October. Hamilton (1930), in a study of Blarina food habits involving 244 stomachs taken throughout the year, listed vertebrates as constituting 4.1 per cent of the diet, and in a later study (1941) based on 460 stomachs, wrote that vertebrates showed a 5.2 per cent frequency of occurrence; in both these studies, 'mice' (voles?) were included in the vertebrates.

The hypothesis that Blarina, at least during the winter months, preys heavily on voles (Eadie, 1944) is not supported by the data from either my work or that of Hamilton (1930,1941). Several variables could account for the apparent conflict. Eadie's work was conducted in an area of fallow fields, the type of habitat favored by voles; much of Hamilton's data came from wooded areas where the voles are not usually found; and mine came from a variety of habitats including both woods and fields. Shull (1907), whose data, like those of Eadie, were based on collections from a grassy area, wrote that the food of Blarina included 40 per cent voles. Eadie discounted the possibility that the vole remains represented carrion because masked shrew scats, collected along with those of Blarina, showed no evidence of feeding on meadow voles.

Blarina obviously feeds on voles, both in the wild and in captivity, even though the voles may be larger (Christian, 1950b, and Phillips, 1956). The reaction of several of my captives, however, indicates that not all shrews will attack voles. I doubt that a vole in the wild could be killed unless it were very young or trapped in a burrow or nest. During their attacks, captive Blarina repeatedly lost contact with their prey and had to locate them again several times before they were killed; in the open where travel in virtually any direction would afford escape, I would imagine most voles would leave a fight at the first opportunity.

The meadow vole is, in general, apparently a more important food item for the shrew than any other small mammal but unless the population of either shrew or vole is high, probably neither much affects the other.

Mice

Several authors have written that mice make up a portion of the diet of Blarina, but none gave any estimate of the numbers eaten or of the percentage contribution to the shrew's diet.

I found the remains of either the white-footed mouse (Peromyscus leucopus) or of the deer mouse (Peromyscus maniculatus) in two stomachs, taken September 30 and October 30. The latter may represent carrion because the day that shrew was taken, a partially eaten deer mouse was found in a nearby snap trap. Peromyscus remains in the two stomachs

had a 2.4 per cent frequency of occurrence and made up 1.3 per cent of the identified volume. Observation of captives indicates that the shrews experience considerable difficulty in catching and killing Peromyscus even in a small cage; unless it were very young, diseased, or blocked from escape, a mouse in the wild should have little difficulty escaping Blarina.

I was unable to find any evidence of predation on the house mouse in the wild and have found no record of this by any other author. The live house mouse offered my captives managed to elude its potential predators, but Hamilton (1930) recorded an instance of a captive 20.5-gram male shrew killing a 16-gram house mouse in a manner similar to that followed by my shrews in killing Peromyscus.

Shrews

Hair, bones, and flesh of the masked shrew were found in the stomach of one Blarina, a 1.2 per cent frequency representing 0.1 per cent of the identified volume. Sorex remains had a 1.0 per cent frequency in 200 winter scats of Blarina reported by Eadie (1944) and, in a later study (1948), a 4.0 per cent frequency in 255 winter scats. Both Hamilton (1940) and Eadie (1949) suggested that Sorex sp. are the prey of the larger short-tailed shrew.

I have no evidence to suggest that in the wild Blarina will, under normal circumstances, prey on other Blarina. I have little doubt that this occurs but the

incidence must be very low. I found but one instance of Blarina remains in a digestive tract, a 1.2 per cent frequency representing 0.2 per cent of the identified volume. The intestine of this adult female shrew contained a few clumps of Blarina hair, some bone, and partially digested flesh; she was taken in a live trap with a dead and partially eaten smaller shrew. The female was released and three hours later retaken in the same trap. Whether the older shrew killed the younger or whether the young represented carrion is unknown. Instances of cannibalism in shrews have been reported by other authors (Townsend, 1935; Manville, 1949; Mann, 1956).

A large number of digestive tracts (46.8 per cent) contained hairs of Blarina but only a few hairs were usually present and no other evidence was found to indicate cannibalism. I conclude, as did Eadie (1944) that these few hairs probably belonged to the individual concerned, perhaps being picked up when the fur was licked or when some ectoparasite was bitten or eaten.

Other Mammals

Eastern cottontail remains were found in one winter-caught short-tailed shrew and, as discussed previously, undoubtedly represented carrion. This shrew's stomach contained 100 per cent flesh mixed with a few cottontail hairs, and the intestine contained an estimated 95 per cent cottontail and 5 per cent insect remains. It is difficult to imagine Blarina capable of obtaining rabbit flesh at this

time of the year unless it chanced upon a dead one.

Being the opportunist that it is, Blarina would probably feed on almost any dead mammal and the various studies have demonstrated its ability to kill the small mammal associates it is likely to encounter, even though they may be almost twice the shrew's size. Blarina travels quite slowly (Layne and Benton, 1954) and most of the potential mammalian prey could easily escape, unless trapped in close quarters with the shrew.

My analyses show that mammals comprised 5.2 per cent of the total volume of identified food of this shrew, and at least one-quarter of this was carrion. Hamilton (1930, 1941) described essentially the same results and most information indicates that mammals represent a relatively minor portion of the diet of Blarina.

Birds in the Diet:

Both Hamilton (1930) and Eadie (1944) reported finding bird remains in Blarina food. Hamilton found two stomachs out of 244, and Eadie noted one scat out of 200 that contained avian material. Brooks (1908) presented pictorial evidence that Blarina had been eating the eggs in a Whip-poor-will nest located on the ground, and he suggested that this shrew may have been responsible for the disappearance of Black and White Warbler nestlings. Various studies on captive shrews have indicated their willingness to eat birds, but it is doubtful that any but nestlings are actually killed and the evidence regarding the eating of entire

eggs is inconclusive. I found nothing to indicate that short-tailed shrews were feeding on birds in the wild.

Reptiles in the Diet:

It has been demonstrated with captive shrews that Blarina will kill and at least partially eat snakes. O'Reilly (1949) described an attack by Blarina on a ribbon snake (Thamnophis sauritus) in which the wounded snake managed to escape by crawling above the ground surface; later the remains of a ribbon snake were found in the same area. Cope (1873) recorded Blarina as eating a large garter snake. One of my captives ignored a garter snake placed in its cage, as did a short-tailed shrew reported by Hamilton (1930), but my captive finally killed the snake, eating very little of it. I obtained no evidence of Blarina in the wild feeding on reptiles and have found no mention, excepting only the reports of Cope and O'Reilly, above, of such predation in the literature. Fed upon only rarely, the reptiles are, with little doubt, insignificant in the diet of the shrews.

Amphibians in the Diet:

I observed salamander remains in the stomachs of three shrews and, although the identifications are not certain, from the appearance of the tiny pieces of skin I believe two stomachs, taken in mid-August and early November, contained the Jefferson salamander (Ambystoma jeffersonianum), and one stomach, collected in late March, had the

remains of a spotted salamander. These salamanders represented a 3.6 per cent frequency and provided 3.1 per cent of the volume of identified foods.

I am aware of only one other author (Hamilton, 1930, 1941) having reported the occurrence of amphibians in the diet of Blarina; from a total of 244 stomachs collected throughout the year, only three, which were all taken in February, contained amphibian remains. It is surprising that more evidence of salamander, toad, or frog remains is not found for in areas of Blarina abundance these amphibians are present, often in numbers, and their acceptability as food has been demonstrated by laboratory studies. Apparently preferences for other foods coupled with the irritating secretions of the amphibians preclude their widespread use as food.

Fish in the Diet:

Although it has never been reported, fish likely form a minor portion of the shrew's diet in areas where anglers leave dead fish along stream banks, or where they happen to be washed up on the shore of a pond or lake. Captive shrews exhibited no hesitation in eating the fish offered to them.

Insects in the Diet:

In every published study of the food habits of Blarina, insects are recorded as at least equal in importance to any other food category; usually insects far

outweigh all other foods, in both frequency of occurrence and volume. The insects have been reported as representing, by volume, 40 per cent (Shull, 1907) and 47.8 per cent (Hamilton, 1930), and by frequency, 95.5 per cent (Eadie, 1944) and 77.6 per cent (Hamilton, 1941) of the diet. In my study, insects were found in 90.0 per cent of the digestive tracts, and they accounted for 48.9 per cent of the volume of identified foods.

Coleopterans

Of the insect orders reported eaten, the coleopterans far exceed all others in frequency of occurrence. I was able to identify beetles in 71.6 per cent of the analyses and they constituted 18.7 per cent of the volume of identified foods. Eadie (1944) found this order represented in 64.5 per cent of the shrew scats he analyzed. Coleopteran families identified most often in the present study were, showing decreasing per cent frequency of occurrence: Elateridae (16.8), Carabidae (14.5), Scarabidae (8.4), Silphidae (6.0), Tenebrionidae (3.6), and Buprestidae (2.4). Eadie wrote that wireworm larvae and pupae (Elateridae) were recognizable in 49 per cent of the scats he examined.

Hymenopterans

Representatives of the Hymenoptera were found in 30.0 per cent of the analyses, providing 5.4 per cent of the volume of identified foods. Members of the family Formicidae (ants) were in 21 of the 25 stomachs yielding

this order. Eadie (1944) found ants in 23.5 per cent of 200 winter shrew scats. Most of the ants found in the present study were eaten in late summer and only one of nine winter digestive tracts contained them. Hamilton (1930) concluded from his studies that ants were virtually never eaten; either a considerable difference in food preferences exists among the different populations of Blarina, or availability of ants was markedly different in the respective collection areas.

Orthopterans

The order Orthoptera was represented in the food analyses by just two identified types: crickets and grasshoppers. On the basis of laboratory studies, both--but especially the crickets--are highly preferred food for shrews. Klugh (1921) remarked that Blarina ate all the crickets which had been common beneath his tent, and Brooks (1908) described a shrew jumping to catch a cricket. The orthopterans present in my analyses showed a 16.9 per cent frequency and made up 9.6 per cent of the volume of identified foods. The comparable figures for the coleopterans and hymenopterans are higher, suggesting that they are more available than the preferred orthopterans. The crickets and grasshoppers were eaten primarily in the summer and fall.

Other Orders

The orders Lepidoptera and Diptera were both represented in eight stomachs, each with a 9.7 per cent frequency. No adults of either group were found; the occurrence is based on identification of larval and pupal forms. The dipterans were eaten primarily in the summer and the lepidopterans primarily in the early fall.

Other identified orders were found in only one or two digestive tracts and probably represent fortuitous discoveries. In one instance, several lice (Anoplura) were present and these may have been picked from its pelage by the shrew; a number of Blarina hairs were present in the same stomach.

Brooks (1908) presented a far from exhaustive list of insects, injurious to man, that he believed Blarina ate: "...grasshoppers, seventeen-year locusts, cut-worms, wire-worms, corn ear-worms, canker-worms, "rose-bugs," white-grubs, May-beetles, cucumber-beetles, plum curculios, grape-curculios, grape-root-worms, potato-beetles, chestnut-worms, and many others..." A number of authors (McAtee, 1926; Balch, 1936; Buckner, 1955) credited Blarina as being an important predator on the cocoons of both the European spruce sawfly and the larch sawfly.

Arthropods other than Insects in the Diet:

Centipedes, found in 9.7 per cent of the digestive tracts, were eaten more often than millipedes, found in

3.6 per cent. No quantitative data on availability were collected, but it is my impression that centipedes were far more numerous than the millipedes. Laboratory studies suggested little, if any, preference between the two, but Hamilton (1930) claimed that centipedes were eaten more readily. Hamilton's stomach analyses showed the centipedes constituting 3.8 per cent and the millipedes 1.7 per cent of the shrew's diet. Eadie (1944) listed both classes (Chilopoda and Diplopoda) together, found them in 30 per cent of the winter scats, and mentioned that millipedes were eaten more often than centipedes.

Pillbugs and Sowbugs were found in 13.2 per cent of the analyses and constituted 8.6 per cent of the volume of identified foods. Most of these were eaten in late spring and fewest in winter. Eadie (1944) listed these as occurring in 23 per cent of the winter scats, and Hamilton (1930) reported them as 6.7 per cent of the diet.

One spider was found in a stomach collected in mid-September. Hamilton (1930) listed arachnids as constituting 2 per cent of the diet of Blarina, and (1941) claimed for them a 7.4 per cent frequency of occurrence; he remarked that both adults and their cocoons are eaten.

I found mites in three stomachs, one in early March and two in late August; these tiny arachnids (some only 1.5 mm. long) were not entire and therefore difficult to identify. If they were ectoparasites from Blarina, their presence would be more easily understood.

Although crayfish have been accepted in captivity, to my knowledge no author has reported their having been eaten in the wild. Since crayfish do occasionally venture out on the ground surface, it is not unlikely that shrews should periodically encounter and eat them.

Annelids in the Diet:

Annelids are a favored food item and even during the winter they were found in the digestive tracts. Earthworm remains were present in 64.0 per cent of the analyses and they comprised 16.4 per cent of the volume of identified foods. As Eadie (1944) pointed out, "...their high frequency in the winter diet indicates that Blarina often feeds below the frost line." This statement is likely true but, considering their storage habits, at least a part of the annelids eaten in the winter probably represent worms caught in the fall and hoarded.

According to Hamilton (1930), annelids comprised 7.2 per cent of the shrew's diet, and (1941), had a 41.8 per cent frequency of occurrence. Eadie (1944) reported this group as occurring in 40 per cent of the shrew scats, and Shull (1907) claimed earthworms to constitute but five per cent of the diet.

Mollusks in the Diet:

Representatives of this phylum were found in 13.3 per cent of the analyses and constituted a minimum of 9.3 per cent of the volume of identified foods. Often appearing

as pieces of nondescript, dark-surfaced, fleshy material, and sometimes accompanied by bits of shell or a radula, these remains were difficult to assign even to the phylum. Slugs have no shells and some remains were likely missed, especially in the intestine. It is not improbable that this group made up a greater part of the diet than was recognized.

On the basis of tenuous evidence I judge that slugs were eaten mostly in the warm months, and snails primarily in the fall, winter, and early spring; bits of shell accompanying the soft parts were found less often during the warm months. Mollusks, primarily snails, were reported by Hamilton (1930) as forming 5.4 per cent of the shrew's diet, and (1941) as having a 5.4 per cent frequency of occurrence. Eadie (1944) found them in only one per cent of the Blarina scats; this low incidence could be attributed to difficulty in identification. Merriam (1884) listed slugs but not snails as items of the Blarina diet.

Various authors stated that the short-tailed shrew readily eats snails (Shull, 1907; Clench, 1925; Ingram, 1942) and the latter author reported finding three species of snails in a shrew's storage chamber: Anguispira alternata, Succinea ovalis, and Ventrindens intertextus. The first species and the latter two genera were fed to my captives and were preferred to certain other species of snails. Ingram wrote that the Anguispira shell was usually opened at the apical whorl, but that the other snails were not

opened in any standardized manner. Both Shull (1907) and Hamilton (1930) remarked that Polygyra sp. were almost invariably opened at the apical whorl, but my captive shrews did not employ any such standardized method with the snails given them.

Vegetable Matter in the Diet:

I found vegetable material in a greater percentage (44.6 per cent frequency) of the shrews than is reported by any other author. Plant matter was recorded by Hamilton (1930) as forming 11.4 per cent of the year-round diet, and (1941) as present in 17.1 per cent of the stomachs; he noted (1930) that during the winter the amount of plant remains increased and then represented 25.3 per cent of the diet. Eadie (1944) claimed only eight per cent of his winter scats contained obvious plant material. Neither Hamilton nor Eadie recorded, as did I, the incidence of grass blades or rootlets.

Although my data show almost half the digestive tracts with plant material, this involved an estimated contribution of only 5.4 per cent to the identified volume. The incidence of plant material was highest during the winter and early spring; several stomachs taken at this time of year were filled with a starchy material, perhaps acorns or fleshy tubers. Various authors have reported the wild diet as including beechnuts (e.g., Merriam, 1884; Harper, 1929), mast (Hamilton, 1929), corn (Seton, 1909), endogone spores (Diehl, 1939), and raspberries (Hamilton, 1941).

Grass and sedge blades, rootlets, and bits of leaves were found in nearly half the digestive tracts, but together constituted probably less than 0.05 per cent of the total volume ingested. Although my captive shrews were not seen to eat any leaves, these plant remains may have been eaten intentionally, as is grass, occasionally, by dogs.

Some stomachs contained a tan or whitish mush with a few larger pieces of similar material; this was so thoroughly chewed that precise identification would have been sheer speculation. The material turned blue with iodine indicating starch presence and, because it resembled nothing of animal nature and it appeared the way chewed nuts or acorns might, I placed it in a category titled "Seeds or Nuts"; this material constituted 2.4 per cent of the volume of identified food. Additionally, some stomachs and intestines contained completely amorphous, starchy material which was assigned as plant material but placed in a separate category, "Unknown", and represented 3.0 per cent of the identified volume.

Although plants and their products are commonly ingested, they apparently assume little importance in the diet except during the winter.

Miscellanea in the Diet:

Sand was present in a large number (83.0 per cent) of the digestive tracts but never in large quantities and I judge most, and probably all, was taken accidentally.

When, for example, Blarina eats an insect, the prey is moistened by the shrew's saliva and, before being swallowed, sand grains adhere to the surface. Further, each earthworm that is eaten probably contains sand grains and these, in turn, would then be contained in the shrew's gut.

While trapping, I used a mixture of peanut butter, rolled oats, and bacon grease which was eaten by the temporary occupants of the live traps. Other authors have reported on unusual foods eaten by wild short-tailed shrews: salty chipped beef and cold fat in a frying pan (Klugh, 1921), bacon (Townsend, 1935), suet (Carter, 1936), and raw beef (Schorger, 1947).

On several different occasions I observed my captives as they ate their own droppings. The feces eaten were, in each case, 12 or more hours old and partially or completely air-dried; no shrew was seen to eat fresh feces. To the best of my knowledge, Crowcroft (1952) and Sharma (1962) are the only previous authors to mention coprophagy in any soricid. Crowcroft described this for Sorex araneus in Britain, and Sharma claimed it to be abnormal behavior in the Indian shrew Suncus murinus.

Lagomorphs, as indicated by the articles of Hamilton (1955) and Geis (1957), and others, commonly practice coprophagy; this habit apparently supplies the diet of mammals with large amounts of the B vitamins, produced by the bacterial flora of the colon (Lorenz, 1954).

Water in the Diet:

Water, although not usually considered as a food item, is important for survival; apparently shrews do not always obtain sufficient water with the usual foods ingested. As discussed previously, free water is not imperative for survival. During the winter my captives, apparently in good health, obtained all their liquids from water contained in the food, by licking the ice in their water cups, and from metabolic water; in the wild I imagine that they similarly lick ice or eat snow during the coldest months. Townsend (1935), Chew (1951), Pruitt (1953), and Mann (1956), all indicated that Blarina requires relatively large amounts of water for survival.

Some experiments tested the amount of water taken daily by my captives which were housed continually in the shade but in unheated quarters. Adult shrews were each supplied, in spill-proof containers, 20 ml. of water daily over three-day periods. No shrews were seen to splash the water when drinking, and to correct for evaporation, an identical control was placed beside the cages. In mid-August, shrews (3 records) averaged drinking 8.8 ml. per day, and in mid-October (4 records) averaged 5.6 ml. per day.

Edgren (1948) tested the mid-summer water consumption of Blarina caged in a laboratory and found a mean of 9.1 ml. per day. I suspect that his animals may have been caged in warmer and drier conditions than mine; such

conditions would suggest a higher rate of water loss by shrews and, consequently, a higher consumption.

Water balance may be critical for short-tailed shrews in the wild, but I doubt that they drink much water; I suspect that the behavior and cool, humid conditions of their micro-environment compensate for low intake of free water, at least during part of the year. Laboratory-housed captives are usually subjected to more heat and less humidity than shrews in the wild, and they drink considerable water. The shrews living in wooded areas or grasslands which are remote from open water, or those virtually anywhere during mid-winter when water is in the form of ice or snow, would not find quantities of free water equal to those taken by laboratory animals.

Correlation between Kinds of Food and Time of Feeding:

Numerous studies, many reviewed by Cloudsley-Thompson (1961), have shown the existence of periodicity in the behavior patterns of animals ranging from protozoans to mammals. Since many of the species on which Blarina preys undoubtedly exhibit periodicity in their behavior, I thought that the ingestion of food might reflect such rhythms. The stomachs and intestines of Blarina were examined separately with the intention of determining the existence of any pattern within the daily diet; the times of capture were known, within several hours, for most of the kill-trapped shrews and the contents of the digestive

tracts could thus be correlated with time of day.

To discover any correlation between food and time, the identified foods, grouped within the various categories, were plotted against the probable hour of ingestion. When the correlation was limited to shrews kill-trapped within any single day (five was the largest number taken in one day), differences in the proportion of foods eaten at various hours existed but, when the data of successive days were grouped, no consistent differences remained. When the year-round data were grouped, the resulting graph showed the various categories of food to be distributed in roughly similar proportions throughout the day.

My data suggest that any rhythmic behavior of the prey has little or no influence on its ingestion by Blarina; that a beetle, for example, is just as likely to be eaten when quiescent as when active. Since each species has its own behavioral idiosyncrasies, the grouping of prey into food categories may well obscure any differences in timing of predation that may exist. Additional study of the temporal relationship between individual species of prey and Blarina should prove interesting; collectively, the members of a shrew population would provide continual, although fluctuating, predation pressure and, thus, an uninterrupted record not possible with most species of predators.

Seasonal Variations in the Diet:

Plate XXXVI presents the distribution, by season, of the various food categories in the diet of Blarina.

Insects are shown to be of major importance in the diet at all seasons, in both frequency of occurrence and volume. They were eaten by proportionately more shrews during the spring than in any other season but, relative to volume, were of greatest significance during the winter. Three insect orders were found to supply more food than all others; the coleopterans were eaten more often and supplied more bulk to the diet than members of the other orders, hymenopterans (primarily ants) were eaten mostly during the summer and were found more frequently but provided less of the diet volume than the orthopterans (crickets and grasshoppers) which were eaten mostly in the summer and fall.

Annelids, second to the insects in importance to the diet, were eaten most often during the summer and least in the winter. They had the least value to the diet volume during the winter but, progressively more important through the spring and summer, were eaten most often in the fall.

The non-insect arthropods and the mollusks were of roughly similar importance in the diet. The arthropods, exclusive of insects, (primarily pillbugs, sowbugs, and centipedes) were eaten by the fewest number of shrews during the winter and were relatively unimportant to the

diet at that season. During the other seasons they formed roughly similar proportions of the diet volume, although they were eaten most widely in the fall. The mollusks were taken in all seasons and were eaten by the most shrews in the spring, yet provided more volume to the diet during the summer.

Vegetable matter (represented at all seasons by leaves of grasses and sedges, and during the late fall, winter, and early spring by seeds and nuts) was of greatest proportionate value during the winter and least in the summer, formed a constant minor contribution to the diet, and gained significance only during the colder months.

Mammals formed a small part of the diet in all seasons, but were most important in the fall and winter. Amphibians were not found in the winter diet, were taken by the most shrews in the spring, and represented essentially similar, but small, contributions to the diet in the spring, summer, and fall.

Storage and Hoarding of Food:

The habit of storing foods is highly developed in Blarina and has been documented by many authors. Audubon and Bachman (1849) found a hoard of beetles, some nearly consumed and others mutilated yet alive, in a chamber off an underground tunnel; the storage of beechnuts was described by Merriam (1884, 1895) who considered that this shrew hoarded foods for the winter; Shull (1907) wrote of the hoarding and temperature-dependent transfer of snail

shells, full and empty, between burrow and surface. Claiming the habit was most pronounced in a nursing female, Hamilton (1931) mentioned that while small items were stored entire, salamanders were cut into several pieces. Ingram (1948) reported that a wild shrew maintained both a possible culture chamber for live snails and a discard chamber for empty shells, the shells being transferred from one to the other as the snails were eaten; by marking the shells, he learned that fresh snails were added to the store although uneaten ones were still available, and that the discard chamber contained shells from both freshly collected snails and those from the culture chamber. Phillips (1956) wrote that a captive male "...kept its den littered with chicken scratch, which it transported a distance of three feet." Apparently nothing else was available for nesting material and grain may have served this purpose.

My captives stored almost any food item they found in excess of their immediate needs; several had more than one storage area. All the hoards were close to the nest, none more than six inches away. Corn, nuts, various grains, beetles and other insects, earthworms, pieces of dry dog food, partially eaten mouse carcasses, and other items were stored in soil depressions and the hoard then often lightly covered with soil. These hoards were commonly beneath or adjacent to the nest, some were beneath a piece of nearby bark, less commonly a corner of the cage near the nest was used, and occasionally dry foods were

stored within the nest itself. Dead mice were commonly stored individually and but partially covered.

Apparently the poisonous saliva of Blarina (Pearson, 1942, and Lawrence, 1945) helps to paralyze prey preparatory to storage so that it often remains alive for extended periods of time yet is unable to escape. Most animal food is bitten several times or partially chewed before storage; attacks which I witnessed were usually concentrated toward the anterior end of the prey and both introduction of saliva and damage to the central nervous system likely contributed to immobilization.

The stored animal food frequently spoiled before being eaten but unless putrefaction was far advanced, the shrews still fed from the decaying mass.

Even the youngest captive shrew, probably no more than two months old, displayed this tendency to store foods. Hoarding was practiced by all my captives without noticeable regard to season, sex, or age; it seems to be an innate behavior pattern of Blarina.

TIMING AND RHYTHMICITY OF ACTIVITY

Few details have been available on the timing of shrew activity; most of the available information is in the form of generalizations and impressions of the various authors. To my knowledge, the only published works describing experimental results on the activity of the short-tailed shrew are those of Pearson (1947) and Osterberg (1962).

Both Seton (1909) and Klugh (1921) wrote that this animal is active both day and night; Klugh claimed that they were but little less diurnal than nocturnal. Similar reports exist for other shrews, including Sorex vagrans (Clothier, 1955), Sorex araneus and Sorex minutus (Crowcroft, 1954), and Cryptotis parva (Hamilton, 1944). There was no sign of cyclic or rhythmic activity in Cryptotis, but Hamilton indicated that several captives in an unheated room were more active at night than during the day. Manville (1949) described Blarina as active all year round, both day and night, and wrote, "I captured three specimens and observed at least twelve others along roads and trails in broad daylight." Pearson (1947) stated, "My impression from trapping experience is that short-tailed shrews are caught more frequently during the daytime in winter and at night in hot weather."

Times of Activity as Determined from Field Captures

When either kill traps or live traps were in operation, they were usually checked at intervals of four hours or less and the timing of these visits was recorded. Whenever an animal was found in a trap, the maximum time interval within which it must have entered the trap was thus known. Many of these intervals were narrowed by allowing for the appearance and condition of the specimens using such criteria as the dampness and behavior of specimens in live traps and the temperature and accumulated snow, rain, or dew for those taken in kill traps.

After each of these time intervals was made as short as the evidence permitted, the mid-point was determined and a period of one hour, centered on this mid-point, was considered as the most probable period during which the shrew entered the trap. This hour-long period is termed a "trap-entry interval." Since most of the maximum time intervals were shortened to two hours or less, it is more than likely that most of these trap-entry intervals actually represent the span of time in which capture occurred.

A total of 172 trap-entry intervals, representing both kill- and live-trapping data from throughout the year, were plotted as lines on a 24-hour chart divided into 15-minute periods. A frequency distribution curve of these trap-entry intervals was then drawn by counting the number of lines extending through each 15-minute period of the

24-hour day; this curve is presented in Plate XXXVII and shows the probable times during which shrews were captured. Assuming that capture is most probable when activity is greatest, this curve might be used as an indication of the timing of activity. Because the data were collected using two different trapping methods, and because of certain other variables, the curve is biased and suggests some inferences which are not supported by other work; this is discussed below.

Diurnal and Nocturnal Activity:

The most striking feature of Plate XXXVII is the marked difference in the probability of capture between day and night. The graph indicates that throughout the year, the probability of capturing shrews during the day, between 0600 (6 A.M.) and 1800 (6 P.M.), is about one-eighth that of capturing them at night, 1800 to the following 0600. The difference is probably not as great as shown. Although kill traps were usually operated through 24-hour periods, some of the live traps, especially those in the open sun, were not. Had the same number of traps been in operation both day and night, I would guess that, judging by the number of traps usually inactivated, the curve for the day might be one-third greater.

The low incidence of captures during mid-day indicates to me not so much that the animals are relatively inactive at that time, but that the activity must be limited to places other than those where the traps were placed.

Blarina activity is not restricted to any one part of the 24-hour day, according to my records on laboratory animals and the observations of Seton (1909), Hamilton (1930), Pearson (1947), Manville (1949), and others; assuming that the animals would have been caught just as readily, day or night, had they been in the immediate vicinity of the traps, it is probable that the diurnal activity is primarily below ground or at least under moderately dense cover. Removal or brushing aside of some debris was necessary to provide an even surface and a small open area for proper placement and function of the traps, and these small cleared areas about each trap may have deterred some daytime captures.

Times of Peak Activity:

More animals were caught at dusk just after sunset than at any other time; they continued to enter the traps until sunrise at which time the captures decreased rapidly. Pearson's (1947) study of oxygen consumption revealed two peaks in Blarina metabolism, one early in the evening and another about dawn. The graph of probable capture times (Plate XXVII) shows a similar pre-sunrise and post-sunset peak of trap entry.

Plate XXVII not only indicates a higher probability of capture at night, it reveals also--assuming that probability of capture equates with activity during the night--four peaks of this activity. Since the majority of the data were gathered in the summer and early fall, these peaks may be primarily a reflection of the behavior at that time

of year. The greatest number of captures occurred at and immediately following dusk, between 1830 and 2030, followed by a second but lesser high point about three hours later, between 2200 and 2300. Approximately 2.5 hours later, activity reached another peak centered between 0015 and 0200; and about four hours later, another activity peak was reached between 0415 and 0630.

The greatest number of captures, and ostensibly activity, is shown as occurring just following sunset. This period, however, as the potential highest peak of activity, is not supported by the majority of my data on laboratory animals whose activity usually reached a maximum peak shortly before sunrise. Because many records used in compiling this curve were from kill-trapped specimens, individuals which might have been caught more readily later in the night were removed from the population just after sunset, and the graph may thus mask the actual situation.

By photographing animals using different runways, Osterberg (1962) determined that during the spring, use by Blarina was highest shortly before sunrise but in the late fall, most travel occurred just after sunset. The majority of specimens represented in my graph were caught during the summer and early fall and thus should have exhibited the summer pattern of activity, described below, which has a definite early morning peak of activity.

Since relatively few specimens were caught during the winter months, field data are insufficient for valid

comparisons of seasonal variations in activity. My experience, however, does not support the impression of Pearson (1947) that these shrews are caught more readily during the daytime in winter. I caught more shrews during the day in winter than in summer, but the majority was still taken either at night or in the subdued light of dawn, dusk, or a heavily overcast sky.

Activity of Captive Shrews

The activity of captives was recorded periodically throughout the year by electric recording devices described earlier. These animals were kept in low-sided, five-gallon aquaria in an unheated garage and never exposed to direct sunlight.

Unlike certain other mammals, shrews exhibit considerable variability in their activity periods. The diurnal thirteen-lined ground squirrel (Citellus tridecemlineatus) or the nocturnal bats show marked uniformity in activity times; the beginning and ending of circadian activity in these animals is quite abrupt, with definite and extended periods of rest. Blarina, on the contrary, is active periodically throughout the day and night; my records show a pattern of activity periods, separated by longer intervals of rest, spaced throughout the 24-hour day. The activity revealed a similarity in basic pattern but the distribution of activity and rest periods differed considerably among individuals in number, extent, and timing. No apparent

differences were found between the patterns of male and female captives. Records of shrew activity which were obtained with the use of the spring-loaded platform (Plate IX, Fig. 1) are presented in **Plate** XXXVIII.

A captive shrew was normally fed by removing the screen top from its cage, depositing the food in the open portion--or activity area--of the cage, adding water to the container, and replacing the screen. Throughout this process the shrew was almost always hidden in his nest but as soon as the screen was replaced, he usually emerged from his hiding place and investigated the food. In order that such feeding would not interrupt the recording of activity, for each of the tests sufficient dry dog food was placed in the cage to last through the experiment. When activity was recorded over a period of several days, water usually had to be replenished and this was done as carefully as possible; I saw no evidence of this disturbing the shrews. Only one experiment, that of a shrew kept in darkness for a two-week period, required modification of this procedure; water was supplied once each night by use of a funnel affixed to the cage top and dry dog food was added twice after the experiment began.

The Basic Pattern:

Figures 1 and 2, Plate XXXVIII, show records taken on July 15 of the activity of two adult shrews caught in the previous year, a male (Fig. 1) and a female (Fig. 2). Both records show a spacing of activity which is greater during

the day than at night, and these periods of activity are relatively short compared with the periods of rest. The activity periods lasted from less than one minute to about one-half hour, with most 10-15 minutes in length; and the rest periods ranged from about one minute to slightly over three hours, averaging about 2.5 hours in length.

The record of the male shows quite clear-cut separation between activity and rest during the daytime, with short intervals of activity averaging about ten minutes each, separated by rest periods approximately three hours long. At night the shrew became more active and the rest periods were shorter, averaging about 1.5 hours, while the periods of activity were of greater length, approximately one-half hour long, with periodic, short, several-minute rests interspersed.

The female's record illustrates a different, yet basically similar, pattern. Her rest periods were shorter, her activity periods tended to be shorter and more interrupted by short rests, and the separation between periods of rest and activity was less distinct than for the male.

Considerable variation in timing and extent of activity was evident among individuals on the same day and in the records of a single animal on successive days. The records of the male and female discussed above illustrate variation between individuals on the same day. The records of a young adult female (Figs. 3 and 4) and a young adult male (Figs. 5, 6, and 7) demonstrate variation in the

patterns of activity shown by some individuals on successive days. Although such variation was common, the basic pattern of activity was still recognizable.

The activity of an old male, weighing 23.4 grams and showing considerable subdermal deposition of fat, was recorded in mid-September using the runway apparatus. This shrew, at least 13 months old, exhibited periods of activity lasting between five and ten minutes and these were separated by periods of rest from one to 3.5 hours long. When observed foraging about the cage, this shrew moved slowly with a waddling gait, considerably different from the usual scurrying behavior of the others. The decreased activity both in timing and extent of this shrew, in contrast with records of other adults at the same time of year, suggests that both excessive fat deposits and age may decrease activity.

During the majority of the experimental runs the temperature, relative humidity, and late in the study barometric pressure, were recorded but I have been unable to recognize any direct correlation between the timing or extent of daily activity with any single factor.

Differences between Summer and Winter Patterns of Activity:

Although within any period of several days the records of activity of any particular shrew, or group of several shrews, often varied considerably, records taken at different times of the year reveal a contrasting pattern.

During the winter, activity is spread throughout the night and day, with much less concentration in the early morning and evening; during the summer, activity is definitely greater through the dark hours and much reduced from the winter level during the daytime. Typical winter patterns of activity are shown in the records of a young adult female not over six months old (Figs. 3 and 4) and an adult male (Fig. 8). The winter pattern was evident with five shrews tested between mid-October and early March: three females (one young adult, mentioned above, and two adults) and two males (one immature judged to be no more than five months old and one adult, described above). This seasonal difference in activity pattern was, thus, present in both sexes and in shrews of differing ages.

It is possible that the winter pattern of activity may have been forced on the animals by their environment. Energy is dissipated rapidly during the winter and the shrews probably need to feed more often when the weather is cold than during the summer. Although I know of no work specifically on Blarina, the temperature-regulating mechanisms of the more primitive mammals are reputedly not so well developed as those of the higher mammals, and the periodic and rather frequent spurts of activity by Blarina may be required to prevent the body temperature from dropping to a lethal level during the winter.

Because of the individual variations in activity, it is difficult to determine when the winter activity pattern

changes to the summer pattern. I was unable to obtain continuous records of activity for my shrews, but judging from the records collected, the change is gradual with most of the captives exhibiting the summer pattern from late April through mid-September and the winter pattern between mid-October and early March. Figures 8, 9, and 10, Plate XXXVIII, show records of the same shrew in February, July, and early October and demonstrate, respectively, winter, summer, and intermediate patterns of activity.

Daily Peaks of Activity:

The daily peak of activity in my captives occurred usually in the early morning, usually between 0200 and 0630, and this tended to be earlier in the summer than in the winter; a comparison of Figures 1 and 2 with Figures 3 and 8 illustrates this trend. The daily peak was most apparent during the summer, least evident during the winter.

A second and lesser peak occurred usually between 1830 and 2100, and this was most pronounced in the fall and winter.

In a study of oxygen consumption by Blarina conducted primarily in June and July, Pearson (1947) determined the times of maximum consumption in seven experimental runs: 0100, 0300, 0500, 0500, 0530, 0630, and 0800, averaging approximately 0500. Pearson wrote that many of the 24-hour records showed two peaks, one early in the evening and one near dawn. Using automatic photographic equipment for recording use of runways in a one-acre plot,

Osterberg (1962) also demonstrated the existence of daily activity peaks but his data do not completely support my own. Data collected by him in April and May showed an activity peak occurring at 0400, but that taken in October and November revealed a distinct peak at 2100. Osterberg's recorded peak activity in the spring corresponds with mine, but that in the fall does not and I am unable to justify the discrepancy.

Peaks of activity have been recorded in the 24-hour rhythm of three other shrews by Crowcroft (1954): A single water shrew (Necmys fodiens) showed a peak in activity just before sunrise, nine common shrews (Sorex araneus) had two major peaks of activity about 0400 and 2000, and one pygmy shrew (Sorex minutus) was most active about 1100.

Rest Periods:

The periods of activity were intermittent with periods of sleep and the shrews differed widely in the lengths of their rest periods. During the summer most rest intervals lasted between two and three hours, and during the winter they were shorter, from about 1.5 to 2.5 hours long; the longest such period was recorded on May 3, 1956, when an adult female spent just under 5.6 hours in her nest.

The records of these rest periods show numerous instances of interruption by short intervals of activity, usually lasting about a minute. These interruptions corresponded to the observed periodic waking of sleeping shrews and their short-lived excursions from the nest during which

they occasionally fed, drank, urinated or defecated, and sometimes simply moved about the cage. These forays were more common during the winter than the summer.

Sleep

Excepting these short-lived forays, the shrews remained in their nests or refuges throughout the rest periods and were apparently asleep for whenever I suddenly lifted a piece of bark or opened a nest box to expose the shrew, it almost always remained in its sleeping position for a few seconds or longer before springing to its feet. Some did not awaken until they were poked.

Most slept in a curled position, either on their sides or in such a way that, with the head tucked under the body, they seemed to be resting either on top of their head or on the back of their neck. Two of the 28 shrews kept as captives usually slept on their backs with their feet against the overlying piece of bark and the tail curved over their ventral surface; one which slept in this latter position invariably permitted the posterior third of his body to project from beneath the bark. A group of five young, all siblings, slept in a group with each periodically waking and trying to burrow deeper into the pile; this almost always partially wakened the siblings and a general rearrangement ensued. Rood (1958) observed similar behavior among young shrews and remarked that his captives occasionally slept on their backs with all four legs in the air; he noted also that, once acquainted, unrelated adults would

sleep together in apparent harmony.

Blarina sleeps with much the same intensity that it spends its wakeful hours. When asleep, my captives seemed oblivious to many stimuli and slept soundly for short intervals, separated by shifts in position and occasional awakening during which they often poked their snouts or heads from the nest, occasionally left the nest for a minute or so, or licked their pelage, then returned to sleep. Even though the breathing during sleep was slower and deeper than when awake, the nose was seldom stationary. The shrews usually awakened if their rostrum or tail was touched, if blown upon, or if I squeaked by drawing air through my lips.

My shrews shifted position at irregular intervals from several seconds to 15, and perhaps more, minutes. This shift seldom resulted in a different basic position; instead, the orientation was usually shifted slightly and some shrews seemed to end essentially the same as they began. Rood (1958) described his captives as shifting position each few minutes.

Every time an unusually long rest interval occurred, the animal had been previously active and feeding over an extended period of time, and these long rest periods invariably fell within the afternoon hours. Whether the prior activity or the ingested food was responsible for these extended rest periods is not known, but I have the impression, without specific evidence to support it, that the more food an individual shrew ate, the longer he slept

and the more difficult it was to wake him.

Activity in Continual Darkness:

Curiosity about the effect of continual darkness on the activity rhythms of Blarina prompted an experiment which, although subject to possible errors, suggests the presence of an interesting phenomenon.

A screen was improvised around a cage identical with those used in the other experimental runs. The cage was suspended on a spring-loaded platform and the contacts set somewhat coarsely so that imbalance of the cage would not cause permanent closure. A funnel was arranged so that water could be provided in the dark without excessive spilling, and a store of dry dog food was placed in the cage to insure that disturbance would be minimal during the test.

A young male shrew, caught the previous week and probably about three months old, was tested to determine his activity pattern over the two days prior to his introduction to darkness; he showed a pattern similar to those of other shrews in summer and was placed in the dark on August 8, 1955. Once each night the shrew was supplied with water, and twice during the experiment, on the fourth and tenth days, food was added, without the use of any lights.

The record of activity showed little or no change over the two-week period, and three representative records are shown in Figures 11, 12, and 13, Plate XXVIII, illustrate

the activity pattern one, eight, and 14 days, respectively, after beginning the experiment. The three records are surprising because of their similarity. The two records of the activity of this shrew taken before the experiment very closely resembled the record of August 9, the first complete 24-hour record following the start of the test. Whatever timed the activity was apparently unaffected by the enclosure and if light was the responsible phasing agent, its effect was retained without any lessening over the two-week period. Lack of the necessary special equipment precluded further investigation of this aspect of behavior.

The existence of rhythmic activity in mammals and other animals has been widely documented, and the persistence of rhythmicity in the absence of various factors thought to act as possible controls has led to the postulation of a "biological clock." Cloudsley-Thompson (1961), after reviewing much of the literature, wrote, "The search for hypothetical 'clock' mechanisms has not yet been successful and on account of the complexity of the problems involved, may well proceed for many years before success is achieved."

Rhythmicity of Activity:

Short-tailed shrews have been shown to have a circadian rhythm of activity characterized by successive activity periods with a daily peak occurring between 0200 and 0630, this tending to be earlier in the summer than the

winter. The existence of a daily peak is supported by my field and laboratory data and the studies of Pearson (1947) and Osterberg (1962), although the conclusions of the latter author do not agree completely with his.

Within the 24-hour cycle is a shorter rhythm, shown by laboratory data to have a usual period of 1.5 to 3.5 hours; the field data suggest a range from 2.5 to 4 hours. Pearson (1947) wrote that his records showed "...clear evidence of a short cycle lasting about 3 hours." The graph presenting Osterberg's (1962) data indicates a period varying between 2.5 and 4 hours.

The periods of activity, of greater length and more closely spaced during the night than the day, indicate a definite nocturnality in the pattern of Blarina activity. The higher incidence of activity during the night is supported by the data of both Pearson and Osterberg.

Since a daily and an approximate 1.5-2.5 hour rhythm of activity existed, I hoped I might discover yet a shorter rhythm, perhaps within the shifting of a position during sleep, or within the blocks of activity separated by the 1.5-3.5 hour rest periods. Using a finely-set contact on the spring-loaded cage platform, it was possible to record all the movements of a shrew, whether asleep or awake.

The resultant record showed only as a solid block of lines when the shrew was active and, when ostensibly asleep, the periodic movements showed no pattern that I

could discern; the record appeared as a random series of lines. The speed of the kymograph was increased to spread the record, but no change in the pattern of the lines was evident.

From the few records obtained in this manner, I can only offer the hypothesis that no regular shorter cycle of activity occurs within the broader usual 1.5-3.5 hour pattern.

SUMMARY

This investigation of the natural history of the short-tailed shrew (Blarina brevicauda Say) is based upon data collected in the field, the laboratory study of 28 captives, and an extensive review of the literature. The field work, conducted near Ann Arbor, Michigan, entailed both live- and kill-trapping in eleven areas of 3-30 acres which represented a variety of common local habitats including moist and dry woods, overgrown and brushy fields, and both moist and dry woods.

Although comparisons are open to some question, the various live traps were 21.3 per cent effective per trap day for all mammals taken and the kill traps were but 1.7 per cent effective. One small experimental trap, equipped with a door which locked only after being opened by an entering animal, offered a degree of selectivity against Blarina; the mechanism might prove useful in studies of small mammals other than this shrew. Live traps measuring 2.5 x 2.8 x 7.0 inches and larger were more effective in capturing small mammals than smaller traps.

Three kinds of apparatus were built to record the activity of captive shrews: (1) a runway equipped with a swinging door which, by closing circuits connected to a recording device, indicated the time intervals spent by a

shrew in the nest and in the activity area of the cage, (2) a spring-loaded platform to support each cage and detect any motion of the occupant, and (3) a constant-speed recorder that provided continuous records of shrew activity.

In contrast to various previous reports, males average longer and heavier than the female shrews. The total lengths of males averaged 120.1 mm. (54 records) and of females 114.3 mm. (57 records); the weights of males averaged 19.1 gm. (134 records) and of females 15.6 gm. (150 records). A comparison of my data with those of other authors indicates that the shrews in the northern portions of their range are heavier and longer than their southern relatives.

Specimens were assigned to one of three age categories: immature, young adult, and old adult. The immature shrews are shorter and less heavy than the older, have comparatively longer tails, more acute rostra, larger and sharper incisors, less well developed scent glands, and less scarring than their older associates.

The pelage is composed of four main types of hair: (1) vibrissae, (2) eyelashes, (3) guard hairs, and (4) underfur. Variations in these types are described and, based primarily on the structure of the apical segments, four types of underfur (A_1, A_2, B_1, B_2) are detailed. The short summer pelage, usually present between late May and mid-August, was found in some shrews from April through November; the winter pelage, having hairs averaging

approximately 2.0 mm. longer than in the summer pelage, was usually present between early September and mid-May but was noted in every month except August. Of the 115 pelts collected, 59 (51 per cent) showed some evidence of molt.

Although the rate and minor details of molting vary among individual shrews, a heretofore unrecognized pattern exists. The fall molt generally begins on the rump and spreads ventrally and, on the dorsum, cranial and caudad. When the molt reaches the midventral area, it spreads to the hind legs, to the tail, and anteriorly. Two small additional centers of molt form on the rostrum and forehead and all eventually meet. The forelegs and the dorsal rostrum are usually the last areas to molt. The spring molt is essentially a reverse of the above. Contrary to previous claims, present evidence suggests that the grossly visible molting process requires approximately one month for completion; the interval between the initial separation of hair from its papilla and the loss of the last old hairs may be closer to three months.

The development of the scent glands noted here supports the correlations established by Pearson (1946) but the value of these glands to the animal is still speculative. Previously undescribed heel organs or, in their place corresponding hair-free areas, were present just above the heel on the lateral surface of each hind leg in every shrew examined. When well-developed, these organs measured

approximately 2.5 x 1.5 mm., and a central, epidermis-free and usually scale-occluded, elongated depression bordered by swollen ridges. In some shrews the loci of these organs were smooth, hairless, and somewhat shiny. I was unable to correlate the development of these structures with age, sex, or sexual condition and further work is necessary to establish the origin and function of the organs.

The literature regarding sense acuity of Blarina is reviewed and simple experiments indicate that sight is poorly developed, hearing is good and capable of perceiving tones of comparatively high frequencies, smell is developed to only a moderate degree, and the animals are very sensitive to touch, especially about the head and tail. No information is available on taste in these shrews and both the range and acuity of all the senses require further investigation.

The voice is apparently the major means of communication although odor and possibly tail position have importance here. Six different vocalizations are described and each is associated with an apparent corresponding mental attitude: (1) a soft, **low-pitched twitter of interest,** (2) the high-pitched squeak of surprise or annoyance, (3) the shrill chatter of extreme annoyance, (4) the musical trill and subsequent slow chatter of extreme excitement, (5) the unmusical trill and subsequent sharp chatter of extreme annoyance coupled with frustration, and (6) an unmusical chitter of interest and excitement. The use of the

soft twitter while foraging, especially when the shrew is in unfamiliar surroundings, suggests a possible echolocation function.

The pattern of the shrew's footprints varies yet trails made in mud or snow can usually be identified by their width, the common presence of a tail mark weaving along the trail, and the random course of the path. Without tracks or trail, Blarina presence is indicated by partially eaten insects or snails, the remnants of small mammals having their brains eaten, the pungent odor of recently used pathways, or the peculiar and diagnostic feces.

The short-tailed shrew was found to occupy four horizontal strata within its habitat: (1) the ground or upper surface of the leaf-litter with evidence of such use provided by the appearance of Blarina in the diet of raptors and the trails left in snow, (2) the litter-soil interface as indicated by the incised pathways although much of the probable extensive use of this stratum leaves little or no record, (3) an upper system of tunnels approximately 1.5 inches in diameter and ranging to over 6 inches in depth, and (4) a lower system of tunnels approximately 2 inches in diameter occurring between 15 and 20 inches beneath the ground surface. The larger size of the deeper tunnels is suggestive of mole rather than shrew excavation; a comparative study of Blarina tunnels in mole-free areas would be instructive.

Using flour dusted on the tunnel walls, I mapped three

different tunnel systems and the lower level tunnels were absent only where the water table came to within 10 inches of the surface. One breeding and several smaller resting nests were located in the underground systems.

The salient features of Blarina reproduction are reviewed and in spite of the past and present work, many problems are yet unsolved. Little convincing evidence exists regarding the existence of a post-partum estrus if the first litter survives and is nursed; data from field and laboratory studies suggest conflicting conclusions. Further work is required to establish any correlation-- if any exists-- between vaginal smears and the estrus cycle. The testes are never completely descended into the scrotum and I have demonstrated a lack of correlation between small testes and sperm absence; the usual criteria for simple determination of sexual maturity are thus not reliable for Blarina. If mature sperm are indicative of sexual ability, sperm smears rather than testis measurements should be used in studies of this shrew. The ages at which males and females attain sexual maturity are uncertain but present data indicate that females may be sexually mature as early as 3.5 months and males at 2 months.

Despite considerable speculation, no study has proved whether pairing occurs during the breeding season or the duration of any such pairing. Studies of other shrew species indicate considerable mortality of the young occurring between birth and leaving the nest. Embryo counts for

Blarina, which average 5.7 per female (130 records), may thus have little meaning as a measure of young added to the population. Most of the data in the present and previous studies indicate that two and perhaps three litters are produced annually by mature females in the wild; previous work has shown that some captive females are capable of producing five litters per season. A possible correlation between the vernal and autumnal equinoxes and the duration of the breeding season for Blarina requires testing under controlled light conditions for clarification. Graphs of calculated birth dates and occurrence of lactating females, based on the data of many authors, indicate that litters may be nursed for about two months whereas a published observation indicates that weaning occurs at about one month; further study is indicated here also.

Home ranges for male shrews, estimated by using the greatest distance between capture points as the diameter of a circular range, averaged .0 (0.3-2.20) acre and for females 0.75 (0.21-1.54) acre. The sizes of the home ranges varied; decreased size and increased overlapping in the autumn was associated with increased population density and may have been related to the changing reproductive status and age of the shrews. A small region of optimal habitat surrounded by less favorable areas tends to cause crowding of animals within the optimal habitat and also generates greater overlapping and smaller sizes of home ranges.

My estimates of population density ranged from zero to 14.3 Blarina per acre, the highest populations occurring between mid-September and early October. The shrews were not equally distributed throughout the areas of study and consequently the density was considerably higher in some places-- and much less in others-- than the calculated averages. Most mortality occurred before the end of the calendar year. After considering the various possible causes of mortality, I concluded that predation and a differential mortality of the older shrews are probably of greatest importance. Although availability of water has been considered a critical factor for shrews, evidence shows that they are able to survive with only a limited intake.

The existence of a three or four year cyclical fluctuation of shrew populations is suggested and comparison with past studies indicates that such fluctuations are probably local phenomena.

Captive shrews accepted any food of animal origin but experienced difficulty in capturing mice and voles even within the confines of the relatively small cages and some shrews showed no interest in killing the potential prey. The brains of small mammals were invariably eaten first and after a mouse or vole was eaten, all that usually remained intact was an empty skin having only a few breaks and some of the less muscular areas such as feet, tail, and anterior portion of the skull. Birds were eaten but their brains were inexplicably left intact, one reptile and various

amphibians were killed but not readily eaten and fish were accepted. All arthropods presented to the captives were eaten and preference was shown for the larger soft-bodied insects, some mollusks were preferred over others, annelids were readily taken with a preference shown for the smaller-sized worms, and grass was refused although many other items of plant origin (seeds, nuts, cookies) were eaten.

Analysis of 83 digestive tracts provided the per cent frequency of occurrence and per cent volume of identified foods (74.9 per cent of the total gut contents). These respective percentages are summarized for the major categories of food as follows: mammals (7.7, 5.4), amphibians (3.8, 3.1), insects (90.8, 71.9), arthropods exclusive of insects (20.5, 11.7), annelids (64.1, 16.4), mollusks (15.3, 9.3), and plant material (44.8, 5.4). Three orders of insects (Coleoptera, Hymenoptera, Orthoptera) represented the bulk of the food in that category and the beetles were, by both volume and occurrence, the most important insects eaten. Seasonal variation in the diet occurred with annelids and molluscs most important in the summer and insects comprising the bulk of the diet in the winter.

A graph demonstrating the probability of capturing shrews within the 24-hour day reveals a pre-sunrise and post-sunset peak, indicating greatest activity at those times. Captives show a similar rhythm with activity greatest between 1200 and 0630, tending to be earlier in the summer and later in the winter. Within this 24-hour cycle,

short periods of activity-- usually lasting between 10 and 15 minutes and averaging longer at night-- alternated with periods of rest lasting about 2.5 hours during the day and 1.5 hours during the dark hours. Attempts to discover a still shorter rhythm proved unsuccessful.

Summer and winter activity patterns differ with the summer pattern, noted between late April and mid-September, having a pronounced pre-sunrise peak and relatively little diurnal activity. The winter pattern, observed from mid-October to early March, shows activity more equally spread throughout the day and night although the pre-sunrise and post-sunset peaks still persist. The rest periods average between 2 and 3 hours during the summer and between 1.5 to 2.5 hours in the winter and the longest recorded period of inactivity was 5.5 hours. One shrew, kept in continual darkness for two weeks, retained the circadian pattern of activity throughout this period.

Considerable data have been gathered and analyzed, more from other studies have been consolidated and compared, and various implications and conclusions have been drawn. As often occurs, however, more questions have been generated than answered.

APPENDIX

LIST OF PLANTS MENTIONED IN THE TEXT, ARRANGED ALPHABETICALLY BY VERNACULAR NAME. THE SCIENTIFIC NAMES FOLLOW FERNALD(1950)

Alternate-leaved dogwood	Cornus alternifolia L.
American elm	Ulmus americanus L.
Asters	Aster sp. L.
Beech	Fagus grandifolia Ehrh.
Black cherry	Prunus serotina Ehrh.
Black oak	Quercus velutina Lam.
Blue beech	Carpinus caroliniana Walt.
Bluejoint	Calamagrostis canadensis (Michx.)
Box elder	Acer Negundo L.
Boneset	Eupatorium perfoliatum L.
Bracken fern	Pteridium aquilinum (L.) Kuhn
Brambles	Rubus sp. L.
Burdock	Arctium sp. L.
Bur oak	Quercus macrocarpa Michx.
Butternut	Juglans cinerea L.
Canada blue grass	Poa compressa L.
Canada thistle	Cirsium arvense (L.) Scop.
Cocklebur	Xanthium strumarium L.
Common burdock	Arctium minus Schk.
Common cattail	Typha latifolia L.
Common chicory	Cichorium Intybus L.

Common milkweed	Asclepias syriaca L.
Common ragweed	Ambrosia artemisiifolia L.
Cottonwood	Populus deltoides Marsh.
Early meadow rue	Thalictrum dioicum L.
Elderberry	Sambucus canadensis L.
Flowering dogwood	Cornus florida L.
Giant ragweed	Ambrosia trifida L.
Goldenrod	Solidago sp. L.
Grasses	family Graminae
Gray dogwood	Cornus racemosa Lam.
Hawthorn	Crataegus sp. L.
Hazelnut	Corylus americana Walt.
Hepatica	Hepatica sp. Mill.
Hog-Peanut	Amphicarpa bracteata (L.) Fern.
Honeysuckle	Lonicera sp. L.
Horsetails	Equisetum sp. L.
Jack-in-the-pulpit	Arisaema triphyllum (L.) Schott.
Jewelweed	Impatiens capensis Meerb.
Joe-Pye-weed	Eupatorium purpureum L.
Maple-leaved viburnum	Viburnum acerifolium L.
Nanneyberry	Viburnum Lentago L.
Orchard grass	Dactylis glomerulata L.
Pignut hickory	Carya glabra (Mill.) Sweet
Pin oak	Quercus palustris Meunchh.
Poison ivy	Rhus radicans L.
Prickly ash	Zanthoxylum americanum Mill.
Quaking aspen	Populus tremuloides Michx.

Red cedar	Juniperus virginiana L.
Red maple	Acer rubrum L.
Red oak	Quercus rubra L.
Red osier dogwood	Cornus stolonifera Michx.
Red willow dogwood	Cornus Amomum Mill.
Rushes	Juncus sp. L.
Sedges	family Cyperaceae
Serviceberry	Amelanchier sp. Medic.
Shagbark hickory	Carya ovata (Mill.) K. Koch.
Shrubby St. John's wort	Hypericum prolificum L.
Skunk-cabbage	Symplocarpus foetidus (L.) Nutt.
Smooth sumac	Rhus glabra L.
Spotted St. John's wort	Hypericum punctatum Lam.
Staghorn sumac	Rhus typhina L.
Sugar maple	Acer saccharum Marsh.
Swamp white oak	Quercus bicolor Willd.
Sycamore	Platanus occidentalis L.
Tall coneflower	Rudbeckia laciniata L.
Tall scouring rush	Equisetum hiemale L.
Virginia creeper	Parthenocissus quinquefolia (L.) Planch.
White ash	Fraxinus americana L.
White melilot	Melilotus alba Desr.
White oak	Quercus alba L.
Wild carrot	Daucus Carota L.
Wild cucumber	Echinocystis lobata (Michx.) T.&G.
Wild grape	Vitis sp. L.
Wild rose	Rosa sp. L.
Willows	Salix sp. L.

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Figure 1. Early September, 1965



Figure 2. Mid-March, 1966

Plate 1. Summer and winter views, from the same position, of the baseball batting area at Saline, Michigan. The meadow edge is shown on the left, the river road and field on the right. The reference stake was an iron subdivision pin.



Figure . Baseball Point area, late [illegible]t, l[illegible].



Figure 2. Drift area for [illegible] River, late March, l[illegible].

[illegible]. Preferred planing habit [illegible] the [illegible] all [illegible] area and a general view of the [illegible] area. The [illegible] Figure [illegible] has the [illegible] subdivisions.



Fig. 1. Cherry tree.



Fig. 2. Bitten end

Fig. 3. View of the cherry in mid-summer, showing the relative size and location of the various parts.



Figure 3. [illegible], [illegible], [illegible].



Figure [illegible], [illegible], [illegible].

[illegible] view of the [illegible] portion of the [illegible] the subject or [illegible] their [illegible]. [illegible] in Figure 1 [illegible] one [illegible] individuals.

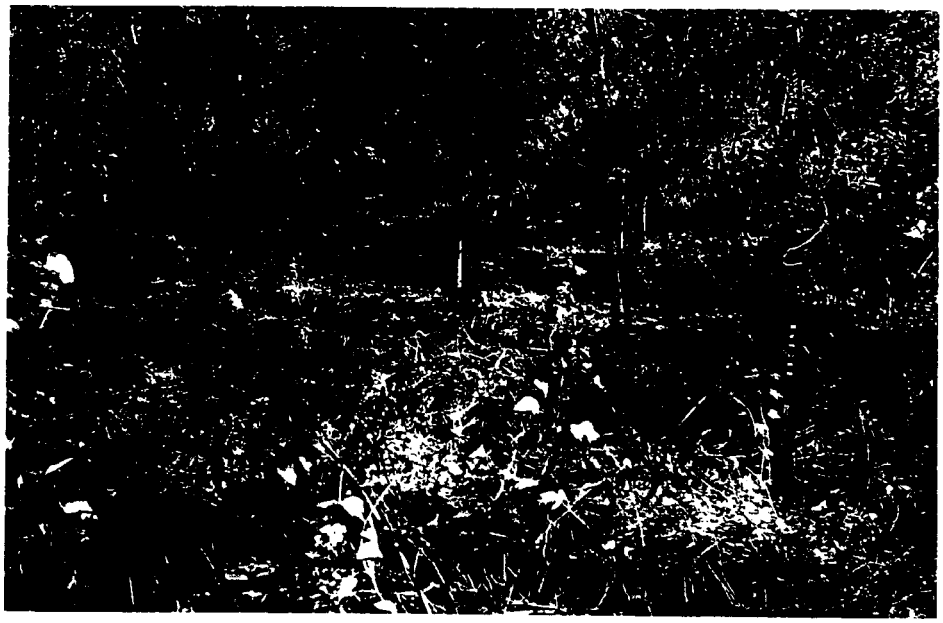


Figure 1. Early [illegible], 1951.



Figure 2. [illegible]rch, 1954

[illegible] [illegible] [illegible] [



Figure 5. [illegible] area.



Figure 6. [illegible] habitat.

Plate VI. Views of the narrow strip of preferred habitat along the border of the [illegible] and the adjacent slope in the [illegible] area. More shrews were taken here than in any other trapping area. The stake has one inch subdivisions. Late October, 1955.

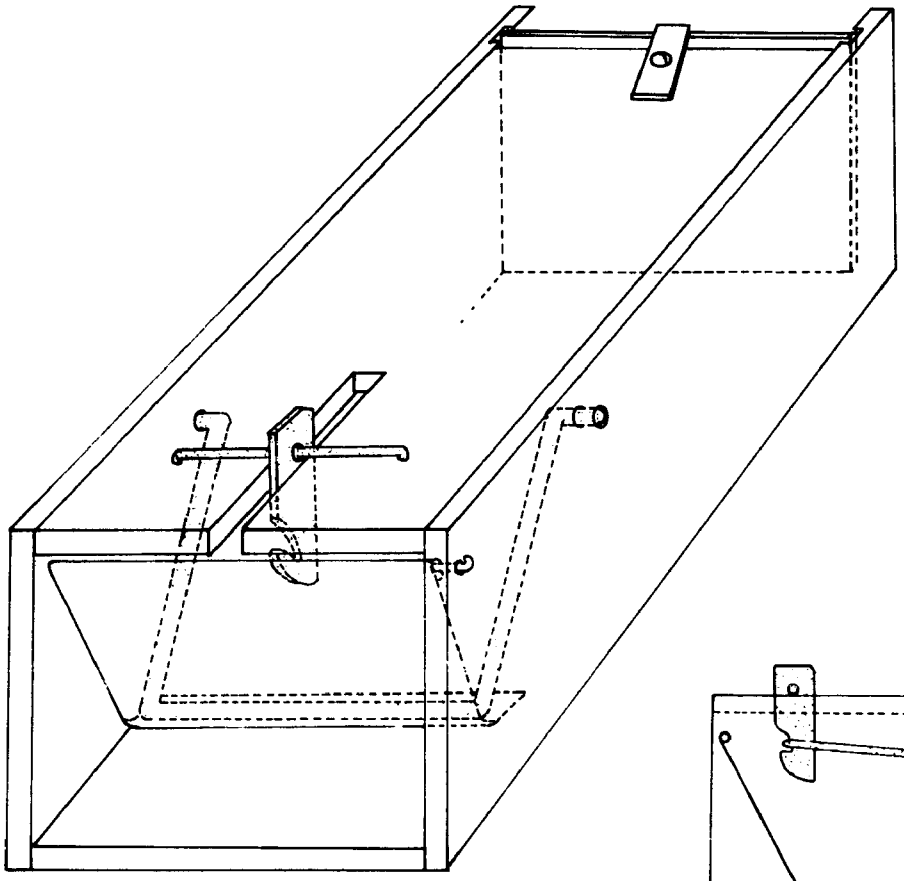


Fig. 1. Assembled trap

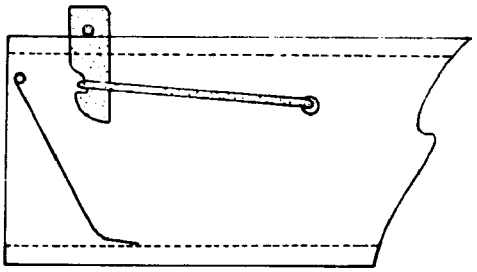


Fig. 2. Side view, set

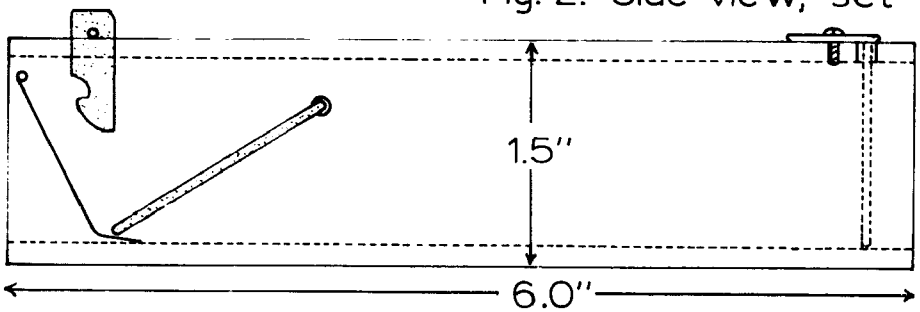


Fig. 3. Side view, tripped

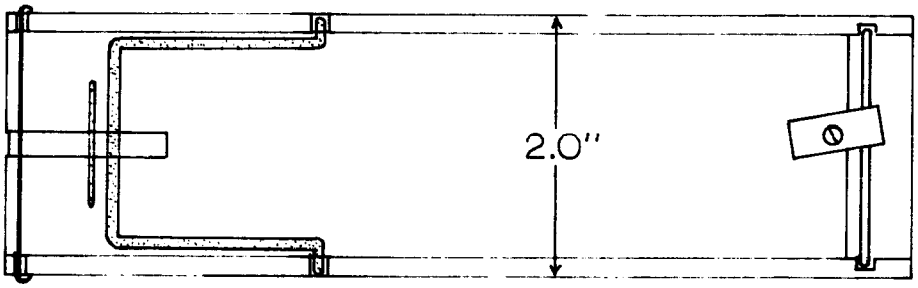


Fig. 4. Top view, without catch

PLATE V.1. Experiment 1 trap showing details of assembly and operation. The basic shell consists of cemented exterior hardboard; the rear door and latch and catch of heavy aluminum; the entry door of light aluminum; and the lock wire of 9 and the hinge wires of 15 auge wires.

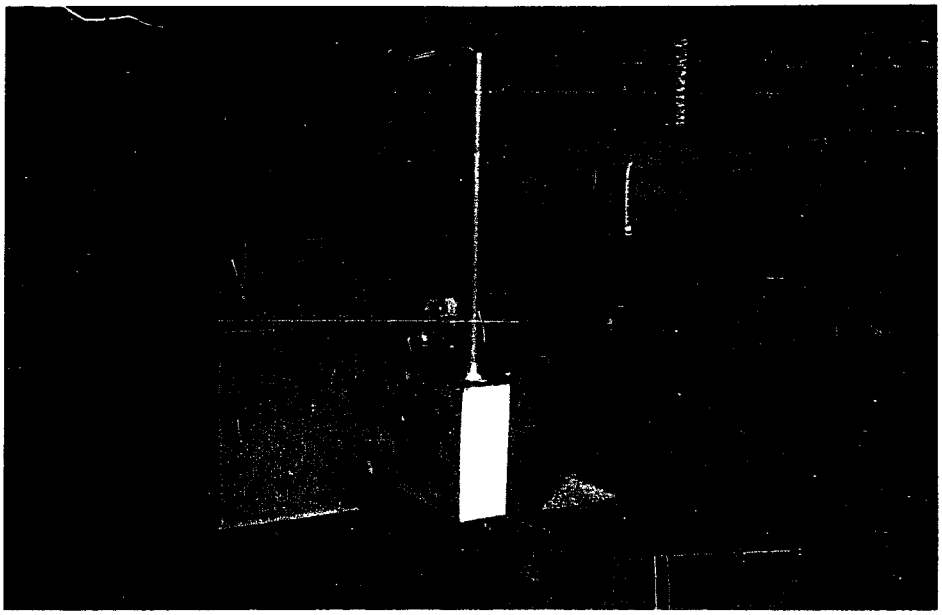


Figure 1. Witch box closed.

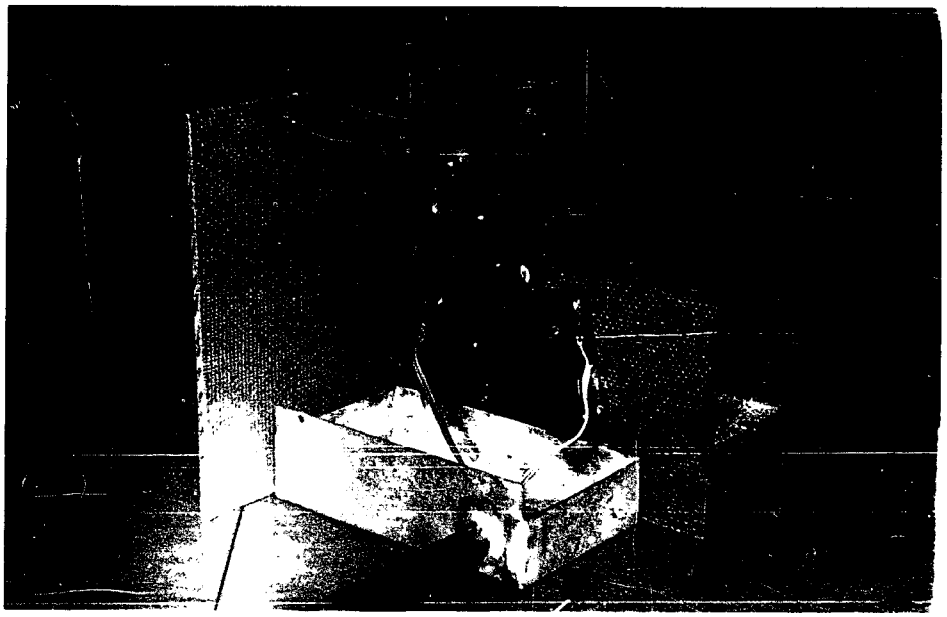


Figure 2. Witch box open showing electrodes.

Frame VIII. Bunny assembly which detected movement of Plasmodium between host activity areas of the cage.

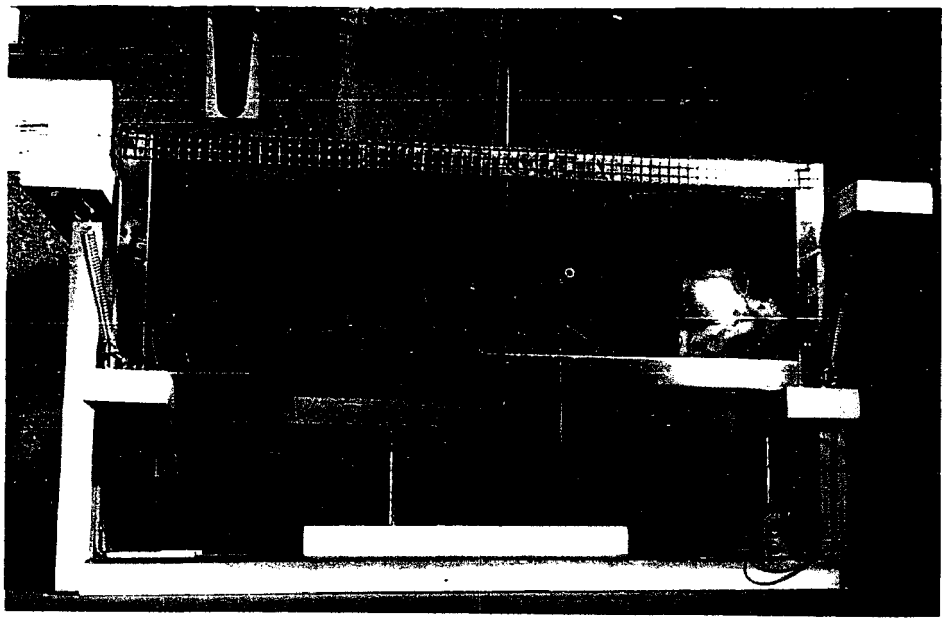


Figure 1. Spring-loaded platform with a rat.



Figure 2. Lower portion of platform with assembly.

...ctivity ...ch... ...per tus... ...rating ...ig. 1) the spring-loaded platform ... ...rim if which a runway ... ...is ...ti... ... ... the switch ... ... to the platform ... ... ver... of the screw.

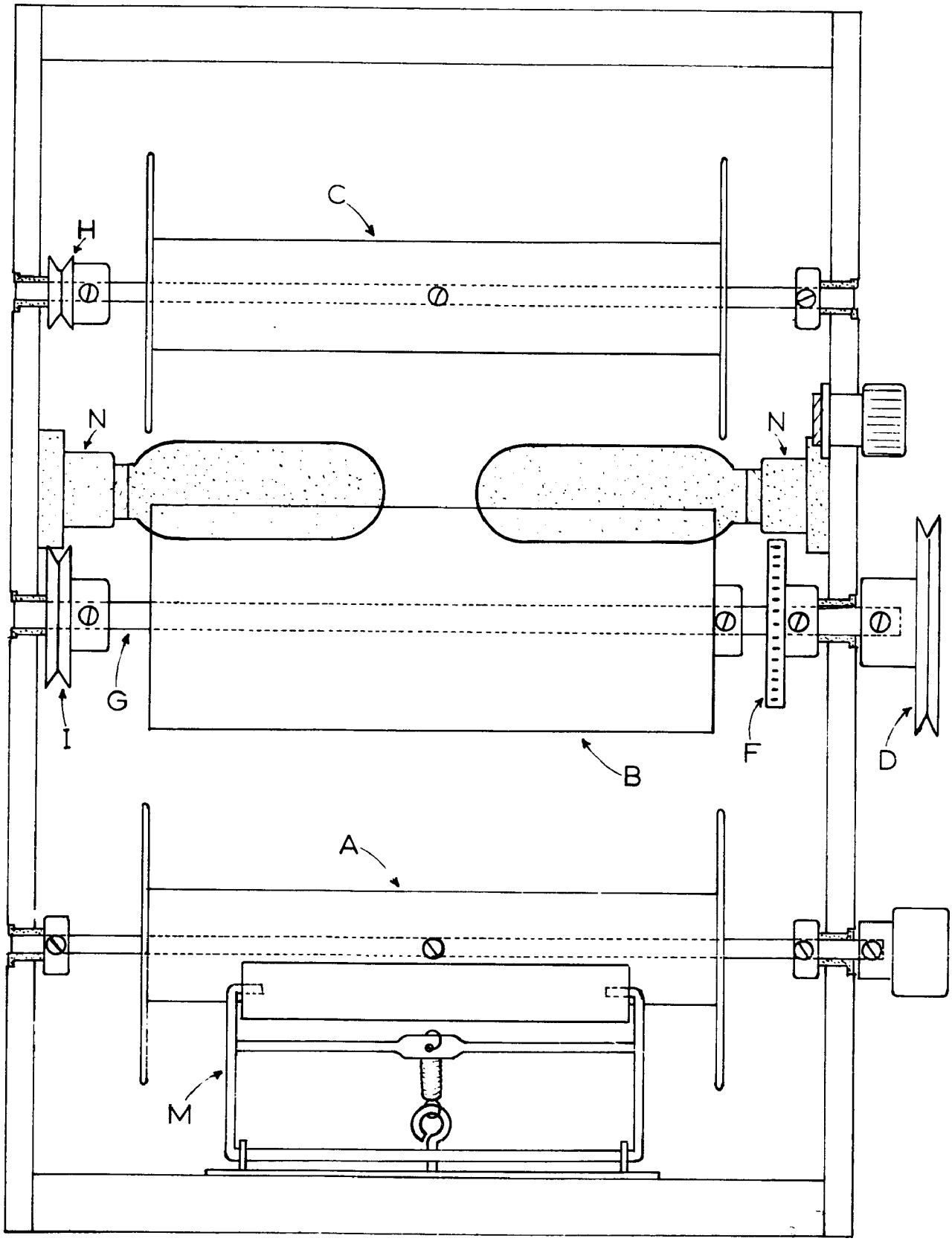


PLATE A. Kymograph with cover removed and pressure rollers omitted. Paper, four inches in width, loaded on roller A passes over the master roller B and is rewound on roller C. More detailed description is given in the text.

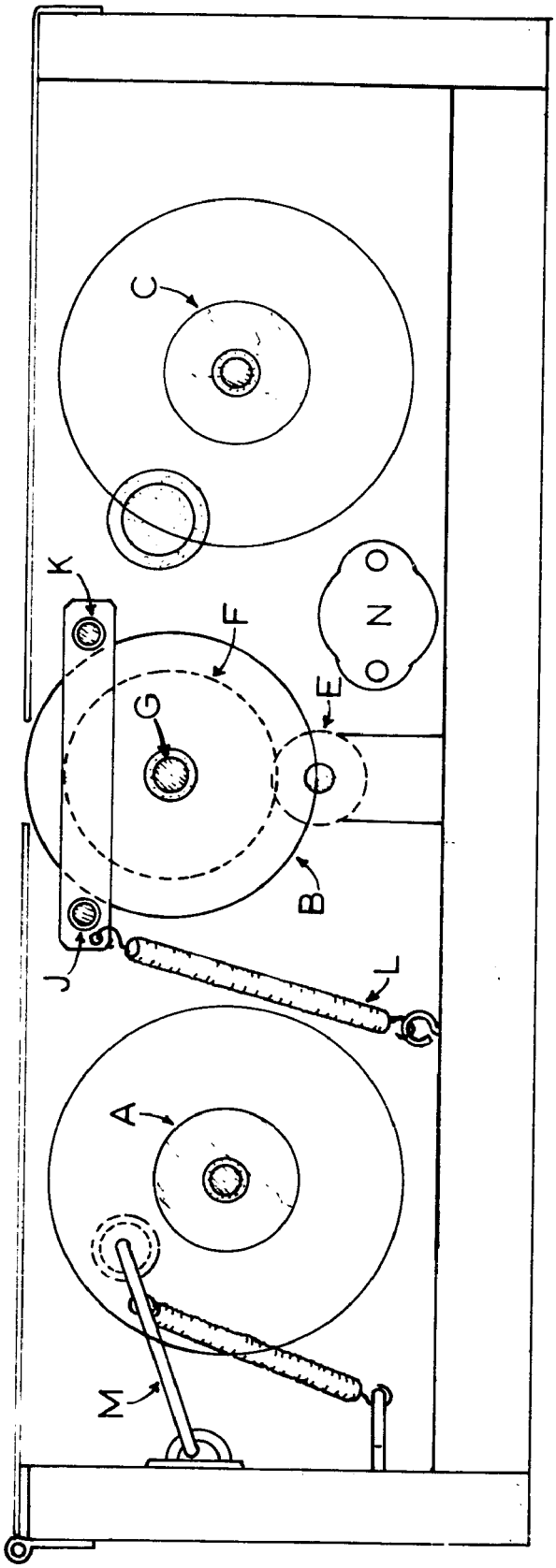


Fig. 41. Kymograph in side view with cover in place and the side removed. The striped circles represent shafts upon which rollers A, B, C, J, and K and gears E and F rotate. Further details are given in the text.

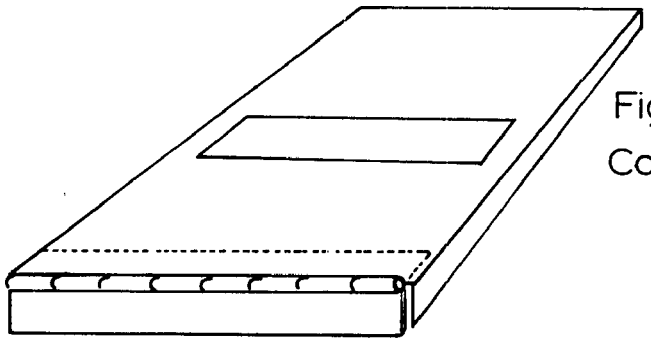


Fig. 1.
Cover

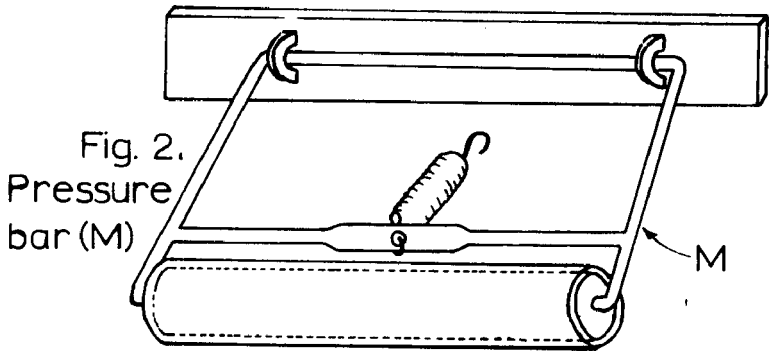


Fig. 2.
Pressure
bar (M)

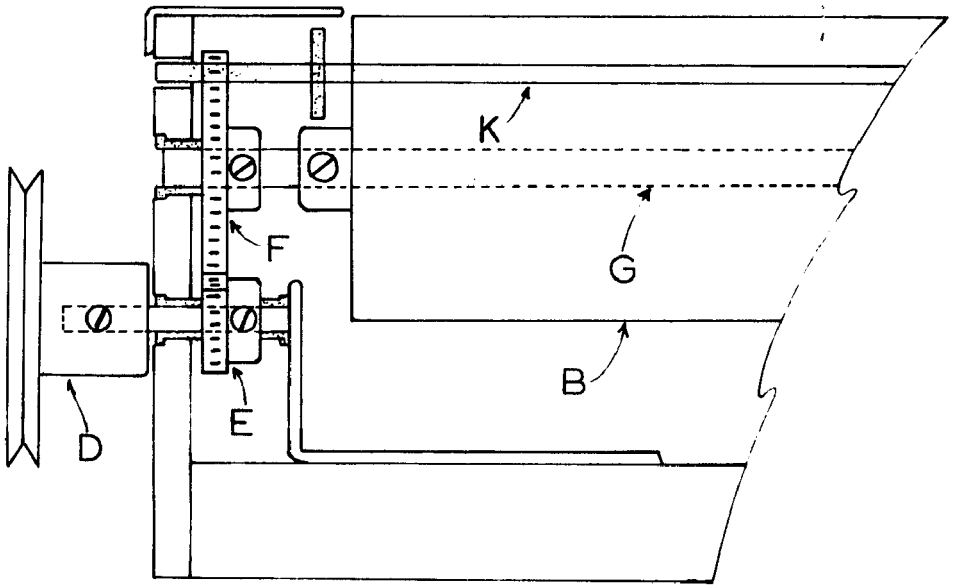


Fig. 3. Master roller drive

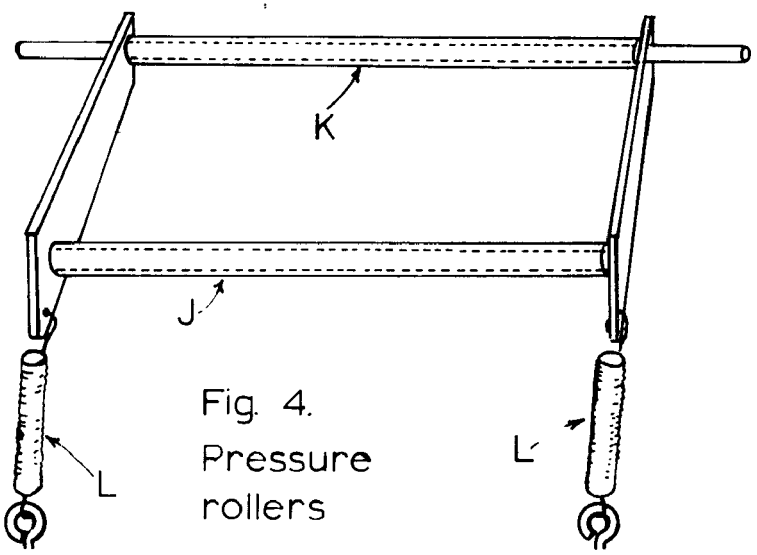


Fig. 4.
Pressure
rollers

PLATE XII. Details of kymograph construction.

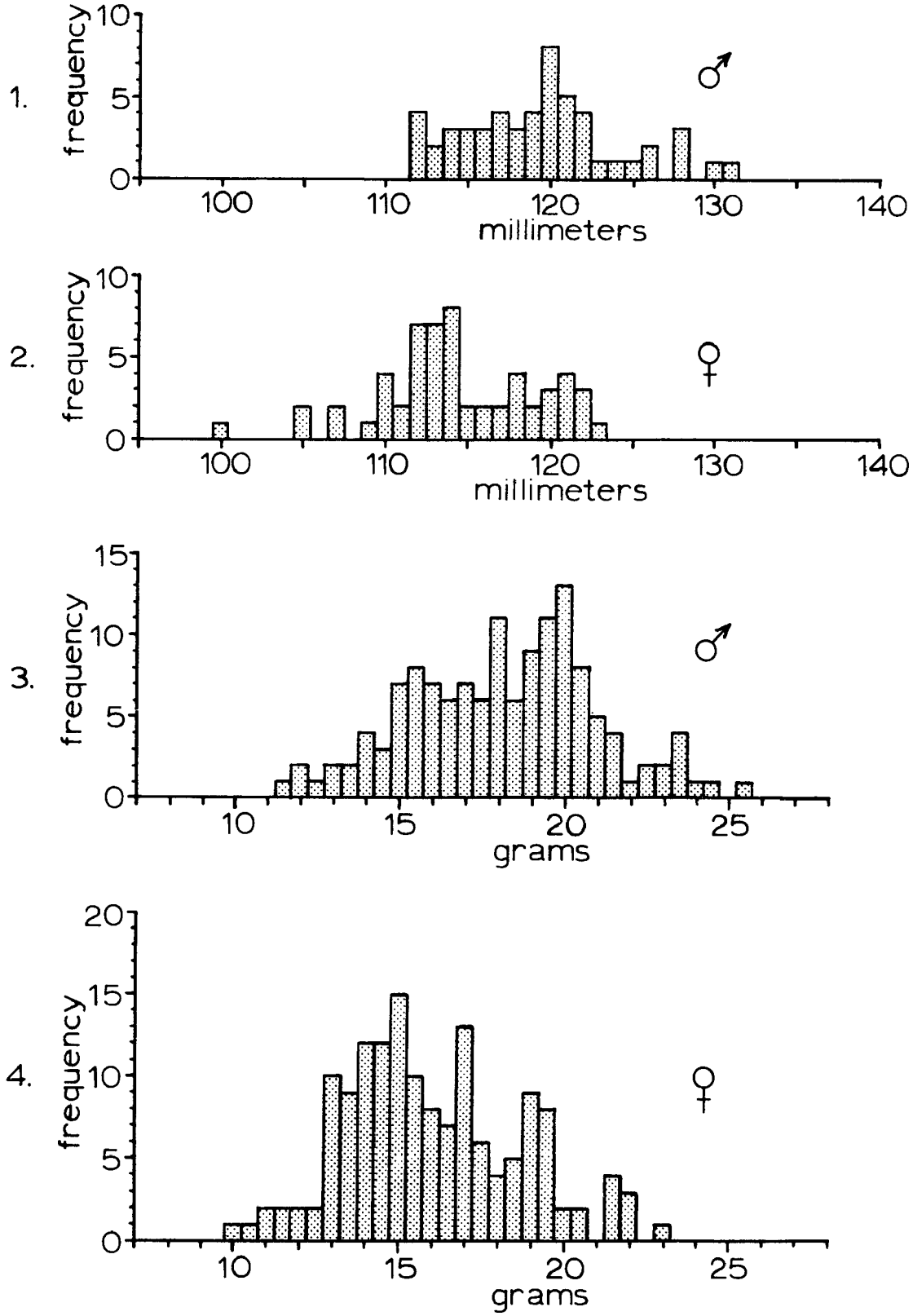


PLATE XIII. Total lengths and weights of male and female Blarina in southern Michigan. Figures 1 and 2 are based on dead specimens only; Figures 3 and 4 are based on both live and dead individuals.

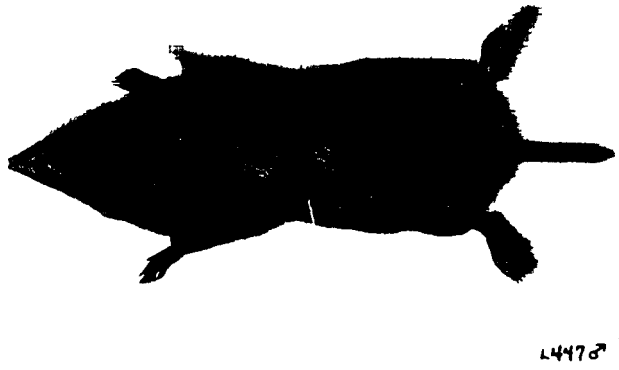


Figure 1. Immature.

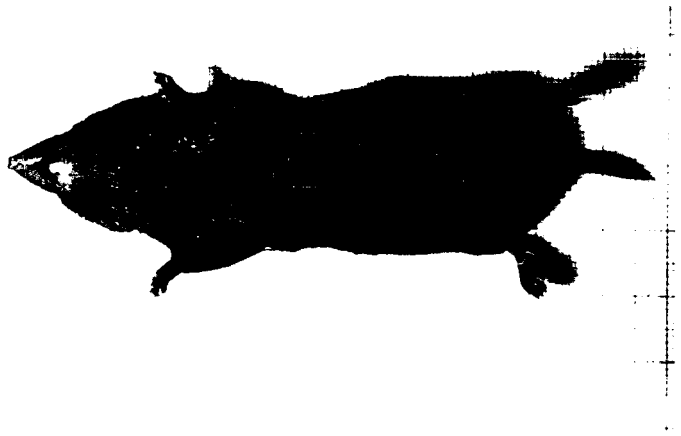


Figure 2. Young Adult.

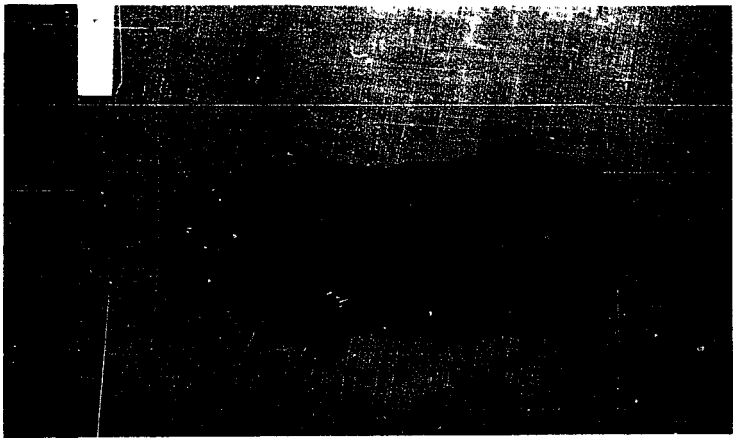


Figure 3. Old Adult

PLATE XIV. Morphological age differences in a series of male Blarina.

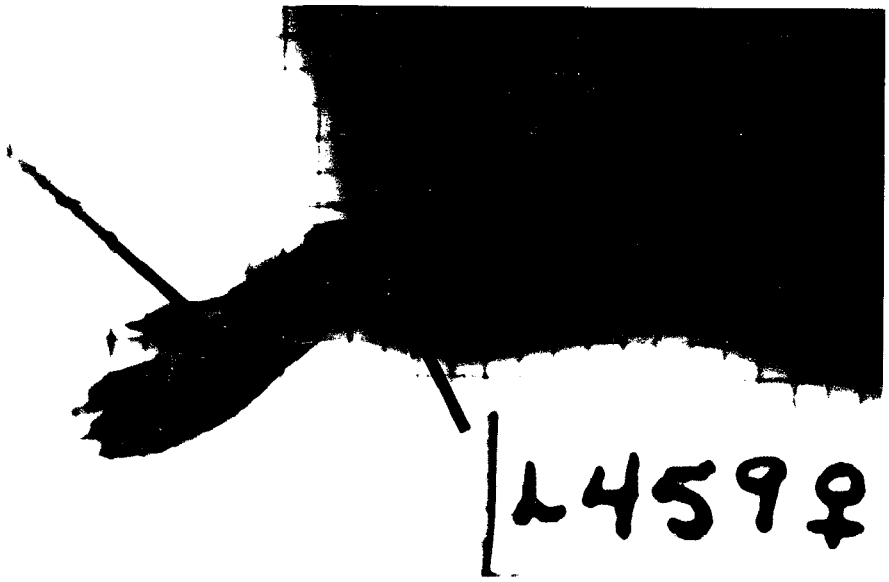


Figure 1. Heel organ with central scab.

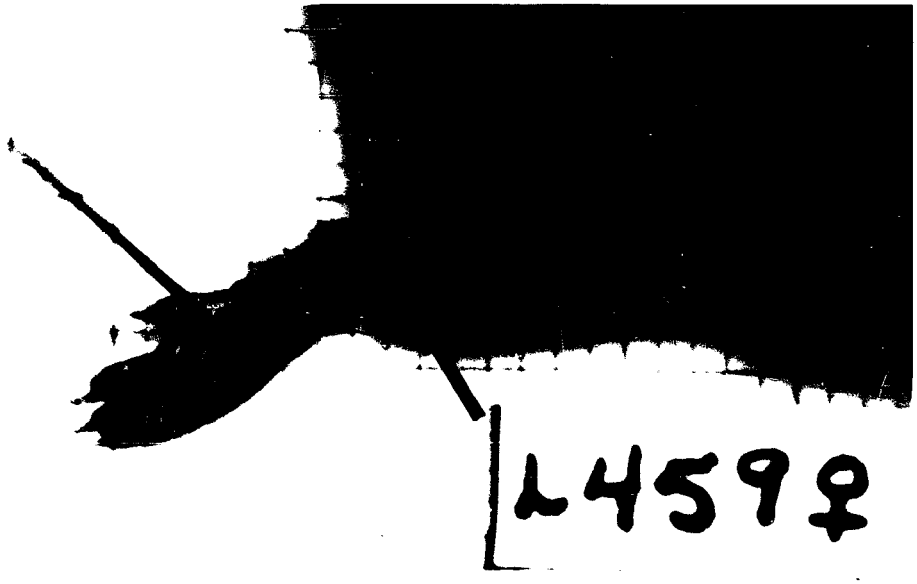


Figure 2. Same as above with scab removed.

PLATE IV. Well-developed heel organs of a female short-tailed shrew.

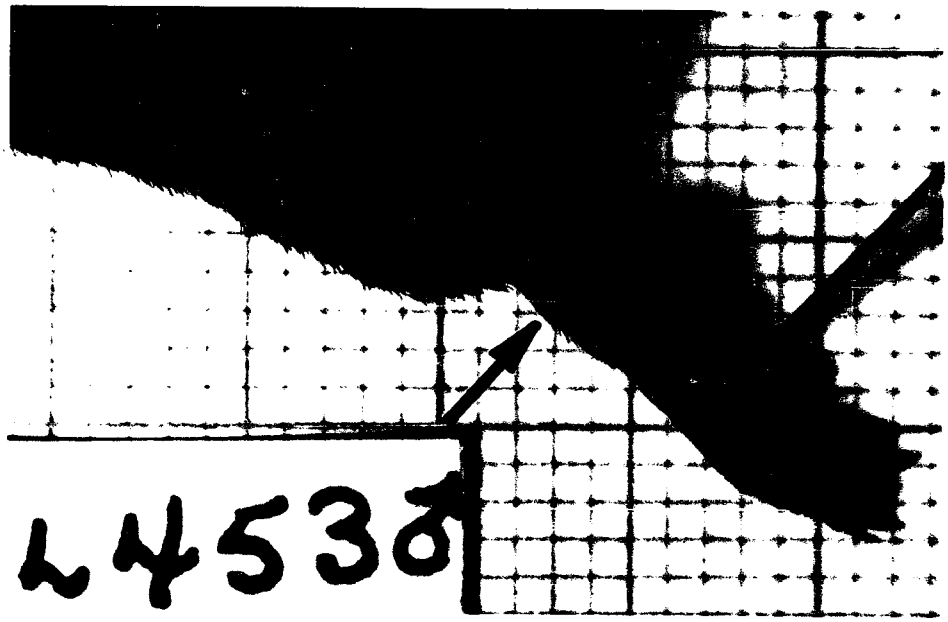


Figure 1. Undeveloped heel organ.



Figure 2. Moderately developed heel organ with small scab.

PLATE VI. Heel organs showing poor and moderate development in male Blarina.

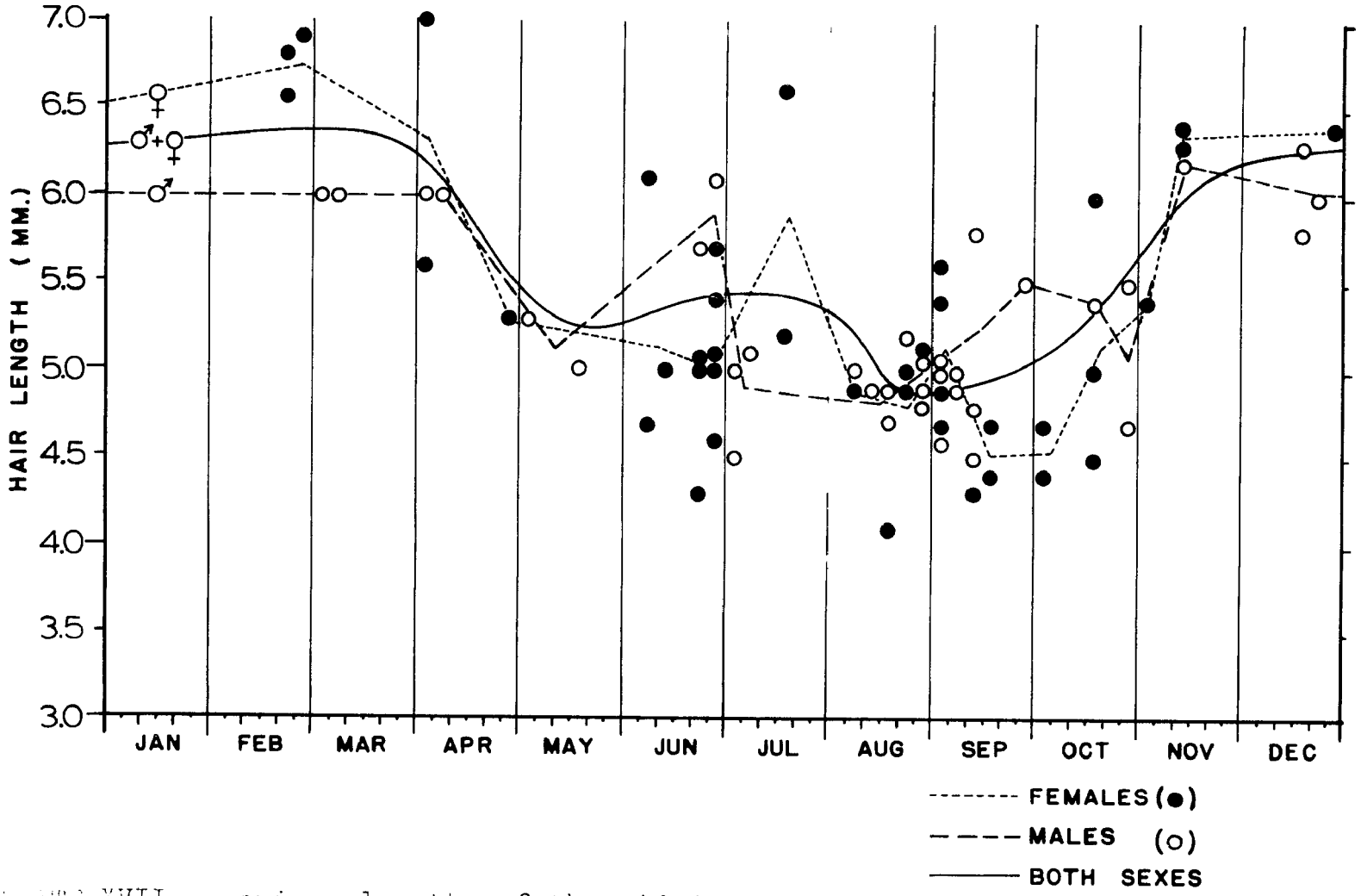
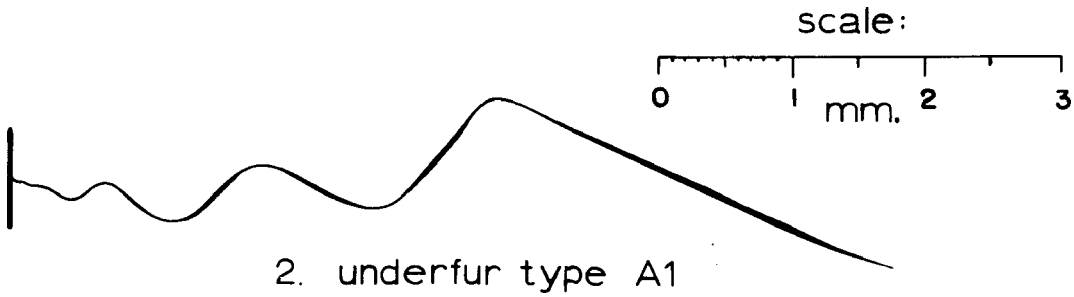


PLATE XVII. Maximum lengths of the mid-dorsal underfur hairs from pelts of Blarina collected throughout the year. The measurements, taken from the base to the tip of the longest unextended hairs in small excised pieces of skin, are grouped in five-day intervals.



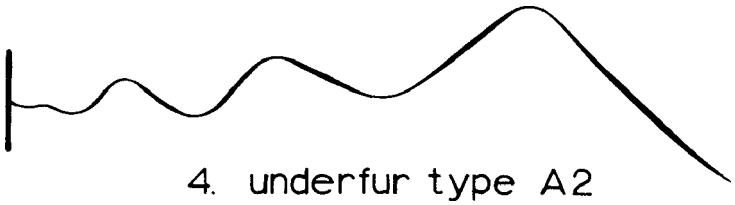
1. guard hair



2. underfur type A1



3. underfur type A1



4. underfur type A2

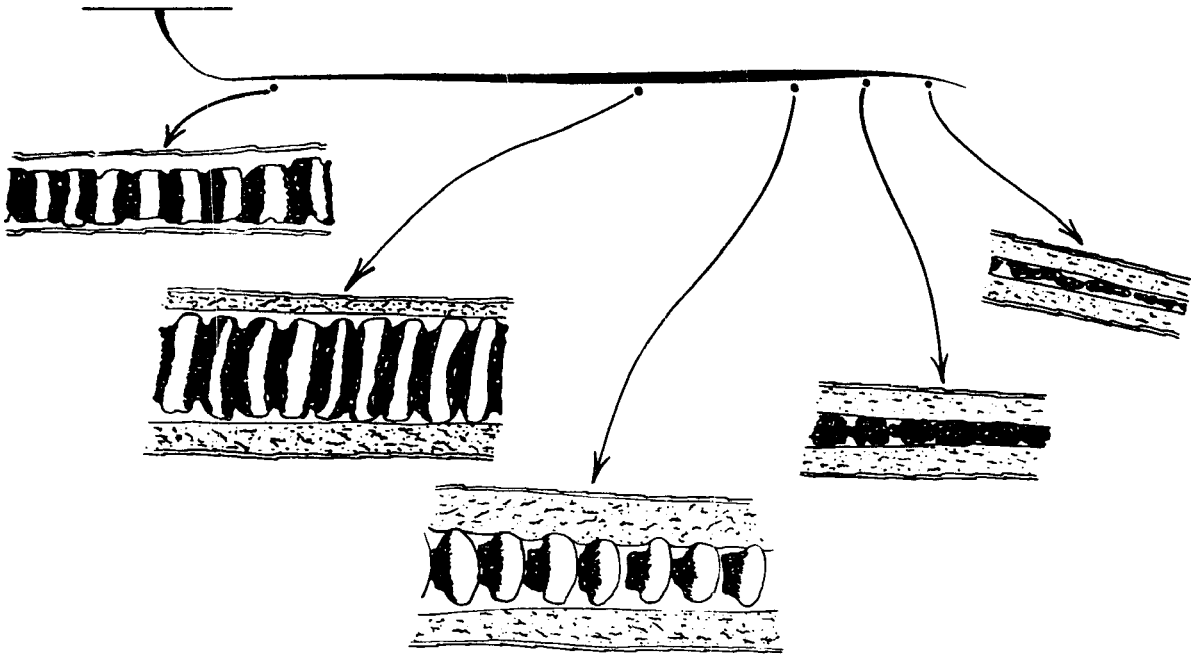


5. underfur type B1

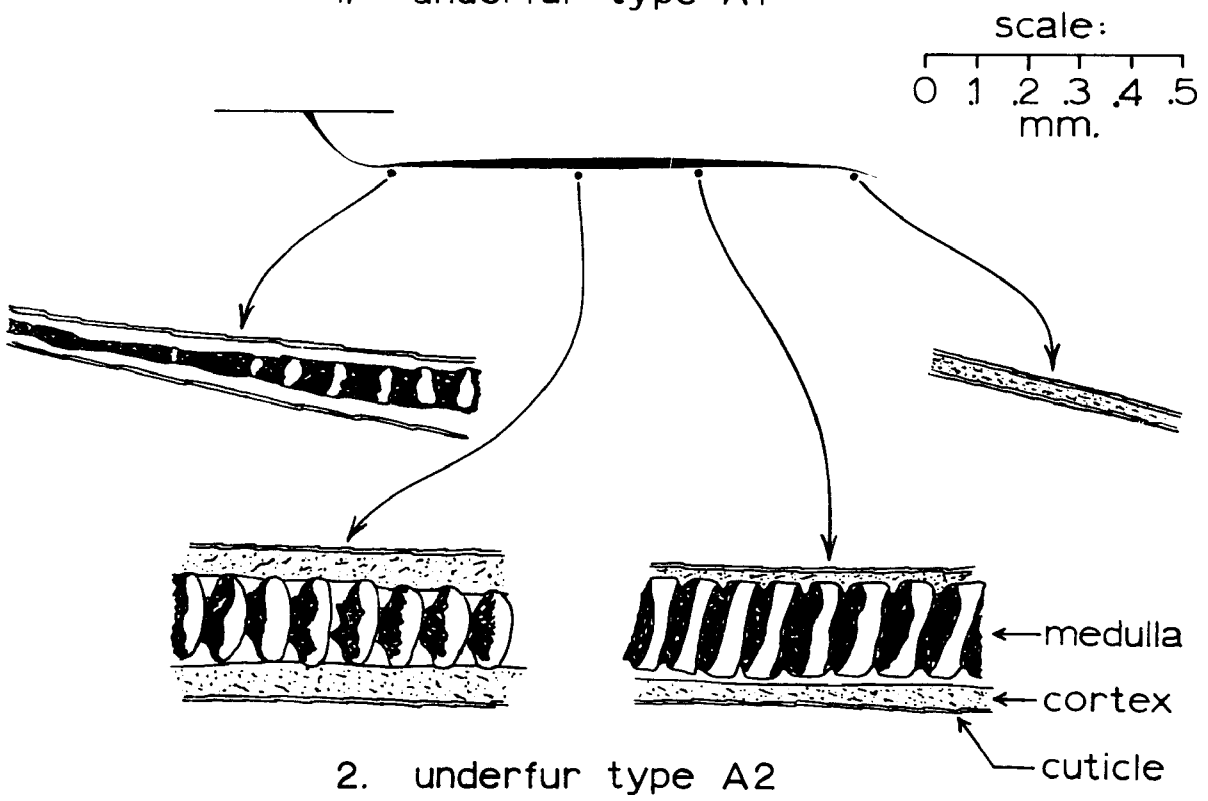


6. underfur type B2

PLATE XVIII. Types of underfur hairs and a guard hair of Blarina. Figures 1, 3, 4, 5, and 6 illustrate typical hairs taken from a summer pelt; Figure 2 shows a hair from the winter pelage. The vertical lines to the left represent the skin surface.

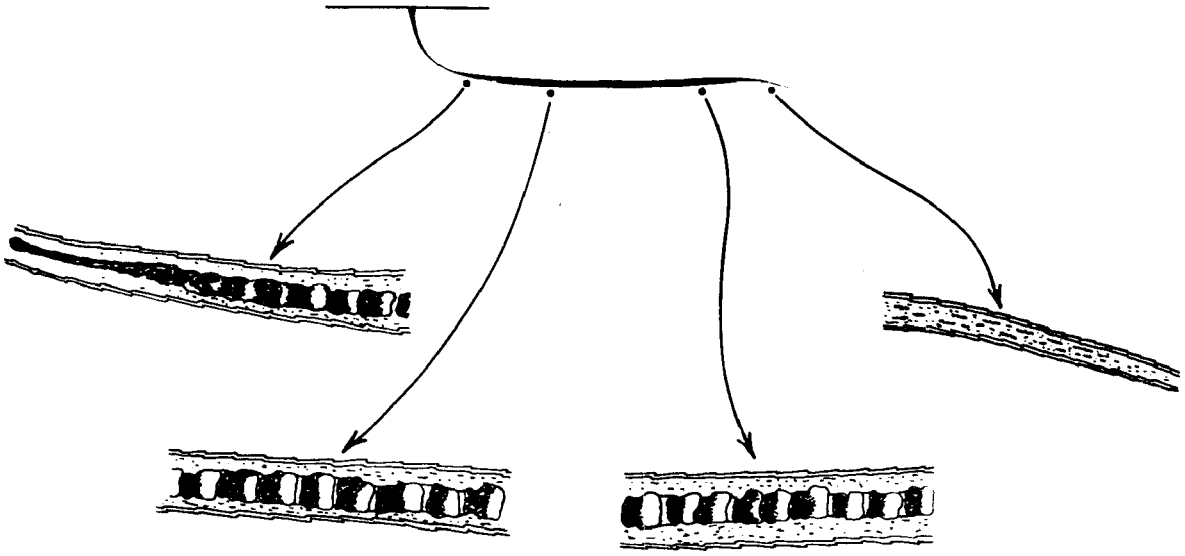


1. underfur type A1

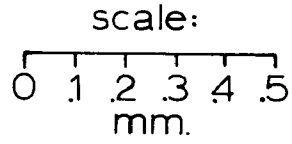


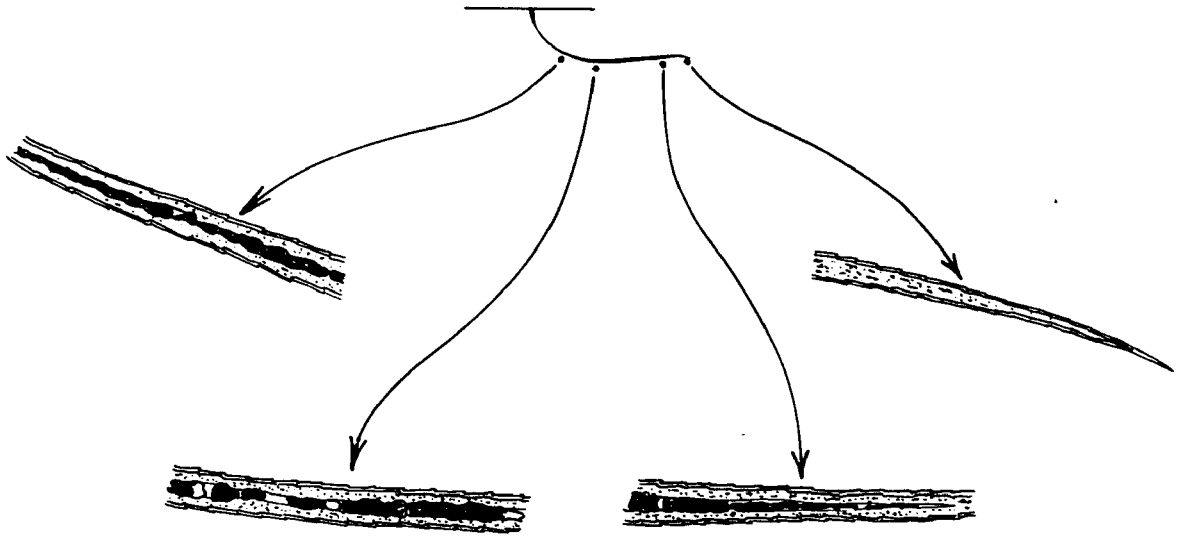
2. underfur type A2

FIG. XXX. Terminal segments of the underfur types A1 and A2 of Ellarina. The distribution of pigment and extent of the cuticle, cortex, and medulla are shown.



1. underfur type B1





2. underfur type B2

PLATE XX. Terminal segments of the underfur types B1 and B2 of Blarina. The enlargements show the relative proportions of the cuticle, cortex, and medulla and the distribution of pigment in both cortex and medulla.

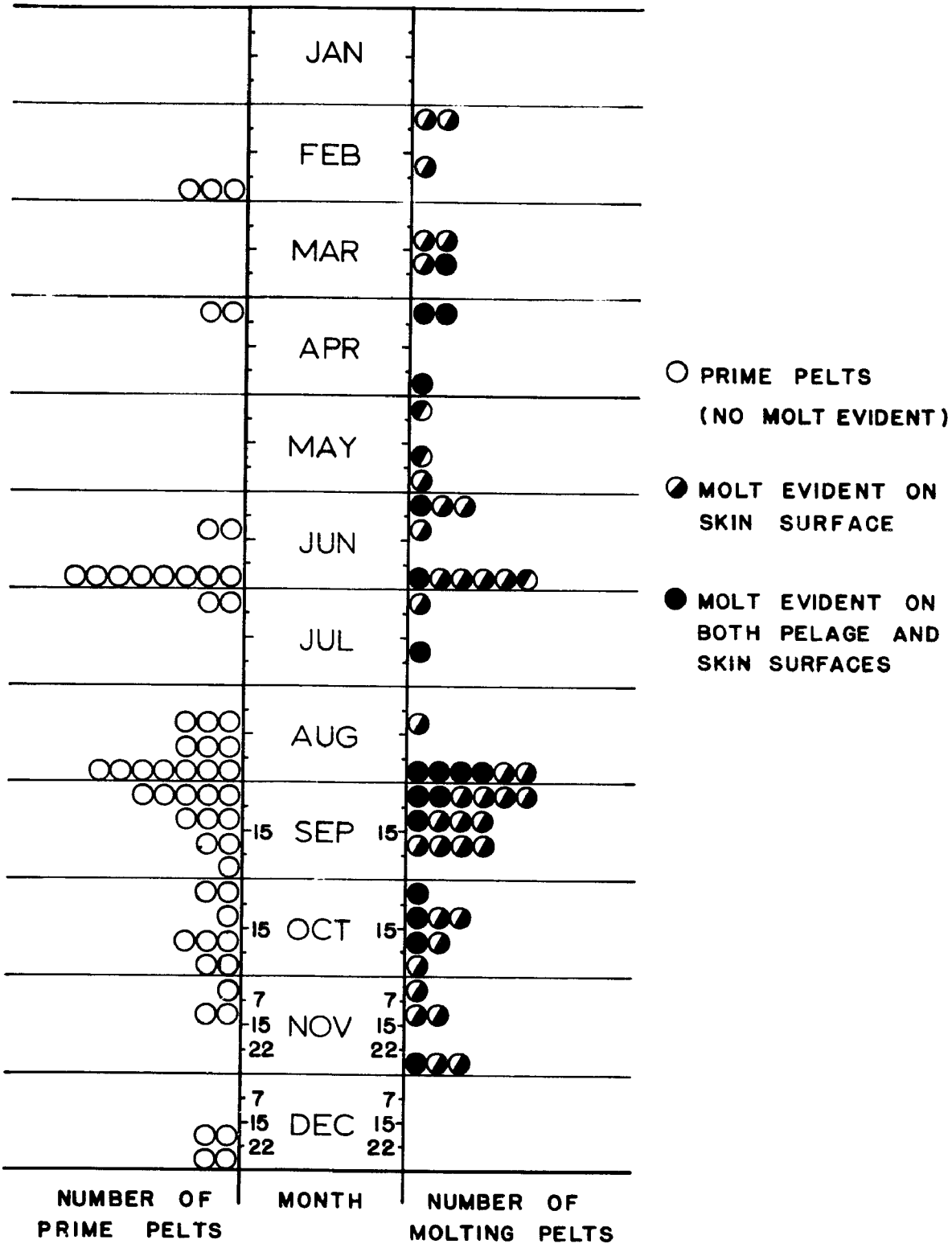


PLATE XXI. Comparison of molting and prime pelts of Marina taken throughout the year. The data are grouped in approximately one-week intervals.

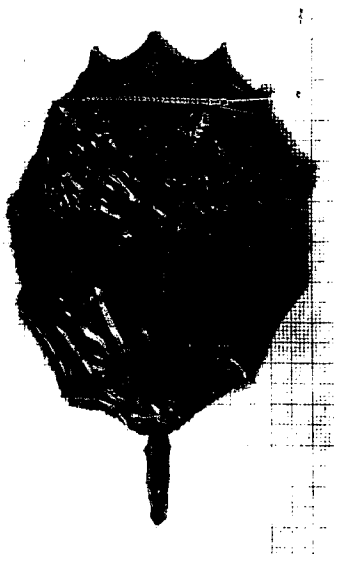


Figure 1

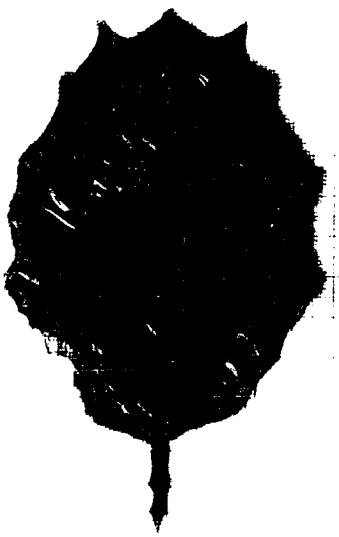


Figure 2

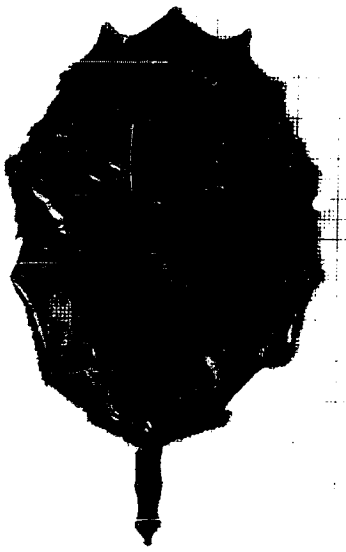


Figure 3



Figure 4



Figure 5



Figure 6

PLATE XXII. Polarina skins illustrating sequential stages of the fall molt. Figures 1 and 2 represent the initial stages and Figure 3 shows essentially the entire pelt in molt.

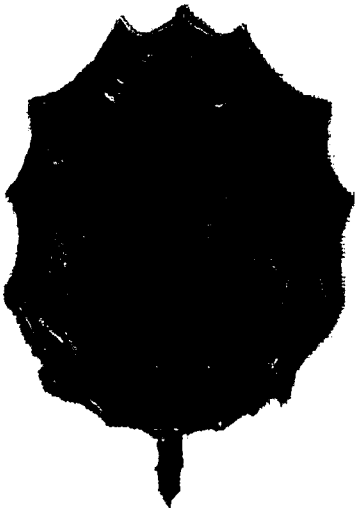


Figure 1



Figure 2

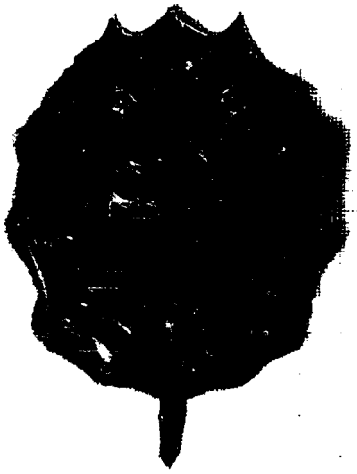


Figure 3



Figure 4

PLATE XXIII. Blarina skins showing sequential stages in the completion of the fall molt. Figure 1 illustrates a pelt almost completely in molt, in Figure 4 the pelt is almost prime.



Figure 1



Figure 2



Figure 3



Figure 4



Figure 5



Figure 6

PLATE XXIV. Blarina skins illustrating selected sequential stages of the spring molt.



Figure 1. Trail entering tunnel in 2.5 inches of snow



Figure 2. Trail exhibiting variation in basic pattern

PLATE XXV. Blarina trails in snow. Two rows of footprints, about 0.5 inch apart, lie within the 1.25 inch wide path. Some prints are opposite, some alternate; the tail mark is shown in both figures.



Figure 1. Trail in t in ...ch illustrati... erratic ...th.

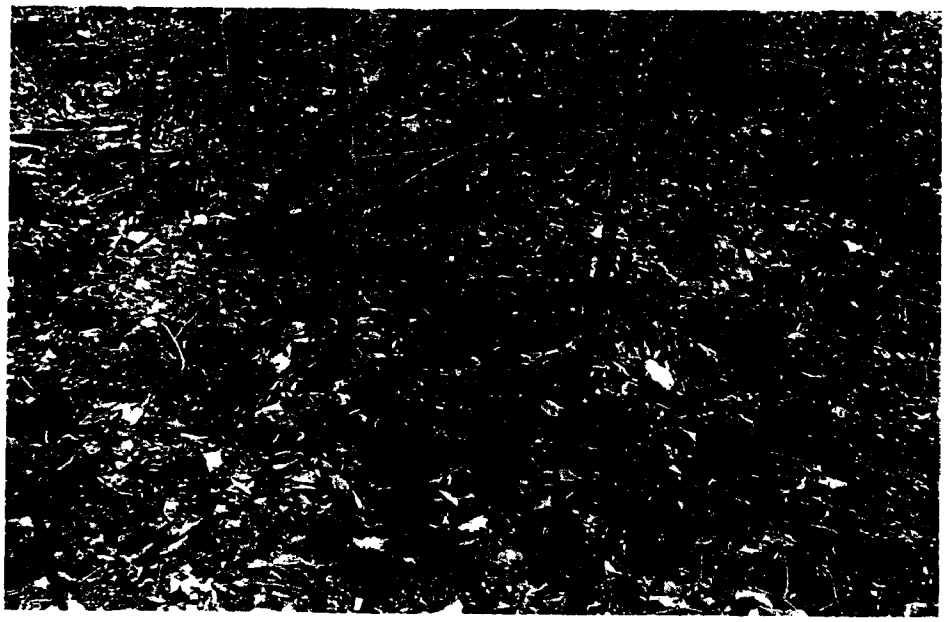


Figure 2. Surface trenches in a moist woods.

PLATE XXVI. Blarina trails. The path in Figure 1 represents the course followed by a foraging shrew; the trenches in Figure 2 developed when subsurface tunnels collapsed and are likely used more for travel than for foraging.

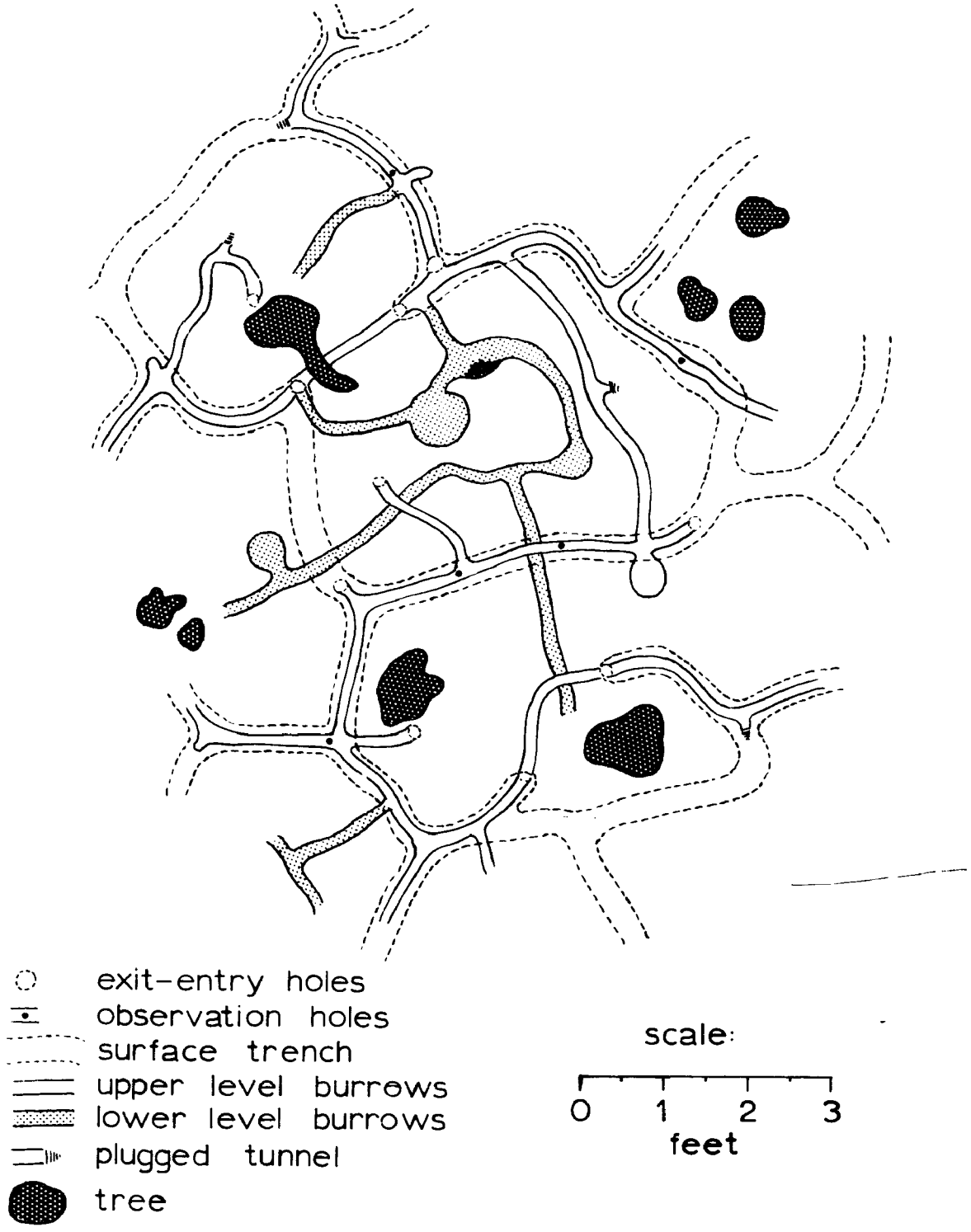


PLATE XXVII. Trench and burrow system of Thomomys talpoides in moist loam soil in an intolerant tree and shrub seral stage within the Crim Area.

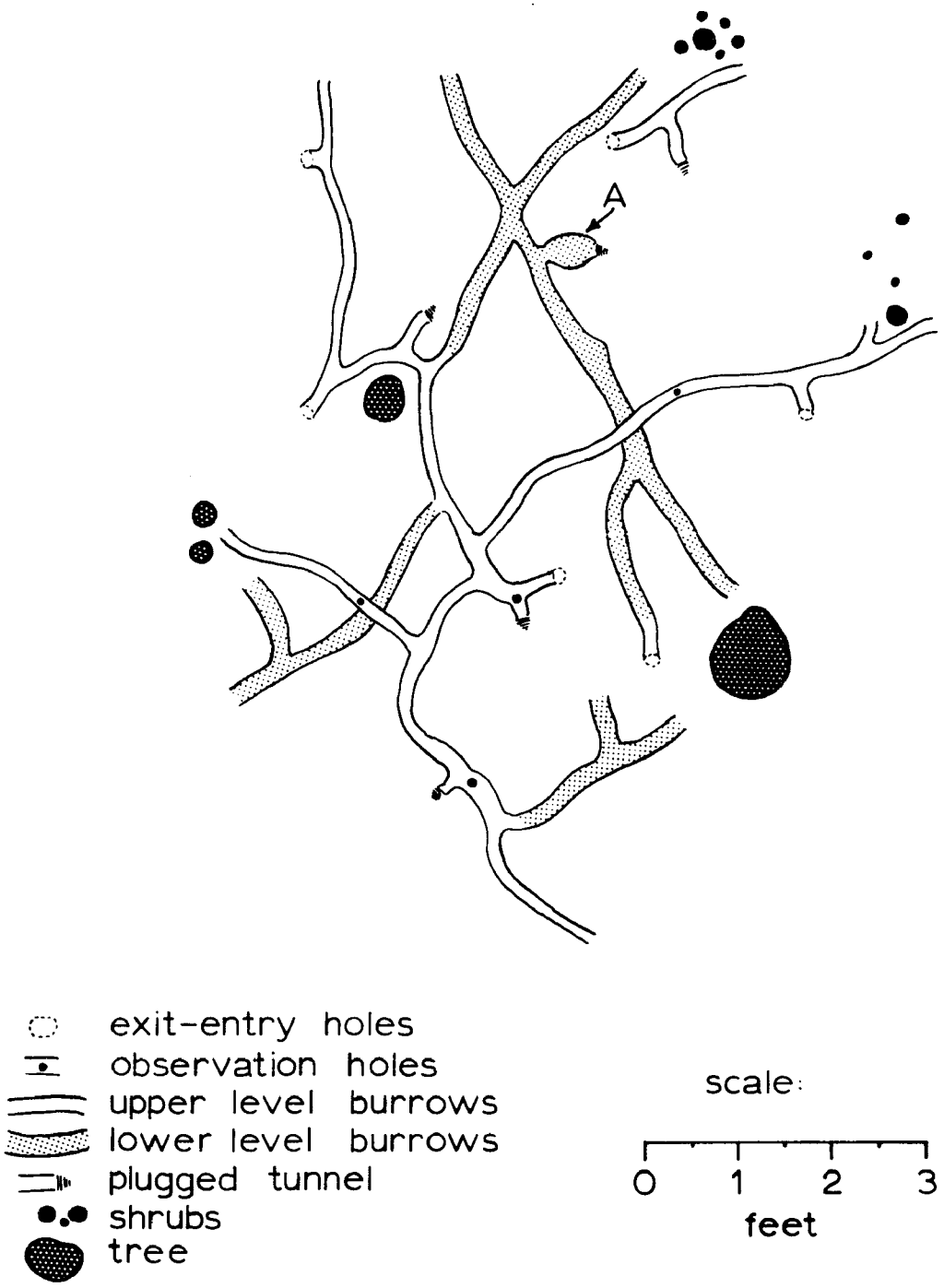
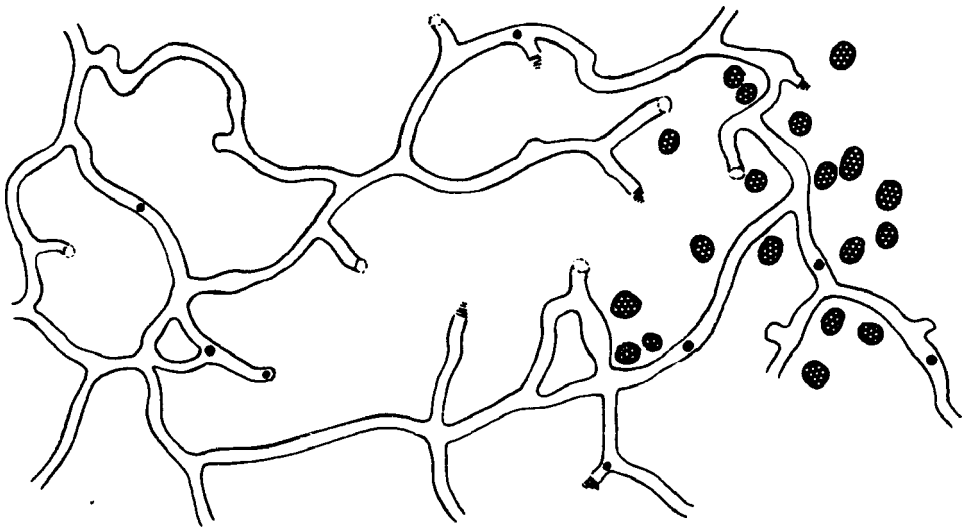


PLATE XXVIII. Burrow system of Blarina in sandy soil within a dry upland wooded plot in the Greene area.



exit–entry holes
observation holes
tunnels
plugged tunnels
cattails

scale:
0 1 2 3
feet

PLATE XXIX. A burrow system of the short-tailed shrew in moist clay soil adjacent to a temporary pond within the Railroad Area.

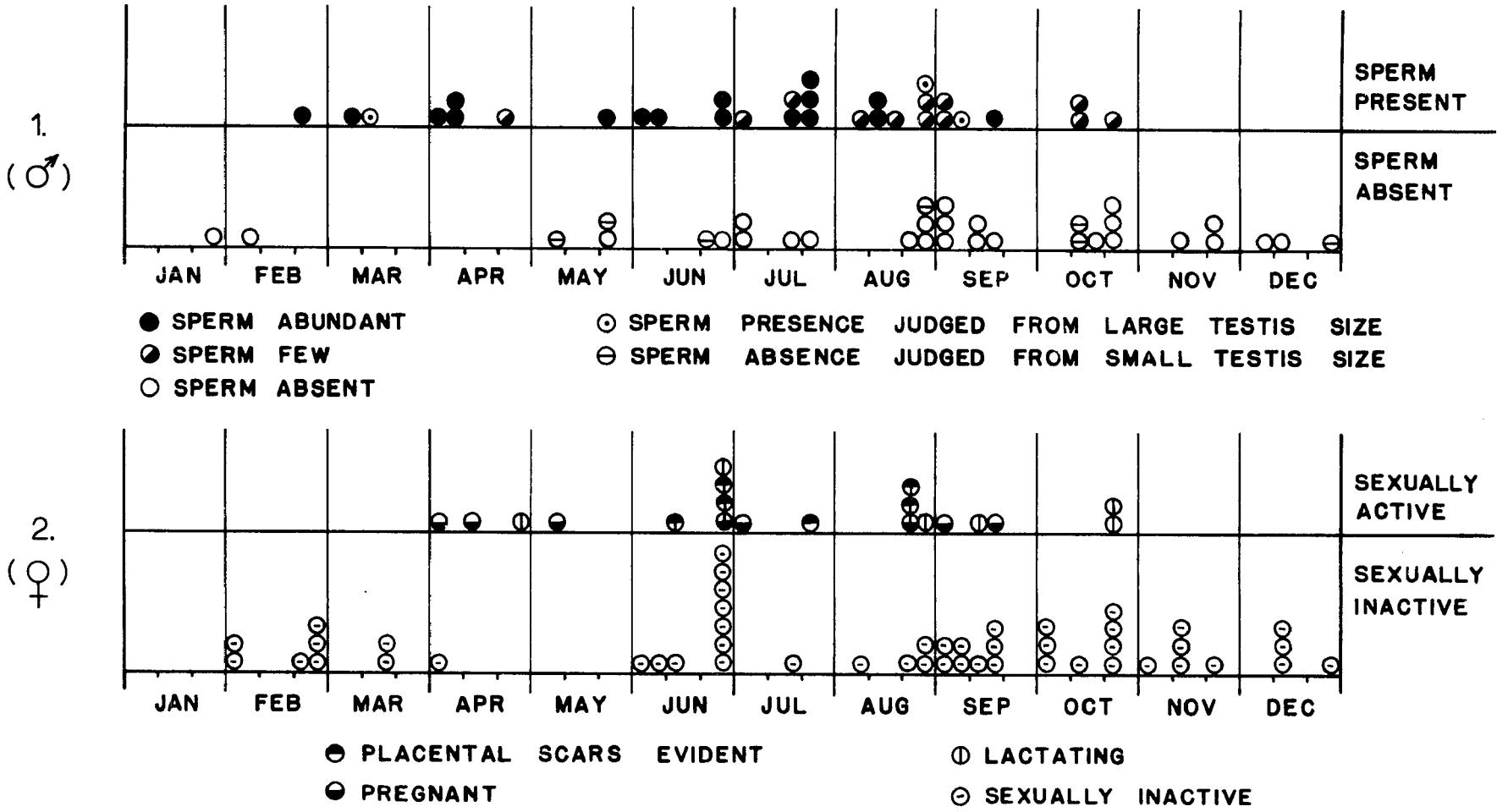
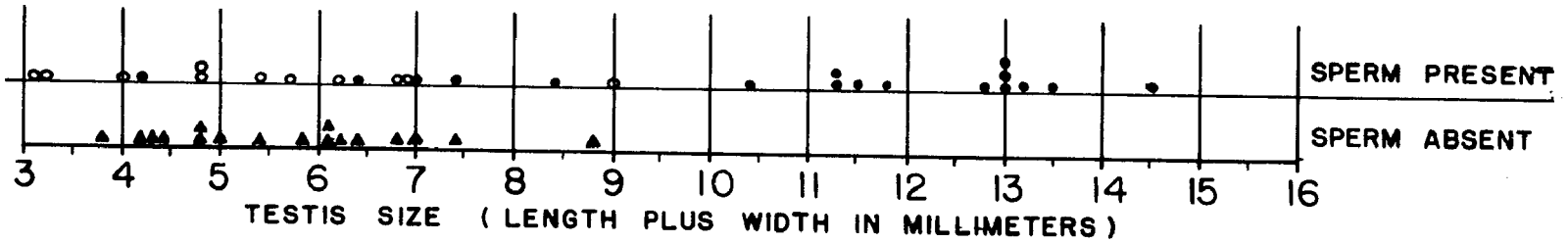
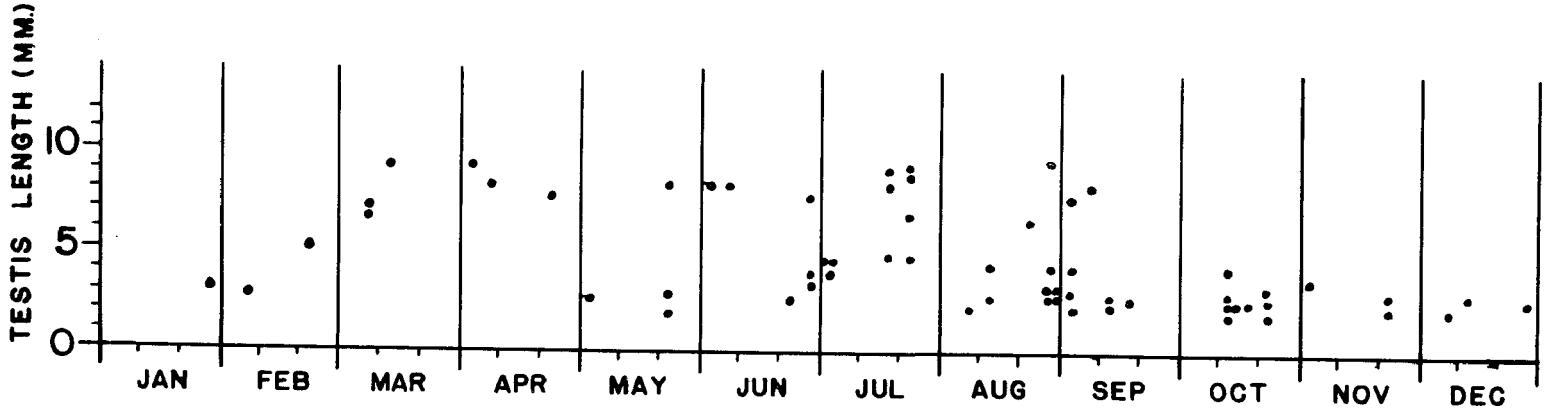


PLATE XXX. Sexual condition of male and female short-tailed shrews throughout the year. Figure 1 illustrates the occurrence of mature sperm in either or both testis and epididymis; figure 2 shows the sexual condition of female shrews. The data are grouped in five-day intervals.



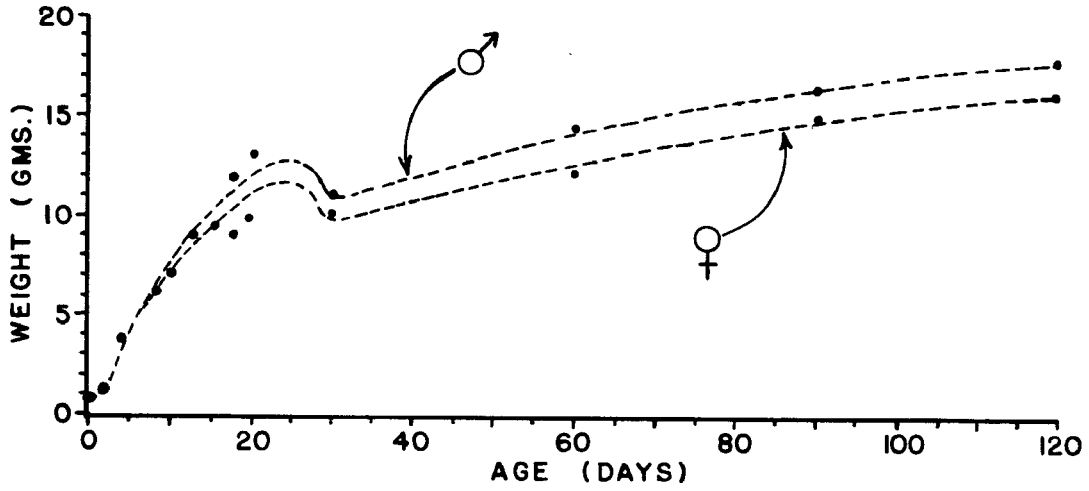
1.

o FEW SPERM
• MANY SPERM
▲ NO SPERM

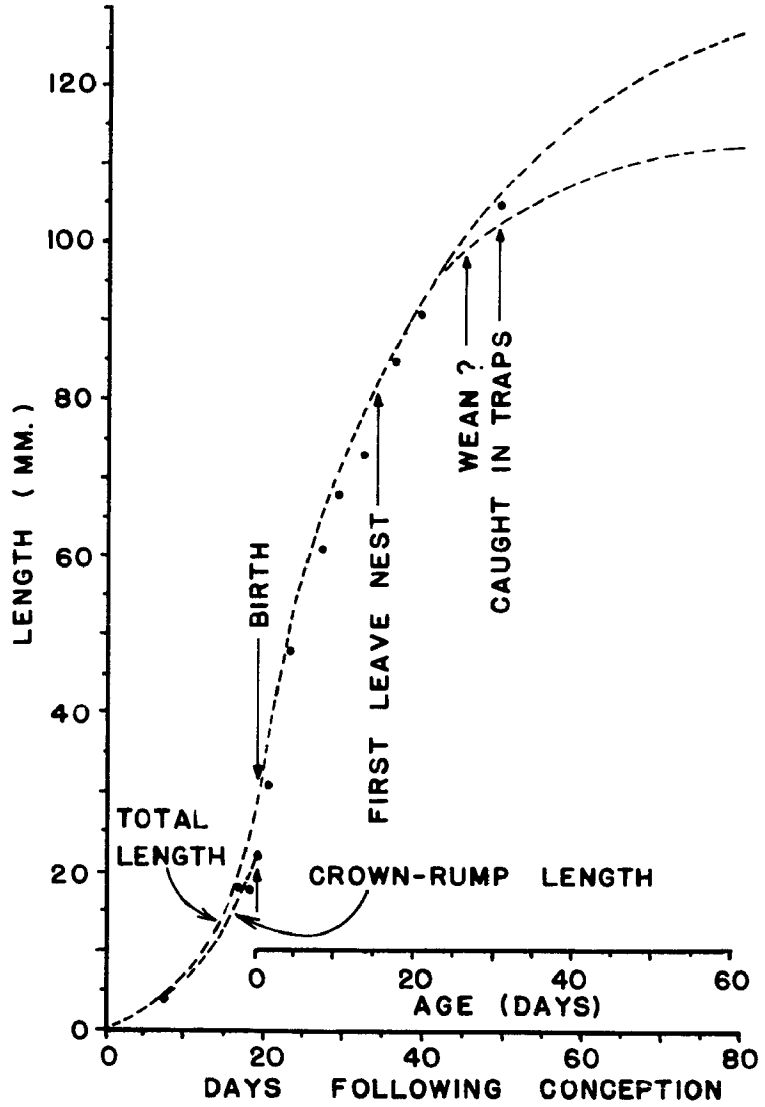


2.

PLATE XXXI. Testis sizes of wild male Blarina in relation to date and sperm presence. Figure 1 presents the relationship between occurrence of sperm and the sum of testis width and length. Figure 2 shows the distribution throughout the year of testis size.



1.



2.

PLATE XXXII. Growth curves of Blarina. Figure 1 illustrates the weight from birth to 120 days of age. Figure 2 demonstrates the length (prior to birth both total and crown-rump lengths are given) in relation to age. Drawn in part from data of Hamilton (1929) and Pearson (1944).

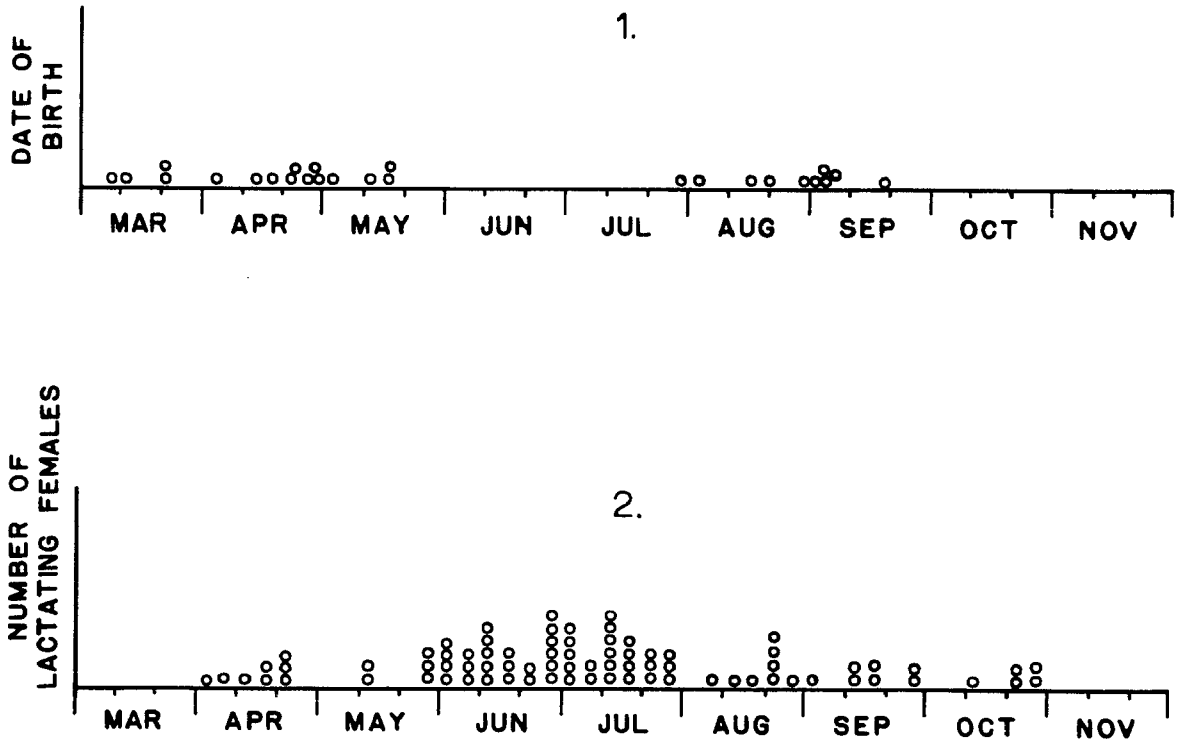
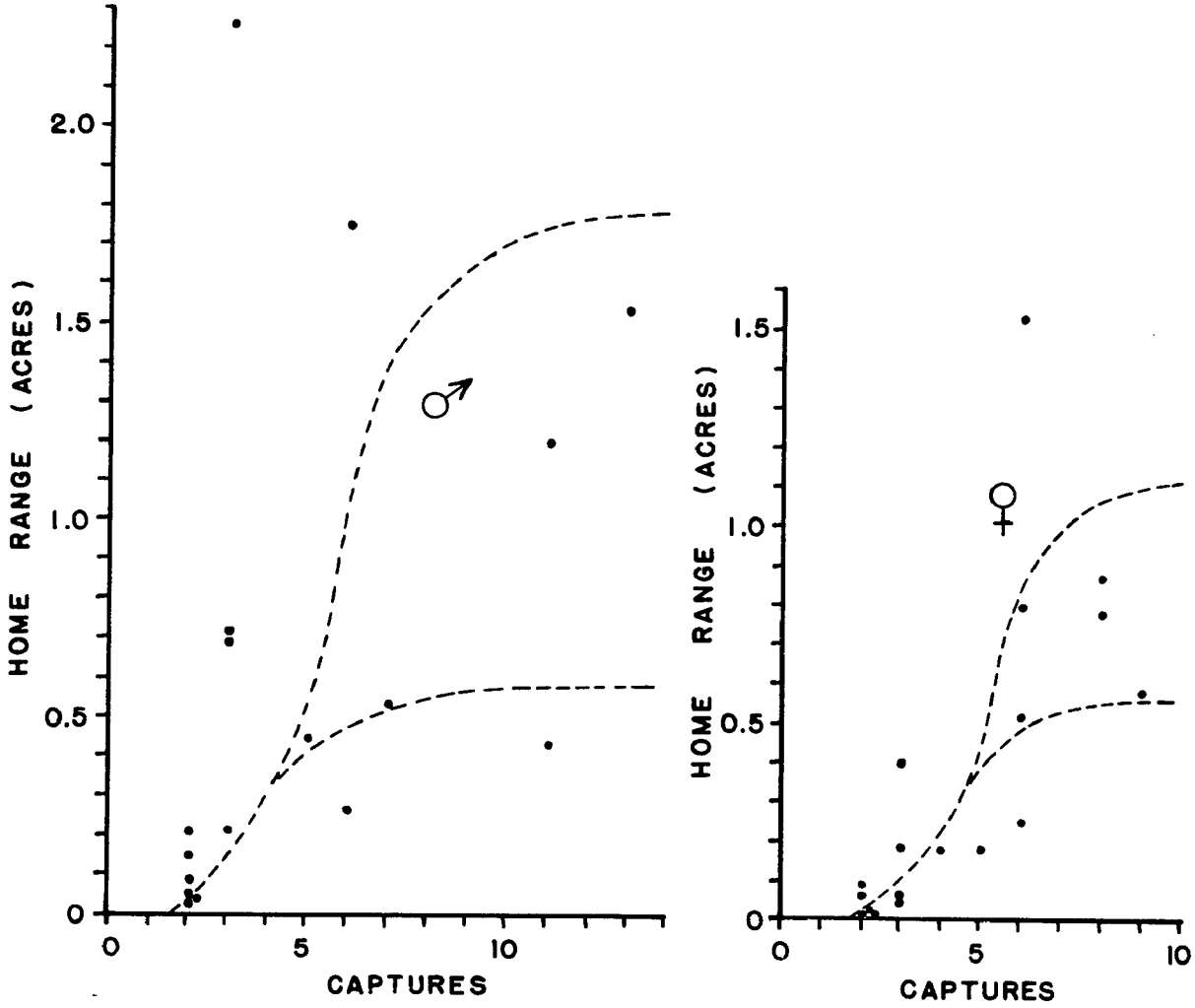


PLATE XXXIII. Birth dates and occurrence of lactation for Blarina. The birth dates (Figure 1) are calculated, as described in the text, from those of the present investigation augmented by those from numerous other publications. The occurrence of lactation (figure 2) is similarly drawn from many sources. Data were obtained from the following: Blair (1936), East (1951), Grimm and Roberts (1953), Hamilton (1932, 1949), Lindsay (1938), Manville (1949), Pearson (1944), Richmond and Nosland (1949), and Townsend (1935).



1. 2.

PLATE XXXIV. The calculated home ranges of Blarina in relation to the number of times each shrew was captured. The double lines represent the estimated range within which most home ranges will lie. These data are taken from Table 6, column 6.

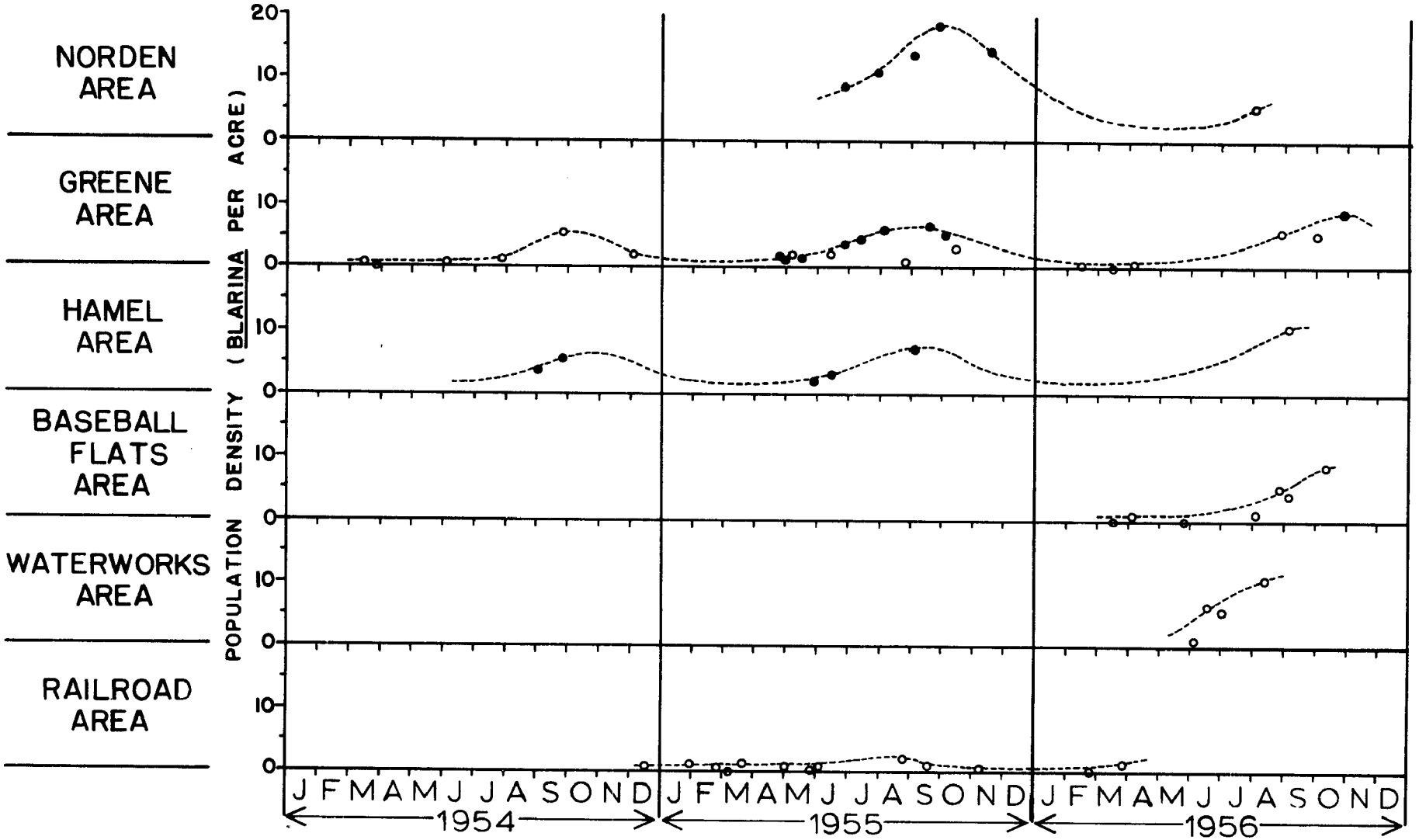


PLATE XXV. Estimated population density of the short-tailed shrew within selected plots in southern Michigan over a three-year period. The solid circles represent estimates based on live trap data, the open circles are based on snap trap data.

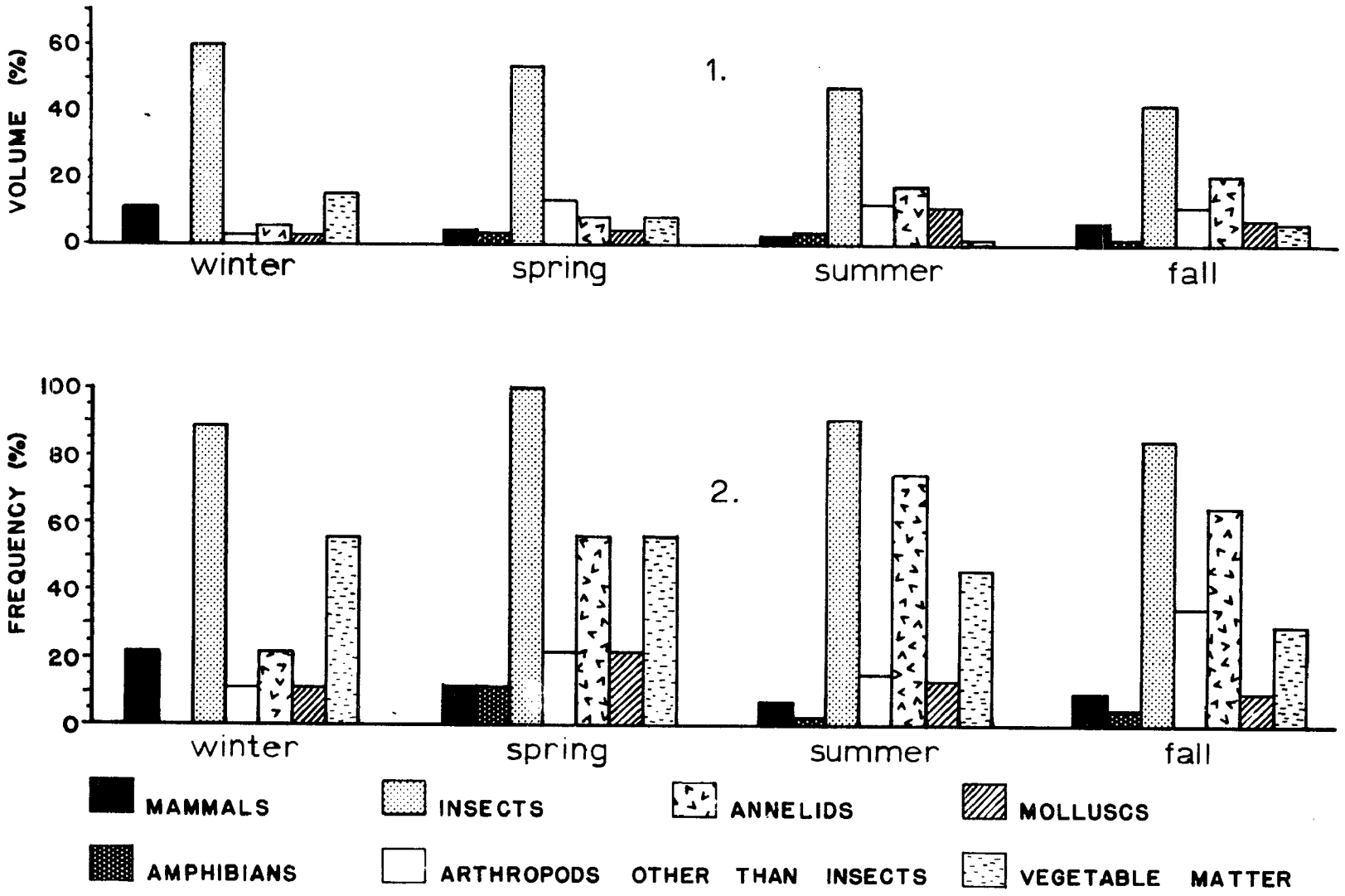


PLATE XXXVI. Seasonal percentage of volume of the identified foods (Figure 1) and frequency of occurrence (Figure 2) of the foods eaten by the short-tailed shrew in southern Michigan, based on the examination of 5 digestive tracts.

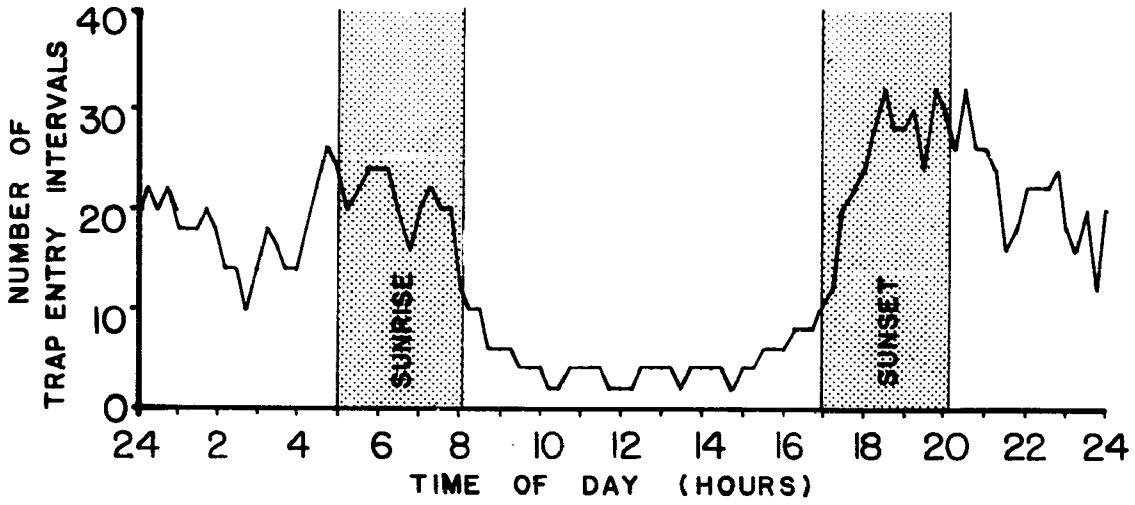


PLATE XXXVII. Composite daily probability of capturing Blarina, based on data collected throughout the year, in relation to the year-round ranges of sunrise and sunset. The number of trap entry intervals was determined by tabulating the occurrence, within each 15-minute period, of plotted lines representing the estimated hour within which each captured shrew probably entered its trap.

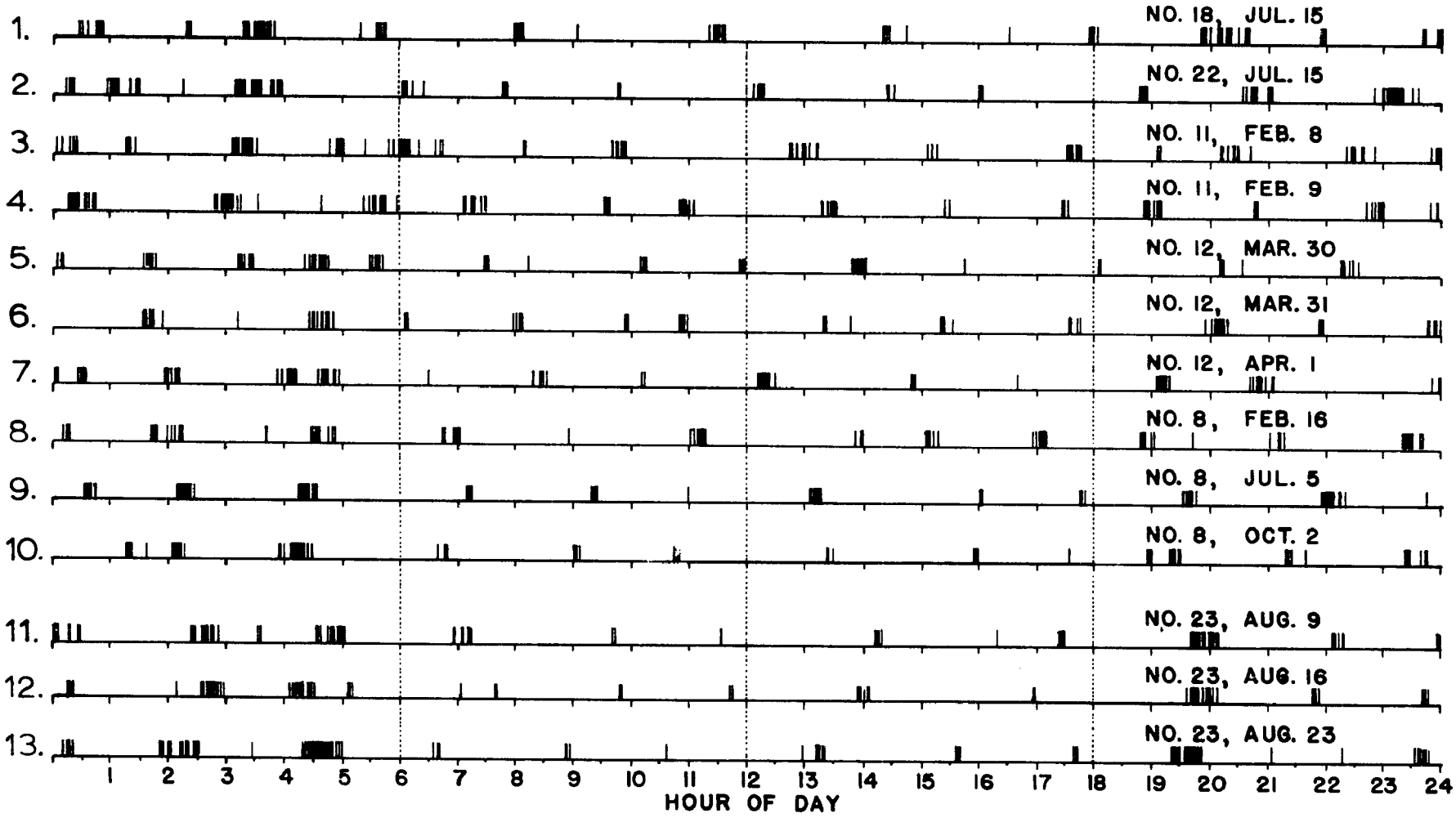


PLATE XXXVIII. Distribution of the activity of captive Blarina throughout representative 24-hour intervals. Figures 1-10 represent records on shrews which were exposed to indirect daylight; figures 11-13 were obtained from an individual which was shielded from all light over a two-week period.