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Mammalian Succession on Lake Michigan Sand Dunes

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MAMMALIAN SUCCESSION ON LAKE MICHIGAN SAND DUNES

by

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INTRODUCTION

The evident succession of communities on the sand dunes along Lake Michigan has prompted many persons to use this area for studying various aspects of succession. The sand dune communities are especially well suited for such studies because of the uniformity of many factors, such as initial substrate and climate. The progressively older dunes, due to the lowering of lake levels during glacial retreat (Olson 1958), should differ only because of "time, the biological processes of succession, and chance events associated with dispersal and colonization" (Krebs 1972: 421).

Cowles (1899) developed his ideas on plant succession while investigating the different vegetation types on the Lake Michigan sand dunes. Shelford (1913) studied the succession of animals, especially invertebrates. Bees (Pearson 1933), ants (Talbot 1934), orthopterans (Strohecker 1937), spiders (Lowrie 1948), and birds (Van Orman 1976) are other faunal groups which have been closely studied in the same communities. Vegetation (e.g. Fuller 1911, 1914 and Morrison and Yarranton 1973, 1974) and physical factors (e.g. Talbot 1934 and Strohecker 1937) have also been studied. Olson (1958) critically reexamined the successional trends on Lake Michigan sand dunes.

However, except for some general statements by Dice (1920, 1925) and Wood (1922), and a few notes by Shelford

(1913), there appear to be no studies of the mammalian components of the successional communities on the sand dunes. This study was initiated to investigate the populations of mammals with respect to current ideas of succession.

STUDY AREAS

Study areas were established within each of five vegetational stages on the sand dunes. Each study area was selected on the basis of consistency of vegetation type, adequacy of size, freedom from human disturbance, and proximity to other study areas.

Area 1. Pioneer dune grasses (Fig. 1). This area was covered by clumps of marram grass (Ammophila breviligulata), sand reed grass (Calamovilfa longifolia), and little bluestem (Andropogon scoparius). These grasses provided the only cover as bare sand existed between the clumps. The sand was loose with continual deposition occurring. Although this vegetation type was found on the foredunes, it also occurred on blowouts where wind erosion had created bare sand and the dune grasses had become established. Large blowouts tended to be freer from human disturbance and were therefore selected as study areas.

Area 2. Cottonwood (Fig. 2). Cottonwood trees (Populus deltoides) were the most obvious vegetation, but were scattered. Dune-building shrubs, primarily dune grape (Vitis riparia var. syrticola), sand dune willow (Salix syrticola), and sand cherry (Prunus pumila), grew extensively throughout the area. The dune grasses also persisted, although marram grass was not as abundant as in area 1. Numerous ponds fringed with dense grasses also existed in this study area.

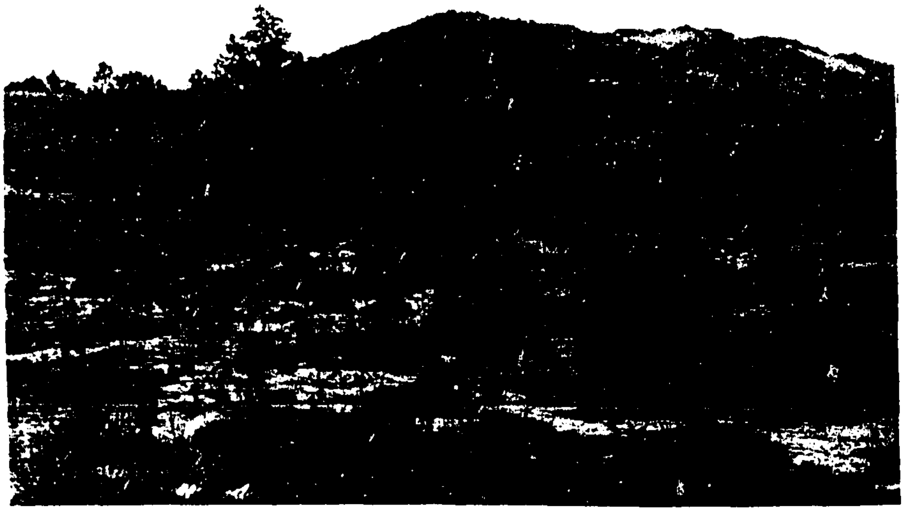

Fig. 1. Pioneer Dune Grass Area. Marram grass and sand reed grass are the grasses seen in this photograph. Cottonwood trees are seen in the left background outside this study area.

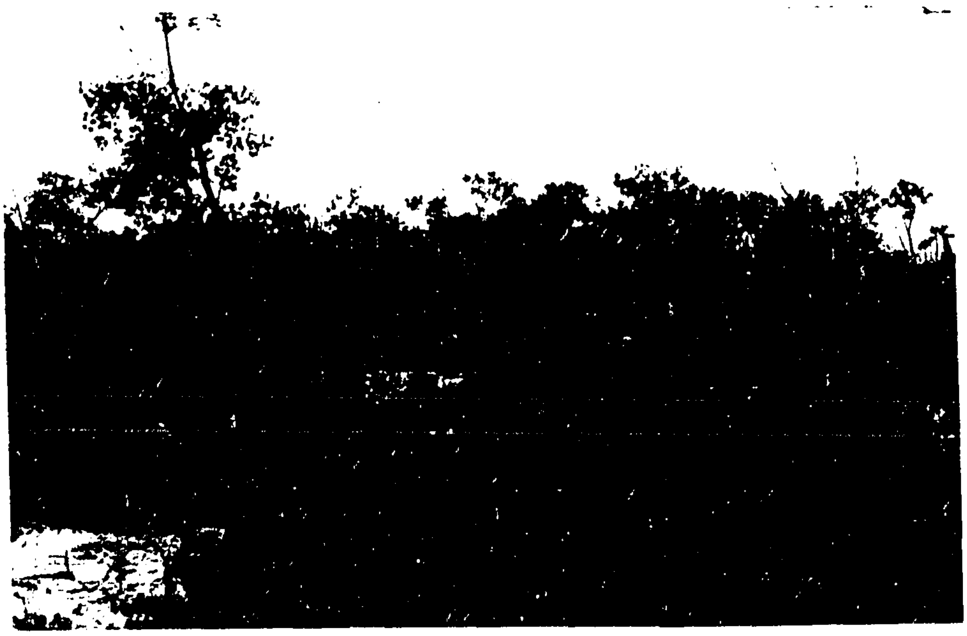

Fig. 2. Cottonwood Area. A cottonwood tree is evident in the left foreground. The shrubs in the foreground are primarily sand dune willow and sand cherry.

Area 3. Jack pine (Fig. 3 and 4). Jack pines (Pinus banksiana) and some red pines (Pinus resinosa) dominated this area which occurred in depressions behind the cottonwood dunes. The trees grew close enough together in places to impede travel. Portions of the area had standing water with many dead trees, apparently a recent condition due to the high level of water in the Great Lakes during the preceding years. There was little ground cover except in scattered openings which contained mostly the same vegetation as that found in the cottonwood area.

Area 4. Black oak (Fig. 5). Black oak (Quercus velutina) was the major canopy species in this area. The understory was comprised mostly of black oak, sassafras (Sassafras albidum), white pine (Pinus strobus), and red maple (Acer rubrum). The canopy trees were widely spaced with the open areas partially filled with the understory species and some grasses.

Area 5. Beech-maple (Fig. 6). Although sugar maple (Acer saccharum) and American beech (Fagus grandifolia) dominated in the canopy, black cherry (Prunus serotina) and red oak (Quercus rubra) were also evident as canopy species in this area. Beech, sugar maple, hemlock (Tsuga canadensis), and white pine comprised the understory. Ground cover varied from very dense to almost none throughout the area.

Plant succession on Lake Michigan sand dunes typically

Fig. 3. Jack Pine Area, from an opening within the area. The grasses in the foreground existed in the openings within this area. The dense growth and lack of ground cover in the actual forest can be seen in the background.

Fig. 4. Jack Pine Area. An overview of the jack pine area and one of the numerous ponds within the sand dune area are seen from one of the surrounding dunes.

Fig. 5. Black Oak Area. The unique topography of the sand dunes is still evident in this area. The large trees are black oaks. Several white pines in the understory are evident in the right foreground.

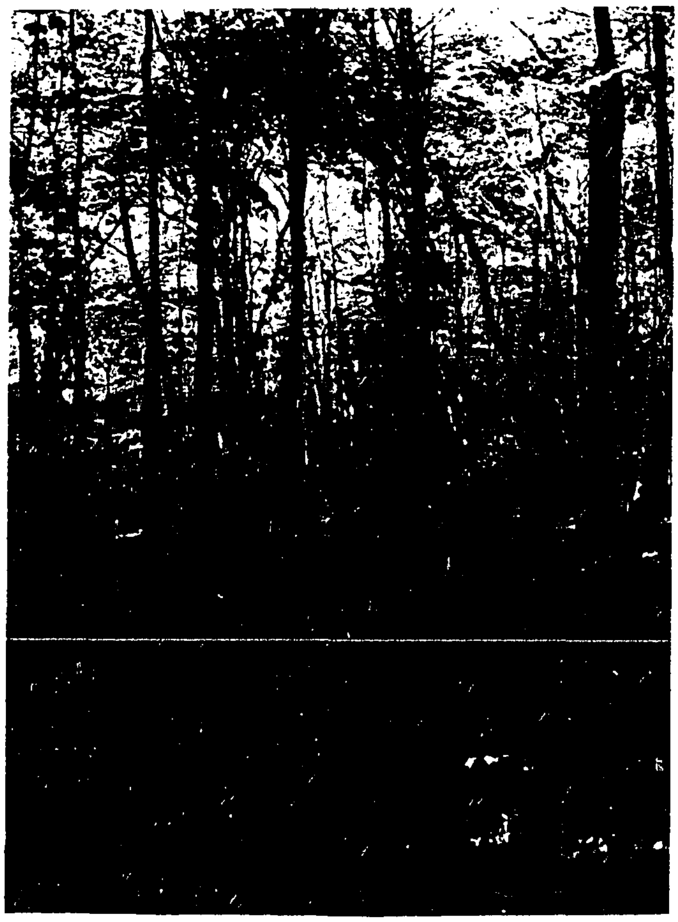

Fig. 6. Beech-maple Area. Although not many canopy trees are evident in this photograph, the limited sunlight reaching the forest floor is an indication that the canopy is dense. Most of the small trees are sugar maple and American beech.

begins with the pioneer dune grasses followed by cottonwood and various shrubs. Pines, mostly jack, white, and red, invade the cottonwood areas, then are replaced by black oak (Cowles 1899, Olson 1958). Olson found black oak remaining dominant on the oldest dunes which he dated at the southern end of Lake Michigan. He believed that succession to a beech-maple forest on southern Lake Michigan sand dunes probably occurs only in special sites (moist and protected slopes), and then not through the above sequence.

Olson (1958) and Van Orman (1976) note that black oak becomes increasingly rare as one proceeds north along the lake shore. Red oak communities appear to be more common on these northern dunes and, due to their more mesic nature (Curtis 1959), may proceed to a climax beech-maple forest more readily than would a black oak community. Beech-maple forests are a larger component of the sand dune ecosystem on the northern dunes than at the southern end of Lake Michigan. Thus the five sand dune communities selected as study areas probably represent a likely succession of communities on the northern sand dunes along Lake Michigan.

Areas 1 through 4 were located in Muskegon State Park, Muskegon County, Michigan (Sec. 28, R 17 W, T 10 N). Area 5 was located in the Hope College Dune Field Station just south of Holland, Michigan in Allegan County, Michigan (Sec. 9, R 16 W, T 4 N).

METHODS

Sampling Time

The five study areas were intermittently sampled for mammals from June to October 1975 (Table 1). All the study areas were sampled four times during this period, but only the last three samples from area 5 (beech-maple) are included because of changes in the sampling methods. The initial sampling in area 5 was considered a pilot study. The communities were sampled at this time of year because most populations of small mammals at this latitude begin breeding in the spring with a resultant increase in their populations throughout the summer and fall (Asdell 1964) even though reproduction may slow markedly during the summer (Blair 1940). Also, any mammals which hibernate would be susceptible to sampling in the summer. The intermittent sampling of all areas throughout the time period was used to detect possible population changes and also to determine whether the scarcity of a species during a trapping period was a result of a low population at that time or a result of an actual scarcity of the species in that habitat.

Study areas 1 through 4 were sampled concurrently during each trapping period (except during trapping period II and III when two areas were offset by one day). Area 5, the beech-maple forest, located some 40 miles south of the other

Table 1. Dates of mammal sampling on Lake Michigan sand dunes during summer and fall, 1975. Dates underlined indicate dates of transect counts.

Study Area		Sampling Periods			
Number	Name	I	II	III	IV
1	Pioneer dune grasses	June 7,8,9	July 9,10,11	August 14,15,16	October 5,6
2	Cottonwood	June 7,8,9	July 10,11,12	August 13,14,15	October 5,6
3	Jack pine	June 7,8,9	July 9,10,11	August 14,15,16	October 5,6
4	Black oak	June 7,8,9	July 10,11,12	August 13,14,15	October 5,6
5	Beech-maple	(May 30,31, June 1)	July 17,18,19	August 22,23,24	September 28,29

areas, was sampled within a week of the sampling in areas 1 through 4. The concurrent sampling was conducted to negate any differing influences of time, primarily weather conditions. Availability of food and population fluctuations were also considered when deciding to sample all areas within a short time span.

Small Mammal Sampling

All the study areas were sampled identically with a variety of methods designed to census different types of mammals. Small mammals were sampled with snap-traps and pit-traps. The snap-traps were "Victor" type mouse traps baited with a mixture of rolled oats and peanut butter. Stickel (1948) and Patric (1970) concluded that bait was necessary when they found that a significantly greater number of animals were caught by baited traps than by unbaited traps. Beer (1964) found the rolled oats and peanut butter mixture to be the most effective for capturing all animals.

The snap-traps were arranged in a North American Census of Small Mammals (NACSM) type A trap line (Calhoun 1963). Two parallel lines 30.5 m apart and 145 m long were located within each study area at least 46 m from any major vegetational change, except in the jack pine area. In this area occasional openings with the same vegetation as found in the cottonwood area were transected by jack pine trap lines. Each trap line consisted of 20 trapping stations with 7.5 m

between adjacent stations. Three snap-traps were placed at each trapping station within 1.5 m of the stake marking each station, resulting in a total of 120 traps set in each study area.

The trap lines were operated for three consecutive nights during each trapping period except during period IV which only had two nights of trapping. Trapping period III was preceded by 14 days of prebaiting (all traps placed and baited but not set). Bait was replaced every three to four days during this prebaiting period. Chitty and Kempson (1949) and Grodzinski, Pucek, and Ryszkowski (1966) suggested prebaiting traps as a means of equalizing the trappability of all individuals in a population.

The pit-traps consisted of two- and three-pound coffee cans measuring 16 cm deep x 12.5 cm wide and 16.5 cm deep x 15.5 cm wide respectively. These cans were placed in the ground with their open end flush with, or slightly beneath, the surface of the ground. They were filled approximately one-third with water to prevent captured animals from jumping out of the traps (MacLeod and Lethiecq 1963) or from destroying one another if multiple captures occurred. Pit-traps sample shrews of the genus Sorex more effectively than other traps as regards both species and numbers (Brown 1967).

Eight pit-traps equidistantly spaced were placed in a line 145 m long midway between the snap-trap lines in each

area. The pit-traps were in operation during the same time as the snap-traps, plus during the 14-day prebaiting period. Pit-traps were not used during the final trapping period in areas 1 through 4 because of time limitations.

Since the sand on the dunes provided a good base for observing tracks of animals, three areas, one square meter each, were marked and brushed clean in each study area. Considerable clearing of the litter in the jack pine, black oak, and beech-maple areas was required. A fine layer of sand was deposited on the clearings in these three study areas to provide a better base for recording tracks. This procedure was followed during each trapping period except the last when no tracking areas were established. Bider (1968) successfully used a sand transect for measuring animal activity in a terrestrial community, and various persons (Sheppe 1965, Justice 1961) have used tracking methods as an indicator of home range and habitat selection and utilization.

All traps and tracking areas were checked each morning of the trapping period. Captures were recorded according to species, trap location and number, and date, and marked for later examination. Traps were rebaited and reset as needed.

The locations of the traps and tracking areas were changed in each trapping period so that a different portion of each habitat was sampled each time with no sampling re-

peated in any given location. This permitted a wide sampling throughout the habitat. Also, any effects of removal trapping (e.g. possible substantial reduction in populations) did not have to be considered when changing the location of traps.

Standard measurements of length and weight of the captured animals were taken in the laboratory. Sex, age, and reproductive condition of each specimen were also determined. Individuals were assigned to an age group (adult or juvenile) on the basis of weight (insectivores) or pelage (rodents). Peromyscus could be determined to be either juvenile (gray pelage), subadults (gray-brown pelage), or adults (rufous-brown pelage) (Burt 1940, Blair 1940). Breeding condition in males was determined by enlarged testes and seminal vesicles (Jameson 1950), in females by lactation, pregnancy, placental scars, and/or corpora lutea (Rolan and Gier 1967).

Diurnal Mammal Sampling

Diurnal squirrels and chipmunks were censused by visual observations, with the aid of 7x35 binoculars, on 305 m transects in each study area. An adaptation of the sample count method by Bond (1957) was used. This consisted of alternate standing and walking periods, each five minutes in duration, during which all mammals observed or heard were noted. The species and its behavior were recorded. The observer began the transect with a standing period, then

proceeded with a slow walking period covering 61 m, followed by a standing period, etc. The entire transect was traversed in 50 minutes.

The width of the census area was 46 m in all habitats (23 m on either side of the observer). The total area censused was approximately 1.4 ha.

The location of the transect in each area was the same throughout the study. The transects were kept separate from the trap lines since the snap-traps might accidentally capture (and remove) some of the animals to be censused visually. The dates when each transect was sampled are shown in Table 1.

All observations and evidence of mammals on the sand dunes were noted. Communication with persons familiar with the animals of the areas produced further information on the fauna of the area.

Density

Density index

The snap-trap lines were designed to obtain indices of the density of small mammals in each study area. These indices were calculated as the number of mammals caught per 100 trap nights, taking into consideration the trap type(s) capable of catching a particular species. For example, if a species was caught only in snap-traps, then only the number of snap-trap nights would be considered when calculating the

density index. The mean number of observations of a particular species per transect served as the density index for the diurnal sciurids.

Estimated density

Actual density was estimated for both the small mammals and diurnal sciurids. The method for estimating the density of small mammals is an adaptation of that used by Golley, Gentry, Caldwell, and Davenport (1965). The area sampled by the trap line is calculated by the formulae

$$A = 2\ (2rL + \pi r^2) \qquad (1)$$

where L = length of trap line (145 m) and r = radius of home range for those species in which r is less than or equal to one-half the distance between the parallel trap lines (15 m) (Fig. 7) and

$$A = 2rL + LD + 2rD + \pi r^2 \qquad (2)$$

where D = distance between the trap lines (30.5 m) for those species in which r is greater than D (Fig. 8). Estimates of home ranges were obtained from the literature. Several assumptions must be made when using these formulae. Home range is assumed to be circular in shape and uniform in size between habitats. The assumption is also made that the three-day trapping periods capture all small mammals within the area estimated by the formulae.

The area censused for diurnal sciurids was the same (1.4 ha) for all species in each area, hence the estimated

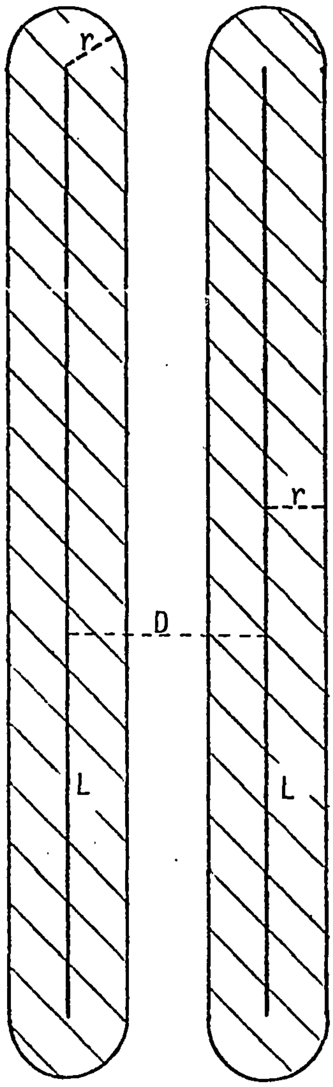

Fig. 7. Area sampled by parallel trap lines for species in which the home range radius (r) is less than or equal to one-half the distance between the trap lines (D).

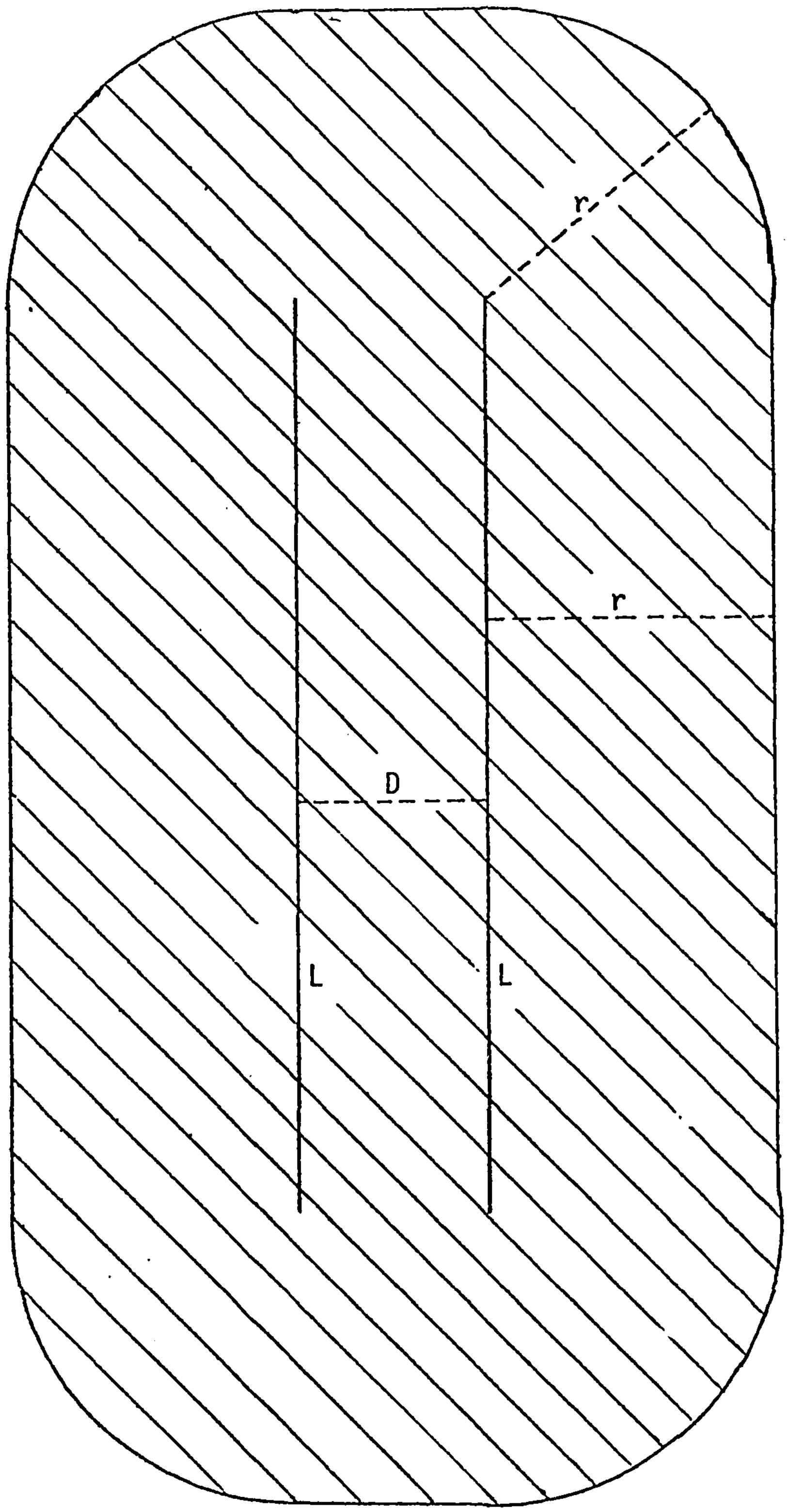

Fig. 8. Area sampled by parallel trap lines for species in which the home range radius (r) is greater than one-half the distance between the trap lines (D).

density was found by dividing the number of mammals observed by the size of the sampled area.

Diversity

The diversity of mammals in each vegetational area was determined by calculating the Shannon-Wiener diversity index H' (Shannon and Weaver 1949) according to the formula

$$H' = -\sum_{i=1}^{s} P_i \ (\log_e P_i)$$

where P_i is the proportion of the ith species in the total sample and s is the number of species.

Statistical procedures follow Steel and Torrie (1960). Chi-square tests were used to determine differences in habitat selection and sex ratios for small mammals. Student "t" tests were used to test differences in the mean number of observations on transect counts.

Names of plants follow Gleason (1952). Names of mammals follow Hall and Kelson (1959).

RESULTS

Quantitative data were obtained on 10 species of mammals from the sand dune communities censused. Trapping resulted in very few captures; only 27 small mammals were taken in 7152 trap-nights (0.38 per 100 trap-nights). The five species censused by trapping and the number captured were the insectivores *Sorex cinereus* (masked shrew), 5, and *Blarina brevicauda* (short-tailed shrew), 10; the cricetid rodents *Peromyscus maniculatus bairdii* (prairie deer mouse), 10, and *Peromyscus leucopus* (white-footed mouse), 1; and the zapodid rodent *Zapus hudsonius* (meadow jumping mouse), 1.

A total of 191 observations of five species of diurnal sciurids was made during 30 transect counts. The observed species and the number of observations were the sciurid rodents *Tamias striatus* (eastern chipmunk), 100, *Spermophilus tridecemlineatus* (13-lined ground squirrel), 36, *Sciurus carolinensis* (gray squirrel), 1, *Sciurus niger* (fox squirrel), 22, and *Tamiasciurus hudsonicus* (red squirrel), 31.

Small Mammals

Peromyscus maniculatus bairdii

The prairie deer mouse, *Peromyscus maniculatus bairdii*, was found in only two areas on the sand dunes, the pioneer

dune grass area and the cottonwood area. The number of prairie deer mice found in the two areas was not significantly different ($X^2 = 1.60$, $P > 0.05$).

The density index of the prairie deer mouse (number of individuals trapped per 100 trap-nights) was calculated using only snap-trap nights since all the prairie deer mice were captured in snap-traps. The density index for this species (Table 2) in the pioneer dune grass area was 0.23 and ranged from 0.00 to 0.42. The three mice found in this habitat were all taken during separate trapping periods and not until after at least one night of trapping. In the cottonwood area the density index was 0.53 and ranged from 0.00 to 1.25.

Blair (1940) calculated an average home range of 0.23 ha for 134 adult prairie deer mice in a blue-grass association in southern Michigan. Accordingly, a home range radius of 27 m was used in estimating the density (Golley et al. 1965). The average density (Table 3) in the pioneer dune grass area was 0.47 mice per hectare with a high of 0.62 per hectare (trapping periods I, II, and IV). The cottonwood area supported an average of 1.09 mice per hectare with a high of 1.85 per hectare (trapping periods I and IV).

Males comprised 70% of the captured mice but owing to the small sample (N= 10) this proportion is not significantly different from an expected 1:1 ratio ($X^2 = 1.60$, $P > 0.05$). The only non-adult mouse taken was a sub-adult male captured

Table 2. Species and density indices (numbers per 100 trap-nights) of small mammals on Lake Michigan sand dunes.

Species	Habitat				
	Pioneer dune grasses	Cottonwood	Jack pine	Black oak	Beech-maple
Peromyscus maniculatus bairdii (prairie deer mouse)	0.23	0.53	-	-	-
Zapus hudsonius (meadow jumping mouse)	-	0.08	-	-	-
Sorex cinereus (masked shrew)	-	-	-	0.13	0.26
Blarina brevicauda (short-tailed shrew)	-	-	-	0.07	0.79
Peromyscus leucopus (white-footed mouse)	-	-	-	-	0.10
Total	0.23	0.61	-	0.20	1.15

Table 3. Species and estimated densities (numbers per hectare) of small mammals on Lake Michigan sand dunes.

Species	Habitat				
	Pioneer dune grasses	Cottonwood	Jack pine	Black oak	Beech-maple
Peromyscus maniculatus bairdii (prairie deer mouse)	0.47	1.09	-	-	-
Zapus hudsonius (meadow jumping mouse)	-	0.12	-	-	-
Sorex cinereus (masked shrew)	-	-	-	0.20	0.40
Blarina brevicauda (short-tailed shrew)	-	-	-	0.12	1.46
Peromyscus leuccpus (white-footed mouse)	-	-	-	-	0.30
Total	0.47	1.21	-	0.32	2.16

in the pioneer dune grass area in October. The average weight of six adult males was 17.5 ± 0.58 gm; the average weight of three adult females was 22.2 ± 1.1 gm. Mice in breeding condition were taken in June (75%), August (100%), and October (100%). No mice were taken in July; consequently, no record of breeding condition could be obtained. One prairie deer mouse, an adult male taken during August, was infected (inguinal region) with a botfly (Cuterebra sp.) larva.

Zapus hudsonius

One meadow jumping mouse was captured. This animal was taken in the cottonwood area in August following the 14-day prebaiting period. The density index (Table 2) was 0.08 mice per 100 snap-trap nights. An average home range for 50 adult Zapus in a blue-grass association in southern Michigan was calculated as 0.36 ha (Blair 1940a). The density of this species was estimated using a home range radius (Golley et al. 1965) of 34 m. The cottonwood area supported 0.49 Zapus per hectare during August and 0.12 per hectare for the entire cottonwood area sampled (Table 3). The individual captured was a reproductively active female weighing 16.6 gm.

Sorex cinereus

Two areas, the black oak forest in October and the

beech-maple forest in August, supported masked shrews. This species was caught in both snap-traps (three individuals) and pit-traps (two individuals). For this reason the density index was calculated using trap-nights from both types of traps. The density index (Table 2) in the oak forest was 0.83 *Sorex* per 100 trap-nights during October and 0.13 per 100 trap-nights overall. The density index in the beech-maple forest was 0.60 *Sorex* per 100 trap-nights during August and 0.26 overall.

Buckner (1966) calculated an average home range for 48 *Sorex cinereus* as 0.55 ± .04 ha, hence a home range radius of 42 m was used in estimating the density of this species (Golley *et al*. 1965). The oak area supported 0.81 *Sorex* per hectare in October and 0.20 per hectare overall; the beech-maple area supported 1.21 *Sorex* per hectare in August and 0.40 per hectare overall (Table 3).

Blarina brevicauda

The short-tailed shrew comprised 37% of all captures of small mammals. Ten individuals were taken -- nine in the beech-maple forest and one in the black oak forest. All *Blarina* were taken during the August trapping period. The number of short-tailed shrews found in the beech-maple area was significantly greater than both the black oak area ($X^2 = 6.40$, $P < 0.05$) and all other areas ($X^2 = 9.00$, $P < 0.01$).

Because this species was captured in both trap types,

its density index was calculated combining trap-nights from both. The density index in the oak forest for the short-tailed shrew was 0.20 per 100 trap-nights during the August trapping period and 0.07 per 100 trap-nights during the entire study. The density index in the beech-maple forest was 1.81 per 100 trap-nights during the August trapping period and 0.79 per 100 trap-nights during the entire study (Table 2).

Buckner (1966) calculated an average home range for 34 short-tailed shrews as 0.39 ± .04 ha, hence a home range radius of 35m was used in estimating density. The density in the black oak area during August was 0.49 per hectare and during the entire trapping period was 0.12 per hectare. The density in the beech-maple area in August was 4.34 per hectare and during the entire trapping period was 1.46 per hectare (Table 3).

Males and females were captured in equal numbers. All the short-tailed shrews captured were adults. The average weight of five adult males was 15.7 ± 0.8 gm; the average weight of four females (one specimen not suitable for analysis) was 14.8 ± 1.2 gm. Five of the nine animals examined (56%) were in breeding condition.

Peromyscus leucopus

One white-footed mouse was trapped in the beech-maple forest during trapping period IV. The density index was

0.10 per 100 trap-nights (Table 2). Burt (1940) calculated a home range of 0.10 ha for adult white-footed mice in oak-hickory woods in southern Michigan. Hence a home range radius of 23.5 m was used to estimate the density (Golley *et al*. 1965). The beech-maple forest supported 0.86 *Peromyscus* per hectare in October and 0.30 per hectare for the entire census periods (Table 3). The captured individual was an adult male weighing 23.9 gm and in breeding condition. Three botfly larvae were located in the inguinal region of this single animal.

Diurnal Sciurids

Spermophilus tridecemlineatus

A total of 36 observations of the 13-lined ground squirrel, *Spermophilus tridecemlineatus*, was made during the four census periods. The mean number of sightings per transect was 0.17 $\pm$ 0.17 (one observation) in the pioneer dune grass area, 5.50 $\pm$ 2.88 (33 observations) in the cottonwood area, and 0.33 $\pm$ 0.21 (two observations) in the jack pine area (Table 4). No ground squirrels were detected in either the black oak area or the beech-maple area. The mean number of ground squirrels observed in the cottonwood area is significantly greater than the mean number of observations in any other area ($t > 4.0$, $P < 0.005$ with 10 df). It should be noted that all the ground squirrels seen in the jack pine

Table 4. Species and density indices (number of observations per transect) of diurnal sciurids on Lake Michigan sand dunes.

Species	Habitat				
	Pioneer dune grasses	Cottonwood	Jack pine	Black oak	Beech-maple
Spermophilus tridecemlineatus (13-lined ground squirrel)	0.17	5.50	0.33	-	-
Tamias striatus (eastern chipmunk)	-	-	4.67	5.67	6.33
Tamiasciurus hudsonicus (red squirrel)	-	-	3.50	-	1.67
Sciurus niger (fox squirrel)	-	-	-	2.17	1.50
Sciurus carolinensis (gray squirrel)	-	-	-	-	0.33
Total	0.17	5.50	8.50	7.84	9.83

area were observed in openings with vegetation similar to the cottonwood area.

A substantial increase in ground squirrels in the cottonwood area was noted during the August census. The mean number of observations per transect in August (period 3) of 8.0 $\pm$ 1.0 was significantly greater than the mean in July (period 2) of 3.5 $\pm$ 0.5 ($t = 4.02$, $P < 0.05$ with 2 df). Each of these census periods had two transect counts, hence were considered more reliable to compare than those census periods with only one transect count (periods 1 and 4).

The average population (Table 5) was 0.1 *Spermophilus* per hectare in the pioneer dune grass area, 4.0 per hectare in the cottonwood area, and 0.2 per hectare in the jack pine area. The population in the cottonwood area increased from approximately 2.2 per hectare in June and July to 5.9 per hectare in August and October.

Most ground squirrels remained visible during the transect counts and did not enter a burrow unless the observer approached them. Only adults and possibly subadults were observed during transect counts even during periods when juveniles were known to be out of the nest because they were being taken in traps.

Twenty-one *Spermophilus* were captured by snap-traps. These captures were considered incidental since the mouse-sized snap-traps were not designed to capture animals of

Table 5. Species and estimated densities (numbers per hectare) of diurnal sciurids on Lake Michigan sand dunes.

	Habitat				
Species	Pioneer dune grasses	Cottonwood	Jack pine	Black oak	Beech-maple
Spermophilus tridecemlineatus (13-lined ground squirrel)	0.1	4.0	0.2	-	-
Tamias striatus (eastern chipmunk)	-	-	3.4	4.2	4.7
Tamiasciurus hudsonicus (red squirrel)	-	-	2.5	-	1.2
Sciurus niger (fox squirrel)	-	-	-	1.5	1.0
Sciurus carolinensis (gray squirrel)	-	-	-	-	0.2
Total	0.1	4.0	6.1	5.7	7.1

this size (average adult weight of 125.5 gm). These specimens did, however, provide some pertinent information. Four of the five individuals trapped in either the pioneer dune grass or jack pine areas were subadults and were captured during the last two trapping periods. Two partial "family groups" were captured in the cottonwood area during 10-12 July 1975. One lactating female and five young were trapped within 23 m of one another; another lactating female and three young were taken within 38 m of one another.

Tamias striatus

The eastern chipmunk was observed more often than any other mammal. A total of 100 observations was made in three study areas. This species occurred in substantial numbers in each of the areas (jack pine, black oak, and beech-maple areas) in which it was found. The mean number of sightings per transect was 4.67 ± 0.56 (28 observations) in the jack pine area, 5.67 ± 0.56 (34 observations) in the black oak area, and 6.33 ± 0.49 (38 observations) in the beech-maple area (Table 4). The only areas with significantly different means were the jack pine area and the beech-maple area ($t = 2.24$, $P < 0.05$ with 10 df).

An increase in the number of chipmunks per transect was recorded in all three of the habitats from June to October. However, none of these increases was statistically significant.

The estimated density (Table 5) was 3.4 _Tamias_ per hectare in the jack pine area, 4.2 per hectare in the black oak area, and 4.7 per hectare in the beech-maple area.

The eastern chipmunk was the easiest mammal to census. Most chipmunks (83%) were vocal, revealing their presence to the observer readily. Few chipmunks (13%) entered and remained in their burrows during the time that the burrows were visible during the transect count.

Seven _Tamias_ were captured by snap-traps. As with the ground squirrels, these captures were considered incidental since the snap-traps are not designed to capture animals of this size (average adult weight of 85.4 gm). The trapped animals did not show the same relative abundance as the animals counted on the transects. Five of the seven animals were trapped in the jack pine area; two animals were trapped in the black oak area; no animals were trapped in the beech-maple area. The six adults were males and were all in breeding condition between June and August. The only non-adult was a subadult female weighing 41.7 gm taken on 6 October.

Tamiasciurus hudsonicus

The red squirrel was observed 31 times in two habitats, the jack pine area and the beech-maple area. The mean number of sightings per transect was 3.50 $\pm$ 0.43 (21 observations) in the jack pine area and 1.67 $\pm$ 0.42 (10

observations) in the beech-maple area (Table 4). The mean number of red squirrels observed in the jack pine area is significantly greater than the mean number of red squirrels observed in the beech-maple area ($t = 3.05$, $P < 0.01$ with 10 df). The approximate density of this species on the sand dunes is 2.5 per hectare in the jack pine area and 1.2 per hectare in the beech-maple area (Table 5).

Sciurus niger

Twenty-two observations of the fox squirrel were made in two of the study areas, the black oak area (2.17 ± 0.31 observations per transect) and the beech-maple area (1.50 ± 0.22 observations per transect) (Table 4). The means are not significantly different. The estimated density is 1.5 fox squirrels per hectare in the black oak area and 1.0 per hectare in the beech-maple area (Table 5).

Sciurus carolinensis

The gray squirrel was observed twice in one habitat, the beech-maple area. The mean number of sightings per transect was 0.33 ± 0.21 (Table 4) and the estimated density was 0.2 gray squirrels per hectare in the beech-maple forest (Table 5).

Observations and Signs of Large Mammals

No animal tracks were observed in the three sand areas

marked and cleared for sampling in each study area. However, signs and observations of mammals throughout the seral stages did reveal extensive use of the sand dune communities by eight species of large mammals (Table 6). Eastern cottontails (Sylvilagus floridanus) were probably the most common of these large mammals. Rabbits were usually found feeding in the cottonwood area and taking refuge in the jack pine area. Signs of red fox (Vulpes vulpes) were common throughout the entire sand dune area. Dens of this mammal were located in a pioneer dune grass area and in the black oak area. Whitetail deer (Odocoileus virginianus) used the jack pine area extensively, but were also found throughout most of the sand dune ecosystem. The remaining species were less common but did occur regularly.

Species Diversity

The Shannon-Wiener diversity index H' of small mammals in the seral stages on the sand dunes was calculated using the overall density index (captures per 100 trap-nights) for each species. The overall density index was used because it takes into account both the trap types which can capture each species and the entire successional community sampled throughout the year. The sand dune communities show a general increase in the diversity of small mammals as succession occurs (Table 7). The pioneer dune grass area supports only one species of small mammal, hence H'= 0.

Table 6. Signs and/or observations of large mammals in the successional stages on Lake Michigan sand dunes. (presence denoted by x).

Species	Habitat					
	Beach	Pioneer dune grasses	Cottonwood	Jack pine	Black oak	Beech-maple
Vulpes vulpes (red fox)	x	x	x	x	x	-
Mephitis mephitis (striped skunk)	x	-	x	x	-	-
Procyon lotor (raccoon)	x	-	-	-	x	-
Odocoileus virginianus (whitetail deer)	-	x	x	x	x	x
Marmota monax (woodchuck)	-	x	x	-	-	x
Sylvilagus floridanus (eastern cottontail)	-	-	x	x	-	-
Didelphis marsupialis (opossum)	-	-	x	x	-	x
Ondatra zibethica (muskrat)	-	-	x (ponds)	-	-	-

Table 7. Species diversity index H' of mammals in the successional stages on Lake Michigan sand dunes. Diversity indices for small mammals (column 2) and for diurnal sciurids (column 3) are calculated using the density indices for each species in each habitat. Diversity indices for all mammals sampled (column 4) are calculated using estimated densities.

	Species Diversity Index H'		
Habitat	Small Mammals	Diurnal Sciurids	All Mammals
Pioneer Dune Grasses	0.00	0.00	0.52
Cottonwood	0.39	0.00	0.61
Jack Pine	-	0.82	0.82
Black Oak	0.65	0.59	0.79
Beech-maple	0.82	0.98	1.49

The diversity index of the jack pine area is also 0, but this is due to the fact that no small mammals at all were taken in this area. Although the cottonwood area supports more animals than the oak area, the diversity index of the cottonwood area (H'= 0.39) is less than that of the oak area (H'= 0.65). The beech-maple area has the highest small mammal diversity index (H'= 0.82) of the sand dune communities.

The total number of observations of each species in each study area was used to calculate the diversity index of the diurnal sciurids in the sand dune communities. As with the small mammals, the diversity index of the diurnal sciurids increases as succession occurs (Table 7). The 13-lined ground squirrel is the only diurnal sciurid which inhabits the first two successional areas, and therefore H'= 0 in both these areas. The jack pine area has the second highest diversity index (H'= 0.82) as regards diurnal sciurids, the opposite situation from the diversity index of the small mammals. Again, the beech-maple area has the highest species diversity index (H'= 0.98).

The only way to combine both the small mammals and the diurnal sciurids in each seral stage is to use the estimated densities of each species in each area. The seral stages show an overall increase in mammalian diversity as succession occurs (Table 7). The only exception to this trend is the black oak area where the diversity index (H'=

0.79) is slightly less than the diversity index of the jack pine area (H'= 0.82). The diversity index of the beech-maple area (H'= 1.49) is much greater than the diversity index of any other area.

Prebaiting

The three-day trapping period following the 14-day prebaiting period (trapping period III) produced some noteworthy results. First, two species were taken only during this trapping period. Second, only during this period were any mammals taken in pit-traps. Third, the number of mammals taken in the beech-maple area was significantly greater during trapping period III than during any other time.

Blarina brevicauda and *Zapus hudsonius* were taken only during trapping period III. *Blarina* was one of the two most abundant small mammals in this study. The 10 individuals of this species represented 37% of the total number of small mammals captured, yet all the short-tailed shrews were captured during only the one trapping period.

The pit-traps, after being in place for 10 days in the black oak area, captured one short-tailed shrew and, after being in place for 16 days in the beech-maple area, captured two masked shrews. The short-tailed shrew captured in the pit-trap was the only one captured in an area other than the beech-maple area. At the time the short-tailed shrew was captured in the black oak area, no shrews were captured

in snap-traps. However, when short-tailed shrews were taken in the beech-maple area, they were all taken in snap-traps. The capture rate (number of captures per unit effort, in this case one unit effort being 100 trap-nights) of the pit-traps in the black oak area during August was 0.38 for Blarina while the capture rate for Blarina of the snap-traps was 0.0 at the same place and time. The capture rate of the pit-traps in the beech-maple area during August was 0.0 for Blarina while the capture rate of the snap-traps was 1.25.

The two masked shrews caught in the pit-traps represented 40% of the total captures of this species: the remaining numbers were caught in snap-traps, one in the beech-maple area following prebaiting and two in the oak area with no prebaiting. The capture rate of the masked shrews was higher with pit-traps than with snap-traps in the one situation where masked shrews were caught and both types of traps were present. During trapping period III in the beech-maple area, the pit-traps had a capture rate of 1.47 while the snap-traps had a capture rate of 0.28. No pit-traps were used in the final sampling period (October) in the oak area when two masked shrews were taken in snap-traps, hence no comparison can be made for that trapping period.

The nine Blarina and three Sorex taken in the beech-maple area following the prebaiting period represent 92%

of the total number of small mammals captured in this area. One white-footed mouse was the only small mammal taken during any other trapping period. The number of shrews taken after prebaiting is significantly greater than the total number of small mammals captured in the beech-maple area during trapping periods without prebaiting ($X^2 = 9.30$, $P < 0.01$).

An overall comparison of the different types of trapping in all five habitats on the sand dunes is shown in Table 8.

Table 8. Numbers (per 100 trap-nights) of small mammals snap-trapped on Lake Michigan sand dunes during different type trapping periods.

Type of trapping period	Habitat				
	Pioneer dune grasses	Cottonwood	Jack pine	Black oak	Beech-maple
No prebaiting	0.21	0.63	-	0.21	0.17
Extensive prebaiting (14 days)	0.28	0.56	-	-	2.78

DISCUSSION

This study of mammals in the seral stages on Lake Michigan sand dunes shows a distinct succession of mammals (Table 9). The types of mammals change through time (time as evidenced by vegetation types) and species diversity increases.

Relationship to Successional Studies

This mammalian succession complements previous faunal studies on the sand dunes. Shelford (1913) described the pattern of change of invertebrates in the habitat gradient from open beach to climax forest. Each seral stage had a more or less characteristic invertebrate community and the sere had an overall increase in species numbers. Strohecker (1937) found an ecological succession of Orthoptera which corresponded in general to the vegetational succession. Strohecker found two major assemblages of orthopterans on the sand dune sere. The first assemblage corresponded to the foredune, poplar, and pine communities and the second assemblage corresponded to the black oak and climax communities. Talbot (1934) discovered a similar relationship between ants and the sand dune communities. She found that the number of species of ants increased correspondingly with the plant succession on the Lake Michigan sand dunes. The ant species were also grouped into two major assemblages:

Table 9. Successional stages on Lake Michigan sand dunes and the mammals found in each seral stage. Numbers in parentheses are individuals per hectare.

Habitat				
Pioneer dune grasses	Cottonwood	Jack pine	Black oak	Beech-maple
Prairie deer mouse (0.47)	13-lined ground squirrel (4.0)	Eastern chipmunk (3.4)	Eastern chipmunk (4.2)	Eastern chipmunk (4.7)
13-lined ground squirrel (0.1)	Prairie deer mouse (1.09)	Red squirrel (2.5)	Fox squirrel (1.5)	Short-tailed shrew (1.46)
	Meadow jumping mouse (0.12)	13-lined ground squirrel (0.2)	Masked shrew (0.20)	Red squirrel (1.2)
			Short-tailed shrew (0.12)	Fox squirrel (1.0)
				Masked shrew (0.40)
				White-footed mouse (0.30)
				Gray squirrel (0.2)

those that tolerate and are most abundant in sandy areas where vegetation is scattered and those that are limited by sand and require humus. Lowrie (1948) found "an ecological succession of spiders which corresponds to the plant succession with very few exceptions" (1948: 334). Beetles exhibit an overall increase in species numbers from the cottonwood stage to the forest stages (Park 1930). The number of species of bees in each plant stage increases to the black oak forest and then declines in the beech-maple forest (Pearson 1933). Van Orman (1976) found that both the number of species of birds and the total number of individuals within each plant community increases from the pioneer to the climax stages. As in previous studies, there appear to be two major assemblages of birds on the sand dunes. One assemblage consists of the birds which inhabit the marram grass-cottonwood and jack pine areas. The second major assemblage consists of the birds inhabiting the black oak and beech-maple forests. As stated previously, the results of this study of mammals basically agree with the results of the other faunal studies conducted on the sand dunes: the succession of fauna corresponds with the succession of flora found on the dunes.

Most of the faunal groups discussed above demonstrated the greatest turnover of species between the jack pine and black oak areas. For the invertebrates studied this change is most likely due to the development of a forest canopy

and humus (Kendeigh 1961). Van Orman (1976) attributed the significant turnover of species between the jack pine and black oak areas to the change from a heterogeneous habitat of pines and open areas to a more homogeneous deciduous habitat.

Mammals do not exhibit such a distinctive turnover between these seral stages. Instead, the greatest turnover seems to be between the cottonwood area and the jack pine area. One group of mammals inhabited the pioneer dune grass and cottonwood areas (prairie deer mouse, meadow jumping mouse, 13-lined ground squirrel) and another group inhabited the forest areas (short-tailed shrew, masked shrew, white-footed mouse, eastern chipmunk, red squirrel, fox squirrel, gray squirrel). The 13-lined ground squirrel is the only mammal found in both sets of areas, but it is only found occasionally in the jack pine area and not at all in the other forest areas. The conifers provide suitable habitat for two new species, the eastern chipmunk and the red squirrel. The red squirrel is a characteristic coniferous species and disappears as the pines are replaced by black oaks, but it is found again in the beech-maple (and hemlock) stage. The eastern chipmunk is found in all the forested areas beginning with the jack pine. The forest structure first seen in the jack pine stage appears to be a more significant factor for mammalian species than for the other faunal groups.

The location of the jack pine area studied (surrounded

by pioneer dune grass and cottonwood areas) taken with the virtual absence of the open country mammals further suggests that the jack pines do not provide acceptable habitat for the mammals found in the earlier stages. The absence of other forest species may be because the isolation of this specific jack pine area from other black oak and beech-maple areas does not allow immigration from the other forested areas. However, jack pine areas in this section of Michigan may not be suitable habitat for small mammals common in forests in this area, especially when populations of such mammals are very low.

The successional stages on the sand dunes each support characteristic communities of mammals. Distinctive mammalian communities in seral stages have been found in other successional studies of mammals. Golley, Gentry, Caldwell, and Davenport (1965) investigated the relationship between small mammals and community development from abandoned fields to climax hardwood forests on the Atlantic coastal plain. They found relatively little overlap of small mammal species in the separate successional stages. They also evaluated the food habits of the small mammals in relation to the community development. The observed relationship reflected the correspondence between vegetation and replacement of mammals. Beckwith (1954) studied ecological succession on abandoned farm lands in southern Michigan. He stated that "variations in mammal populations are closely

associated with changes in plant communities" (1954: 374) due to the mammals' dependence on plants for their food and shelter. Beckwith's findings show that the successional stages support different types of mammals: prairie deer mice use the initial stages of succession, meadow voles are most common during the middle stages, and short-tailed shrews and white-footed mice are common during later stages. Pearson (1959) concluded from his study of small mammals and old field succession in New Jersey that vegetation was the most important factor in determining the distribution and density of small mammals. He found that changes in the types and amount of vegetative cover can explain the occurrence and relative abundance of small mammals in the various seral stages. Wetzel (1958) investigated mammalian succession on stripped land along river bottoms in Illinois. *Peromyscus maniculatus bairdii* was the initial mammal in this sere with populations of *Peromyscus leucopus* developing in later seral stages correlated with forest development. Mammal populations in portions of a hydrosere (sedge mat to white cedar to upland maple-basswood) in Minnesota were studied by Gunderson (1949). He found that the seral stages had distinctive mammalian communities. As evidenced in these studies, communities of mammals are correlated with vegetation types.

Successional studies of mammals have also provided data on the number of species and abundance through the

seral stages. Smith (1940) found that the number of species of mammals increased in a succession from abandoned eroded farmland to the climax prairie. The subclimax stage contained the largest population of rodents. Golley, Gentry, Caldwell, and Davenport (1965) found that the populations of small mammals increased progressively through the initial seral stages, declined to the lowest level in the fourth stage, then increased slightly in the final stage. The successional trend in biomass was similar to that observed for population levels. The number of species tended to decrease through the sere. A study of mammals of upland secondary succession in southern New England (Hirth 1959) showed that the most common small mammals (white-footed mice and short-tailed shrews) were most abundant in the midseral stage. In old field succession in New Jersey (Pearson 1959) the number of mammal species decreased through the sere. The relative abundance of the total small mammal fauna followed the same pattern as noted by Golley, Gentry, Caldwell, and Davenport (1965). Pearson reasoned that this distribution (increase, decrease, increase) was "a reflection of the change from a well developed grassland stage ... to a developing forest aspect afterwards" (1959: 255). Aldrich (1943) found that both the number of species and total abundance of mammals in a swamp sere in northeastern Ohio increased from a sedge meadow (*Juncus*-*Scirpus* associes) to a swamp shrub stage (*Cephalanthus*-*Alnus* associes) and then decreased in the swamp forest (*Acer*-*Ulmus*-*Fraxinus* associes).

These studies generally conflict with the results of the sand dune study in which both species numbers and total abundance increased through the entire sand dune sere.

A possible reason for this conflict is the difference in the trend in diversity between primary and secondary successions. Changes in vegetation diversity during succession have been investigated. Two different trends can be seen in the results of these studies. One pattern has been an increase in diversity during succession as reported by Golley, Petrides, and McCormick (1965), Holland (1971), Margalef (1958), and Reiners, Worley, and Lawrence (1971). The second pattern has been an initial increase in diversity followed by a decrease during the later stages of succession as reported by Whittaker (1953, 1956, 1960), Margalef (1963), AuClair and Goff (1971), and Shafi and Yarranton (1973). Theoretical reasons for the second pattern have been suggested (Margalef 1958, Loucks 1970). Morrison and Yarranton (1973) found an increase in vegetation diversity during a primary sand dune succession. They concluded that diversity apparently decreases during the relatively later part of secondary successions but not during primary successions. This finding was based on their study and a review of the literature. Shafi and Yarranton (1973) suggested that the difference in the pattern of diversity change between primary and secondary successions is attributable to the influence of environmental heterogeneity on diversity. The

initial environment for most primary successions, especially sand dune successions, is more uniform than the initial environment for secondary successions. In secondary successions preexisting environmental heterogeneity can lead to a marked heterogeneity in vegetation during the early stages of the sere (Shafi and Yarranton 1973).

The faunal studies of the sand dune succession have indicated an overall increase in species numbers, a general indicator of species diversity. The diversity of mammals in this primary succession shows a continual increase. This is demonstrated using either the black oak forest as the climax stage with the beech-maple forest as a variation (Olson 1958) or the beech-maple forest as the final stage.

The successional studies of mammals discussed previously have been conducted in secondary successions. Although a species diversity index was not calculated in any of these studies, an examination of the results (species numbers combined with abundance) indicates that species diversity does not appear to continually increase as in the sand dune sere. As with the vegetation studies noted previously, most mammalian successions on secondary seres exhibit an irregular trend in diversity whereas this mammalian succession on a primary sere exhibits a continual increase in diversity. Perhaps the reason for this difference can be attributed to a dependence of mammals on vegetation diversity. If vegetation diversity is a primary

factor in determining mammalian diversity, the expected trends would be those observed in the studies of mammalian succession.

Small Mammal Populations

The very low number of small mammals found on the sand dunes deserve special mention. Since the number of animals captured per trap night partially depends on the pattern of traps, it is best to compare these results with results from identical sampling methods. Results of other studies using identical NACSM trap lines have ranged from 0.8 animals per 100 trap nights for a population low of Microtus in Indiana (Krebs, Keller, and Myers 1971) to 11.2 and 13.2 animals per 100 trap nights in forests in Alberta and New York, respectively (Calhoun 1963). The density index for small mammals on the sand dunes is generally lower than the results obtained in these other habitats.

Low populations of small mammals might be expected in the first two areas because of the limited amounts of resources and the harsh microclimate (Chapman et al. 1926), but the forests appear to provide resources for more animals than are present. No small mammals were found in the jack pine area and very limited numbers were found in the black oak and beech-maple forests. In a similar inland oak forest in southwestern Michigan the white-footed mouse, Peromyscus leucopus, was the most common, and apparently the only sig-

nificant, small mammal (Hodgson and Brewer 1975). Only one white-footed mouse was captured in this study. Wood (1922) and Dice (1925) reported finding this species in sand dune areas. The conspicuous lack of this species from the forests on the sand dunes in this study probably accounts for much of the overall scarcity of small mammals on the sand dunes studied.

Possible reasons for the significantly low numbers of small mammals, and especially the lack of *Peromyscus leucopus*, on the sand dunes are as follows: (1) The bait, trap, or trap arrangement could be ineffective for trapping small mammals. This seems doubtful, however, considering the results of this method as reported elsewhere (Calhoun 1963) and the apparent ease of trapping *Peromyscus leucopus* (Myton 1974); (2) Annual fluctuations in small mammal populations could cause unusually low populations to occur. Smith, Gentry, and Pinder (1974) found significant changes in numbers and species composition of small mammal populations in an eastern hardwood forest in six years of study. They felt that the population of the small mammal community might be determined directly or indirectly by the numbers of the other species present, the effects of temperature and precipitation, and the probable interaction of these physical and biological variables. No data were collected in the present study to analyze this possibility; (3) Sand dune areas are a partial island. No immigration is

possible from the lakeward side. Some of the sand dune communities (jack pine area) are of a localized nature. Occasional extinctions could leave some areas empty. Colonization of these empty areas by mammals could be slower than larger, inland areas. Similar to islands (MacArthur and Wilson 1967), the sand dune areas have reduced immigration and emigration. Annual fluctuations in small mammal populations as noted by Smith et al. (1974) could create extinctions of species in localized areas which could, due to their location, be difficult to recolonize; (4) Subtle environmental changes such as pesticide or toxic chemical levels may have reduced small mammal populations in these as well as some other habitats (Woodwell 1967).

No *Microtus* were found inhabiting any of the sand dune communities. Although records of *Microtus* exist for Lake Michigan sand dunes (Pruitt 1954, specimens at Chicago Field Museum of Natural History and Michigan State University Museum), neither Shelford (1913), Wood (1922), nor Dice (1925) found voles to be common on the sand dunes. The herbaceous layer in the sand dune communities probably does not provide suitable habitat for *Microtus* because of the lack of adequate ground cover (Whitaker 1967).

Role of Mammals in Plant Succession

Most studies of mammalian succession have not emphasized the role of mammals in the plant succession; they

have dealt with the dependence of mammals on vegetation (Smith 1940, Beckwith 1954, Verts 1957, Wetzel 1958, Pearson 1959, Golley, Gentry, Caldwell, and Davenport 1965, Shure 1970, M'Closkey 1975). The dependence of mammals on vegetation for food, shelter, and breeding habitat appears to be a primary factor in determining the distribution of mammals.

The role of mammals in plant succession is difficult to quantify, although possible effects have been described. Krefting and Ahlgren (1974) stated that small mammals may influence the pattern of vegetational change in postfire succession through the consumption of seeds, notably jack pine seeds by deer mice. Dice (1969) describes several classical examples of the control by mammals on succession, specifically the beaver-meadow complex and herbivore grazing in grasslands. Dice notes that animals' roles in succession are usually very local, however.

Any role of mammals in sand dune succession would probably be through seed dispersal and destruction of seeds or young plants. Small mammals on Lake Michigan sand dunes probably do not have a significant effect of plant succession because of their very low numbers. The diurnal sciurids observed on the sand dunes could have a more significant effect due to their gathering and storing of seeds. Although ground squirrels acquire extensive caches of seeds (Howell 1938), the primary grass on the dunes grows mostly

by rhizomes (Olson 1958), therefore seed dispersal (or destruction) may not be an important factor in the early stages. The dispersal of seeds of shrubs by ground squirrels may help to speed the spread of the cottonwood stage. The red squirrel and eastern chipmunk in the jack pine area could significantly affect the distribution of jack pines, again by seed dispersal. Extension of the distribution of conifers by the red squirrel would be an evolutionary advantage for this species which is a characteristic coniferous species. The same is true of the fox squirrel and extension of the black oak area. Eastern cottontails probably have the greatest effect of any mammals on the plant succession of the sand dunes. Because of the large populations of this mammal and its affinity for herbaceous growth (Peterson 1966), this mammal could retard the growth of grasses and shrubs in the early stages of succession, thereby slowing the overall succession. Both eastern cottontails and white-tailed deer might retard the expansion of the forested areas by their browsing on twigs, barks, and buds. On the sand dunes a localized vegetational change, such as the loss of a tree by girdling by mammals, could be significant because of the unstable condition of the dunes once vegetation is removed.

Prebaiting

Some researchers have found that some species of small

mammals are not adequately trapped until after five to ten days of trapping (Calhoun 1963, Myton 1974) or longer (Olsen 1975). This has been explained in at least two different ways: (1) social dominance by some species prohibits other species from being trapped until the dominant species is removed and (2) differences in trappability or ecological differences in the use of habitat (such as fossorial species) do not allow some species to be trapped very quickly. The extensive prebaiting period was used in this study to permit the traps to become accepted as part of the environment. For those areas in this study in which the species are easily trapped, the prebaiting does not seem to have any effect, whereas in the beech-maple area the short-tailed shrew, primarily a fossorial mammal, was trapped at a significantly greater rate after allowing the traps to be in the area for 14 days. This supports the hypothesis that some species are not readily trapped because of their habits, such as being fossorial, rather than because of the dominance of any other species since no "dominant" species were removed in the beech-maple area prior to capturing the shrews. The lack of any common "dominant" species that might have prevented the shrews from being trapped even after prebaiting prevents these results from being a definite falsification of the dominance hypothesis. Perhaps an extensive prebaiting period should be used to census small mammal communities when using a short period of actual trapping.

SUMMARY

Mammals were studied in the classical example of ecological succession on the sand dunes along Lake Michigan. Study areas were established in five seral stages: pioneer dune grass, cottonwood, jack pine, black oak, and beech-maple.

Small mammals were sampled with trap lines of snap-traps and pit-traps. Diurnal mammals were sampled using transect counts. Observations of large mammals were made throughout the sand dune area.

Quantitative data were obtained on ten species. *Peromyscus maniculatus bairdii* and *Blarina brevicauda* were the most common small mammals; *Tamiasciurus hudsonicus* and *Tamias striatus* were the most common diurnal sciurids. The results basically agree with the results of other faunal studies on the sand dunes: the succession of fauna corresponds with the vegetational succession. However, mammals exhibit the biggest turnover of species between the cottonwood and jack pine stages instead of between the jack pine and black oak stages as found in the other sand dune faunal studies.

The successional stages on the sand dunes each support characteristic communities of mammals which corresponds to the findings in other successional studies of mammals. In the sand dune sere species diversity increases continual-

ly. Other successional studies of mammals have exhibited an irregular trend in diversity. A possible explanation for this difference is discussed.

Small mammal populations on the sand dunes were found to be very low with a conspicuous lack of Peromyscus leucopus. These low populations could be due to ineffectiveness of the sampling, annual fluctuations in small mammal populations, the location of the sand dune areas as partial islands with reduced immigration, or subtle environmental changes such as pesticide or toxic chemical levels.

The ground and tree squirrels could play a significant role in plant succession on the sand dunes through their gathering and storing of seeds. The effects of eastern cottontails on retarding plant succession is probably the most pronounced effect by any sand dune mammal.

Trapping results after prebaiting traps during a portion of this study provided data to support the hypothesis that some species of mammals are not readily trapped because of their habits rather than because of the dominance of any other species.

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