DISTRIBUTION AND ABUNDANCE OF BOG-INHABITING PSELAPHID BEETLES

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ABSTRACT.—The distribution and abundance of pselaphid beetle populations in a relict sphagnum bog are related to microhabitat variables and the ecology of each species. In northern Illinois, eleven pselaphid species with boreal affinities exhibited distributional patters related to stages in the bog sere. Each successional stage was characterized by unique moss species and microclimatological conditions comprising the microhabitats: the sphagnum mat, ericaceous shrubs, tamarack forest, and a swamp forest ecotone. Physical preferenda and predator-prey relations appeared to isolate sympatric beetle populations. Seasonal shifts in population between stages were affected by changing microclimate. Early successional stages were dominated by boreal species, where highest densities were attained with maximum development of the moss substratum.

Although the development of vegetational components through the various stages of bog succession is well known, e.g., Transeau (1903), Dachnowski (1912), Dansereau and Sogadas-Vienna (1952), and Heinselman (1963), little attention has been devoted to the faunistic relationships of the bog sere. It generally is accepted that the biota of relict bog communities in northern United States is of boreal origin (Braun 1928). Shelford (1963) concluded that there was no clear line of distinction between bogs of temperate regions and those characteristic of northern coniferous forests. Ross (1958) has shown that large number of insect species are abundant in both taiga and tundra and are almost entirely restricted to these major ecological formations. It is not unexpected, therefore, that certain boreal insect taxa have southern representatives which occur in bog habitats of temperate regions.

The Pselaphidae is a family of clavicorn beetles in the superfamily Staphylinoidea. Pselaphids are small beetles averaging about 1.5 mm in length. The world fauna consists of approximately 7500 described species (Park 1964) with the Nearctic complex being represented by some 500 species (Park 1958). The family is nearly global in distribution, with species occupying a variety of habitats to which they are often exceedingly specific (Park 1949). The basic, and probably ancestral, habitat is the mor-type organic layers of forest floors and their extensions or equivalents (Park 1942).

The studies of Transeau (1903), Dachnowski (1912) and other early botanists on bog development provided a classical description of physiographic succession. Between each successive community of the bog sere, often within short and distinct spatial limits, vegetational components and physical characteristics change abruptly. Populations of bog-inhabiting pselaphid beetles occur within moss and litter microhabitats throughout all stages of bog succession, although various species exhibit predilection for habitats of particular successional stages. In the present investigation, combined field and laboratory studies were used to assess the dominant physical and biotic mechanisms which segregated these sympatric populations.

BOG DEVELOPMENT

The Historical Aspect. Pleistocene glaciation covered most of Canada, northern United States, and mountain chains to the south. The last of the ice sheets, the Wisconsin (Fig. 1), had a significant effect upon the present topography and biota of glaciated areas. The biota of glaciated regions became established after a series of migrations related to ensuing climatic changes. With the renewal of milder climates and the consequent recession of the glaciers, displaced biotic associations spread in the direction of available habitats. Relict colonies — groups of plants and animals unlike those of the surrounding and dominant vegetation, but belonging to some distinct formation—remain as evidence of past climatic conditions (Braun 1928). As this sequential migration proceeded northward, boreal bogs characteristic of northern Canadian forests (Shelford 1963) remained as glacial relicts. These glacial hydrophytic relicts and their associated fauna have persisted in the more extreme habitats where the influences of the post-Wisconsin xerothermic period have not been strong enough to displace them. Replacement of surrounding vegetation by more southern types continued until present-day conditions were attained.

The Bog Concept. In eastern North America, bogs are frequent throughout glaciated territory and often occur to its southern limits. They are, however, most common within limits of the Canadian spruce-fir forests. Bog formations are present in several phytogeographical areas: the deciduous forest (Braun 1947, 1950), the tall grass prairie, the Canadian forest (Shelford 1963), and the taiga (Dansereau and Segadas-Vianna 1952). Conditions conducive to bog development occurred in closed depressions—kettle holes in glacial moraines, the quiet bays of lakes, or in calm situations in stream channels. The term "bog" has been used in ecological literature in many different senses. It sometimes has included marshes and swamps as well as bogs. Those who have used the term have emphasized various characteristics: vegetational (Carpenter 1938, Gates 1942), physical (Gates 1942, Potzger 1934, Transeau 1905), and physicochemical (Rigg 1916). Althought physical conditions often favor peat formation, Gates' (1942) definition of a bog as an area "vegetated by a flora in which peat-forming types of plants are particularly abundant" is followed in this text. In bogs the water table is at or near the surface and the soil is of organic (peat) origin, while swamps are characterized by a water table which is above (Potzger 1934) the surface and the soil is of either inorganic or humus nature.

Bog Succession. Bog succession has long been recognized in its broader aspects. Burns (1909) discussed early successional stages in bog lakes. The complete sequence from open water to mesophytic forests was described by Whitford (1901), Transeau (1903, 1905), Dachnowski (1911), and Dansereau and Sefiadas-Vianna (1952). Heinselman (1963) discussed a variety of successional processes beside that of the classical basin-filling pattern. The treatment by Dachnowski (1912) of vegetational succession in Ohio lakes and peat deposits is well known, and variations of this work have been reproduced in many texts. Fuller (1925) in an outline of Chicago area vegetation, listed the principal plant species associated with each of the major stages of bog sucession.

Marginal vegetation often will develop as a part of typical pond succession preceding bog development (Buchsbaum 1937). Such floating aquatics and emergent vegetation usually establish the initial stage of bog succession — the floating sphagnum mat. This mat forms around the anchorage of sedges and rushes, and often continues to propagate vegetatively (Rigg 1940). Expan-

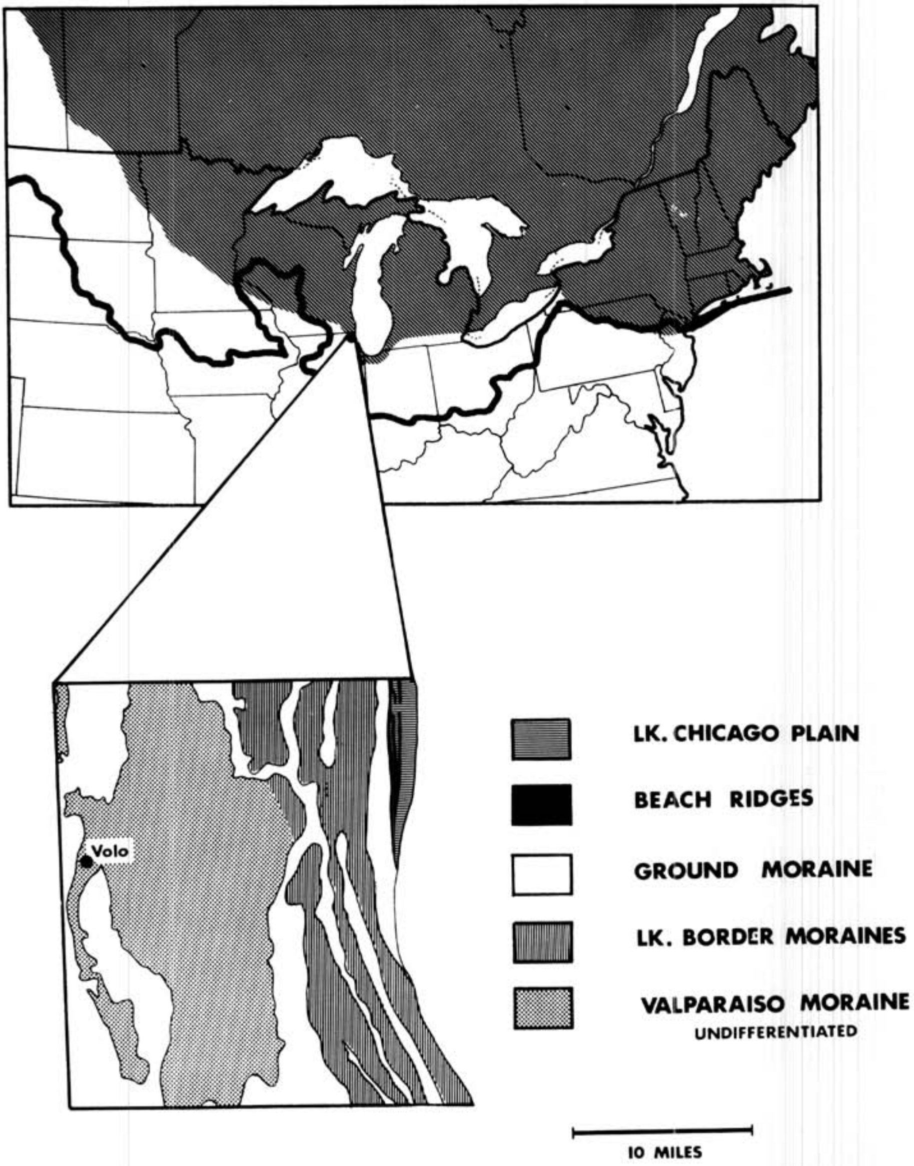

FIGURE 1. Southern limits (solid line) of Wisconsin glaciation in central and northeastern United States (after Hough 1958) and the general present-day distribution (shaded areas) of bog plants (after Transeau 1903). The distribution of bog-inhabiting pselaphid beetles closely approximates that of bog vegetation. Insert: morainic systems of Lake County, Illinois showing the location of the study area (modified from Fryxell 1927).

sion and centripetal encroachment of the mat proceeds over newly deposited layers of peat. The weight of accumulating materials causes a gradual sinking and an eventual filling to the bottom. Succession of vegetation is parallel to the filling-in of the water basin and its structure is parallel to the physiographic stages of development.

A consolidation phase follows with the establishment of a continuous sphagnum substratum which may vary in composition and structure. The differences in successive botanical features within a given geographic area is due primarily to fluctuations in water level. The sphagnum mat prepares a footing for the second stage—the ericaceous shrub zone. Sphagnum forms characteristic elevated hummocks around the bases of these shrubs. Shrubs initiate the transition to the next stage, through stabilization of the substratum by the binding action of their root systems, raising of the substratum by increased vegetative deposition, and modification of the physical environment. The next zone usually supports an association of tamaracks or tamarack-spruce in more northern localities. The substratum becomes noticeably drier, although infrequent pools may be found. Associated with reduced light intensities, a luxuriant fern growth is common. Sphagnum is no longer the dominant floor cover and other mosses and herbaceous vegetation appear. This stage is apparently a rather stable entity in bog succession, and it is not uncommon to find extensive bog areas covered by this single vegetational feature. Transitional woody associations often follow as the next stage; these are not restricted to bog sere, but are current subclimax types throughout their respective regions. The decline in edaphic influences eventually results in a merger with climax mesophytic communities of the surrounding area.

THE STUDY AREA

Sayer Bog, referred to in early literature (Waterman 1921, 1923, 1926; Kurz 1928), is now known as Volo Bog. This area was originally secured by the local Nature Conservancy and was placed under the administrative auspices of the University of Illinois. It is located one mile northwest of Volo, Lake County, Illinois, NE ¼ Section 28, T. 45N, R. 9E of the Grays Lake Quadrangle; alt. 229 m.

The Cary substage of the Wisconsin glacier extended west as far as central Minnesota and covered most of the territory north of the driftless area in Wisconsin. It reached its maximum southern extension in northeastern Illinois, northwestern Indiana and northern Ohio. Carbon-14 dating has placed the age of terminal Cary substage deposits at about 14,000 years (Hough 1958). The oldest and most pronounced morainic system established in northeastern Illinois during this period was the Valparaiso moraine, which averaged about 10 miles in width and marked the southern rim of the Lake Michigan basin. The bogs located in Lake County, Illinois (Volo Bog and others) occur in this Valparaiso drift (Fig. 1). This moraine is characterized by a clayey till of sand and gravel, frequently containing large percentages of calcium carbonate (Waterman 1926). The pollen sequence in Volo Bog (Artist 1934) follows the generalized pattern established for the Lake Michigan Region (Fuller 1935), with the postglacial sequence having been: *Abies-Picea*, *Picea-Pinus*, and *Pinus*-deciduous species. There is no definitive evidence to postulate an extensive postglacial tundra devolpment in this area.

Unusual smoothness (very few kettle holes or deep-set undrained depressions) characterizes the Valparaiso moraine in the Chicago Region. Most of the depressions of this drift have been drained into the river systems of the region, but a section on the edges of the drainage basins of the Fox and Des Plaines Rivers still contains a few poorly drained or undrained depressions, and it is in these that the bogs are found. Nearly all the lakes in this moraine topography have become swamps due to their initial shallowness (Bretz 1955). Since sphagnum was found to be dying out in most localities, Waterman (1921, 1923, 1926) believed this indicative of a move toward a drier habitat and that the bogs in northern Illinois were disappearing as the environment became unfavorable. Both Artist (1934) and Emerson (1921) failed to find sphagnum producing spores in this region and attributed this to unfavorable conditions brought about by alkaline waters, although the former reported no pH above 6.0 in sphagnum zones. In the course of this study, sporophytes of *Sphagnum teres* Angstr. have been recorded on consecutive years (1962-1963) in Stage II of Volo Bog.

Vegetational Associations

In the present study, the sucessional patterns in Volo Bog were subdivided into four basic stages (Fig. 2), which agree substantially with the floristic delineations of Fuller (1925). A complete floral anaylsis was not attempted. Emphasis was placed upon composition of the bryocophilous communities of the floor which comprised the pselaphid habitats (Table I). Only the charac-

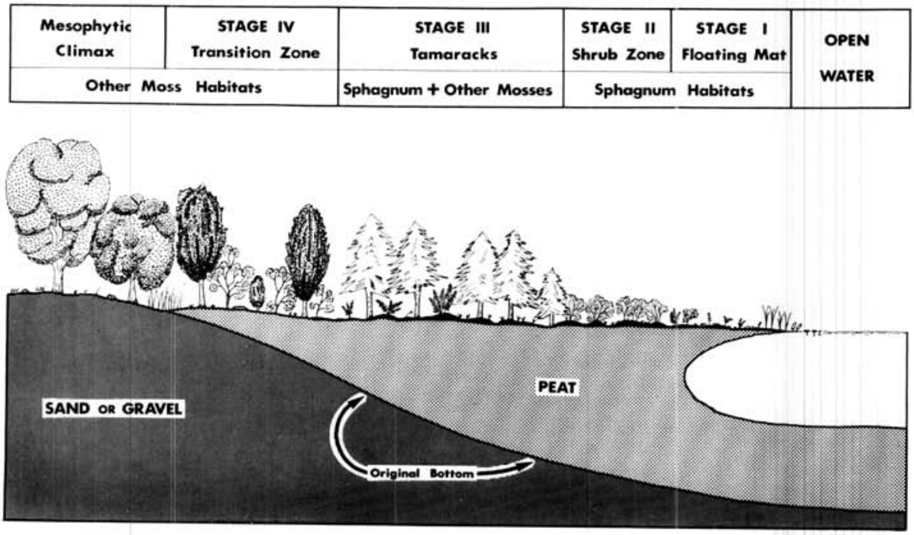

FIGURE 2. Diagrammatic cross section of bog succession depicting successional development at Volo Bog, with dominant vegetational features and seral stages. Areas represented by each association: Stage I, 0.12 ha; Stage II, 0.39 ha, Stage III, 2.85 ha, Stage IV, 14.12 ha.

TABLE I. Characteristic floral components of the successional stages of Volo Bog. Index species or those reaching their maximum density are indicated by an asterisk. All species in left-hand column are mosses.

STAGE I FLOATING MAT—SEDGE ZONE

**Sphagnum cymbifolium* Ehrh.
**Sphagnum recurvum* Beauv.
Aspidium Thelypteris Sw.

**Carex* sp.
Juncus sp.
Menyanthes trifoliata L.
Typha latifolia L.

STAGE II SHRUB ZONE

**Aulacomnium androgynum* Schwaegr.
Climacium dendroides (Hedw.) Web. and Mohr
Dicaranum scoparium Hedw.
Helodium paludosum (Sull.)
**Sphagnum teres* Anstr.
Tetraphis pellucida Hedw.

Calopogon punchellus (Salisb.) R. Brown
Drosera rotundifolia L.
**Oxycoccus oxycoccus* (L.) MacMillan
Pogonia ophioglossoides (L.) Ker.
**Rhus vernix* L.
**Sarracenia purpurea* L.
**Vaccinium corymbosum* L.

STAGE III TAMARACK ZONE

*_Aulacomnium androgynum_ Schwaegr.
Brachythecium sp.
*_Calliergon cordifolium_ (Hedw.) Kindb.
Helodium paludosum (Sull.) Aust.
Heterophyllium haldanianum (Grev.) Kindb.
Mnium affine var. _rugicum_ (Laur.) BSG
Plagiothecium sylvaticum (Brid.) BSG
Pohlia nutans (Hedw.) Lindb.
Polytrichum commune L.
*_Sphagnum magellanicum_ Brid.
*_Sphagnum squarrosum_ Crome

Ilex verticillata (L.) Gray
*_Larix laricina_ Koch
Onoclea sensibilis L.
*_Osmunda cinnamomea_

STAGE IV TRANSITION ZONE (subclimax)

Aulacomnium androgynum Schwaegr.
Brachytecium sp.
*_Calliergon cordifolium_ (Hedw.) Kindb.
Helodium paludosum (Sull.) Aust.
Hetermophyllium haldanianum (Grev.) Kindb.
Mnium affine var. _rugicum_ (Laur.) BSG
Mnium cuspidatum Hedw.
Plagiothecium sylvaticum (Brid.) BSG
*_Thuidium delicatulum_ (Hedw.) Mitt.

*_Ilex verticillata_ (L.) Gray
Iris versicolor L. (in atoll)
*_Onoclea sensibilis_ L.
Populus tremuloides Michx.

teristic vascular species of each stage are given to establish a comparative framework. The bryocophilous associations of bogs have been demonstrated to be reliable indicators of floor stratum development and existing microclimatic conditions of these habitats (Reichle and Doyle 1965). A more detailed discussion of the specific climatic influences and ecological factors characteristic of these microhabitats will be developed in subsequent sections.

The Bog Pselaphid Fauna

Pselaphids occurring in bogs are almost entirely bryocophilous, inhabiting the abundant moss floor cover in all sucessional stages. In eastern North America, bog pselaphid distributions follow quite closely the distribution of bog plants described by Transeau (1903) (Fig. 1). The relict bog biota does not extend southward beyond the Wisconsin terminal moraines to any appreciable extent and, in this pattern, reflects the historical relationship of these associations with glacial events. Pselaphid beetles occurring in bogs may be divided into two main groups: (i) index species restricted to bogs and comprising the dominant elements of the total population, and (ii) species occurring in later successional stages in niches ecologically equivalent to those of their normal swamp forest habitats. The index bog species appear to be glacial relicts of more extensive boreal populations (Reichle 1966).

In Table II are listed the ecological distributions of 22 common bog-inhabiting species in temperate North America. Thirteen species have been recorded from Volo Bog during the present study.

TABLE II. Bog-inhabiting Pselaphidae—a listing of their specificity and ecological distribution. Astersks indicate those species found at Volo Bog.

Species	Forest					Prairie		Bog, Swamp	
	under bark	leaf mold	log mold	tree-holes	ant nests	sod	ant nests	sphagnum bog moss mat	moss cover on swamp floor
Batrisodes furcatus (Brendel)	+	+	+	+				+	+
**Batriscodes golbosus* (LeConte)	+	+	+	+	+		+	+	+
Batrisodes nigricans (LeConte)								+	
**Batrisodes striatus psotai* Park								+	
**Bibloplectus* sp.								+	+
**Bythinopsis tychoides* (Brendel)								+	
**Decarthron abnorme* (LeConte)								+	?
**Decarthron defectum* Park								+	
Lucifotychus minor (LeConte)		+	+					+	
**Melba* (population B-11)								+	
Pselaphus bellax Casey								+	
**Pselaphus ulkei* Bowman								+	
**Reichenbachia borealis* Casey								+	
Reichenbachia corporalis Casey								+	?
**Reichenbachia puncticollis* (LeConte)								+	
**Reichenbachia scabra* Brendel								+	
Reichenbachia spatulifer Casey								+	
**Rhexidius canaliculatus* (LeConte)		+	+	+				+	+
Rhexius insculptus		+	+			+		+	
**Rybaxis clavata* Brendel								+	
Rybaxis transversa Fall								+	
Rybaxis varicornis Brendel								+	

Only three of the Volo species show a definite association with habitat types other than those characteristic of sphagnum bogs—*Batrisodes globosus*, *Bibloplectus* sp., and *Rhexidius canaliculatus*, are all immigrants in later stages of bog succession. *Both Batrisodes globosus* and *Rhexidius canaliculatus* are ubiquitous, and occupy a variety of different habitats. The remaining bog species are not dispersed indiscriminately throughout the bog sere but, instead, display a definite predilection for specific habitats. The nature of their relationships and the resulting distributional patterns within the bog sere form the subject of subsequent discussion.

PROCEDURES

During 1962 and 1963, weekly collections were made of pselaphid populations in each of the four stages of bog succession: sphagnum mat, shrub zone, tamarack fores, and transitional mesophytic forest (Fig 2, Table I). Two replicate moss samples (800 cm^2) were taken at random in each stage every week, following a transect from open water to the peripheral boundaries of the bog. At each sampling point, mean depth of the moss habitat was measured; this later permitted densities to be expressed per unit volume as well as unit area of habitat. Simultaneous with these collections, micro- and macroclimatic variables were measured in each stage. Field samples were then transported to the laboratory in large plastic bags for arthropod extraction.

Pselaphids and other microarthropods were extracted from moss using modified Tullgren funnels. Each funnel was constructed of galvanized metal 45 cm high, having a 71° slope, 30 cm top diameter, and 2.5 cm diameter opening at the bottom. Nine cm below the funnel top, a No. 4 screen was suspended inside on supporting brackets. The funnel was covered by a conical metal shade, containing a 60 watt incandescent light bulb. Moss samples were kept in funnels until dry—usually around 60 hours. Efficiency of pselaphid yield using this method exceeded 95% for all species.

METHODS AND MATERIALS

U. S. Weather Bureau data for Cook County, Illinois, were used for reference macroclimate information. Maximum-minimum thermometers were used to record weekly temperature fluctuations within the woody vegetation cover. Recording thermographs supplied more detailed temperature values immediately above the moss floor cover. Temperature determinations within microhabitats were made with an electronic thermometer probe (Model TLB, Tri-Instruments). Field determinations of relative humidity within the moss habitats were made with an electric hygrometer indicator (Hygrodynamics Inc.). The narrow-range sensing elements (Model H-103) had an accuracy of ± 2.0% R. H. Continuous humidity readings above moss habitats were obtained from recording hygrothermographs. Moisture contents of mosses were based on 40°C air-dry Tullgren funnel weights.

Culture chambers for pselaphids were modifications of the plaster-charcoal technique (Rohde 1956). Polyethylene containers, 6 cm by 6 cm by 2 cm, with friction-top lids, incubated at 17°C were suitable for maintaining pselaphids, predators, and prey in the laboratory for many months. Experiments on survivorship and behavioral responses to environmental stresses were performed with similar cultures.

RESULTS AND DISCUSSION

Seral Distributions. The preferred habitats of pselaphids in all successional stages were the well-developed moss growths. Forty additional 800 cm^2 random moss samples were taken between 15 July and 12 August, 1963, in each of the four successional stages, and the sample distributions of pselaphids were subsequently compared with Poisson distributions having the same mean (Table III). Since the sample data were a composite of several genera, frequency analyses also were determined for each species, if they were sufficiently abundant to enable statistical treatment. In all cases examined, the distributions did not deviate from that found for the composite populations. Therefore, it was assumed that the overall generic treatment did not mask contrasting lower-level species distributions. For each successional stage the mean (x) number of pselaphids per sample and the variance of each mean (s_x^2) are given (Table III). In the first three stages where

TABLE III. **Comparison of observed and theoretical frequencies of pselaphids found in each of forty 800 cm^2 random moss samples, with calculations of X^2 for goodness-of-fit of data to a Poisson distribution. Collections taken: Stage I, July 15; Stage II, July 31; Stage III, August 7; Stage IV, August 12, 1963.**

stage	mean number of individuals per sample	variance	χ^2	degrees of freedom	P
I	**1.68**	**3.287**	**17.69**	**4**	**$P < 0.005$**
II	**2.10**	**3.785**	**23.03**	**4**	**$P < 0.001$**
III	**0.88**	**1.745**	**15.90**	**3**	**$P < 0.005$**
IV	**0.60**	**0.708**	**5.69**	**2**	**$0.05 < P < 0.10$**

the distributions were nonrandom, the variances were greater than their means. The contagion can be resolved, therefore, as a "patchy" or "clumped" distribution of individuals rather than what is termed a "regular" distribution where the number of individuals in each sample closely approximates the mean and the variance approaches zero. There was also a significant increase ($P < 0.005$) in occupancy of sphagnum hummocks in younger successional stages (chi-square contingency test). The clumped distributions previously discussed may be interpreted by the fact that, although percentage moss floor cover was greater in younger stages, microhabitat heterogeneity (hummocks) resulted in clumped pselaphid distributions.

In Stage I the moss habitat was virtually uniform in floral composition, with two species of mosses predominating — *Sphagnum recurvum* and *S. cymbifolium*. The habitat, however, was not uniform in structure (Fig. 3). The typical floating mat of bogs was not represented at Volo; instead, the mat was impregnated with a dense stand of *Typha latifolia*. Sphagnum tended to form clumps at the bases of cattails, leaving either thinly-covered or inundated regions in between. This habitat was characterized by a pselaphid fauna of ten species (Fig. 4). *Reichenbachia borealis* attained its peak abundance in this stage, representing 60% of the mean annual pselaphid population. *Decarthron defectum* also reached peak distribution with 9% of the population. Although represented by only 12% of its total bog numbers in Stage I, *Bythinopsis tychoides* was still a dominant species with over 16% of the population in this stage. *Reichenbachia puncticollis* and *Decarthron abnorme* were species unique to Stage I habitats, although collectively they accounted for less than 2% of the population.

Stage II was characterized by a dense moss floor cover. *Sphagnum teres* was the dominant bryophyte in this zone at Volo, forming a continuous growth which was only occasionally disrupted by grasses or invaded by other mosses — notably *Aulacomnium androgynum*. Large dense hummocks of sphagnum formed about the bases of shrubs, attaining greatest development around *Rhus vernix*. This shrub has a characteristic basal-branching growth pattern which establishes an excellent foundation for hummock development. A clumped pselaphid distribution was correlated with this hummock development, with an increased frequency of pselaphids in the denser hummocks—a phenomenon which became even more striking as aggregations developed in late autumn and early winter. Stage II hummocks were inhabited by eight species of pselaphids (Fig. 4). Characteristic species and their respective mean annual percentage composition of the population were *Rybaxis clavata* (14%),*Pselaphus ulkei* (11%), and *Reichenbachia scabra* (4%). A major part of the population consisted of *Reichenbachia borealis* (34%) which progressively diminished in importance as the bog sere matured, although continuing as a conspicuous element of the fauna. *Bythinopsis tychoides* was rather uniformly distributed throughout the bog sere.

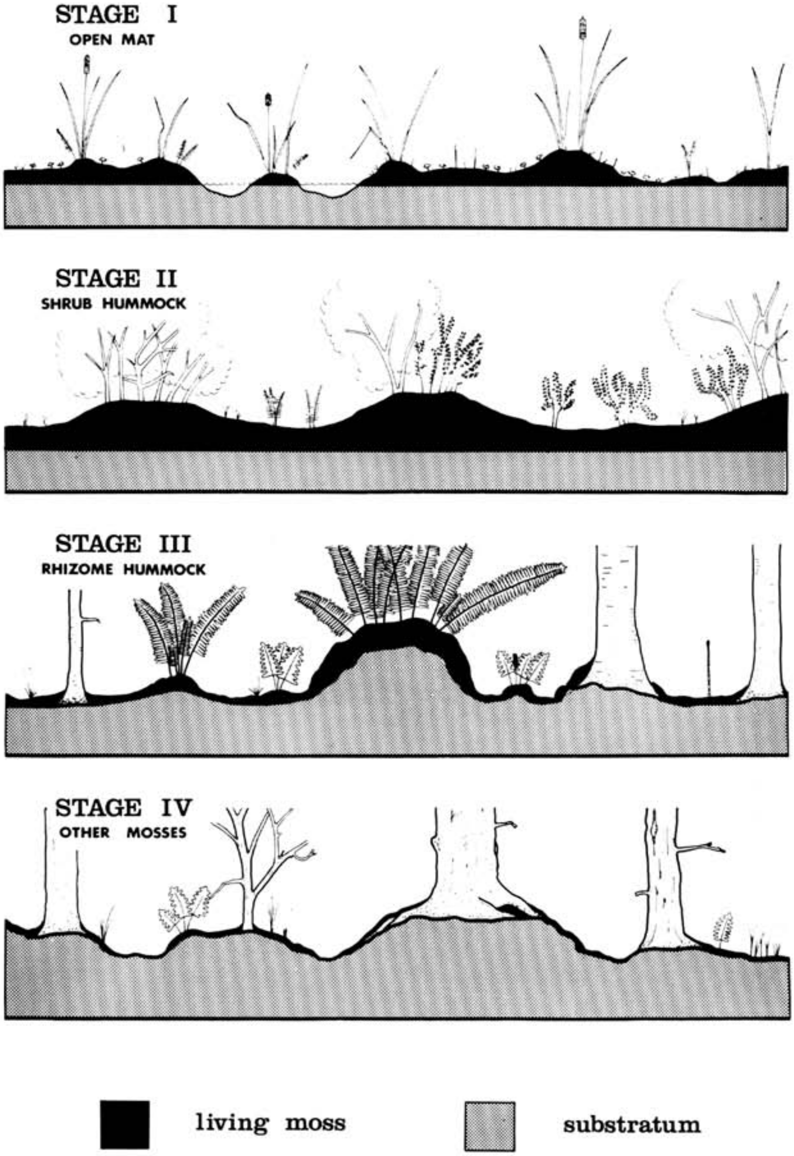

FIGURE 3. Comparative development of moss microhabitats at Volo Bog: Stage I, *Sphagnum recurvum* on the floating mat with early hummock formation; Stage II, *Sphagnum teres* in characteristic hummocks about the bases of shrubs; *Sphagnum squarrosum* and *S. magellanicum* persisting on fern rhizomes—intermittent regions, as in Stage IV, covered by a sparse growth of nonsphagnum mosses.

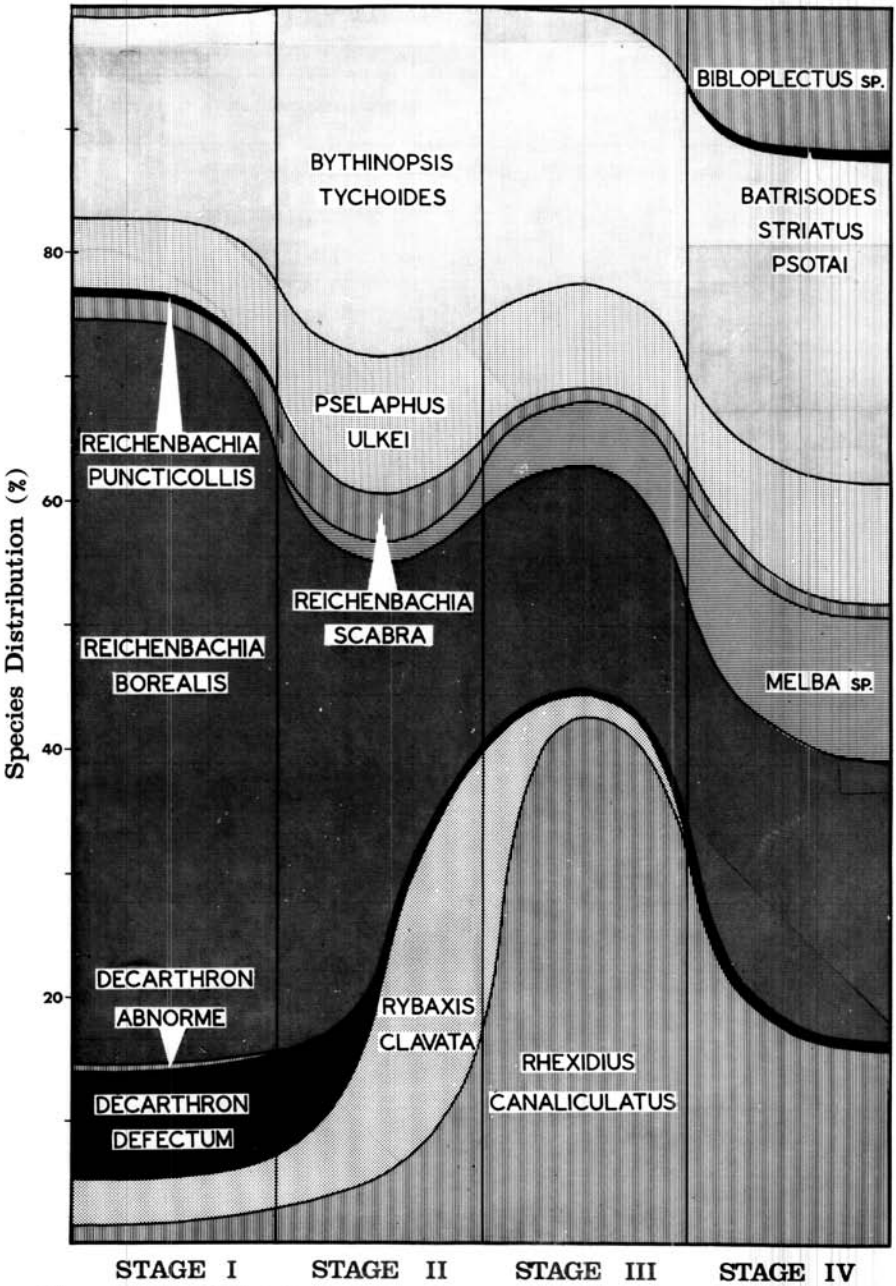

FIGURE 4. Seral distribution of pselaphid beetles at Volo Bog. Shaded areas show the percent of the annual population represented by each species. Species are listed in those stages where they reach peak distribution.

However, in Stage II *Bythinopsis* was most abundant and amounted to over 28% of the resident population.

In Stage III the floor cover of sphagnum (primarily *S. magellanicum*) diminished considerably, with growths usually occurring on the basal rhizome masses of the ferns *Osmunda cinnamomea* and *Onoclea sensibilis.* Numerous other bryophytes (Table I) occupied floor habitats in intermittent regions. Empirical observation would suggest a clumped distribution which, in fact, did occur. A greater percentage of the optimal sphagnum habitats were occupied, since fewer hummock habitats were available and the moss floor cover in between was poorly developed. In Stage III 70% of the hummock samples were occupied (containing 91% of the total fauna) compared to 62% occupancy in Stage II. The structural change in Stage III moss habitats was paralleled by a marked adjustment in the pselaphid fauna (Fig. 4). *Rhexidius canaliculatus* developed as a major component (43%) of the fauna, in association with the fern rhizome sphagnum hummocks. The populations of *Decarthron defectum* and *Rybaxis clavata*, characteristic of earlier successional stages, were no longer important aspects of the fauna. *Reichenbachia borealis* and *Bythinopsis tychoides,* although decreasing in percentage composition, continued as major elements of the fauna. Two new genera, *Bibloplectus* and *Melba,* make their appearance in the sere.

The nonsphagnum mosses of Stage IV presented a shallower but more continuous habitat. Although the microtopography of the area was heterogeneous, with elevations and shallow but extensive depressions with many exposed roots, the mixed-moss associes were nearly uniform in growth. For the first time in the bog sere, there was associated with this general consistency of the moss habitat a randomly distributed pselaphid population (Table III). This distributional pattern occurred only in the transition zone between true bog and mesophytic forest in a moss habitat devoid of sphagnum and its characteristic hummocks. In these transitional, nonbog habitats strong remnants of the bog pselaphid population still remained — *Bythinopsis tychoides* (28%), *Reichenbachia borealis* (25%), and *Rhexidius canaliculatus* (19%). However, sizable populations of swamp forest species *Melba* (12%) and *Bibloplectus* (13%) developed in the ecotone. *Batrisodes striatus psotai* appeared for the first time in this stage and, although a minor element of the fauna, has not been reported from other habitats and appears to be characteristic of late stages of bog succession.

Density. Density may be expressed as a function of unit area or unit volume of habitat. The objectivity of surface area or volume density measurement depends, to a large extent, upon the nature of the habitat being studied (Macfadyen 1952). In bog succession, not only did percentage floor cover of moss vary with maturity of habitat, but depth of moss growth also varied with hummock development (Fig. 3).

When the annual mean pselaphid abundance was expressed on an area basis (Table IV), Stage II appeared as the most productive habitat (49.74 indiv./m^2). Following in decreasing order were Stage III (40.79 indiv./

TABLE IV. Annual mean density of pselaphid beetles in each stage of bog succession expressed both per unit area and volume of moss habitat. Conversion from surface area to volume based upon mean moss depth in each stage.

SUCCESSIONAL STAGE	number of indiv./m² ± SE	$\bar{x}$ moss depth (cm)	number of indiv./10³ cc moss
I	29.39 ± 4.84	6.0	0.49
II	49.74 ± 11.28	8.5	0.59
III	40.79 ± 10.85	5.0	0.82
IV	30.30 ± 9.35	3.0	1.01

m²), Stage IV (30.30 indiv./m²), and Stage I (29.39 indiv./m²). This ordination approximated the degree of moss surface area coverage in each successional stage. However, when numbers of individuals per volume of habitat were compared, densities progressively increased through the sere (Table IV). Maximum densities (per unit volume) were attained in mature successional stages characterized by the greatest number of codominant species (> 10% of total population). In Stage IV, with the highest per unit volume density (1.01 indiv./10³ cc), six species exceeded 10% of the total population, while Stage I (0.49 indiv./10³cc) had only four codominant species.

Biomas. Dry weights of each species were determined from specimens frozen and dried in a vacuum desiccator (Table V). Although their range in size did not exceed 1 to 2 mm, considerable variation in mass existed between species. With the exception of *Batrisodes striatus psotai,* which occurred only rarely in Stage IV, larger species were associated with younger successional stages (Fig. 4, Table V). This observation subsequently will be discussed in relation to the role of the size of the moss interstices as a limiting factor in beetle distribution. Based upon annual population structure (Fig. 4, Table VI), and species weights (Table V), biomass estimates

TABLE V. Freeze-dry weights of eleven species of pselaphid beetles from Volo Bog (means calculated from pooled weights of 10 individuals).

Species	Sample size	$\bar{x}$ dry weight (μg per individual)
Batrisodes striatus psotai Park	5♂, 5♀	206.8
Bibloplectus sp.	5♂, 5♀	14.6
Bythinopsis tychoides (Brendel)	10♀	50.0
Decarthron abnorme (LeConte)	5♂, 5♀	110.0
Decarthron defectum (LeConte)	5♂, 5♀	56.0
Melba sp.	10♀	32.0
Pselaphus ulkei Bowman	5♂, 5♀	87.7
Reichenbachia borealis Casey	5♂, 5♀	126.7
Reichenbachia scabra Brendel	5♂, 5♀	92.9
Rhexidius canaliculatus (LeConte)	5♂ 5♀	34.5
Rybaxis clavata Brendel	5♂, 5♀	140.4

were calculated for each stage of bog succession. These estimates were based upon sampling of a total bog area of about 17.5 hectares, and did not include the total of some 19 ha included within the nature preserve, since a portion of the peripheral acreage to the south was occupied by a swamp community. Mean annual standing crop for each stage of bog succession was: Stage I, 3.01 mg/m^2; Stage II, 4.45 mg/m^2; Stage III, 2.52 mg/m^2; Stage IV, 1.88 mg/m^2. These estimates are based upon the average annual population structure, and do not include any of the seasonal fluctuations in numbers and mass or population shifts between different habitats. Maximum biomass occurred in earlier successional stages. Biomass also was correlated with degree of moss habitat development, and progressively decreased through the sere. This ordination is partially a result of a similar pattern in pselaphid densities, but was reinforced by size of species in each successional stage. Larger species were typically associated with the looser moss growths of earlier successional stages. Comparable biomass data for pselaphid populations in other ecosystems is nonexistent. Park, Auerbach and Wilson (1953) reported the density of a pselaphid population of an Illinois prairie to be 194,000 beetles per acre. Greatest densities in the bog sere were attained in Stage II with 104,000 beetles per acre.

Seasonal Population Fluctuations. Analysis of variance of the seasonal density of pselaphids in each successional stage revealed a significant

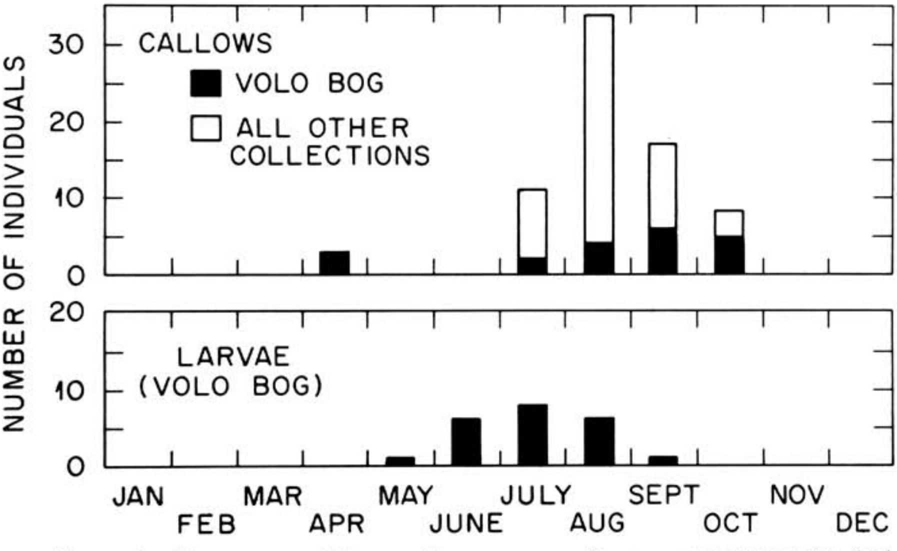

Figure 5. Frequency and temporal appearance of new pselaphid adults (callows) and larvae. Data from other geographic localities corrected for seasonal disparities and superimposed on the Volo time sequence. Values for Volo Bog are numbers of individuals per m^2 of moss habitat; other locality values are cumulative numbers collected and are comparable only in their relative temporal distribution.

($P<0.005$) effect of season on population size (Table VI). In early spring (April) highest densities occurred in hummock habitats in all stages. This was attributable to the rising water table following thaw and spring rains, which inundated the depressions and caused concentration of individuals in hummock "islands." A secondary population peak occurred in early autumn (September) and appeared to result from several factors. During the arid months of late summer and early autumn, the population shifted into the more protected moss habitats of Stages II and III. These habitats later served as winter hibernacula. This same interval included the period of emergence of new adults (Fig. 5)—a result of larval development which was probably initiated earlier that same year during the periods of high population density. Such seasonal fluctuations may be expected to vary over successive years due to varying climatic conditions. Low densities during December and January were most likely due to winter mortality and/or vertical movements into deeper peat layers. Even though no individuals were taken during January, the presence of mature individuals as early as February indicated that some adults did successfully overwinter.

The population distribution among successional stages revealed several density shifts with seasonal aspect (Table VI). During the winter months greater densities occurred in moss microhabitats in Stages I and II, which offered maximum depth stratification and climatic melioration during cold periods. Stage IV, with its shallow and sparse moss cover, had lowest densities. In spring the population moved out of hibernacula into the less protected habitats of Stages III and IV. Flooding of the floating mat, due to the rising water table, resulted in emigration from Stage I during this period. Lower densities in Stage I during late summer may have resulted from higher temperatures on the exposed mat, while drying out of the moss mat was an important factor causing lower densities in Stage IV. Stages II and III continued to vacillate during this period. With the less drying conditions of autumn, population density differences between stages were minimal. With

TABLE VI. Seasonal abundance (number individuals per m²) of pselaphid beetles in each successional stage of Volo Bog.

Season		Stage I	Stage II	Stage III	Stage IV
Winter	$\bar{x}$	33.62	44.08	17.00	6.92
(Jan.-Mar.)	SE	22.03	26.98	12.06	6.22
Spring	$\bar{x}$	29.72	84.72	75.00	77.50
(Apr.-June)	SE	0.77	29.00	32.25	15.05
Summer	$\bar{x}$	24.48	42.71	44.27	25.00
(July-Sept.)	SE	1.38	12.77	14.33	7.16
Fall	$\bar{x}$	30.73	27.43	26.91	11.79
(Oct.-Dec.)	SE	3.17	12.90	5.14	6.04

the onset of winter climatic extremes, the population shifted into the protected hummock habitats of Stages I and II.

It would be premature to extrapolate these seral relations at Volo Bog to bog succession in other localities. Much will depend upon the quality of the fauna represented and the degree of development of the particular area. An important consideration is that this seral distribution shows only a secondary correlation with gross vegetational features, being a more direct result of paralleled development of moss microhabitats. Atypical bogs, or ones which have been disturbed, most often have been found to be characterized by a fauna related to the condition of the moss floor cover, rather than the aboveground vegetation cover.

Biotic Influences

Life Cycle. Little is known about the life cycle of pselaphid beetles. The nearctic fauna is composed of over 500 species, and the complete life history of none is known. Knowledge of the ecological requirements of developmental stages would be of great value in demographic studies of pselaphid populations. The larval stages of only two nearctic species have been described (Bőving and Craighead 1931). In the present study, larvae were extracted from moss, but attempts to rear these individuals were unsuccessful. Park (1947a,b) has conjectured about the absence of life history data, and has suggested several alternative means of obtaining information about the population dynamics of pselaphids.

Evidence for termination of the pupal stage was obtained from appearance of newly emerged adults (callows) in the population (Fig. 5). These records included nine bog-inhabiting species collected from 23 different localities over a three-year period (Reichle 1964). Callow adults taken from Volo Bog best represented the seasonal emergence of adults, since they were obtained from uninterrupted sampling throughout the year. The temporal occurrence of callows from all other localities was equated to the time sequence at Volo Bog by Hopkins' Bioclimatic Law (Graham 1952). An autumnal pulse of callows occurred at Volo which was reinforced by the frequency and temporal appearance of individuals in other localities. The records in April probably represented a spring emergence of lesser magnitude. Park, Auerbach and Wilson (1953) found similar biomodal peaks of callow abundance in their study of the pselaphid beetle population of an Illinois prairie.

Data for the bog population indicate a single annual generation: (i) adults overwinter within the frozen moss habitats of the bog; (ii) adult aggregations in spring and late summer could facilitate mating; and (iii) larval stages were present during the summer months. One annual pulse of larvae occurred, with maximum numbers appearing in July two months before peak callow densities (Fig. 5). No larvae were found in early spring which might have correlated with spring callows, making it unlikely that the latter represented a second generation. Furthermore, assuming equal developmental rates, a second vernal generation would necessitate larval development as early as mid-February when individuals were inactive and the moss microhabitats were frozen. It is most probable that the three callows records in April represented individuals which pupated late the preceding autumn, overwintered as pupae, and emerged in the spring.

Predator-Prey Relations. Beetles of the family Pselaphidae are predators upon the microarthropod fauna of soil and litter habitats. Park (1932, 1933, 1947a) considered the feeding relations of pselaphids that were associated with ants. The feeding habits of five nonmyrmecophilic species were studied by Engelmann (1956). This study presents further information on the selective feeding behavior of six additional bog-inhabiting species. All observations were made on established cultures in transparent rearing chambers described previously. Feeding habits under laboratory conditions may vary from those existing under normal environmental situations, and this factor should be considered in interpreting results.

All positive (+) records of predation were noted (Table VII). The absence of feeding (—) was equally as significant, since this indicated that beetles starved without accepting these prey. Collembola served as the major food source for all bog pselaphid species, and were abundant constituents of the moss fauna in every stage of bog succession. Most bog pselaphids accepted only a specific group of prey. Entomobryid collembolans were eaten by most of the bog pselaphids, although *Bythinopsis tychoides* accepted only podurid and isotomid collembolans.

TABLE VII. Selective feeding behavior of pselophid beetles. The last five species are specific bog-inhabiting form.

	Collembola										
	Entomobryidae	Poduridae	Sminthuridae	Isotomidae	Acarina	coleopterous larvae	*Drosophia* larvae	Phoridae (larvae)	ant larvae	earthworms	tubifex worms
Ceophyllus monilis‡									+		
Tmesiphorus costalis‡	+	—	—	—		+			+		
*Cedius spinosus**	+	—	—	—		+					
*Bibloplectus sp.**	—	+	—	+							
Euplectus sp.†	—	+	—	+	+	—	—			+	+
Batrisodes globosus	+	—	—	+	+	—	+	+	+	+	+
Bythinopsis tychoides	—	+	—	+	—	—	—	—			
Decarthron defectum	+				—		—	—			
Pselaphus ulkei	+	—	—		—		—	—			
Reichenbachia borealis	+	—	—			—	—	—			
Rybaxis clavata	+				—		—	—			

‡ Park (1932, 1933).
* Engelmann (1956).
† Wagner (1962).

Batrisodes globosus, probably the most vagile pselaphid in temperate North America, exhibited the most generalized feeding behavior. *Bythinopsis tychoides* and *Reichenbachia borealis,* with a congruent bog distribution, possessed different prey species. Prey specificity may well serve as an ecological isolating mechanism, removing these species from direct competition. While fluctuations in the abundance of some potential prey were noted between the different successional stages, there were no qualitative distinctions in prey between stages which might have limited pselaphids to particular habitats.

Relatively little is known about the food chains of bog arthropods. Cragg (1961) covered some aspects of the ecology of the soil fauna in English moors. Preliminary reports of a basic food cycle in sphagnum bogs have been made by Smirnov (1958, 1961). The basic energy flow pattern depicted in Fig. 6 for the terrestrial bog sere sumarizes the arthropod data from Volo. Sphagnum mosses and, to a lesser extent, higher vegetation are the basic contributors to detritus. Collembola and Acarina feed upon sphagnum through all stages of decomposition as well as the fungal growths supported by the detritus food base. Ptiliid beetles and insect larvae of several orders are fungal-feeders. Detritus also supports sizable populations of lumbricid and enchytraeid worms. Pselaphid beetles in turn prey upon a variety of these fungivorous and saprophagous invertebrates. The larger arthropod predators are primarily carabid and stayphylinid beetles and spiders which, subsequently, are the food of secondary vertebrate predators. The aquatic insect-nematoceran-ant food chain of Smirnov (1961) undoubtedly underestimated the role of Formicidae in all trophic levels of the moss community.

There are few records of predation on pselaphid beetles. The fact that other elements of the arthropod fauna are probably the major predators contributes to the paucity of such information. Staphylinid and carabid beetles have been observed to attack pselaphids in the laboratory and it is possible that these may be important predators in nature. Predation by salamanders has been reported by Park (1947a, 1964) and Park and Edgren (1950). Salamanders, however, have not been collected from the moss habitats at Volo Bog. Although stomach analyses of *Bufo americanus and Pseudacris triseriata triseriata* from Volo Bog have not yielded pselaphids, the presence of numerous microarthropods suggests that these toads and chorus frogs may be likely predators of pselaphids.

Insectivorous plants, when present, constitute a "predator" of considerable magnitude. The sundew *Drosera rotundifolia* was rare at Volo Bog, and its effect was of little importance. The pitcher plant *Sarracenia purpurea* was locally abundant, and accounted for a sizable toll upon the pselaphid population. From analyses of the contents of 17 pitchers eight pselaphids were recovered. Half of these individuals were *Decarthron defectum.* One *Reichenbachia borealis* was identified, while the remaining specimens were *Brachyglutini* (*Reichenbachia* or *Rybax-*

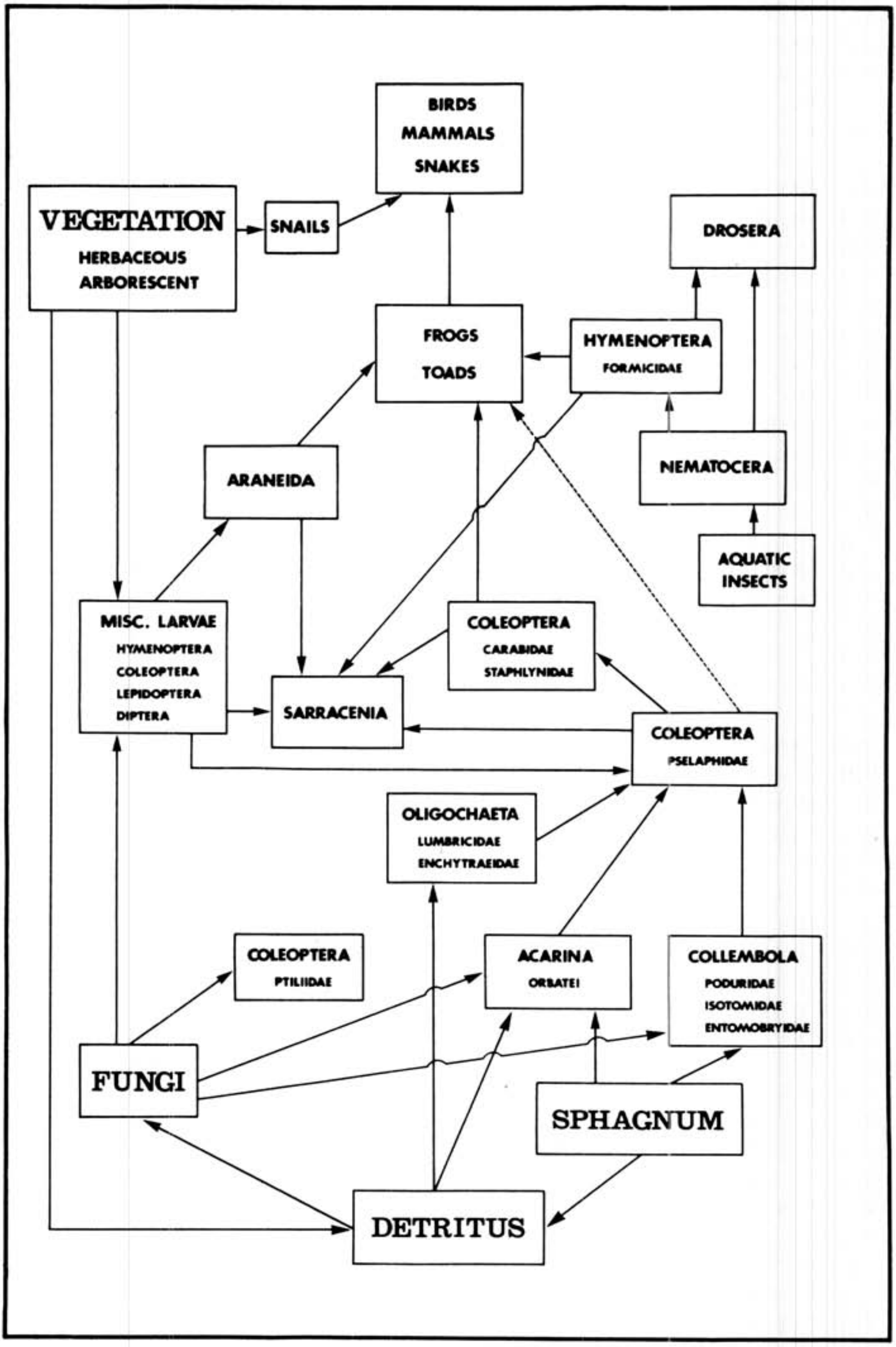

FIGURE 6. Principal pathways of energy flow in the bryocophilous community of sphagnum bogs.

is). The high incidence of *Decarthron defectum* trapped in pitchers may be correlated with its temperature preferendum. This species was characteristic of early successional stages where pitcher plants are most abundant, and its high temperature preferendum suggests stratification in upper moss layers in proximity to pitcher openings.

Parasitism. Parasitism may also play an important role in the population dynamics of a species by influencing densities, distributions, and intra- and interspecies competition. Several records of pselaphid parasitism can be reported for bog populations. Larval mites of the family Erythraeidae have been collected with mouthparts inserted through intersegmental membranes of *Reichenbachia spatulifer* and *R. borealis,* and scutacarid mites have been observed on *Reichenbachia borealis.* All of these mites are parasites of insects and other arthropods and show little, if any, host specificity. The erythraeids are parasitic in the larval stage and as nymphs, and adults are predators on other small arthropods.

The Laboulbeniales is a group of fungi which grow almost entirely on the external surfaces of insects. They are normally commensal and harmless to the host, living off the chitinous cuticula. Occasionally, with soft-bodied species, labouls may penetrate the body cavity with extensive rhizoidal processes. Since these fungi are transmitted from one living insect to another at times of direct contact, i.e., copulation, they tend to exhibit specific host relationships (Steinhaus 1949). Bog-inhabiting pselaphid beetles were infested by at least four species of Laboulbeniales. Comparatively high incidences of infestation occurred with *Autophagomyces bryaxalis* Thax. and *Pselaphidomyces pselapti* Speg. These two species commonly are found on the same individual, although *A. bryaxalis* appears to have broader host range. Two undescribed species — *Autophagomyces* sp. on *Decarthron defectum* and *Adelomyces* sp. on *Pselaphus ulkei* and *P. bellax*—were also present on bog species. Additional infestation records of bog-inhabiting pselaphid beetles exist (personal communication, R. K. Benjamin): *Autophagomyces bryaxalis* on *Reichenbachia puncticollis; Autosphagnomyces* sp. on *Rhexidius canaliculatus; Pselaphidomyces pselapti* on *Reichenbachia puncticollis; Corethromyces elegans* on *Rhexidius insculptus.* The occurrence of these fungi on pselaphid beetles cannot be dismissed lightly. Their influence upon the dynamics of the bog population, however, must await further study.

Behavioral Patterns. Many terrestrial arthropods possess characteristic locomotory rates which vary according to environmental stresses such as predator-prey interactions, responses to climatic variables, and structure of the habitat itself. For the bog-inhabiting pselaphids, a positive correlation has been demonstrated between body size and locomotory rate (Reichle 1967). Such behavior may be important within the interstices of the moss habitats, since larger species are typically associated with looser sphagnum growths. In loose moss habitats the larger agile species could respond more swiftly to predators, prey, and climatic changes. In crevices of denser habitats, speed and agility would be of lesser consequence, and the ability to maneuver within the moss interstices could shift the competitive balance in favor of smaller species.

Body contact with foreign surfaces often has an inhibitory effect upon locomotor activity. Low thigmokineses are typical of crevice-dwelling animals, and often are associated with their aggregative tendencies. Under natural conditions, such reactions will lead animals into sheltered places where they not only are protected from predators but also receive optimal climatic melioration. Bog pselaphids as a group exhibit thigmokinesis. In laboratory cultures, *Reichenbachia borealis* consistently localized ($P < 0.001$, chi-square contingency test) in corners and along side walls of chambers (Reichle 1964). There also was a significant ($P < 0.001$) preference exhibited for vertical surfaces. This response results from a negative geotrophism common in these species. Presumably, such behavior is associated with the stratified nature of their habitat and their preference for the upper living moss layers. It was common during field collections to find the majority of individuals localized near the surface of moss habitats.

The majority of species in the Pselaphidae are capable of flight. Flight activity is characteristically nocturnal, although this behavior is more typical of tropical regions and drops off sharply in temperate climates. Continuous light trap collections were maintained at Volo Bog from May to October 1962 without any records of pselaphids. This is contrasted by records of *Decarthron abnorme*, *D. defectum*, *Reichenbachia distans*, and *Brachygluta intricata* at light in early July in Wisconsin. Apparently under certain conditions, norturnal flights of bog pselaphids may occur. Although flights were not of sufficient range for migration between isolated bog localities, they could afford dispersal between habitats within the bog itself. The correlation of early summer flight activity with copulatory behavior and the appearance of new adults in the population, suggests a functional role of this behavior pattern in population dynamics.

Physical Environment — Microhabitat Factors

Temperature. Temperature extremes in bogs often exceed those of neighboring communities. Rigg (1947), in studies of air and soil temperature in a coastal sphagnum bog of the Pacific Northwest, found freezing temperatures in all months except August with temperatures consistently lower than those of the surrounding region. He attributed this to three basic factors: (i) setting of cold air in the bog depression, (ii) persistence of low temperatures in underlying peat from the preceding winter, (iii) cooling by evaporation and thermal radiation. Correlated with the successional development of bogs, there occurs a drop in substratum temperatures from the floating mat to the tamarack zone, and thereafter a general rise through later successional stages (Burns 1911). In Stage III, however, tamaracks have been found to exert their greatest modifying effect upon microclimate only during the summer months when in full foliage (Turnock 1955).

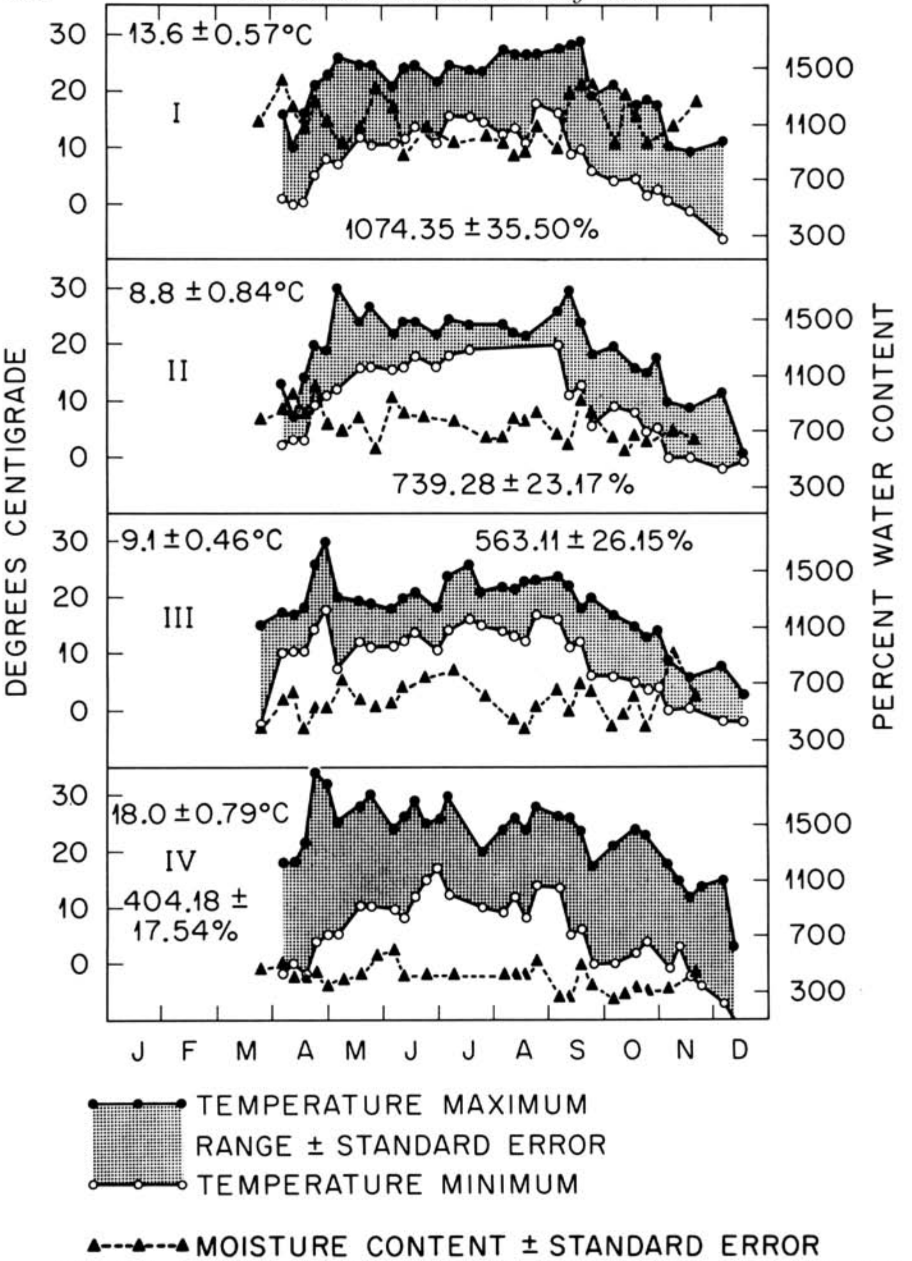

FIGURE 7. A comparison of the temperature regimes and moisture content of moss microhabitats in each stage of bog succession. Temperature curves show weekly extremes and weekly range. Values associated with each graph are (1) mean annual temperature range ± one standard error and (2) mean annual moisture percentage ± one standard error. Records taken beneath the moss mat: Stage I (6 cm), Stage II (8.5 cm), State III (5 cm), and Stage IV (3 cm).

Macroclimate temperature data for the Volo Bog region were obtained from U. S. Weather Bureau reports for the northwestern part of adjacent Cook County. Temperature regimes from March through December averaged 10.5°C with a range of from -20.5 to 35.0°C. In the Stage III tamarack forest at 10 feet, the temperature range for this same period was -30.5 to 32.0°C. Compared with regional conditions, not only did the bog have lower minimum temperatures but it also was subject to freezing temperatures during a greater portion of the year. Only between May and August were bog habitats free of freezing temperatures. Direct interception of incident radiation by the exposed sphagnum mat resulted in overall temperature regimes than those of the tamarack forest. Similar microclimatic differences also were evident between the moss microhabitats of different successional stages.

In analyzing the seral distribution of pselaphids in the bog, temperature conditions were characterized for the major moss habitats in each successional stage (Fig. 7). The annual extremes and the mean weekly temperature range ± one standard error were: Stage I, -5.5 to 29.0°C, 13.6 ± 0.57°C; Stage II, -2.0 to 30.5° C, 8.8 ± 0.84°C; Stage III, -3.0 to 30.0°C, 9.1 ± 0.46°C; Stage IV, -12.0 to 34.0°C, 18.0 ± 0.79°C. Sphagnum habitats in Stage I and the sparse moss habitats of Stage IV exhibited the greatest temperature variation. The more protected and denser moss growths of Stages II and III showed maximum temperature melioration.

Vertical temperature stratification within the respective moss habitats resulted in considerable melioration of above-ground environments (Fig. 8). Surface temperatures throughout the year showed a general decrease from pioneer to mature successional stages. The most abrupt temperature decline occurred between Stage I and Stage II. In Stage II evaporaiton in the absence of direct sunlight resulted in considerably lower temperatures. Shad-

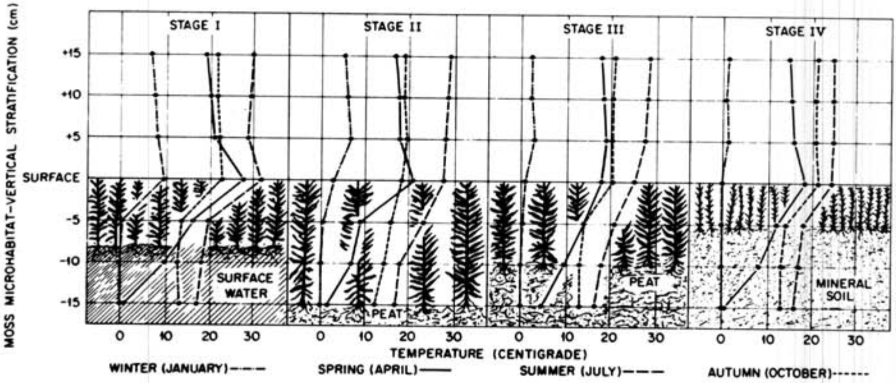

FIGURE 8. Vertical temperature stratification above and within successive moss layers for each season and successional stage. Growth habits of mosses in each stage are diagrammatically illustrated: first three stages sphagnum mosses, Stage IV nonsphagnum mosses.

ing by tree cover slightly enhanced this effect in Stage III. With increasing depth within the moss mat, obvious temperature differences between stages began to disappear. Seldom did temperatures above 20°C occur below 5 cm depth, and at 15 cm all localities had relatively uniform temperatures for any season. Norgaard (1951a) recorded only a 4°C range over 24 hours for summer temperatures at 10 cm depth in sphagnum, while temperature variations on the surface approached tenfold. With exception of the dormant winter season, however, pselaphid populations are generally confined to upper moss layers where temperature characteristics of moss habitats in different stages are distinctly different.

In the laboratory, July temperature preferenda were obtained for five bog pselaphids by Reichle (1967). The recorded temperature preferenda (Table VIII) correlated with temperature conditions of microhabitats where each species had peak distributions. *Decarthron defectum* and *Rybaxis clavata*, both characteristic of early successional stages, possessed the highest temperature preferenda (28.5 and 28.3°C, respectively). These preferenda corresponded to the higher moss surface temperatures in Stages I and II, and these species were rarely found in later successional stages. *Pselaphus ulkei* reached its peak distribution in the cooler moss habitats of late succession and, correspondingly, possessed the lowest temperature preferendum (19.5°C). *Reichenbachia borealis* and *Bythinopsis tychoides* were dominant species throughout bog succession. Their intermediate temperature preferenda were apparent adaptations to the broader temperature range encountered between different microhabitats. Whenever two species were codominants in a given microhabitat, e.g., *Reichenbachia borealis* and *Decarthron defectum* in Stage I and *Rybaxis clavata* and *Pselaphus ulkei* in Stage II, they possessed different temperature preferenda. This suggests that temperature stratification between microhabitats may be an isolating mechanism separating these sympatric populations. Similar temperature stratification of populations has been demonstrated for Danish bog spiders (Norgaard 1951a, b, 1952). In the case of

TABLE VIII. Temperature and relative humidity preferenda of five bog-inhabiting inhabiting pselaphids (after Reichle 1967).

Species	temperature preferendum (°C) (mean ± standard error)	humidity preferendum (% R.H.)	locomotory rate (cm/min ± S.E.)
Bythinopsis tychoides	21.5 ± 0.81	> 95%	21.4 ± 0.68
Decarthron defectum	28.5 ± 0.55	> 95%	29.2 ± 1.07
Pselaphus ulkei	19.5 ± 0.86	> 95%	43.6 ± 1.00
Reichenbachia borealis	21.9 ± 0.99	> 95%	58.1 ± 1.30
Rybaxis clavata	28.3 ± 0.41	> 95%	67.1 ± 1.65

Reichenbachia borealis and *Bythinopsis tychoides*, with similar temperature preferenda (Table VIII) and congruent distributions throughout the bog (Fig. 4), each species had distinct feeding habits (Table VII). Different ecological niches would remove these populations from direct competition.

Year-round field collections of beetles and the postulated life cycle suggest that adults successfully overwinter within the interstices of the frozen moss mat. *Reichenbachia borealis* collected during the summer months and acclimated for 24 hours at 17°C showed a temperature preferendum of 21.9°C. However, *R. borealis* survived at temperatures between 4 and 27°C; $LD_{50\text{-}24\text{ hr}}$ for temperature extremes were 1.5 and 33°C. Tolerance of extremely low temperatures, even in summer-adapted individuals, is indicative of the ability of these species to survive winter conditions. Collections of frozen moss will yield immobile individuals, which become active upon warming. Park, Auerbach and Wilson (1953) reported similar cases of cold hardiness for Illinois prairie pselaphids. The preferendum of the bog species, *R. borealis,* was only slightly below maximum tolerated temperatures, leaving a delicate compensation zone between preferred and lethal temperatures. Since high lethal temperatures are often approached in the upper moss layers, maximum lethal temperatures, rather than low temperatures, may be one of the critical factors affecting the distribution and abundance of the pselaphid population.

Moisture conditions. High humidities are characteristic of bog situations. Sheltered bog depressions have poor air circulation, and the saturated moss floor cover provides an excellent evaporating surface. Burns (1911) studied evaporation rates in a tamarack bog over a seven-week period in midsummer and gave the following relative values (no time units or evaporating surface areas stated): sedge zone, 321.7 cc; sphagnum under tamaracks, 275.0 cc; surrounding oak-hickory forest, 860.0 cc; adjacent field, 1056.0 cc. Since under given conditions the rate of evaporation is inversely related to moisture content of the air, these relative rates suggest high humidities within the bog proper. Although relative humidity of bog air is generally higher than for the surrounding region, it undergoes considerable daily fluctuation. Generally, near-saturated atmospheres develop during the night but these may drop by 50% during the day. Typically, the relative humidities within the interstices of sphagnum moss are high and undergo little fluctuation, even during the drying conditions of late summer. Moss habitats in the different successional stages vary in the degree to which humidity is accentuated, this being dependent upon relative depth and density of the moss growths (Table IX). The wetter mosses of pioneer stages have near-saturated atmospheres immediately beneath the surface, although microhabitat differences between stages are erased in lower moss layers. Stage IV microhabitats exert little modification upon humidity beyond that which can be accounted for through reduced wind velocities near the ground surface. Reduced air movement is an important fac-

TABLE IX. Relative humidity stratification in July for the four successional stages, showing comparative effects of moss microhabitats.

Levels	Stage I	Stage II	Stage III	Stage IV
15 cm above	60.0%	51.5%	52.0%	62.5%
10	61.5	54.0	52.5	63.5
5	63.0	56.5	56.5	64.5
0 surface	66.5	71.0	66.0	70.0
5	96.0	95.0	71.5	73.5
10	100.0*	100.0*	73.5	
15 cm below		100.0*	95.0	

* Supersaturation.

tor resulting in higher relative humidities immediately above and within moss habitats in all stages.

Reichle (1967) found that five different species of bog-inhabiting pselaphids consistently chose the most saturated atmospheres in experimental humidity gradients (Table VIII). Although all species preferred situations exceeding 95% R.H., they differed in the rates at which they responded. Presumably, such response times may give an indication of the relative tolerance of each species to adverse humidity stress. Ranking the species in order of increasing response time gave *Rybaxis clavata* < *Decarthron defectum* < *Pselaphus ulkei* < *Bythinopsis tychoides* < *Reichenbachia borealis*. Regression of response times on locomotor rates was not significant, indicating that these reactions were independent of locomotor ability. In the bog, optimum humidities are found in moss microhabitats in all stages except Stage IV.

Reichenbachia borealis and *Bythinopsis tychoides,* with greater tolerances of humidity extremes, were the only species of this group with significant distributions in the dryer nonsphagnum moss habitats of Stage IV. Conversely, *Rybaxis clavata* and *Decarthron defectum,* with rapid responses to changing relative humidities, were sharply limited to the saturated habitats of pioneer sucessional stages.

An important factor involved in the humidity relations of bog microhabitats is the moisture content of the substrata and mosses. Although there was considerable seasonal variation within each habitat type (Fig. 7), mean annual moisture contents were significantly different ($P < 0.01$). Moisture contents of mosses progressively decreased through the sere. Greatest differences occurred between the sphagnum moss habitats of Stages I through III. As sphagnum receded from open water and its growth habit became more elevated, the water content of its free haline cells decreased. These data corresponded to relative humidity values for these same habitats. A saturated moss mat and highest humidities occurred in pioneer stages, where ground water was abundant. The moss mat in Stage I received moisture from emersion in the bog lake as well as from precipitation. Although water content of the moss mat most quickly responded to precipitation, it was closely correlated to fluctuations in water level. Succeeding stages in the sere were characterized by elevated moss growths and drier moss mats. Mosses in Stages II through IV became increasingly dependent upon precipitation to maintain their moisture levels.

Other Physical Factors. Different vegetational components and moss habitats of the various successional zones interact to modify incident light intensities by as much as 60%. Greatest light reduction occurred within stratified layers of the moss microhabitats (Reichle 1964). At a 5 cm depth in all moss growths, light intensity was reduced to less than 20 ft-c. Associated with the low illumination levels of moss microhabitats was a characteristic negative phototaxis displayed by the pselaphid fauna. *Reichenbachia borealis* showed a significant ($P<0.01$) negative orientation to a collimated 70 ft-c light source. This is in the same range as illumination levels within the upper moss layers and well below light intensities on the moss surface. Similar behavior patterns have been reported for *Batrisodes globosus*, and have been suggested as selective mechanisms restricting species to protected habitats (Park 1947a). Although *Reichenbachia borealis* preferred low illumination levels, it was not entirely removed from photoperiodic influences. While high daytime intensities may be limiting, darkness and higher humidities may contribute to the nocturnal activity patterns characteristic of most pselaphids.

Wind velocity can often exert an indirect effect upon other climatic parameters. Accelerated evaporation rates due to air movement can severely limit the distribution of organisms with high moisture requirements. High evaporation rates and enhanced heat dissipation also will contribute to lower temperatures. Reduction in air movement through the various stages of bog succession was directly related to the degree of vegetational development (Reichle 1964). Air movement also was sharply reduced within the deeper layers of moss. Decreased circulation within the moss mat undoubtedly contributed the higher relative humidities within the interstices of the moss habitat.

Throughout the sere there was a successive development from a peaty substrate to mineral soils. Highest acidity was attained in early stages paralleling the development of sphagnum, although Stage I was influenced by the nearly neutral waters of the bog lake. Mean annual pH of the sphagnum zones were: Stage I, 6.5; Stage II, 5.1; Stage III, 6.1 (Reichle and Doyle 1965). When allowed to orientate on a substrate pH gradient from 3.2 to 9.0 (citrate-phosphate buffer), bog pselaphids displayed no predilection for substratum pH. Consequently, pH was not considered as a significant factor affecting their distribution in the bog.

The larger pselaphid species tend to be associated with habitats affording larger physical "living-space." Considerable variation in size of moss interstices occurred between microhabitats of the different successional stages. Sphagnum growths were characteristically looser in pioneer stages, with more compact

TABLE X. Interstitial volumes of sphagnum microhabitats in different stages of bog succession. Water-displaceable volumes measured from ten replicate 1510 cc moss cores from each stage.

	Stage I	Stage II	Stage IV
mean displaceable volume (cc)	1330.0	1396.5	1301.5
± S.E.	±9.08	±5.48	±5.58
mean dry weight (g)	14.4	11.3	26.8

growths occurring in later successional stages. Significant differnces ($P<0.05$) in interstitial volumes between stages were demonstrated by displacement measurements (Table X). Water-displaceable volumes of sphagnum mosses decreased with successional development. Denser moss habitats were correlated ($P<0.02$) with greater moss dry weights per unit volume of habitat. Vertical stratification with increasing compactness with depth also occurred within any given moss habitat. This tended to mask overt successional distinctions between size of habitat interstices and size of pselaphid inhabitants. Nevertheless, it is noteworthy that the large species, *Rybaxis clavata, Reichenbachia borealis* and *Pselaphus ulkei,* were either limited to or reached their peak distribution in looser moss habitats of pioneer successional stages. The smaller genera, *Bibloplectus* and *Melba,* seldom occurred in sphagnum, but were characteristics of the more compact nonsphagnum moss and litter habitats of late bog succession. *Rhexidius canaliculatus,* one of the smallest species occurring in Volo Bog, was abundant in Stage III within the deep and compact sphagnum hummocks on fern rhizones. Interspecies competition may be manifest through maneuverability of species within the microhabitaa. Body size-interstitial volume adaptations could be associated with predator-prey relations, and could operate by segregating species to particular microhabitats.

SUMMARY

1. A relict beetle population (Pselaphidae) with boreal affinities, comprised of 11 species, was found to inhabit an isolated northern Illinois bog. All species were residents of moss microhabitats, and did not occur in similar habitats of adjacent communities. The distribution and abundance of this fauna throughout the bog sere was examined and correlated with changing ecological conditions of microhabitats. Microclimate, predator-prey relations, and behavioral patterns appeared to be the dominant factors isolating sympatric populations. Faunistic successional patterns paralleled the vegetational sequence, and were closely related to the structure and composition of the moss mat.
2. Succession at Volo, Bog, Lake County, Illinois, was classified as follows: Stage I — the floating sphagnum mat composed almost entirely of *Sphagnum recurvum,* which formed a compact mat exposed to environmental extremes

and changing water levels; Stage II — a shrub zone of heaths and *Rhus vernix,* which stabilized the peat substratum and facilitated characteristic hummock development of *Sphagnum teres*; Stage III—a tamarack (*Larix laricina*) forest characterized by a drier substratum and the appearance of nonsphagnum mosses, with *Sphagnum squarrosum* and *S. magellanicum* persisting only about the rhizones of the ferns *Osmunda cinnamomea* and *Onoclea sensibilis*; Stage IV—a transitional subclimax swamp forest, characterized by the absence of sphagnum and a diverse, but poorly developed, moss floor cover. Development of moss microhabitats was inversely related to overall succession and maturity of the respective bog communities.

3. Pselaphid populations of pioneer successional stages exhibited clumped distributions, with greatest densities occurring in optimal hummock habitats. In the absence of hummock formations in Stage IV, the population was randomly distributed. Greatest occupancy of hummock habitats occurred in early successional stages, where microclimates afforded greatest melioration of environmental extremes. Seral distribuitons were modified by seasonal aspect, though its imprint upon microclimates. Drier conditions of late summer resulted in a population shift into the more protected habitats of intermediate successional stages. Aggregations also developed here in winter hibernacula and in early spring, when rising water inundated all but elevated hummock habitats.
4. Population peaks in spring and autumn were influenced by these climatic phenomena and also by the appearance of new individuals in the population. Annual records of newly emerged callow adults and larvae suggested a life cycle with only one generation per year. Larvae appeared in late spring following adult aggregations; adults emerged in late summer and overwintered within the frozen moss mat.
5. Maximum species diversity was associated with pioneer successional stages and maximum structural development of microhabitats. Mean annual density was highest in Stage II (49.7 indiv./m^2) and only slightly lower in Stage III. Density progressively decreased through Stages III and IV. Biomass showed a similar relationship: Stage I, 3.01 mg/m^2; Stage II, 4.45 mg/m^2; Stage III, 2.52 mg/m^2; Stage IV, 1.88 mg/m^2. Biomass was positively correlated with the degree of moss habitat development.
6. With many sympatric species populations occurring within and between each stage of bog succession, ecological isolating mechanisms removed species from direct competition. Distinct microclimatic and physical conditions of habitats, temperature preferenda, and predator-prey relations segregated populations within the bog sere.
   a. Bog pselaphids exhibited behavioral responses favoring saturated atmospheres and

low illumination levels and consequently, a predilection for the dark, moist moss habitats of sphagnum bogs.

b. Each species possessed a distinct temperature preferendum characteristic of the microclimate in moss habitats where it reached peak distribution. In certain cases where several species were codominant, temperature preferenda and stratified temperature regimes within moss habitats served to further restrict species contact.

c. Larger species were associated with loose moss growths of early succession affording greater "living-space." Conversely, minute species were typical of the compact moss growths of late succession. Body size adaptations to moss interstices appeared to be related to predator-prey relations and interspecies competition.

d. Pselaphids were found to prey upon a variety of soft-bodied microarthropods, including Collembola, immature Acarina, and dipteran larvae, although each species was typically a predator of a specific group. Different feeding patterns, in lieu of climatic isolating mechanisms, served to separate the congruent bog populations of *Reichenbachia borealis* and *Bythinopsis tychoides* from direct competition.

7. Although most species were distributed throughout the bog sere, the majority had peak distributions in particular successional stages *Reichenbachia puncticollis, R. borealis, Decarthron defectum* and *D. abnorme* were index species of early (Stage I) bog succession. *Bythinopsis tychoides, Reichenbachia scabra, and Rybaxis clavata* were characteristic inhabitants of sphagnum hummocks in Stage II. *Rhexidius canaliculatus* was the dominant species in the dense sphagnum habitats in the tamarack forest. The transitional swamp forest zone was an ecotone between the true bog fauna and other lowland species. The typical species of this stage (*Batrisodes striatus psotai*, *Bibloplectus* sp., and *Melba* sp., seldom penetrated the extensive bog populations of earlier successional stages.

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