THE SPIDER FAUNA OF BEAVER ISLAND, ITS COMPOSITION, ECOLOGICAL DISTRIBUTION AND ORIGIN

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ABSTRACT

THE SPIDER FAUNA OF BEAVER ISLAND,
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by Leslie C. Drew

A total of 211 species of spiders was collected from the 58-square mile Beaver Island located in northern Lake Michigan. Qualitative and quantitative collecting methods disclosed the ecological distribution of the species throughout the island.

Quantitative collecting was performed in specific ecological communities to ascertain the structure of the spider population with reference to frequency, density and food-getting behavior. Diurnal and seasonal succession was studied in the Old Field community.

The populations inhabiting the leaf litter stratum of the mixed hardwood-conifer community on the island and the adjacent mainland of the Lower Peninsula were compared. The statistical characteristics of these populations are evaluated by means of Fisher's Index of Diversity. The evolution of this particular population on the island is discussed.

Leslie C. Drew

The origin of the spider fauna of Beaver Island is examined with reference to post-glacial history, current climate, agents of distribution and the influence of the surrounding mainlands of Wisconsin and Michigan.

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by

Leslie C. Drew

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INTRODUCTION

Zoogeographers have used glacial and post-glacial events to interpret existing distributional patterns of many animal groups. Smith (1957) in his studies of vertebrates, primarily amphibians and reptiles, distributed in northeastern United States, concludes that the ebb and flow of changing climates during and following the last glacial epoch accounts for the present disruptive patterns of several species. Van der Schalie (1963) makes use of post-glacial stream confluence to account for the distribution of fresh-water mussels in the northern Great Lakes region. The araneologist is concerned with <u>when</u> and from <u>where</u> certain species came to the island. <u>How</u> for most species is aerial distribution; however, spiders as waifs can also gain access. These facts of spider distribution are best exposed by quantitative census to determine what species are present and then making use of known distribution data.

The present study is concerned primarily with the composition and origin of the spider fauna on Beaver Island. It also includes population profiles of established island habitats and a comparison of a specific ecological situation on the island with that of a similar one on the adjacent mainland of Michigan.

A DESCRIPTION OF BEAVER ISLAND

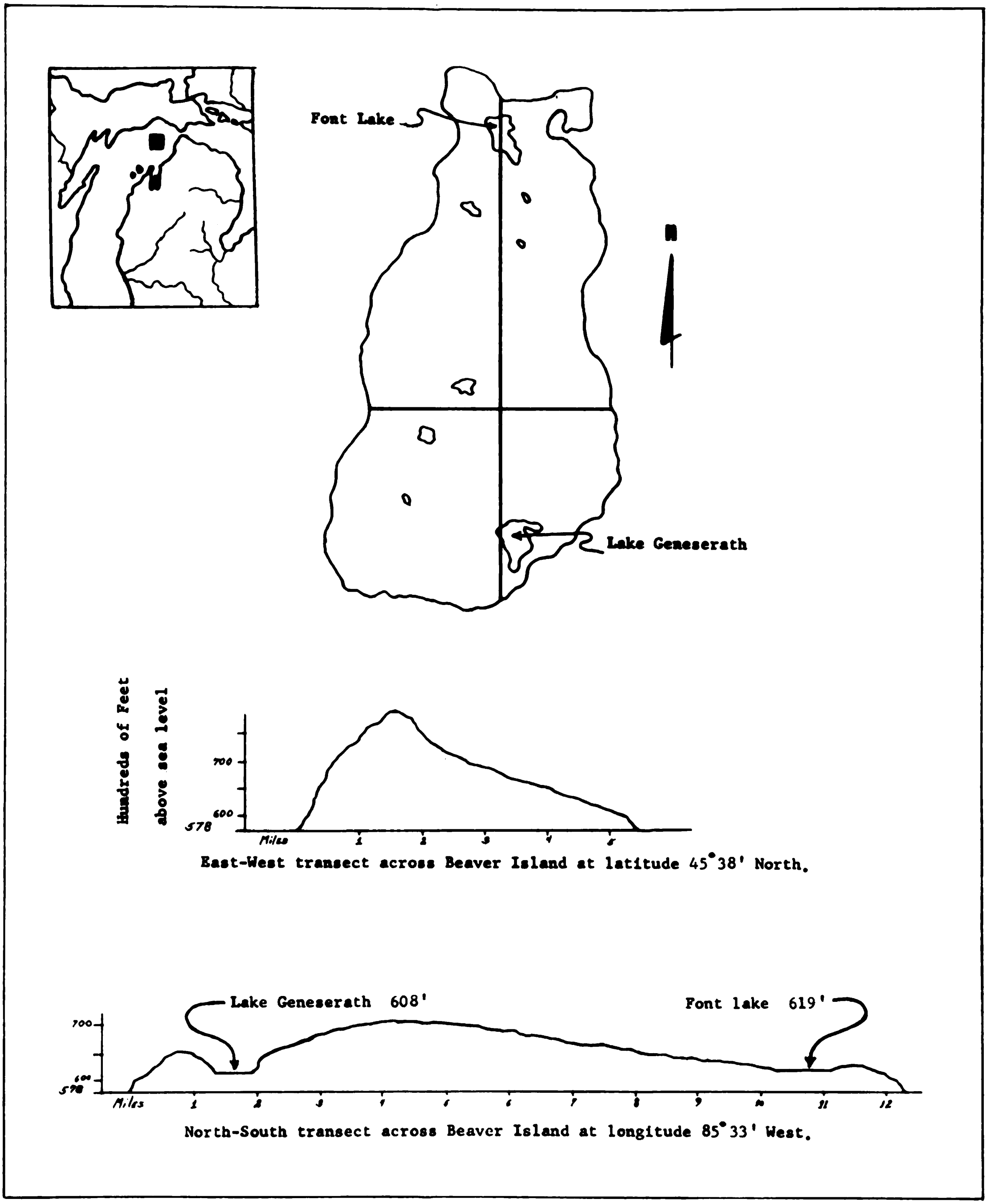
Physiography, Climate, Soils and Vegetation

Beaver Island, with an area of 58.4 square miles (37,376 acres), occupies the position in northeastern Lake Michigan between 45°34' - 45°46' north latitude and 85°29' - 85°38' west longitude. Politically, the island is part of Charlevoix County, Michigan. The island is 19 miles west of Emmet County in the Lower Peninsula of Michigan and 15 miles south of Mackinac County in the Upper Peninsula. Beaver Island is 13.2 miles long (north-south axis) and 6.4 miles across at its greatest width. Elevations vary from 578 feet above sea level, the level of Lake Michigan (1956 map n4530-W8530/15, 1-62,500, of the United States Geological Survey of Washington, C. C.), to 790 feet, the site of the fire tower south of Fox Lake. The greater portion of the island is 22-172 feet above the level of the Lake. St. James, the only settlement on the island, is 15 feet above lake level and is situated along the margins of Beaver Island Harbor at the northeastern tip of the island.

Two Silurian-Devonian limestone formations, Bois Blanc and Detroit River, underlie the island; the Bois Blanc formation is under the northern third and is exposed at two sites along the northern shoreline; the Detroit River formation is under the remaining portion of the island. Both are tilted and dip to the southeast. This bedrock is mantled with glacial till of varying thickness giving rise to the gentle rolling topography of the island (Fig. 1). Eight inland lakes differing in size, bottom-type and depth are scattered over the island. Three major and a number of intermittant streams are located in the south-central and southeastern areas. These flow directly into either Lake Michigan or Lake Geneserath which in turn drains into Lake Michigan. The beaches, forming the shoreline, range from limestone outcrop and boulder to cobble, pebble and sand. Exposed dunes occur behind the shoreline along the northern part of the western margin; and captured vegetated dunes occur just behind the south-central shoreline.

The climate of Beaver Island is seasonally affected by Lake Michigan. During the summer, shore stations to the west, north and east of the island have their mean daily maximum during July. This daily maximum occurs in August on the island. However, during the winter when the Lake is partially or wholly covered by ice, the climate is continental, similar to that of the mainland and the mean monthly temperatures are coincident. Annual precipitation shows further Lake influence. During the summer, this area of the Lake receives 6.2% less precipitation than the surrounding shore stations, and 4.5% more winter precipitation (Blust

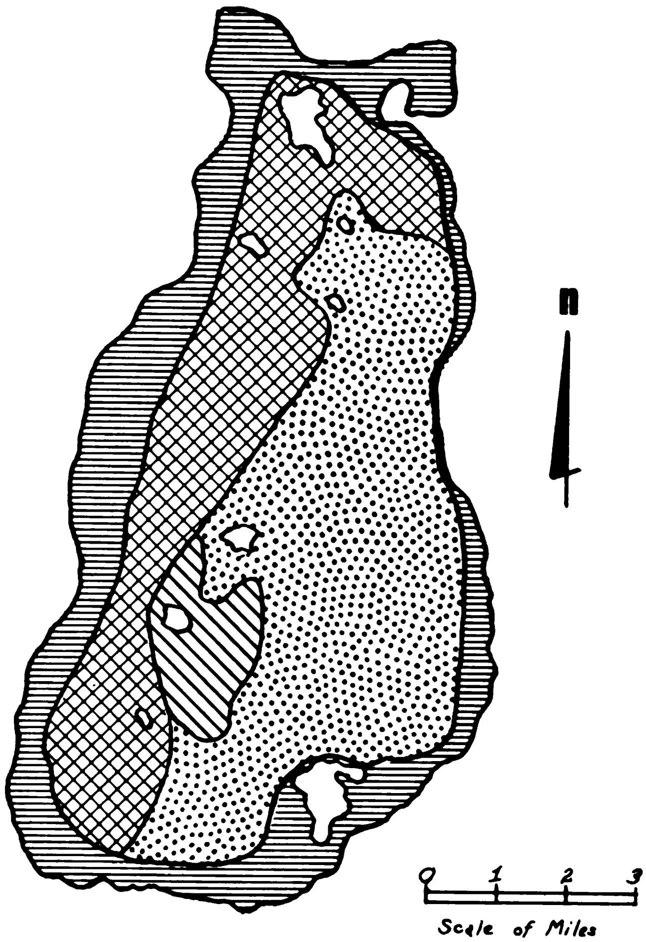
Figure 1. The topography of Beaver Island.



and DeCook, 1960). This fluctuation is attributed to the presence of the vast mass of open water during the summer and its stabilizing or tempering influence on atmospheric storm cells. During the winter, the island intercepts storms due to the unequal heating of the tree shrouded island area as opposed to the relatively uniform surrounding ice. The average annual precipitation is 24.72 inches. September receives the maximum and January the minimum. The mean annual temperature is 43.8°F.; the mean daily maximum 75.8°F.; mean daily minimum 16.6°F. The highest maximum recorded is 97°F. and the lowest minimum -28°F. During the summer, the prevailing winds are from the west-southwest with occasional periods of variable winds from the east-northeast. During the winter months, the prevailing winds are from the north-northwest. The growing season, extending from 14 May to 15 October, is 156 days long. This is comparable to that of the interior counties 200 miles to the south in the Lower Peninsula.

The soils of Beaver Island are agriculturally poor and are quickly depleted under cultivation. According to Veatch (1953), four types occur on the island. The distribution and classification of soils is given in Figure 2.

The vegetation of the island has been studied by Fuller (1918), Darlington (1940) and the Game Division of the



Eastport. Wet land sands; primarily young lacustrine sands on both wet and dry sites.

Kalkaska-Rubicon. Sands and light sandy loams, locally gravely and cobbly.

Munuscong-Detour-Alpena-Rubicon. Wet flats of stony sandy loams and stony clay.

Emmet-Roselawn. Mostly sandy loams. In part deep sands or reddish clay at shallow depths.

Figure 2. The soils of Beaver Island according to Veatch, 1953.

Michigan Conservation Department. Darlington (op. cit) reported that the island has 30 of the 33 plant communities found on the mainland of Michigan. The Game Division mapped the cover types in 1945 and has updated the map periodically. Figure 3 depicts the current distribution of the major vegetative types of the island. The areal distribution and major species of these types are presented in Table 1.

Post-Glacial History of Beaver Island

Studies evaluating the influences of pre- and post-glacial events as well as past climates on current distributional patterns have been reported by many authors. Notable among these are Dillon (1956), Martin and Harrell (1957), Smith (1957), Howden (1963) and van der Schalie (1963). Studies to evaluate these influences on the distribution of spiders are handicapped because: most of these organisms are passively dispersed by aerial means; relict populations have yet to be recognized; and, relatively few conclusive studies have been done on geographic variations. Nonetheless, some species must have been carried to and deposited on the varying amounts of exposed land of the northern basin of Lake Michigan during the post-glacial epoch. Therefore, the sequence of events that compose the post-glacial history of Beaver Island is pertinent to this study.

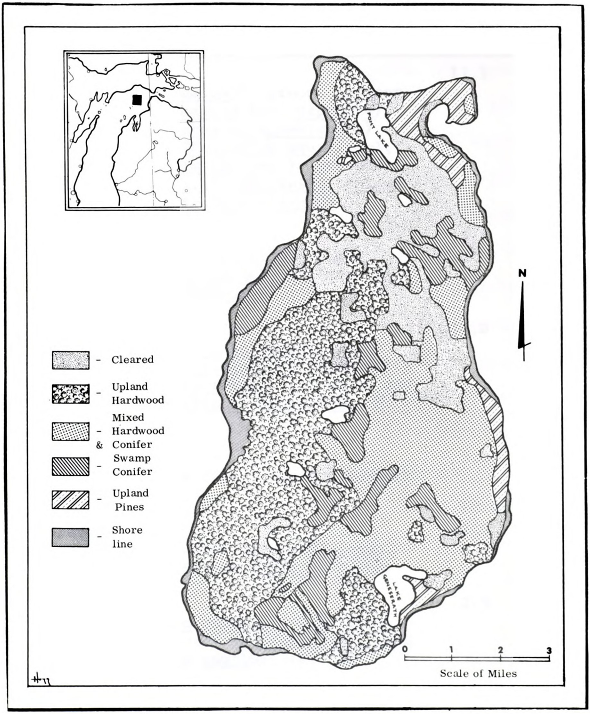


Figure 3. A generalized cover-type map of Beaver Island.

Table 1. Major plant species and areal distribution of vegetative types on Beaver Island[1]

Cover types and major species	Area sq. mi.	%
Cleared Lands apple (*Pyrus malus*)[2], ground juniper (*Juniperus communis* var. *depressa*), blackberry (*Rubus allegheniensis*), bracken fern (*Pteridium aquilinum*), milkweed (*Asclepias spp*.), grasses (*Poa compressa*, *P. pratensis*, *Phleum pratense* and *Agropyron repens*).	17.5	30.0
Upland Hardwood beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), eastern hemlock (*Tsuga canadensis*).	13.2	22.7
Mixed Hardwood-Conifer balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), northern white cedar (*Thuja occidentalis*), white and yellow birch (*Betula papyrifera*, *P. lutea*).	17.0	29.1
Swamp Conifer northern white cedar, eastern hemlock, balsam fir	5.3	8.9
Upland Pines red and white pine (*Pinus resinosa*, *P. strobus*, red oak (*Quercus rubra*)	2.9	4.8
Shoreline willows (*Salix cordata* and *S. glaucophylloides* var. *glaucophylla*), sand cherry (*Prunus pumila*), red osier (*Cornus stolonifera*), marram grass (*Ammophila breviligulata*), balsam-poplar (*Populus balsamifera*).	2.5	4.4
	58.4	100%

1 Modified from Fuller (1918), Darlington (1940) and Ozoga (1963).

2 Species names follow those in Fernald (1950).

Geological evidence indicates portions of the present basin of northern Lake Michigan were alternately exposed and submerged. This evidence consists of beaches and wave-cut terraces, and shallow-water sediments underlying more recent deep-water sediments above and below the present lake level. Interpretations of this evidence have been reported by Leverett and Taylor (1915), Stanley (1938) and Hough (1955, 1958, 1962, 1963). The sequence of events composing the post-glacial history is fairly well established. However, the duration of various stages is somewhat controversial. Radiocarbon dating techniques, used since 1949, have given rise to diverse chronologies. By way of illustration, the dates for wood samples from the Two Creeks Forest (the unofficial standard reference material) varies from 11,400 years before the present (Arnold and Libby, 1949, 1951) to 11,850 $\pm$ 140 years Before Present (Broecker and Farrand, 1963). The variance is compounded by suggested dates for what is sometimes called the Two Creeks Interval or the Two Creeks Low-water Stage. Zumberge and Potzger (1956) date this at 11,000 Before Present; anthropologists use the date of 12,450 years Before Present (C. E. Cleland, pers. comm.). Consequently, the time intervals of post-glacial events are, at best, tentative. The radiocarbon dates recorded by Hough (1958) are used for the post-glacial events of interest to the present study.

Concepts of post-glacial climates and concomitant forest types have been postulated from pollen profiles by Deevey (1949) for the northeastern region of the United States and by Zumberge and Potzger (1956) for two sites in southwestern Michigan. There is considerable agreement between these two studies; and when differences do occur, it is probably regional. These data have been incorporated in the following account with the realization that studies on post-glacial succession dynamics (Wright, 1964) may modify them somewhat.

Lake Algonquin was the first major lake stage following the retreat of the Valders, the last glacial ice, from the Lake Michigan basin. It came into being 8,800 years Before Present and maintained a level of 605[1] feet Above Tide for 800 years. Portions of the present Beaver Island were above this level (Table 2). Deevey postulates that a tundra flora followed the northward retreat of ice through the entire glaciated region. In the pollen profiles at South Haven, Michigan, Zumberge and Potzger have identified spruce-fir pollen at this age level and conclude, as does Deevey, that the climate was cool and moist.

1 The elevations are average values representing a vertical range of about five feet (Hough, 1958).

Table 2. Lake stages during the post-glacial history of Beaver Island

Lake stages	Elevation	No. of Islands	Total shoreline in miles
Algonquin	605 ft.	5	11.2 miles
Chippewa	230 ft.	1[1]	185.0 miles
Nipissing	605 ft.	12	59.7 miles
Algoma	596 ft.	1	37.0 miles
Lake Michigan	578 ft.	1	41.6 miles

1 Really a peninsula (Fig. 4). The shoreline measured was that which extended from present Lake Charlevoix on the south, the Mackinac River on the north to the present Straits of Mackinac.

As new discharge routes were uncovered by the north-northeastward retreating ice, the lake level dropped gradually to a low of 230 feet Above Tide. This recession, which occurred over a period of 1500 years, exposed increasing amounts of the former lake bed and, thus, united the former isolated islands into a peninsular body broadly connected to the present Lower Peninsula (Fig. 4). The pollen profiles reflect a climatic change during this stage. The spruce-fir pollen is overlain by increasing amounts of pine pollen indicating a warmer and drier climate. Zumberge and Potzger identified a shift from jack-pine to white and red pine during this period.

The low-water stage of 230 feet Above Tide, known as Lake Chippewa, remained for 700 years (6,500-5,800 Before Present). An increasing amount of oak pollen occurs with that of pine in the South Haven profile which indicates a continuation of the warm dry climate.

Isostatic rebound in the northeastern portion of the Great Lakes region gradually decreased the northern discharge route at North Bay, Ontario. As a result, the water level in the northern Lake Michigan basin rose once again to 605 feet Above Tide. This latter level was determined by the elevations of the discharge route from the southern portion of the basin and that of Port Huron in Lake Huron. This gradual increase in water level, termed the Transition by Hough (1958), occurred over a period of 1800 years (5,800-4,000 years Before Present) and fragmented the extensive continuous shorelines of the previous stage. The climate remained warm but became more humid as evidenced by pollen of oak, beech, hemlock and elm in the profiles. Smith (1957) and Hough (1958) report this to be the Climatic Optimum or Thermal Maximum of the geologists.

The re-establishment of the 605 feet Above Tide level, known as the Lake Nipissing stage, lasted for 1000 years (4,000-3,000 years Before Present). During this stage, Beaver Island was a series of 12 or more islands (Table 2) of various sizes and elevations. Deevey (1949) refers to this stage as the Thermal Maximum, as do Zumberge and Potzger (1956). The basis for this conclusion by Deevey is the occurrence of oak and hickory pollen. He also assumes a steppe-like vegetation developed or there was an extension of the western grasslands into the recently glaciated northeastern region. There is no palynological evidence to substantiate this assumption. However, the present distributional patterns of some organisms is best explained by the occurrence of such vegetation (Smith, 1957). The profile at South Haven, Michigan records the occurrence of oak and pine during this stage.

Lake Nipissing was brought to a close by erosion of the sill in the discharge route at Port Huron. This resulted in a new level, 596 feet Above Tide, known as Lake Algoma, which lasted 800 years (3,000-2,200 years Before Present). During this stage, present day Beaver Island was exposed as one single island with a shoreline of 37 miles (Table 2). Also during this stage, the climate became cooler and more moist much like that of the present. The evidence for this conclusion is that oak-hickory pollen deposits in the profiles of Wisconsin and Minnesota are overlain by pollen of species presently occurring in these areas (Deevey, 1949).

Continued erosion at Port Huron in conjunction with a lateral shift of the Detroit River dropped the water level of the lake to 580 feet Above Tide--present day Lake Michigan. There have been minor fluctuations during the last 2200 years but none of the magnitude of preceding stages.

MATERIALS AND METHODS

Qualitative and quantitative collecting was accomplished with the following equipment: a 12-inch diameter insect net attached to a three-foot handle; a 30-inch square beating net of medium weight canvas suspended from the tips of a wooden collapsible X-shaped frame; a wooden frame enclosing one square foot; two sifting boxes, one 13" x 13" with 5/16" mesh screen bottom, and the other 10" x 10" with 1/16" mesh screen; an aspirator; and a 5-cell head lamp.

The methods varied according to the purpose for collecting. General collecting to determine the composition of the spider fauna included visual searching during the day and night hours with and without the above equipment. Sweeping with the insect net, beating with the beating net and sifting leaf litter were the methods used to collect for the spider population profiles of specific ecological communities.

In studying the population of old fields, use was made of the sweeping methods advocated by Barnes (1953). One sample includes those spiders collected in 200 strokes over a distance of 100 paces. Each stroke of the net covers an approximate 6-foot arc through the standing vegetation; and a return stroke is taken before stepping forward one pace.

The populations inhabiting clumps of junipers, white cedars and shrubs of forests were sampled by use of the beating net. The method used in these situations was to place the net under boughs or branches which were then struck twice with a three-foot, 12-ounce stick. After two such blows, the spiders were collected from the net by means of an aspirator. One sample consists of those spiders dislodged by 200 such blows which usually covered more than one bush or tree.

Spider populations of the leaf litter stratum were studied by sifting the specimens out of one square-foot samples of litter. In an attempt to assure random selections of samples, these procedures were followed: a two-digit random number (from the tables of Dixon and Massey, 1957) determined the number of paces along a directional line to the starting point; the end of a 100-foot steel tape was secured to the ground by means of a six-inch lag screw; the last digit of another two-digit random number determined the distance in feet along the tape to the sample, where the wooden frame that encloses one square foot was placed. The leaf litter enclosed by this frame was gathered by hand and placed in a paper bag, the top of which was folded down several times, secured with paper clips, and marked as to distance from the starting point and sample number. Later, the contents of each bag was sifted and the spiders collected by use of the aspirator. All specimens from one bag, constituting one sample, were put into the same vial containing 70% alcohol for identification later.

The results of the quantitative sweeping, beating and sifting can be expressed in terms of frequency and density as applied by Barnes (1953) and Barnes and Barnes (1954, 1955) in studies of the spider populations in various real communities. Frequency as defined by Barnes and as used here is a statistical expression of the number of times a particular species occurs in a given number of samples taken from an existing community. Frequency is expressed as a percentage and is derived by using the following formula:

$$\% \text{ Frequency} = \frac{\text{No. of samples with particular species}}{\text{Total number of samples}} \times 100.$$

Density is defined as the average number of individuals of a particular species per sample and is calculated as follows:

$$\text{Density} = \frac{\text{Total number of specimens of a particular species}}{\text{Total number of samples}}$$

These two expressions provide a graphic representation of the population structure of specific communities.

The Index of Diversity was calculated for the species occurring in the leaf litter communities of mixed hardwood-conifer forests on Beaver Island and on Waugoshance Point, Emmet County--that portion of the Lower Pêninsula closest to Beaver Island. Such an index is based on the relationship between the total number of individuals and the number of species contained in samples. This index was evolved by Fisher, Corbet, and Williams (1943) and is known as the logarithmic series. It is expressed by this formula: $S = \alpha \ln(1 + N/\alpha)$. Wherein α is a constant independent of sample size and, thus, becomes an expression of the diversity of species in relation to the total number of individuals. The comparison of such indices from areas that were once geographically continuous could possibly reveal changes in the population structure of presently ecologically similar communities.

Quantitative sweeping and beating samples were taken during the course of one day. This was not feasible with the leaf litter samples taken on the island and on the mainland. However, these samples were taken within a one week period.

Collecting on the island was done during the spring, summer and fall of 1961, 1962 and 1963. The specimens collected during this study have been deposited in the collections of the Entomology Museum, Michigan State University, East Lansing, Michigan.

RESULTS

The Spiders of Beaver Island

Of the 211 species known to occur on Beaver Island, 114 or 54.1% are web-weaving species and 97 or 45.9% are hunting species. These two descriptive categories, used throughout the remainder of this report, require definition: web-weaving species are those which capture their prey by entanglement in an aerial web; hunting species are those which capture prey by sheer physical acumen, speed or stealth, in the presence or absence of a web. These categories, derived in part from Comstock (1948) and Gertsch (1949), are applied to families known to occur in this temperate area.

A listing of the families, genera and species which comprise the fauna of the island together with pertinent ecological data for Beaver Island is presented below. A summary table (Table 3) follows this listing.

THE SPIDERS OF BEAVER ISLAND

Class Arachnida

Order Araneae

Suborder Labidognatha (Araneomorphae)

Section Ecribellatae

Superfamily Epeiroidea

Family Theridiidae--Comb-footed Spiders

Members of this family are usually associated with irregular or mesh webs placed in a variety of ecological situations.

Achaearanae tepidariorum (C. L. Koch, 1841). Under logs and in abandoned buildings in swamp-conifer forest; in and on buildings in St. James and cottages along east coast.

Argyrodes trigona (Hentz, 1850). Shrubs and low tree branches of mixed hardwood-conifer forest.

Crustulina stricta (O. P.-Cambridge, 1861). Juniper stands south of Font Lake.

Dipoena nigra (Emerton, 1882). Low branches of conifers of mixed hardwood forest.

Enoplognatha marmorata (Hentz, 1850). Under stones in gravel pits; on shrubs in upland hardwoods.

Euryopsis funebris (Hentz, 1850). Leaf litter of upland hardwoods; on sand under juniper bushes.

Robertus laticeps (Keyserling, 1884). Litter of swamp-conifer forest.

R. riparius (Keyserling, 1886). Litter of upland hardwoods and mixed hardwood-conifer forests.

Steatoda albomaculata (De Geer, 1778). Under debris at dump sites; under flat stones (2" to 6") behind foredune along northwest shoreline.

S. borealis (Hentz, 1850). Under bark and in litter of upland hardwoods; in rolls of birch bark in swamp-conifer forest.

Theridion differens Emerton, 1882. In rock piles, juniper stands, and on shrubs of upland hardwoods.

T. frondeum Hentz, 1850. Low branches and shrubs of all forest types; vegetation of old fields.

T. glaucescens Becker, 1879. Vegetation of roadsides and old fields; cedar stands.

T. murarium Emerton, 1882. Juniper stands; shrubs of hardwood-conifer forests; cedars; on buildings where mature males were occupying webs with immature females.

T. ornatum Hahn, 1831. Low branches and shrubs of upland hardwood-conifer forests; in crevices of stone wall.

T. petraeum L. Koch, 1872. Rock piles; vegetation at meadow-cedar edge.

T. sexpunctatum Emerton, 1882. In rock piles sheltered by shrubs.

Theridula emertoni Levi, 1954. On vegetation of clearings in upland hardwood forest.

Family Linyphiidae--Sheet-web Weavers

Most species of this family construct rather conspicuous dome-shaped or flat webs at various heights above ground level in standing vegetation. Some are found only in the litter on forest floors.

Bathyphantes pallida (Banks, 1892). Leaf litter of mixed hardwood-conifer forest.

Centromerus cornupalpus (O. P.-Cambridge, 1875). Leaf litter of swamp-conifer forest.

C. latidens (Emerton, 1882). Leaf litter of mixed hardwood-conifer forest.

C. persoluta (O. P.-Cambridge, 1875). Leaf litter of swamp-conifer and mixed hardwood-conifer forests.

Drapetisca alteranda Chamberlin, 1909. On webs closely applied to bark of beech and sugar maple saplings.

Frontinella communis (Hentz, 1850). (F. pyramitela[1] of Chamberlin and Ivie, 1944). Bowl-like web suspended in spaces of juniper bushes and bracken ferns.

Helophora insignis (Blackwall, 1841). Flat webs in low shrubs of upland hardwood forest.

Lepthypantes appalachia Chamberlin and Ivie, 1944. Litter of swamp-conifer forest.

L. nebulosa (Sundevall, 1830). Webs in shrubs bordering cleared fields and on juniper bushes.

L. subalpina (Emerton, 1882). On webs in roadside vegetation and in rock piles.

1 Following the suggestion of Levi and Levi (1961), the name changes proposed by Chamberlin and Ivie (1944) are not used pending further study.

Linyphia marginata C. L. Koch, 1834. Under dome-shaped webs in roadside vegetation; on low shrubs in mixed hardwood-conifer forest; and cedars of swamp-conifer forest.

L. waldea Chamberlin and Ivie, 1943. Under flat webs suspended in vegetation bordering lakes and marshes.

Macrargus multesimus (O. P.-Cambridge, 1875). Leaf litter of hardwood-conifer forest.

Microneta viaria (Blackwall, 1841). Leaf litter upland hardwood forest.

Pityohyphantes costatus (Hentz, 1850). Conspicuous flat webs on shrubs and low tree branches of all forest types.

Pusilla mandibulata (Emerton, 1882). Flat webs suspended near bases of shrubs on sand beaches.

Family Micryphantidae--Dwarf Spiders

Most of the species belonging to this family are small, less than 2 mm., and live near the ground under various kinds of leaf litter.

To avoid repetition in the following list, all species followed by a phrase describing a forest type were found in leaf litter. Exceptions to this will be described.

Ceraticelus alticeps (Fox, 1891). Mixed hardwood-conifer forest.

C. atriceps (O. P.-Cambridge, 1874). Herbs of mixed hardwood-conifer forest.

C. emertoni (O. P.-Cambridge, 1874). Vegetation of old fields.

C. fissiceps (O. P.-Cambridge, 1874). Shrubs of mixed hardwood-conifer forest.

C. laetabilis (O. P.-Cambridge, 1874). Herbs of apple orchards; shrubs and leaf litter of upland hardwood and hardwood-conifer forests.

C. minutus (Emerton, 1882). Upland hardwood and hardwood-conifer forests.

Ceratinella brunnea Emerton, 1882. Swamp-conifer and mixed hardwood-conifer forests.

Ceratinopsis nigriceps Emerton, 1882. On webs at distal ends of cedar and juniper branches.

Cochlembolus pallidus (Emerton, 1882). Hardwood-conifer forest.

Collinsia oxypaederotipus (Crosby, 1905). Upland hardwood forest.

Cornicularia clavicornus Emerton, 1882. Hardwood-conifer forest.

C. indirecta (O. P.-Cambridge, 1874). Hardwood-conifer forest.

C. minuta Emerton, 1882. Swamp-conifer forest.

C. pallida Emerton, 1882. Hardwood-conifer forest.

Eperigone maculata (Banks, 1892). Upland hardwood forest.

E. trilobata Emerton, 1882. Shrubs and leaf litter of upland and hardwood-conifer forests.

Erigone alsaida Crosby and Bishop, 1928. Leaves of shrubs in upland hardwood forest at night.

E. atra Blackwall, 1833. Upland hardwood forest.

E. dentigera O. P.-Cambridge, 1874. Vegetation bordering lake shores; herbs of upland hardwood forest.

Floricomus plumalis (Crosby, 1905). Hardwood-conifer forest.

Grammonota pictilis O. P.-Cambridge, 1875. On cedar trees and in leaf litter of swamp-conifer forest.

G. spinimana Emerton, 1923. Hardwood-conifer forest.

Maso sundevalli (Westring, 1851). Swamp-conifer and hardwood-conifer forests.

Minyriolus castaneus (Emerton, 1882). Upland hardwood forest.

Oreonetides vaginatus (Thorell, 1872). Mixed hardwood-conifer forest.

Pelecopsis moestum (Banks, 1892). Hardwood-conifer forest.

Pocadicnemis hartlandiana Emerton, 1913. Hardwood-conifer forest.

P. pumila (Blackwall, 1841). Upland hardwood forest.

Sciastes terrestris (Emerton, 1882). Hardwood-conifer forest.

Sisicottus montanus (Emerton, 1882). Hardwood-conifer forest.

Scironis tarsalis (Emerton, 1911). Mixed hardwood-conifer forest.

S. montigenus Bishop and Crosby, 1938. Hardwood-conifer forest.

Sisicus penifusiferus Bishop and Crosby, 1938. Hardwood-conifer forest.

Tapinocyba minuta (Emerton, 1909). Hardwood-conifer forest.

T. simplex (Emerton, 1882). Hardwood-conifer forest.

Tunagyna debilis (Banks, 1892). Hardwood-conifer forest.

Walckenaer vigilax (Blackwall, 1853). Vegetation of old fields.

Family Epeiridae--Orb-web Weavers

Some taxonomic schemes reduce this family to subfamily status under the family Argiopidae. I prefer the workable arrangement proposed by Kaston (1948) which gives full family status to Epeiridae and eliminates Argiopidae. The species listed below all build orb webs of various size, complexity and inclination, though most are vertical or near vertical.

Subfamily Argiopinae

Argiope trifasciata (Forskål, 1775). On vertical webs suspended in juniper bushes and standing vegetation of old fields.

Subfamily Epeirinae

Acanthepeira stellata (Walckenaer, 1805). Webs on vegetation of inland lake shores and on shrubs and herbs of sandy beaches.

Araneus diadematus Clerck, 1757. Webs in vegetation at old field-woods edge.

A. marmoreus Clerck, 1757. Shrubs of upland hardwoods, mixed hardwood-conifer forests and vegetation of old fields.

A. nordmanni (Thorell, 1870). Shrubs of upland hardwood forest; and beach.

A. solitarius (Emerton, 1884). Shrubs of upland hardwood forest.

A. thaddeus (Hentz, 1847). Shrubs of upland hardwood forest.

A. trifolium (Hentz, 1847). Herbs of open areas in upland hardwood forest, old fields and beach shrubs.

Araniella displicata (Hentz, 1847). Vegetation of old fields; herbs and shrubs of open woods.

Cyclosa conica (Pallas, 1772). Shrubs of upland and mixed hardwood forests.

Epeira cornuta (Clerck, 1757). Shrubs of upland and mixed hardwood forests; beach shrubs.

E. patagiata (Clerck, 1757). Herbs and shrubs of upland and mixed hardwood forests; vegetation on beaches.

E. sericata (Clerck, 1757). Trees and shrubs of upland and mixed hardwood forests; frequently on buildings.

Eustala anatera (Walckenaer, 1841). Marsh vegetation; shrubs of upland hardwood forest.

Larina borealis Banks, 1894. Vegetation of open areas in upland hardwood forest, junipers and grassy fields.

Mangora gibberosa (Hentz, 1847). Vegetation of abandoned orchards.

Neoscona arabesca (Walckenaer, 1837). Shrubs and herbs of upland hardwood forest; junipers and old fields.

Zygiella nearctica Gertsch, 1964. Low branches of trees and shrubs of mixed hardwood-conifer forests; herbs and shrubs of beach along eastern shore line; on buildings.

Family Tetragnathidae

These species also spin orb webs which may vary from near horizontal to vertical in position.

Subfamily Tetragnathinae

Leucauge venusta (Walckenaer, 1837). Shrubs and herbs of upland hardwood forest.

Pachygnatha kuratai Levi, 1951. Vegetation bordering inland lakes and marshes.

Tetragnatha elongata Walckenaer, 1805. Shrubs and herbs of hardwood forest; on cedar trees along stream course; vegetation of beaches.

T. extensa Linnaeus, 1757. Vegetation around buildings; shrubs of upland hardwood forest.

T. guatemalensis O. P.-Cambridge, 1889. Shrubs and low tree branches of hardwood-conifer forests; beach shrubs.

T. harrodi Levi, 1951. Cedar trees; vegetation of clearings in upland hardwood forest; vegetation on beach.

T. laboriosa Hentz, 1850. Shrubs of upland hardwood forest; vegetation of old fields, beaches and roadsides.

T. pallescens F. O. P.-Cambridge, 1903. Juniper stands near open water and beach vegetation.

T. versicolor Walckenaer, 1841. On cedars bordering inland lakes and Lake Michigan; junipers and grass of open fields.

Family Mimetidae--Pirate Spiders

These species are reported to prey exclusively on other spiders.

Ero leonina (Hentz, 1850). Leaf litter of mixed hardwood-conifer forests.

Mimetus epeirodes Emerton, 1882. Vegetation of old fields and under debris in dumps.

Superfamily Lycosoidea

Family Agelenidae--Funnel-web Weavers

Most species of this group inhabit moist situations such as under leaf litter, under loose bark of logs and stumps in forests; others place their sheet webs at various heights above ground level in standing vegetation.

Agelenopsis emertoni Chamberlin and Ivie, 1935. Vegetation of old fields.

A. pensylvanica (C. L. Koch, 1843). On and near buildings in St. James.

A. potteri (Blackwall, 1846). Shrubs of mixed hardwood-conifer and upland hardwood forests; in rock piles; and on buildings.

A. utahana (Chamberlin and Ivie, 1933). Shrubs and hollow stumps of upland hardwood forest; leaf litter of upland hardwood and hardwood-conifer forests.

Cicurina arcuata Keyserling, 1887. Leaf litter of upland hardwood and hardwood-conifer forests.

C. brevis (Emerton, 1889). Leaf litter of upland hardwood and mixed hardwood-conifer forests; vegetation of roadsides.

C. lowriei Levi, 1951. Shrubs and herbs of mixed hardwood-conifer forest.

Coras montanus (Emerton, 1889). In the leaf litter and hollow stumps of upland hardwood forest.

Cryphoeca montana Emerton, 1909. Litter of swamp-conifer forest.

Wadotes calcaratus (Keyserling, 1887). In brush piles and leaf litter of upland hardwood and mixed hardwood-conifer forests; under debris on beach along the west side of the island.

Family Hahniidae

These spiders spin delicate small sheet webs in moist situations, especially in forest litter.

Neoantistea agilis (Keyserling, 1887). Leaf litter of upland hardwood and mixed hardwood-conifer forests.

N. riparia (Keyserling, 1887). Leaf litter of upland hardwood forest.

Family Pisauridae--Fisher Spiders or Nursery-web Weavers

The species of this family do not build snares for capturing prey but rather are active hunters. Most are associated with moist habitats often near or on open water.

Dolomedes scopularis C. L. Koch, 1848. Under vegetative debris along shores of inland lakes and along sandy beaches on east coast.

D. scriptus Hentz, 1845. In shallow depressions under logs along shore line of Fox Lake.

D. tenebrosus Hentz, 1844. Under vegetative debris along shore line and on vegetation bordering shore line.

Family Lycosidae--Wolf Spiders

Most members of this family are active hunters that pursue their prey. However, some are sedentary and build more or less vertical burrows that may be topped by turrets of vegetative debris.

Subfamily Lycosinae

Arctosa littoralis (Hentz, 1844). Under debris on sandy beaches during the day or running along water's edge at night.

Geolycosa missouriensis (Banks, 1895). In vertical burrows with turrets in soils of mixed hardwood-conifer forests and juniper-grass fields. The deepest burrow was 11 inches; the average depth of six burrows was 8-3/4 inches.

G. wrightii (Emerton, 1912). In vertical burrows of varying depths in sandy areas of beaches. The depths of the burrows seem to vary seasonally: shallow (9" to 15") in early summer; deeper (18" to 27") in the fall.

Lycosa avida (Walckenaer, 1837). Under beach debris along northwest rocky shore line.

L. baltimoriana (Keyserling, 1876). Under debris on sand beaches and wandering on soil surface under shrubs behind foredunes.

L. frondicola Emerton, 1885. Leaf litter of upland hardwood forest.

L. helluo Walckenaer, 1837. Under debris on sandy beaches; in leaf litter and under stones in upland hardwood forest.

L. pratensis Emerton, 1885. In upland hardwood forest litter; in crevices between cobblestones on beaches.

Pirata arenicola Emerton, 1909. Under debris and on vegetation along shore lines of inland lakes.

P. marxii Stone, 1890. Leaf litter of mixed hardwood-conifer forest.

P. minutus Emerton, 1885. In rock piles and in litter at old field-wood's edge.

P. montanus Emerton, 1885. In sunflecks on leaf litter of upland hardwood forest.

P. pirata (Clerck, 1757). Between pebbles and rocks of beach along southeast shore line; under debris along west shore line.

Tarentula aculeata (Clerck, 1757). On leaf litter of mixed hardwood-conifer forests; under beach debris; and in open grassy fields.

Subfamily Pardosinae

Pardosa distincta (Blackwall, 1846). In rock piles; leaf litter of mixed hardwood-conifer forests; vegetation along shores of inland lakes; under vegetative debris on sand beaches.

P. fuscula (Thorell, 1872). Under debris on sand beaches.

P. lapidicina Emerton, 1885. On and between pebbles and rocks along Lake Michigan shore line.

P. mackenziana (Keyserling, 1876). On shrubs of upland hardwood forest, junipers, cedars and vegetation of roadsides.

P. milvina (Hentz, 1844). Old fields and shrubs of upland hardwood forest.

P. modica (Blackwall, 1846). Marsh vegetation.

P. moesta (Banks, 1892). Grass of old fields and shore lines of inland lakes.

P. saxatilis Hentz, 1844. Grassy clearings in upland hardwood forests and along shore lines of inland lakes; rock piles; soil surfaces of old fields.

P. xerampelina (Keyserling, 1876). In rock piles; on stony beaches; on roadside vegetation and in litter of upland hardwood forest.

Superfamily Gnaphosoidea

Family Gnaphosidae--Running Spiders

These species are primarily nocturnal, hunting spiders. During the day they may be found in shallow depressions or crevices or under stones, logs and debris.

Subfamily Gnaphosinae

Gnaphosa muscorum (L. Koch, 1866). Under stones and logs along shores of inland lakes; soil surface of old fields.

Subfamily Drassodinae

Drassodes neglectus (Keyserling, 1887). In rock piles; under logs of mixed hardwood-conifer forests; soil surface of old fields.

Drassyllus niger (Banks, 1911). Leaf litter of upland hardwood forest.

Haplodrassus signifer (C. L. Koch, 1839). In debris under cedar trees.

Herpyllus vasifer (Walckenaer, 1805). In leaf litter of mixed hardwood-conifer forests; under stones in old fields.

Zelotes subterraneus (C. L. Koch, 1839). Under debris in dumps; in rock piles; on vegetation of roadsides; and on shrubs of upland hardwood forest.

Superfamily Clubionoidea

Family Clubionidae--Sack Spiders

Many of these hunting spiders may be found in silken retreats in rolled leaves of shrubs and weeds. Others are found under stones, boards and in leaf litter of several forest types.

Subfamily Clubioninae

Clubiona canadensis Emerton, 1890. On cedars; under loose bark; and on shrubs of swamp-conifer forest.

C. chippewa Gertsch, 1941. On shrubs of upland hardwood forest.

C. mixta Emerton, 1890. On beach vegetation along western shore line.

C. moesta Banks, 1876. On shrubs of upland hardwood forest.

C. obesa Hentz, 1847. On shrubs of upland hardwood forest; under debris and logs on beaches of inland lakes and Lake Michigan.

C. pallens Hentz, 1847. Shrubs of hardwood-conifer forests.

C. riparia L. Koch, 1866. On shrubs of upland hardwood forest; under stones behind foredune along western shore line.

C. trivialis C. L. Koch, 1843. On cedars.

Subfamily Liocraninae

Agroeca ornata Banks, 1892. In leaf litter of upland hardwood and swamp-conifer forests.

A. pratensis Emerton, 1890. On shrubs and in leaf litter of upland hardwood forest; in leaf litter of mixed hardwood-conifer forest.

Phrurotimpus alarius (Hentz, 1847). Leaf litter of upland and mixed hardwood forests.

P. borealis (Emerton, 1911). Leaf litter of mixed hardwood-conifer forest.

Subfamily Micariinae

Castianeira cingulata (C. L. Koch, 1842). In leaf litter of mixed hardwood-conifer forests; under beach debris along northern portion of eastern shore line.

C. descripta (Hentz, 1847). In litter and under stones of upland hardwood forest; under debris and amongst rocks of beaches surrounding island.

Micaria emertoni Gertsch, 1935. In leaf litter of upland hardwood forest.

M. longipes Emerton, 1890. On beach vegetation and under stones behind foredune along sandy western shore line.

Superfamily Thomisoidea

Family Thomisidae--Crab Spiders

The spiders of this family capture their prey by either lying in ambush or wandering about. They do not make webs.

Subfamily Misumeninae

Misumena vatia (Clerck, 1757). Vegetation of old fields and beaches; on juniper bushes.

Misumenops oblongus (Keyserling, 1880). Vegetation of old fields.

Oxyptila americana Banks, 1895. Leaf litter and debris of all forest types; relatively more common in deciduous litter.

Xysticus elegans Keyserling, 1880. Vegetation bordering marshes and grass-juniper fields; litter and shrubs of upland hardwood forest.

X. ferox (Hentz, 1847). Under debris in dumps and on juniper bushes.

X. gulosa Keyserling, 1880. Vegetation of old fields and under stones at field-wood's edge.

X. luctans (C. L. Koch, 1845). Old fields and grassy juniper stands.

X. pellax O. P.-Cambridge, 1894. On juniper bushes.

X. triguttatus Keyserling, 1880. Vegetation of old fields.

Subfamily Philodrominae

Ebo latithorax Keyserling, 1883. On beach vegetation.

Philodromus cespiticolus (Walckenaer, 1802). Shrubs of upland hardwood forest; on cedars and junipers; vegetation of old fields and beaches.

P. imbecillus Keyserling, 1880. Vegetation of old fields; shrubs and herbs of mixed hardwood-conifer forest.

P. infuscatus Keyserling, 1880. Vegetation of old fields; sandy surface and vegetation of beach along western shore line.

P. pernix Blackwall, 1846. Leaves of shrubs, bark of trees in upland hardwood forest; on cedar trees.

P. placidus Banks, 1892. On juniper bushes.

P. rufus Walckenaer, 1825. Shrubs and herbs of upland hardwood forest; on cedar trees; vegetation of old fields and roadsides.

Thanatus formicus (Clerck, 1757). Vegetation of old fields; grassy openings in mixed hardwood-conifer forest; on clumps of beach grass.

Tibellus maritimus (Menge, 1874). Roadside vegetation and juniper bushes.

T. oblongus (Walckenaer, 1802). Shrubs of upland hardwood and mixed hardwood-conifer forests; junipers; and vegetation of old fields.

Superfamily Salticoidea

Family Salticidae--Jumping Spiders

These hunting spiders are reported to have the keenest vision of all spiders. They hunt in broad daylight capturing their prey by stalking slowly and jumping quickly.

Evarcha hoyi (Peckham, 1883). Vegetation of old fields; grassy openings in upland hardwood forest.

Habrocestum pulex (Hentz 1846). On and in leaf litter of upland hardwood forest; in rock piles of old fields.

Habronattus agilis (Banks, 1893). Cedar trees and vegetation of old fields.

H. borealis (Banks, 1895). Herbaceous beach vegetation along southeastern shore line; old fields near open water.

H. calcaratus (Banks, 1904). Under stones in old fields.

Icius elegans (Hentz, 1846). Vegetation of old fields and field-wood's edge.

I. similis Banks, 1895. Shrubs and herbs of upland hardwood forest.

Metacyrba undata (De Geer, 1778). Under debris and on vegetation of old fields; on buildings.

Metaphidippus flavipedes (Peckham, 1881). Most frequently on cedar trees; shrubs and herbs of upland and mixed hardwood forests; vegetation of most beaches along shore line.

M. protervus (Walckenaer, 1837). Shrubs of upland and mixed hardwood-conifer forests; vegetation of marshes and old fields.

Neon nellii Peckham, 1888. Leaf litter of all forest types.

Paraphidippus marginatus (Walckenaer, 1837). Shrubs and herbs of all forest types; vegetation of shore lines.

Phidippus clarus Keyserling, 1884. Shrubs and herbs of upland hardwood forest; vegetation of clearings in old fields and flower gardens; under debris in dumps.

P. purpuratus Keyserling, 1884. Under stump fragments, bark, stones and boards in forests and fields.

Salticus scenicus (Clerck, 1757). Shrubs of upland hardwood forest; vegetation of old fields, beaches and flower gardens; in and on buildings.

Sitticus palustris (Peckham, 1883). Vegetation of old fields; shores of inland lakes and northern shore lines.

Section Cribellatae

Superfamily Dictynoidea

Family Dictynidae--Mesh-web Spiders

Most of these species build small dense webs at the tips of dried weeds, at the distal ends of shrub and conifer branches, or under the rolled edges of leaves. Some are found only in leaf litter.

Dictyna annulipes (Blackwall, 1846). On grasses in clearings of upland hardwood forest; on beach vegetation.

D. bostoniensis Emerton, 1888. On cedar trees and herbaceous vegetation near open water; old fields.

D. brevitarsus Emerton, 1915. Leaf litter of mixed hardwood-conifer forests.

D. coloradensis Chamberlin, 1919. On beach vegetation; on junipers; vegetation of old fields and roadsides.

D. foliacea (Hentz, 1850). In grassy areas of old fields.

D. maxima Banks, 1892. Under leaves of shrubs in upland-hardwood forest.

D. minuta Emerton, 1888. On cedar trees.

D. sancta Gertsch, 1946. Herbaceous vegetation of beach along northeastern shoreline.

D. sublata (Hentz, 1850). On cedars, shrubs and herbs of upland hardwood forest.

D. volucripes Keyserling, 1881. Shrubs and herbs of upland hardwood forest; vegetation of grassy fields.

Lathys foxii Marx, 1891. Leaf litter of all forest types.

L. pallida (Marx, 1891). Leaf litter of all forest types.

Family Uloboridae--Hackled-band Orb Weavers

Hyptiotes cavatus (Hentz, 1847). Low tree branches and shrubs of mixed hardwood-conifer forest.

Family Amaurobiidae--Hackled-band Weavers

Subfamily Amaurobiinae

Callobius bennetti (Blackwall, 1846). Under logs and in leaf litter of all forest types; in rock piles; on cedar trees.

Subfamily Ixeuticinae

Titanoeca americana Emerton, 1888. Leaf litter of mixed hardwood-conifer forests.

Walmus borealis (Emerton, 1909). Leaf litter of upland and mixed hardwood forests.

TABLE 3. Summary of the spiders of Beaver Island

Families	Genera	Species
Theridiidae	10	18
Linyphiidae	11	16
Micryphantidae	22	37
Epeiridae	11	18
Tetragnathidae	3	9
Mimetidae	2	2
Agelenidae	5	10
Hahniidae	1	2
Pisauridae	1	3
Lycosidae	6	23
Gnaphosidae	6	6
Clubionidae	5	16
Thomisidae	8	19
Salticidae	11	16
Dictynidae	2	12
Uloboridae	1	1
Amaurobiidae	3	3
Total: 17	108	211

The number of species known to occur on the island is approximately one-half that which occurs on the mainland of Wisconsin or Michigan (Tables 4 and 5). This reduced number not only reflects the absence of many species but of families as well. Of these, the absence of Oxyopidae and Anyphaenidae should be noted for representatives of these families are relatively abundant in specific ecological situations. Muma and Muma (1949), Whitcomb et. al., (1963) and Brady (1964) report species of Oxyopidae to be very abundant in old fields and grassy areas. Of the two oxyopid species occurring in Michigan (Drew, in preparation), Oxopes scalaris is fairly common in areas of the Southern Peninsula that are ecologically similar and geographically near the island. Therefore, its absence is that much more noticeable. The lack of representatives of the family Anyphaenidae is of equal interest for these are also relatively abundant (Lowrie, 1948). Here, however, we may be confronted with geographical distribution entirely, because the four species recorded for Michigan have been collected from southern counties only (Drew, op. cit.). This same distributional pattern applies also to Wisconsin (Levi and Field, 1954; and Levi, Levi and Kaspar, 1959).

The absence of representatives of eight other families (Atypidae, Oonopidae, Dysderidae, Scytodidae, Pholcidae,

Table 4. Web-weaving families of Beaver Island, Michigan and Wisconsin

Families	Beaver Island	Michigan	Wisconsin[1]
Pholcidae	-	1,1[2]	2,2
Theridiidae	10,18	15,43	14,41
Nesticidae	-	-	1,1
Linyphiidae	11,16	14,23	16,33
Micryphantidae	22,37	30,56	37,67
Epeiridae	11,18	17,36	20,43
Theridiosomatidae	-	1,1	1,1
Tetragnathidae	3,9	3,15	4,14
Oecobiidae	-	1,1	-
Dictynidae	1,1	3,25	4,15
Uloboridae	1,1	2,3	2,2
Amaurobiidae	3,3	3,4	3,3
	63,114	89,208	104,222
	54.1%	51%	51.2%

1 Modified from Levi and Field (1954) and Levi, Levi, and Kaspar (1958).

2 The number preceeding the comma is the number of genera; that following the comma is the number of species.

Table 5. Hunting families of Beaver Island, Michigan and Wisconsin

Hunting families	Beaver Island	Michigan	Wisconsin
Atypidae	-	1,1	1,1
Oonopidae	-	1,1	-
Dysderidae	-	-	1,1
Scytodidae	-	1,1	1,1
Mimetidae	2,2	2,5	2,5
Agelenidae	5,10	5,15	6,15
Hahniidae	1,2	3,4	3,4
Pisauridae	1,3	2,7	2,5
Lycosidae	6,23	7,35	8,36
Oxyopidae	-	1,2	1,2
Gnaphosidae	6,6	11,21	12,28
Clubionidae	5,16	8,29	7,28
Anyphaenidae	-	3,4	2,3
Thomisidae	8,19	12,42	11,35
Salticidae	11,16	23,49	28,48
	45,97	80,216	85,212
	45.9%	49.0%	48.8%
Total[1]	108,211	169,426	189,434

[1] Figures are total number of genera and species for each geographical area compared in Tables 4 and 5.

Nesticidae, Theridiosomatidae and Oecobiidae) (Tables 4 and 5) will be discussed below.

Two species which are frequently found on the surrounding mainlands were not collected on the island. These are: Argiope aurantia, the banded orb-weaving garden spider; and Phidippus audax, a usually common and most conspicuous jumping spider. Despite repeated collecting attempts throughout the growing season, neither mature nor immature forms of these two species were found.

Spider Populations of Specific Communities

Old Fields. The spider populations representative of this community inhabit the upper portions of standing vegetation. In order to learn more about diurnal and seasonal succession in the old field community, collecting was done during the morning and afternoon hours on the same day in July; and in July and September.

On 13 July 1963, six sweeping samples were taken during two different periods of the day: three at 10:00 A.M. and three at 2:00 P.M. The afternoon samples were taken from the same areas as those in the morning. Of the 14 species collected, six were present in both samples, five unique to the morning samples and three unique to the afternoon samples (Fig. 5). Each series of samples had one species that was not collected in subsequent quantitative

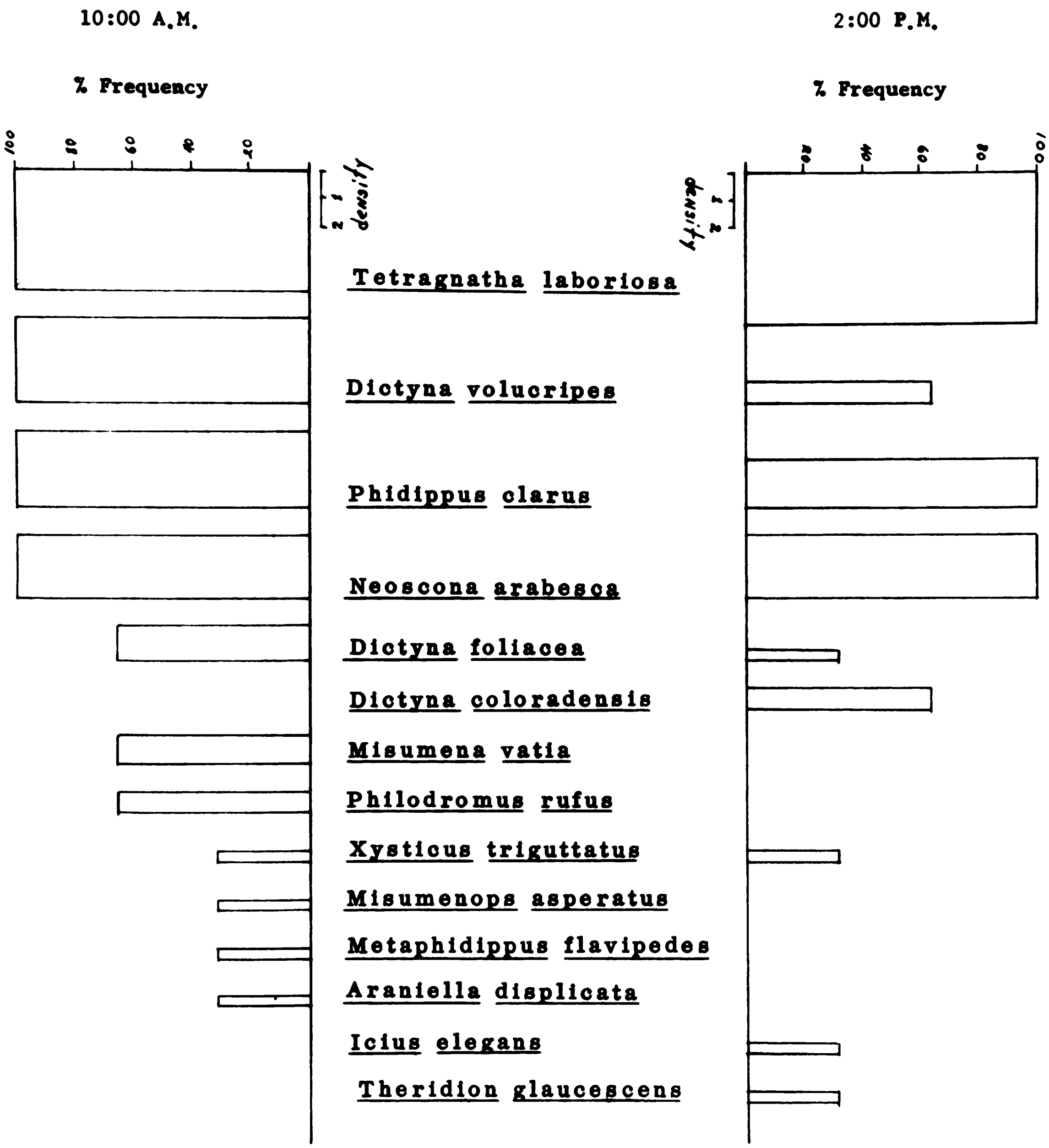
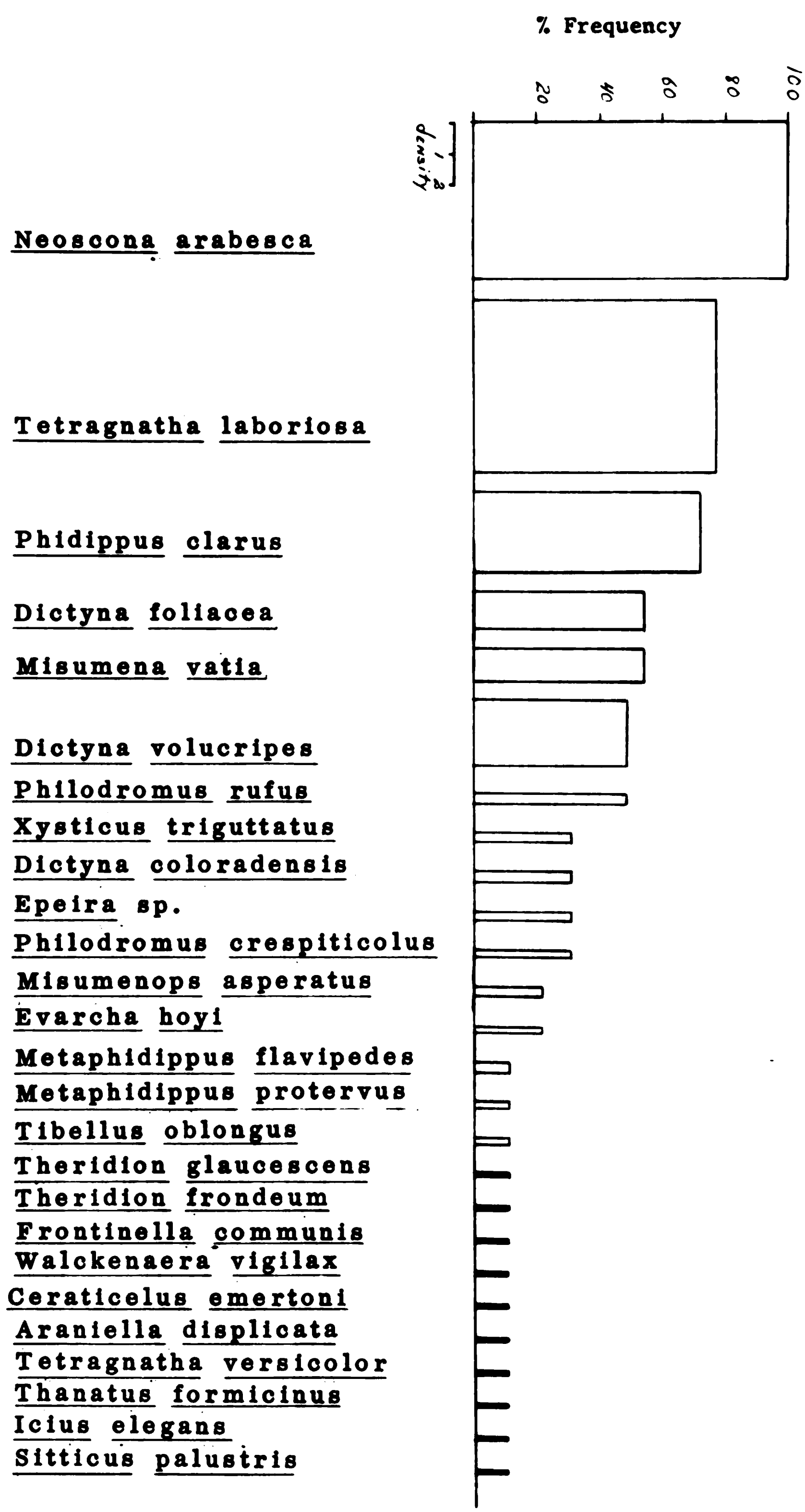


Figure 5. Frequency-density diagrams of the spider populations at different times on the same July day in the old field community.

collecting in this community. They were *Metaphidippus flavipedes* in the morning sample and *Dictyna coloradensis* in the afternoon sample. *Tetragnatha laboriosa* was the most abundant species in both series of samples. It had a frequency of 100% in both series; but a density of 4.0 in the A.M., and a density of 5.3 in the P.M. In the morning samples, *Dictyna volucripes*, *Phidippus clarus* and *Neoscona arabesca*, in this order, followed *T. laboriosa* in abundance. In the afternoon series *N. arabesca* followed *T. laboriosa* at the same value of abundance as in the morning. *P. clarus*, at a somewhat lesser figure, was next most abundant and replaced *D. volucripes* in order of abundance. The abundance of the latter species was greatly reduced and was equaled in abundance by a congenic species, *D. coloradensis*, which was not present in the morning series.

The first series of samples evaluating seasonal succession was taken during morning hours in July 1963. Nine sweeping samples gave evidence that 26 species were present in this community (Fig. 6). The three most abundant species had densities greater than the remaining 23. Thirteen of the 26 species were web-weavers, including two of the most abundant. *Neoscona arabesca* the most abundant species had a frequency of 100% and a density of 5.1. *Tetragnatha*

Figure 6. Frequency-density diagram of the spider populations in the old field community, July 1963.



laboriosa had a greater density, 5.6, but a frequency of 77.8%. The two most abundant hunting species, Phidippus clarus and Misumena vatia followed but in greatly reduced abundance.

A series of five sweeping samples taken in the mornings of the first week in September 1963, contained a total of 14 species (Fig. 7). A considerable reduction in abundance as compared with the July samplings is apparent. Also, there were present six species not collected in July. T. laboriosa was most abundant with a frequency of 60% and a density of 4.6. It was followed by Philodromus crespiticolus, Icius elegans, Dictyna bostoniensis and Acanthepeira stellata at much lower values. Of these last four species, only I. elegans was present in July (Fig. 6), and then at a much lower abundance. Dictyna volucripes was present but replaced by D. bostoniensis in abundance. N. arabesca was present but two other web-building species, Acanthepeira stellata and Araniella displicata were each more abundant. Of the 14 species collected in this series, seven were web-building species and seven were hunting species.

Upland Hardwood Forest (Beech-Maple). Two strata of this community were sampled during August 1963. Eight beating samples of the herb-shrub stratum and 36 square-

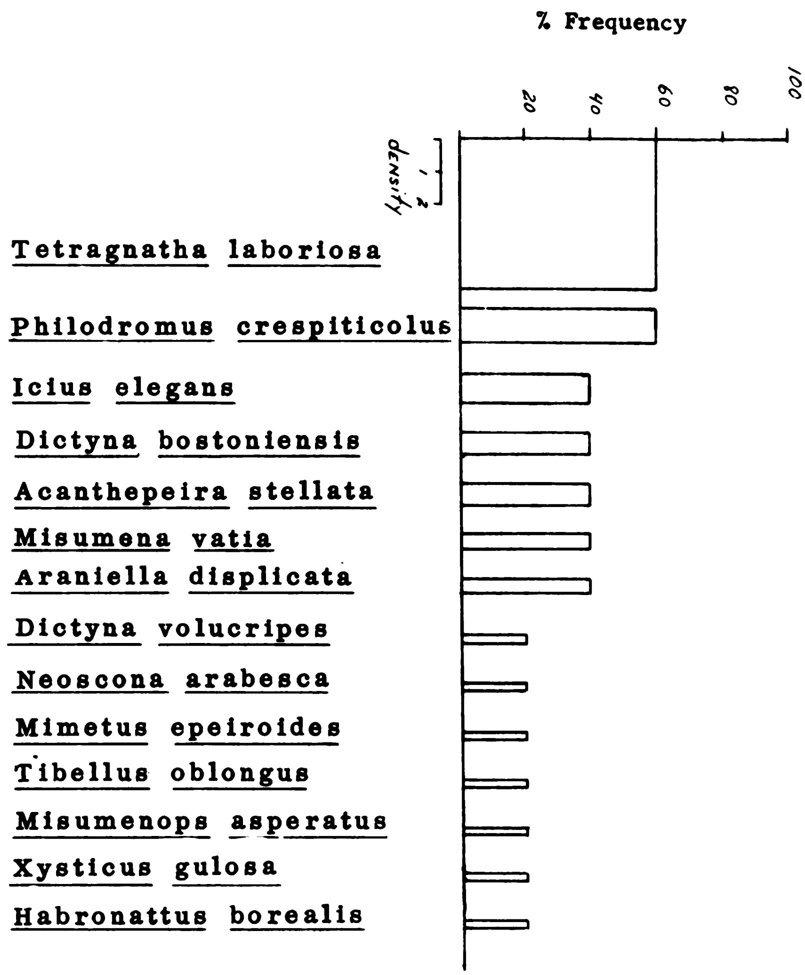


Figure 7. Frequency-density diagram of the spider populations in the old field community, September 1963.

foot samples of the leaf litter stratum were collected. Because two sampling techniques were used in these two distinct habitats, the results are not comparable. However, together they reveal the population structure of this community.

The results of the eight beating samples show a total of 17 species inhabiting the herb-shrub stratum (Fig. 8A); eleven of these are web-building species and six hunting species. Pityohyphantes costatus was most abundant with a frequency of 50% and a density of 4.5. The hunting species, Paraphidippus marginatus was next most abundant followed by the web-building species Helophora insignis.

The results of the 36 square-foot samples of leaf litter contained eleven species, seven web-building and four hunting species (Fig. 8B). Of the 36 samples taken; 17 did not contain spiders; 12 contained one specimen each; six contained two specimens (not of the same species in each case); and one contained four specimens of four different species. Oxyptila americana was most abundant with a frequency of 16.7% and a density of 0.2. Walmus borealis and Phrurotimpus alarius followed in equal but lower numbers.

Juniper Bushes, (Juniperus depressus). During July 1963, a series of three beating samples were taken in

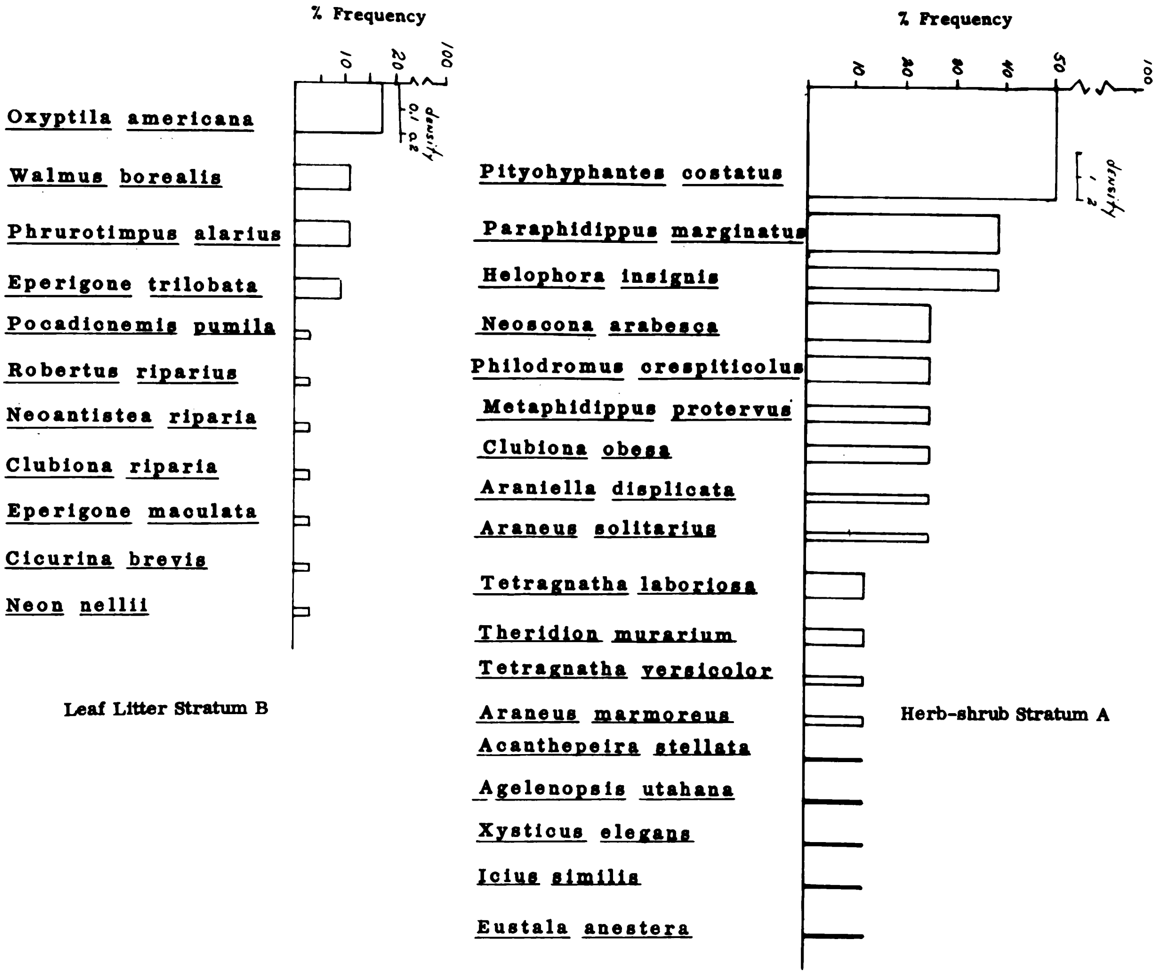


Figure 8. Frequency-density diagrams of spider populations inhabiting the herb-shrub and leaf litter strata of the upland-hardwood forest, August 1963.

juniper clumps (3' to 5' high and 5' to 12' in diameter) to ascertain the spider populations of this community. Eleven of the 15 species collected were web-building species, the remaining four were hunting species (Fig. 9). However, the combined densities of the four hunting species, 11.3, nearly equals that of the eleven web-building species, 13.5. Metaphidippus flavipedes was the most abundant with a frequency of 100% and a density of 8.0. Neoscona arabesca followed with the same frequency and a density of 4.7. The abundance of the remaining 13 species was considerably lower than these two species.

White Cedars, (Thuja occidentalis). In late July 1963, a series of three beating samples were taken in this conifer community. Two of the three most abundant species collected were hunting spiders, Metaphidippus flavipedes and Philodromus imbecillus (Fig. 10). Their combined densities, 6.3, was slightly less than that of Grammonota pictilis the most abundant species with a density of 6.7 and a frequency of 100%. Among the 12 species collected, seven were hunting and five were web-building species.

The Spider Populations of a Similar Habitat on the Island and on the Mainland of Michigan

This investigation was done to ascertain the similarities and dissimilarities of the spider populations

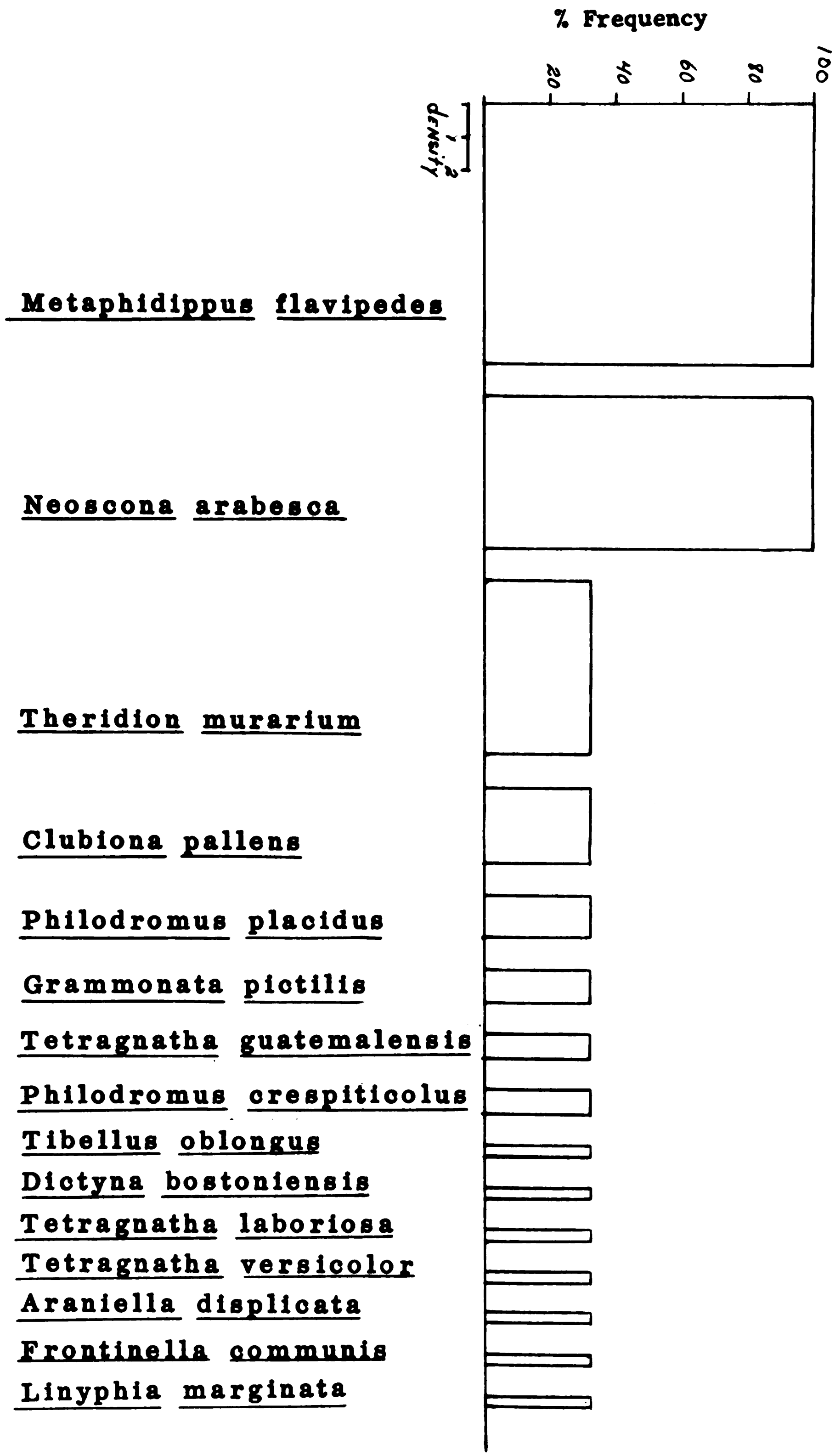


Figure 9. Frequency-density diagram of the spider populations inhabiting junipers (*Juniperus depressus*), July 1963.

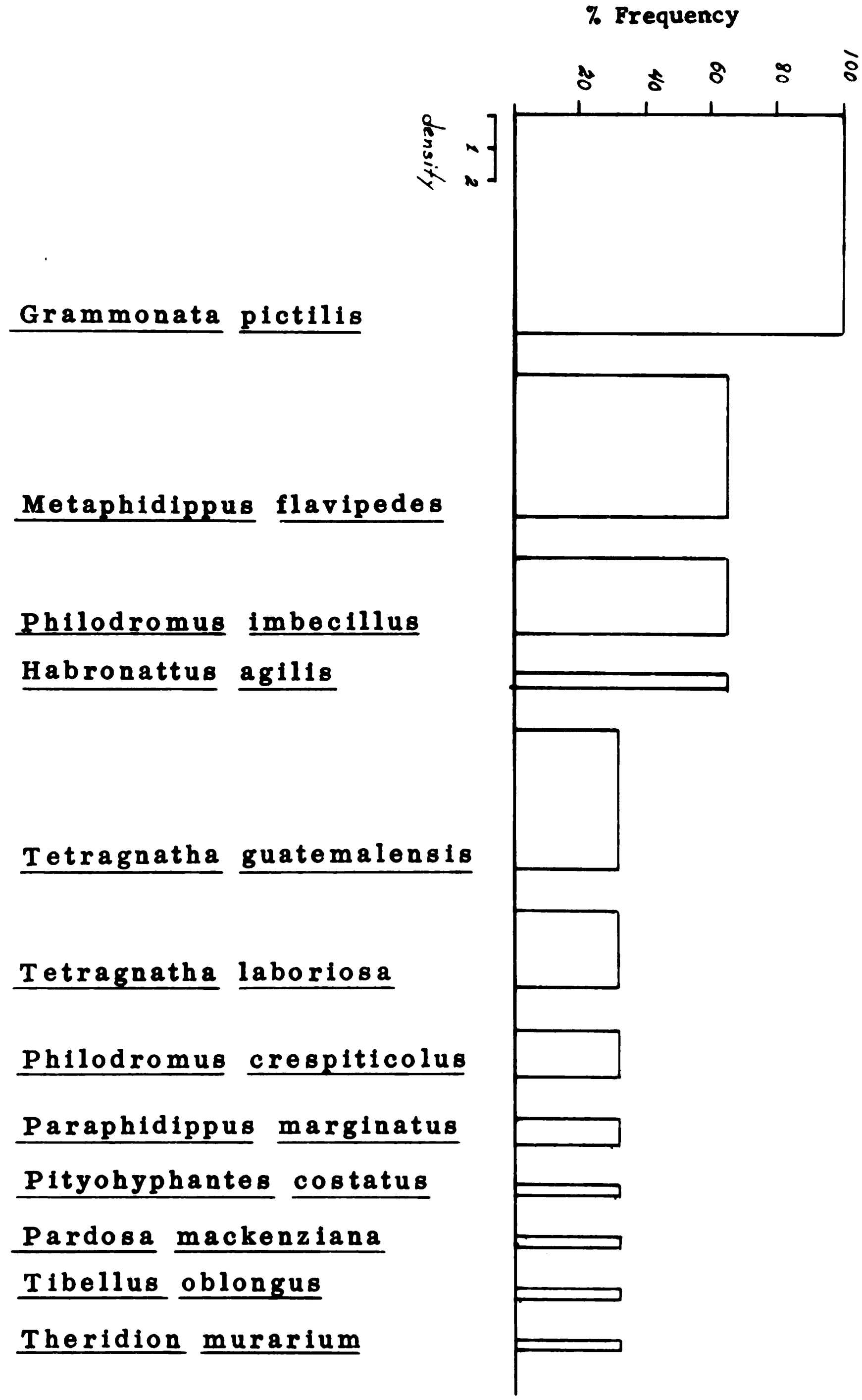


Figure 10. Frequency-density diagram of the spider populations inhabiting northern white cedars, August 1963.

inhabiting a specific ecological community occurring on the island and on the mainland. The comparison was made in terms of the number of individuals per species, the number of species in each community, and making use of these figures, the calculation of Fisher's Index of Diversity.

This study was conducted during September 1963 by analyzing 110 square-foot samples of the leaf litter stratum of two stands of mixed hardwood-conifer forest: 55 samples from the northeast portion of the island; and 55 from a similar stand, 19 miles over water to the east, on Waugoshance Point in Emmet County.

The sites studied have a number of similarities, other than forest cover, and fewer dissimilarities. The readily apparent similarities and their implications are: both are located at 45°45' north latitude and back of the shoreline, therefore, each is subjected to the same overall meteorological factors; both are generally level and vary in elevation from two to five feet above lake level, thus each has been subjected equally to the recent fluctuations of Lake Michigan; both have the same soil type (Eastport), therefore the same general drainage features; both were submerged by Lake Algonquin, were part of the exposed land mass during the Lake Chippewa Stage and were submerged once again by Lakes Nipissing and Algoma, therefore, both sites have had equal time for vegetational and soil development; and both stands border and gradually merge, on their landward sides, into oak-pine forests. Over and above the fact that one site is on an island and the other is part of the mainland, the most conspicuous difference is that the island site is located on an east-facing coast while that on the mainland is located on a west-facing coast.

No definite phytosociological analysis was made in either stand. However, the major dominant trees present are: balsam fir (Abies balsamea), white spruce (Picea glauca), northern white cedar (Thuja occidentalis), white birch (Betula papyrifera), quaking aspen (Populus tremuloides), bigtooth aspen (P. grandidentata). Scattered amongst these species are: white pine (Pinus strobus), red pine (P. resinosa), hemlock (Tsuga canadensis), and red oak (Quercus rubra). Both stands are considered to be more closed than open. That is, the conifer species are of such abundance that even though the deciduous trees may be bare of leaves, the forest still has the appearance of being in leaf-out condition during the entire year. As a consequence, the litter layer of this forest type is never exposed to wind penetration as is that of a homogeneous deciduous forests. Also, the litter layer is in relatively continuous shade. Both these factors, reduced wind penetration and abundant shade, would be conducive to restricting the spiders to the litter and preventing, or at least greatly reducing aerial dispersal of the species present. For, as Duffey (1956) concluded, it takes a combination of rising temperatures which induce aeronautic behavior and winds of sufficient velocity to carry the exposed spiders to new or less densely populated habitats. It is assumed, therefore, that these populations present in this stratum of mixed hardwood-conifer forest are confined populations.

The leaf litter, or L layer, habitat of this forest is in part Type I Curled and in part Type II Needle according to classification by Heatwole (1961). That is the interstices, which are of importance to the resident fauna, vary from fairly large due to the curled or rolled deciduous leaves to small and angular in the conifer litter. Further, because the samples were collected in September before leaf fall, the litter had been subjected to the chemical and physical processes of humification for at least a year.

Sampling of the leaf litter habitat was done randomly eliminating the preference of either of the two litter

types. This sampling method satisfied the major criterion for using Fisher's Index of Diversity in that the specimens, and not the samples, must be randomly selected. The assumption that the spiders in this specific community are randomly distributed is based on the conclusion put forth by Cole (1946), who found that of the cryptozoa distributed under various sized boards placed on a forest floor, only spiders displayed a random distribution.

The results revealed that a total of 78 species of 52 genera representing 15 families inhabited this leaf litter community. Table 6 contains a listing of these species together with the number of individuals per species for each of the two sites. Of the 78 species present, 25 (32.1%) were common to both areas, 34 (43.6%) were present only in the island study site, and 19 (24.3%) occurred only on the mainland site.

Further summation of the data is contained in Table 7. There were 14 families represented by 59 species and 424 specimens in the island's community, and 13 families represented by 44 species and 162 individuals in the mainland site. Categorized in terms of food-getting habits, 39 or 66.1% of the island's 59 species and 25 or 56.8% of the mainland's 44 species were web-weavers; 20 or 33.9% of those on the island and 19 or 43.2% of those on the

Table 6. Species inhabiting leaf litter of mixed hardwood-conifer forest on Beaver Island and on Waugoshance Point

Species	Number of Individuals Beaver Island	Mainland
Theridiidae		
Euryopis argentea	-	3
Paidisca unimaculata	2	-
Robertus laticeps	2	-
R. riparius	20	2
Theridion frondeum	-	1
T. ornatum	-	3
T. sexpunctatum	2	-
Linyphiidae		
Centromerus latidens	6	-
C. persoluta	9	1
Helophora insignis	1	2
Lepthyphantes nebulosa	1	-
L. zebra	2	1
Micryphantidae		
Ceraticelus alticeps	1	-
C. communis	-	1
C. fissiceps	4	2
C. laetabilis	5	-
C. minutus	1	-
C. rugosa	-	4
Ceratinella brunnea	11	1
Cochlembolus pallidus	15	-
Cornicularia clavicornis	2	-
C. indirecta	3	-
C. minuta	-	1
C. pallida	3	-
Eperigone maculata	2	-
E. trilobata	1	4
Floricomus plumalis	3	-
Maso sundevalli	3	1
Pelecopsis moestum	5	2
Pocadicnemis hartlandiana	2	-
Sciates truncatus	4	-
Scirites pectinatus	-	1
Sisicottus montanus	12	7
S. monitgenus	2	-

Table 6. (continued)

Species	Number of Individuals Beaver Island	Mainland
Micryphantidae (cont'd.)		
Sisicus penifusiferus	7	-
Tapinocyba minuta	24	-
T. simplex	22	-
Tunagyna debilis	2	-
Epeiridae		
Epeira patagiata	-	1
Mimetidae		
Ero leonina	1	-
Tetragnathidae		
Tetragnatha harrodi	-	2
T. laboriosa	-	1
Pachygnatha kuratai	9	-
Agelenidae		
Agelenopsis utahana	1	4
Cicurina arcuata	-	2
C. brevis	10	-
C. robusta	-	1
Cryphoeca montana	7	-
Hahniidae		
Hahnia cinerea	12	2
Neoantistea riparia	3	3
Lycosidae		
Lycosa gulosa	3	-
L. pratensis	1	2
Pardosa milvina	1	2
Pirata marxii	1	-
Schizocosa crassipes	-	1
Gnaphosidae		
Zelotes subterraneus	3	-

Table 6. (continued)

Species	Number of Individuals Beaver Island	Mainland
Clubionidae		
Agroeca ornata	1	-
Clubiona kastoni	-	2
C. pallens	-	3
C. riparia	2	8
Phrurotimpus alarius	12	4
P. borealis	-	4
Scotinella divestus	-	1
Thomisidae		
Oxyptila americana	49	37
Philodromus aureolus	1	-
Thanatus coloradensis	-	1
Tibellus oblongus	1	-
Xysticus elegans	1	2
Salticidae		
Neon nellii	29	4
Paraphidippus marginatus	1	1
Dictynidae		
Dictyna bostoniensis	-	5
D. brevitarsus	5	-
D. coloradensis	2	-
Lathys foxii	13	4
L. pallida	30	17
Amaurobiidae		
Callobius bennettii	2	1
Titanoica americana	2	-
Walmus borealis	42	10
	424	162

Table 7. Comparisons of the spider populations inhabiting leaf litter

Families	Beaver Island No. of species	Beaver Island No. of individs.	Mainland No. of species	Mainland No. of individs.
Salticidae	2	30	2	5
Thomisidae	4	52	3	40
Clubionidae	3	15	6	22
Gnaphosidae	1	3	-	-
Lycosidae	4	6	3	5
Hahniidae	2	15	2	5
Agelenidae	3	18	3	7
Tetragnathidae	1	9	2	3
Mimetidae	1	1	-	-
Epeiridae	-	-	1	1
Micryphantidae	22	134	10	24
Linyphiidae	5	19	3	4
Theridiidae	4	26	4	9
Dictynidae	4	50	3	26
Amaurobiidae	3	46	2	11
Totals	59	424	44	162
Web-weaving species	39 (66.1%)		25 (56.8%)	
Hunting species	20 (33.9%)		19 (43.2%)	
Index of Diversity	18.62 (17.07-20.17)		19.88 (17.20-22.36)	

Index of Diversity for combined samples:
17.50 (16.53-18.47)

mainland were hunting species. These data indicate the mainland populations of web-weaving and hunting species are much more nearly equal in number. On the island, the number of web-weaving species dominates the hunting species nearly 2 to 1. In addition, the total number of individuals from the island sample is 2.62 times larger than that of the mainland.

Of the 55 samples collected on the island, four were without spiders as were 15 of the 55 samples collected on the mainland. However, the Index of Diversity for each community showed no significant difference: 18.62 (17.07-20.17) for the island; 19.88 (17.20-22.36) for the mainland. Further, when the Index is calculated on the combined samples (78 species and 586 individuals), again there was no significant difference; 17.50 (16.53-18.47). According to Williams (1944), these results would indicate that the samples were from the same population. These results reflect a further characteristic of this Index: the values are small and there are a large number of individuals representing a much smaller number of species.

CONSIDERATIONS ON THE ORIGIN OF THE ISLAND FAUNA

Zoogeographic Aspects

Studies by several authors on the impoverished vertebrate faunae of the island have indicated that relatively little morphological variation has taken place, and the species present are for the most part identical with those of the mainland of Michigan. Effects of isolation have been recorded by Hatt, *et*. *al*. (1948) for one species of amphibian, the Redbacked Salamander (*Plethodon cinereus cinereus* (Green)), and two species of snakes, the Milk Snake (*Lampropeltis triangulum triangulum* (Lacèpéde)) and the Water Snake (*Natrix sipedon sipedon* (Linnaeus)). Hatt *et*. *al*. (*op*. *cit*.) conclude that fifteen of the remaining 16 species of the herpetological fauna have been derived from the Southern Peninsula of Michigan. The one exception is the Painted Turtle (*Chrysemys picta marginata* Agassiz), which is similar to those found in the Northern Peninsula of Michigan and in Wisconsin. According to Ozoga and Phillips (1964), the mammal populations of the island most closely resemble those of the Northern Peninsula. With the exception of the Western House Wren (*Troglodytes aedon parkmanii* Audubon), the avifauna resembles the Southern Peninsula (Hatt, *et*. *al*., 1948). To date, 163 bird species have been recorded for the island (Drew and

Phillips, 1964). This figure represents less than half the number of birds that could reach the island (by flying) from the adjacent mainland of Michigan.

The data on the herpetological and mammal faunae suggest accidental introductions, with the exception of the amphibian and snakes mentioned above, rather than relict populations derived from individuals which made use of the exposed dry land during the low-water or Lake Chippewa stage. The open water separating the island from the mainland masses is considered to be an effective barrier to most terrestrial vertebrates. However, during the winter when the island is ice locked to the mainland, some species may use this bridge to gain access to or leave the island (Ozoga and Phillips, 1964).

The relative ease of transport (winds/air currents) available to many species of spiders rules out obvious terrestrial barriers. This is reflected by the fact that of the 211 species presently known to occur on the island, 167 species or 79.1% are common to Wisconsin to the west and Michigan to the north and east. Further, a western component, species occurring in Wisconsin and not in Michigan, is represented on the island by 20 species or 9.5% of the total. The majority of these 20 species presently occur in northern Wisconsin (10 species) or are scattered over the entire state (five species); and the remainder (five species) are either west-central or southern in distribution. There are 16 species (7.6%) on the island that occur in Michigan and not in Wisconsin. Of this number, 15 occur on adjacent mainland to the north and east; and only one is from the southern portion of the state. In conjunction with these components, there are eight species or 3.8% of the total that are unique to the island; they have not been recorded for the surrounding mainlands of Wisconsin or Michigan. These species currently have known distributions confined to the northeastern regions of the United States. The above figures strongly suggest the influence of the nearby mainlands on the island with reference to the source of spider species. That the vagaries of the wind may be important in distribution is reflected by the number of species presently unique to the island as well as those in common with Wisconsin and not Michigan, and conversely.

Wind as a Factor in Distribution

Aerial dispersal by several species of spiders in boreal and temperate regions of North America and Europe have been recorded by many investigators. Air-borne spiders have been observed 60 miles from the nearest mainland

(Darwin, 1896) and at an altitude of 5,000 feet (Glick, 1939). This means of dispersal is characteristic of the juveniles of many species soon after hatching. Several species of the families Linyphiidae and Micryphantidae, all small (1 mm. to 3 mm.) spiders even as adults, make regular use of this means of dispersal to the point that members of these families are described as having aeronautical behavior. This behavior appears to be correlated with population density (Duffey, 1956) and occurs during the fall, winter and spring. Consequently, year round fluctuating winds could be mixing spiders from several populations and depositing them in other areas. This means of dispersal undoubtedly accounts for the disruptive distribution patterns of many species of spiders.

Besides the direct influence of winds, there is the indirect influence as shown by surface current patterns on lakes. These patterns are induced by the transfer of kinetic energy from the wind to the surface of the water through wind stress. Because of this, currents respond quickly to changes in the intensity and direction of winds (Sverdrup, *et*. *al*., 1942).

The most recent study on the surface current pattern in Lake Michigan was done by the Great Lakes Research Institute (Ayers, *et*. *al*., 1958). This study revealed that under the influence of the prevailing westerly winds of June, believed to approximate the normal summer circulation, the northern region of this Lake is dominated by the outflow current as it flows toward the Straits of Mackinac (Fig. 11). The current originates near the center of the western shore of the lake and dips into the lower end before flowing northward along the west coast of Michigan. This pattern coincides with that found by Harrington (1895). The second phase of the surface current study was conducted during August after the Straits region had been under the influence of an easterly wind for eight days. The pattern at this time was a strong southward current that flowed from the Straits along the eastern edge of the lake to the lower end before turning northward (Fig. 12).

Evidence to support the role of surface currents in spider dispersal was found during the course of this study. Living representatives of 17 species were found trapped in the surface tension 25 to 30 feet off the eastern shoreline of the island (Table 8). Of these, 14 species are known to occur on the island, Wisconsin and Michigan. The remaining three species have not been collected on the island. Of these, one species occurs in northern Wisconsin and two in the Southern Peninsula of Michigan. They

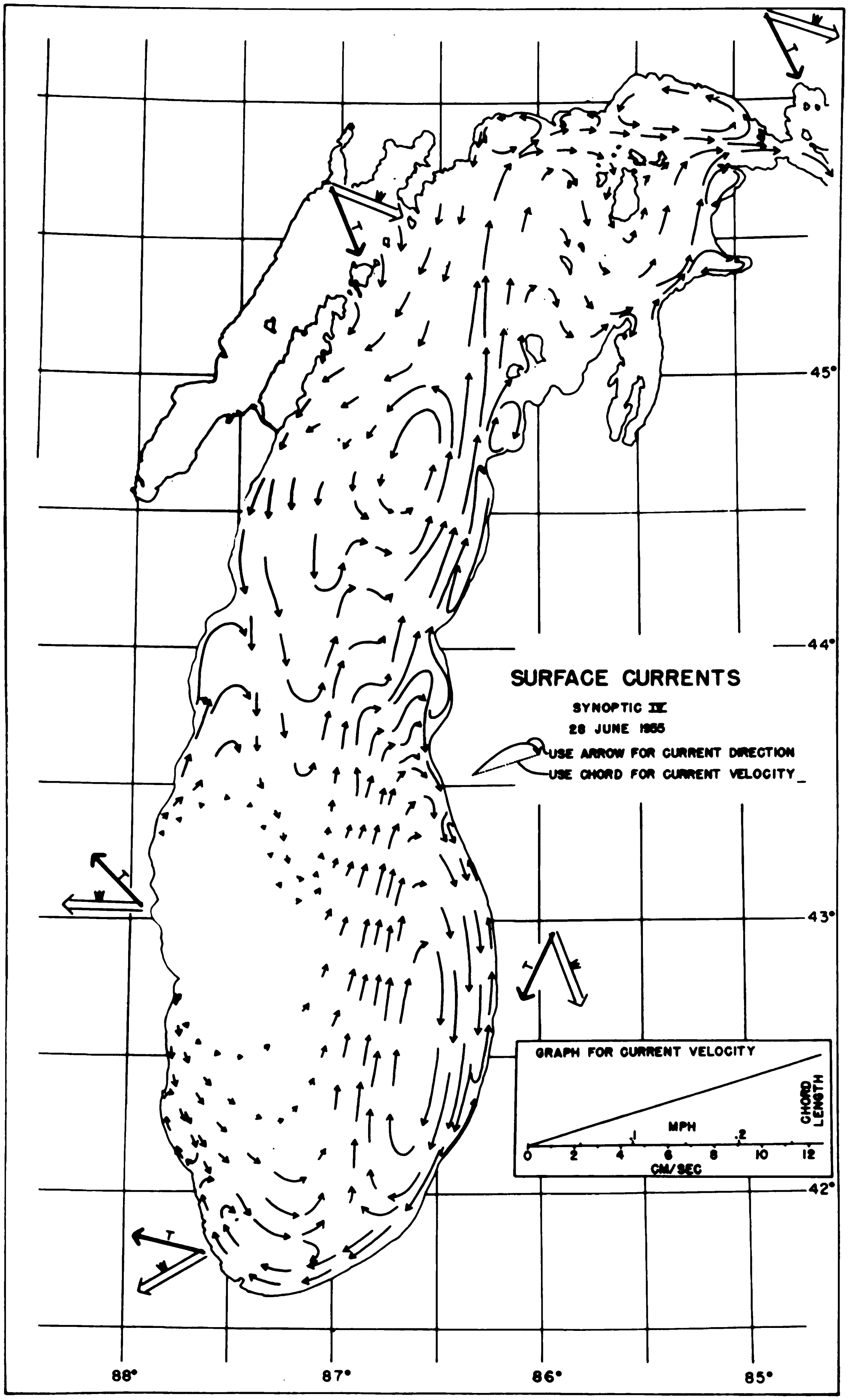


Figure 11. Summer surface currents in Lake Michigan according to Ayers, et. al., 1958.

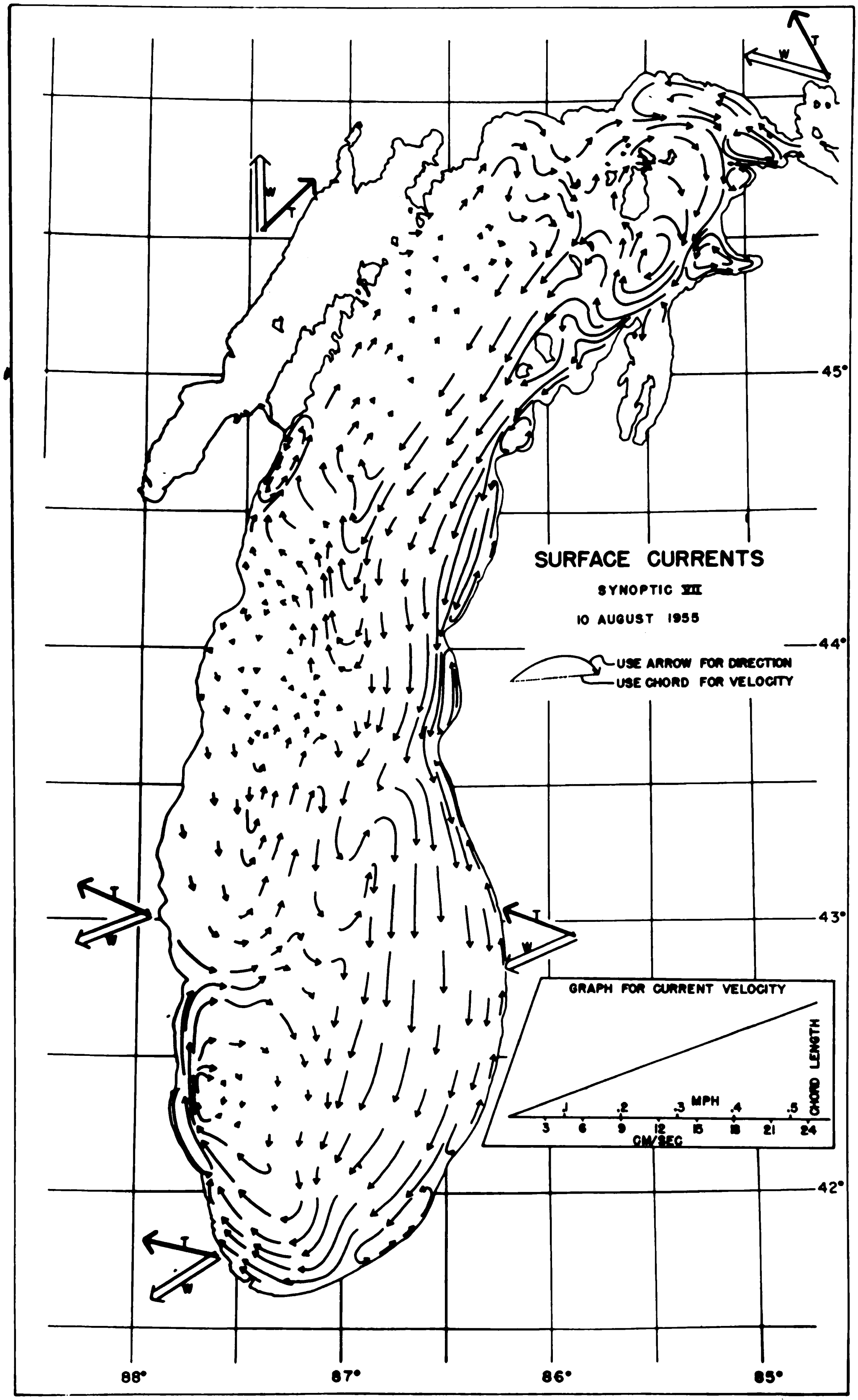


Figure 12. Variation of summer surface currents in Lake Michigan according to Ayers, et. al., 1958.

Table 8. Species found on the surface of Lake Michigan

Families and species	No. of individuals	Sex[1]
Theridiidae		
Theridion frondeum	4	M
T. glaucescens	1	M
Linyphiidae		
Bathyphantes pullatus	1	M
B. pallida[2]	2	M,F
Micryphantidae		
Ceratinopsis laticeps[3]	1	M
Erigone atra	3	2M,1F
Minyriolus arenarius[3]	1	F
Tetragnathidae		
Tetragnatha laboriosa	1	F
Gnaphosidae		
Drassyllus sp.	1	Imm.
Clubionidae		
Micaria montana	1	Imm.
Thomisidae		
Philodromus rufus	1	F
Tibellus oblongus	1	Imm.
Xysticus spp.	3	Imm.
Salticidae		
Icius similis	2	M
Phidippus rimator	1	Imm.
Talavera minuta	1	M

1 M = males, F = females, Imm. = immature.

2 Occurs in northern Wisconsin but not in Michigan nor the island.

3 Occurs in southern Michigan but not in Wisconsin nor the island.

evidently became trapped in the surface tension after being deposited by dying winds and were then carried by currents eddying off the shore of the island. There is no way of determining the period of time the spiders were trapped in the surface tension. However, the flexible metabolic requirements of spiders and the fact that their need for water is more critical than for food gives them a distinct advantage to survive such transport. It should be noted that these specimens were found during periods of no appreciable wind. Possibly, with winds of sufficient velocity, spiders could be extricated from the surface tension and continued on their passive journey.

Distribution Through Human Activities

Human activities may have influenced spider distribution. Travel, trade and agricultural activities on the island and between the island and mainlands have existed for some time.

Some species could conceivably have reached the island on the canoes and boats of Indians and early white settlers. Quimby (1960) maintains that the Chippewa, Potawatomi and possibly the Ottawa Indians used the islands in northern Lake Michigan as hunting and fishing sites during the summer months. Visitations to the island by early white settlers for exploratory or social activities are well known (Bald, 1961). Sporadic boat travel to and from Beaver Island continued and later, as it exists today, became more regular. No doubt, species traveled aboard as accidental passengers.

Early in the 20th century, large quantities of potatoes and fish packed in boxes and crates were exported from the island to mainland ports (pers. comm., Capt. Forrest Pratt, 1962). It is conceivable that before these crates and boxes were returned, spiders could have secreted themselves or laid egg sacs in or on them.

During the lumbering days in Michigan and Wisconsin, some of the logs were floated down rivers that drained into Lake Michigan (i.e., the Muskegon, Pere Marquette, Manistee and Menominee Rivers) (Bald, 1961). Some of these logs could have passed the mill sites and reached the open water of the Lake. Once there, currents could have carried the logs to the island. The logs, in turn, could have carried spiders or spider eggs in bark crevices; and when the logs were washed ashore, these waifs may have established themselves on the island.

In summarizing the information on the origin of the spider fauna of Beaver Island: some species may have been present since portions of the present island were exposed above post-glacial Lake Algonquin about 9000 years ago; other populations could have occupied the mass of exposed area during the low water stage which was later fractionated and isolated from the mainland mass by the formation of Lake Nipissing 3000 years ago; still others have been carried to the island by wind, air and lake currents during this latter time and up to the present; and some species were transported to the island through the activities of man.

DISCUSSION

Composition of the Spider Fauna of Beaver Island

The composition of the current spider fauna of Beaver Island is due to the interaction of the present climate of the region, the influence of the surrounding mainlands, the ecological diversity of the island, and the impact of restricted area.

The fauna is derived from at least four sources. Of the 211 species known to occur on the island, 20 species or 9.5% are common to the mainland of Wisconsin; 16 species or 7.6% are common to the mainland of Michigan; eight species or 3.8% are endemic to the island; and 167 or 79.1% presently occur on the mainlands of Wisconsin and Michigan. The large percentage (79.1%) in common with the two surrounding mainlands is a direct result of the current climate in this region of the Great Lakes, the mixing of species attributable to the winds sweeping over these areas and the similarity of post-glacial histories. Pollen profiles indicate that the present cool, moist climate was initiated approximately 2200 years ago during the Lake Algoma stage in the Lake Michigan basin (Hough, 1958, Deevey, 1949). This in conjunction with the fact that species occurring in a given area are present as a consequence of similar adaptations to the physical factors of the environment (Allee et. al., 1949) indicates that there has been sufficient time for the establishment of the current spider fauna in this area.

A measure of the ecological diversity of the spider fauna of a region is to evaluate it on the basis of food-getting behavior, web-weaving or hunting. Basic to this criterion, is the assumption that during the initial colonization of a pristine area there would be an imbalance of behavior types due to fortuitous immigration; but through time and biological maturity of the communities within an area, a balance of behavior types would be reached. This implies that available niches would be filled by species that were structurally, physiologically and behaviorally adjusted; and competition for similar niches would occur and some forms would be absent because of unavailable niches.

The application of this behavioral criterion to the surrounding mainlands discloses a Wisconsin fauna of 51.2% web-weaving and 48.8% hunting species, and a Michigan fauna of 51.0% web-weaving and 49.0% hunting species (Tables 4 and 5). Thus the ecologically diverse mainlands support spider faunae that are almost equal in web-weaving and hunting species.

The spider fauna of Beaver Island is composed of 54.1% web-weaving species and 45.9% hunting species (Tables 4 and 5). These percentages indicate an ecological situation slightly favorable to the web-weaving species which, in turn, possibly have easier access to the distributing winds than do hunting species. Implied in this evaluation is the assumption that some of the hunting species present on this island may have reached it by wandering over the exposed but presumably ecologically suitable peninsula during the 700-year long Lake Chippewa stage of the Lake Michigan basin. With the submergence of major portions of this land mass, the immigration of hunting species has been more limited than has that for the majority of web-weaving species.

Of the 27 families known to occur in this region (Tables 4 and 5), 10 are not represented on the island. The absence of these may be accounted for on the basis of the restricted area of the island or, as Anderson (1960) defines this phrase, dearth of niches. This indicates that the available niches are occupied, leaving little if any chance for encroachment by ecologically similar but less favored forms. This may in part account for the absence of species of Oxyopidae and Anyphaenidae. These species are hunting spiders that are usually abundant in grassy fields and shrubs of wooded areas. Quantitative sampling of these areas (Figs. 5-8) reveals that hunting species of the families Salticidae, Thomisidae and Clubionidae are abundant and may be filling these niches quite adequately. Or, possibly, the absence of oxyopid and anyphaenid species represents a stage in the ecological evolution of the spider fauna. Perhaps these species occur in the relatively youthful stages of the development of a community; or, become established during the later or more mature stages.

The remaining eight families are relatively rare on the surrounding mainlands where they are represented by one species each. The exception - Pholcidae - is represented in Wisconsin by two species of two genera, but neither are abundant (Levi and Field, 1954).

Spider Populations of Specific Communities

The structure of the spider populations inhabiting four real communities has been graphically presented in

Figures 5-10. These population profiles indicate that two or three species dominate each community in abundance.

With reference to food-getting behavior, web-weaving species dominate the following communities: Old Field (September), 57.2%; Beech-Maple shrubs, 62.0%; and the Junipers, 66.7%. Hunting species dominate the leaf litter community of Beech-Maple forest, 54.6%; and the Northern White Cedars, 58.3%. The Old Field community in July was equally balanced with 50% of each type species.

Diurnal succession in the Old Field community in July revealed that *Dictyna coloradensis* is more active later in the day than is *D. volucripes*. This behavioral difference may be of value in future descriptions of these two morphologically similar species.

Two species, *Tetragnatha laboriosa* and *Philodromus crespiticolus* occur, at varying rates of abundance, in all of the communities sampled. Evidently these communities are microclimatologically similar and/or these two species have a wide range of tolerance.

The Spider Populations of a Similar Habitat on the Island and on the Mainland of Michigan

The results of the logarithmic series of Fisher, *et. al.*, indicate that the species-diversity values of the leaf litter populations on the island and the mainland are similar. Moreover, the value obtained from the combined samples indicates the samples could be from the same population. This similarity of spider faunae could only have developed during the time since the two sites were exposed after the demise of Lake Algoma 2200 years ago even though they have been separated for approximately 5000 years.

Because both sites currently support ecologically similar communities, it is quite probable that the environmental factors of each are identical. Because these factors may have adverse as well as beneficial effects on individuals occurring in specific habitats within the communities, the abundance of the species present can be favorably or unfavorably affected. Clark et. al. (1964) maintain that effects of environmental factors tend to combine multiplicatively and are reflected by the relative abundance of the individuals of a species which inhabits a community. Basically, it is this relative abundance that is evaluated by species-diversity values. Thus, the similarity of the spider populations inhabiting the leaf litter of these ecologically similar though geographically separated sites is the product of the interaction of environmental factors and the tolerance ranges of the individuals comprising a species.

This similarity of the populations inhabiting the separated communities does not mask a number of dissimilarities. In 51 samples from the island, 424 individuals were collected and from 40 mainland samples, 162 individuals. These figures yield crude densities (Odum, 1959) of 8.3 spiders/sq. ft. of litter contrasted with 4.1 spiders/sq. ft. of litter. This dissimilarity indicates that the carrying capacity of the island is much greater than that of the mainland.

Also, on the island, the web-weaving species dominate the hunting species almost 2 to 1 (1.95 - 1). The community on the mainland supports a more nearly balanced proportion of 1.32 - 1 a figure very similar to the ratio for the entire mainland of Wisconsin or Michigan. Thus the web-weaving species are favored in some manner in the island community.

These two dissimilarities appear to be reflections of a more biologically interesting feature--the establishment and subsequent divergence of the populations currently occupying these similar but separated communities.

The premise that the island populations originated independently is based on several geological features outlined and discussed above. The island populations are not isolated portions of established populations but rather are the results of fortuitous immigrations from parental populations. This implies the formation and development of a gene pool that initially would be quite different from that of a segment of the mainland populations. This possibility could be explained in terms of the founder principle of Mayr (1963) which postulates that the small gene pool would, in time, develop into a large population in which the genes have adaptive values different than those of the parental population. These changes are the end results of genetic drift, recombinations and to a lesser extent mutations. This genetic substrate in the confines of the simplified island environment and under the protection of isolation could contribute to high population densities. In addition, because of the aeronautic behavior of many families of web-weaving species, a predominance of these over the hunting species would be expected in such isolated situations.

SUMMARY AND CONCLUSIONS

A total of 211 species representing 17 families and 108 genera have been collected on this 58-square mile island during the course of this study. Though this number may seem large, it is just less than one half of the number recorded for Wisconsin and for Michigan. This disparity in species number takes on added interest because the island has 30 of the 33 plant communities found in Michigan and was once connected to that mainland. The primary means of dispersal available to most spiders is on wind and air currents. Thus, the species found on the island have reached it either by this passive means or by individual effort--wandering--during the 9000 years since portions of the island were first exposed and, later, temporarily landlocked to the mainland of Michigan. The following statements summarize some of the findings concerning the spider fauna of Beaver Island:

1. The fauna has four geographic components: species in common with both Wisconsin and Michigan; species in common with Wisconsin only; species in common with Michigan only; and, species endemic to the island. The major portion (167 species, 79.1%) is common with the surrounding mainlands; the minimal portion (8 species, 3.8%) represents the endemic component.
2. The spider populations inhabiting specific communities are structured with reference to the parameters of frequency and density and the food-getting behavior of each species.

3. Positive evidence in the form of 17 species indicates access to the island is accomplished through indirect effect of the wind, namely, surface currents of Lake Michigan.
4. The carrying capacity of the hardwood-conifer leaf litter community on the island is more than twice that of the mainland.
5. There are no significant differences between Fisher's Index of Diversity values for the island and mainland populations inhabiting the hardwood-conifer litter. The calculated values indicate these populations could be segments of the same population even though they are currently separated by 19 miles of open water.
6. The similarity of the Index values is attributed to the interaction of environmental factors and the tolerance ranges of the individuals composing the populations. These interactions accumulate multiplicatively and determine the abundance of the populations.
7. The present populations of the leaf litter community are not an isolated segment of the mainland populations but have been established independently.

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