Studies on the Biology and Ecology of Michigan *Phalangida (Opiliones)*

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INTRODUCTION

In the United States, research in the Order Phalangida (Order Opiliones) has been concerned primarily with taxonomy, as seen in the contributions by C. M. Weed, N. Banks, C. R. Crosby, and others. The phalangids of some states have been studied systematically, notably those of New York (Bishop, 1949) and Ohio (Walker, 1928). In contrast, like those of most of the remaining states, Michigan's phalangid fauna has been sampled only incidentally. T. H. Hubbell, Museum of Zoology, The University of Michigan, and the late R. R. Dreisbach, Midland, Michigan, made it a practice to preserve Michigan daddy-long-legs as they took them with other invertebrates of more direct concern. But publications on Michigan Phalangida are few, and the literature that is useful in studying the state's representatives of this order is quite limited. The most helpful material is to be found in the treatments by Edgar (1966) and Bishop (1949), together with the key and descriptions of species in the monograph of the genus *Leiobunum* by Davis (1934).

Although approximately 160 species of daddy-long-legs, belonging to 44 genera, 9 families and 3 suborders, occur in North America, only a small fraction (21 species, 8 genera, 3 families, 1 suborder) are found in Michigan, viz.,

Order Phalangida
    Suborder Cyphophthalmi—no representatives
    Suborder Laniatores—no representatives
    Suborder Palpatores
      Family Nemastomatidae Simon
        Genus *Crosbycus* Roewer
          C. dasycnemus (Crosby)
      Family Ischyropsalidae Simon
        Genus *Sabacon* Simon
          S. crassipalpe- (L. Koch)
      Family Phalangiidae Simon
        Genus *Caddo* Banks
          C. agilis Banks
          C. boöpis Crosby
        Genus *Odiellus* Roewer
          O. pictus (Wood)
          O. argentus Edgar
        Genus *Phalangium* Linnaeus
          P. opilio Linnaeus
        Genus *Opilio* Herbst
          O. parietinus DeGeer

Genus *Leiobunum* C. L. Koch
    L. calcar (Wood)
    L. cretatum Crosby and Bishop
    L. flavum Banks
    L. lineatum Edgar
    L. longipes Weed
    L. nigripes Weed
    L. nigropalpi (Wood)
    L. politum Weed
    L. serratipalpe Roewer
    L. ventricosum (Wood)
    L. verrucosum (Wood)
    L. vittatum (Say)
Genus *Hadrobunus* Banks
    H. maculosus (Wood)

Eighteen of the phalangid species found in Michigan have been reported only from the Western Hemisphere. The three remaining species, *Phalangium opilio, Opilio parietinus,* and *Sabacon crassipalpe,* are more or less world-wide in distribution. Undoubtedly the best known of these is *P. opilio.* It is unique in our own fauna in that it is the only species that seems to be able to reproduce and maintain itself in habitats more or less strongly influenced by man. Forster (1947) reports it to be the only non-endemic species in New Zealand and never found in unsettled areas. Indeed, it appears to be man's closest phalangid fellow traveler.

The genus *Leiobunum* is notable because 12 of the State's 21 species are included in it. About 20% of the North American forms belong in *Leiobunum.* Its members typically are abundant in the forest and are more likely to be collected than any other genus. *Leiobunum* includes species reported from South America, Europe, the Middle East and the Orient.

Other Michigan genera are interesting because of their spatial and temporal distributions. *Odiellus* includes 15 species additional to the two found in Michigan; its range includes Southern Europe and North Africa as well as North America. The fossil species, *C. dentipalpus,* has been recovered from baltic amber (Bishop and Crosby, 1924) and would seem to extend the early range of the genus to Northern Europe. The reporting of *C. agilis* in Japan by Suzuki (1958) and others further complicates the zoogeography of this very interesting genus. The genus *Crosbycus* has a solitary species *(dasycnemus)* which, together with the rather large non-American genus *Nemastoma,* makes up the Family Nemastomatidae.

Most Michigan phalangids have the main parts of their ranges in the eastern and southern United States. *Hadrobunus maculosus* is found in the northern portion of this area, while *H. grandis* occurs in the southern. Careful study needs to be done to distinguish these forms more clearly. *Leiobunum flavum* and possibly *L. verrucosum* are southern species (Bishop, 1949). Their northern limits lie probably in the southern portion of the

Lower Peninsula. There is some evidence to indicate that *L. longipes* reaches its northern limits in Wisconsin (Levi, 1952) and the Upper Peninsula of Michigan. Published records indicate that *L. vittatum* and *L. politum* are two of the most common species in the eastern half of the United States. These species were taken very frequently in Michigan and the former from a great diversity of habitats. Both have been reported from widely separated latitudes—from Texas to Manitoba.

The compilation in the Appendix summarizes records of collections of phalangids from Michigan reported for the first time. Collections were made from all 83 counties of the State. The number of collections per county bears no consistent relationship to the number of species secured. Three counties, Cheboygan, Gratiot, and Washtenaw, were collected from more extensively than the others.

My own collections of Michigan phalangids were prompted by a desire not only to ascertain their geographic distribution within the state but also to know more about their general biology and ecology. I therefore made detailed observations of selected species, both in the field and under laboratory conditions, with respect to such aspects of their life histories as development and growth, mating behavior, food habits, and physiological capabilities. These observations are reported in the present paper as a contribution to knowledge of the natural history and habitat characteristics of this widely distributed but not well-known group of terrestrial arthropods.

This paper is divided into three principal sections. The first section deals with the biology of four species of the genus *Leiobunum;* these were the most abundant species found in a sustained study of the phalangids of a mesic deciduous woodland carried out in 1957 and 1958 at the University of Michigan Biological Station, and they yielded a considerable body of information about their life history and ecology. The second section presents the results of laboratory experiments to ascertain the limits of tolerance and optimal conditions for temperature and moisture, factors of obvious importance in the phalangid environment. The third section attempts to integrate field and laboratory observations in analyzing the habitats of most of the Michigan species of phalangids as they were recorded in the course of state-wide collecting.

ACKNOWLEDGMENTS

BIOLOGY OF FOUR SPECIES OF LEIOBUNUM

The site for this study was a woodland on Grapevine Point, Douglas Lake, Cheboygan County, Michigan. Here, about 85% of the trees were *Acer saccharum* with a diameter 1–5 cm. A few *Betula papyrifera, Fagus grandifolia, Quercus rubra* and *Tilia americana,* 5–20 cm. in diameter, constituted nearly all the remaining tree species. Small woody and low herbaceous species of *Aralia, Gaylussacia, Galium, Trillium, Ribes,* and *Polygonatum,* together with several mosses and lichens, were the primary ground vegetation associated with the above tree canopy and are evidence of a mesic moisture regime. Considerable shelter and shade for the resident animals were afforded by the moderate to dense plant growth.

A fairly homogeneous area of approximately 50 x 80 meters was gridded with stakes set at 10 meter intervals. Sampling units (quadrats) of 1 x 10 meters and 1 x 1 meters were easily located and delimited by reference to the established grid. When quantitative collections were made from specific quadrats, care was taken not to cast a shadow upon the area under examination. To insure a minimum of disturbance both to the litter and the animals, walking in the gridded area was kept to a minimum, occurring along boundary lines and outside the quadrat under study.

Although phalangid eggs are deposited in ground litter, the young soon ascend into higher vegetational strata, including tree canopy, and thereafter spend part of their lives out of easy reach of the collector. In the present study, collections were made first from the litter, low herbage, and the lower parts of tree trunks. White sheets were then spread on the ground, covering the area of a 1 x 10 meter sampling unit, and specimens were collected from the higher vegetation by vigorous shaking of the tree trunks. Shaking was done as uniformly as possible, to restrict collection to the canopy area directly above the sampling area. Trees with trunks larger than 10–12 cm. in diameter proved difficult to shake, but these constituted only a small percentage of the trees in the gridded area. There was no indication that phalangids seek out larger trees in preference to the smaller ones.

Phalangids can be handled in a number of ways. The most expeditious method is to pick them up with the thumb and first two or three fingers. This frequently results in loss of legs, however, and if living individuals in perfect condition are desired, an insect net may be used to sweep through low vegetation. Small specimens are best taken up with a moist camel hair brush. Occasionally the phalangid sought is so small that it must be moved by handling pieces of litter upon which it walks. Small, difficult-to-see specimens in litter are best recovered by sifting the litter through half-inch mesh screen onto some light background such as a white sheet. All of the known specimens of *Crosbycus dasycnemus* collected thus far in Michigan have been found in litter subjected to sorting in Berlese funnels or recovered from pit traps. Animals on trunks a few feet above one's reach may be stimulated to move downward by gently prodding from above with the end of a stick. This procedure is risky since many simply leap away from their perch when

startled; when they begin falling freely it is extremely difficult to follow their descent in dim light, especially if air is moving and if they tend to drift away from a vertical path, and on the ground they usually remain motionless and sink deeper into the litter as one disturbs the leaves in searching. All except the heaviest-bodied species float down without injury. Those that lose legs easily (for example, *Leiobunum longipes, L. politum, Hadrobunus maculosus* and *Caddo agilis*) may often be collected in perfect condition by prodding and directing them into a live cage.

To expose the genitalia at the time of preservation, for subsequent aid in identification, some investigators have recommended putting pressure on the abdomen of sexually mature specimens (Weed, 1889; Walker, 1928). However, this rarely results in sufficient extension of these organs, and damage to the body or distortion of the typical body contours is likely to occur. Since it is not difficult to dissect out the genitalia if necessary, I suggest that no special efforts be made to expose them at preservation.

Quantitative samples were taken regularly during the summers of 1957 and 1958. By the time collecting began in mid-June, three of the four species of *Leiobunum* studied had hatched from the egg wintering-over stage. Development of all four species was followed until mating and oviposition were completed in late August. In only *L. longipes* were all the life history stages observed. Considerably more information was gathered about this species and, as a consequence, it is discussed in more detail.

A series of 24-hour collections was made in July and August, 1958, to investigate diurnal behavior and vertical migration of phalangids. Four different quadrats per week were collected once each at regular intervals— at 4:00 P.M., 11:00 P.M., 3:00 A.M., and 9:00 A.M.—during the 24-hour period. These times were selected to secure specimens under widely varying daily conditions of light, temperature and moisture. An old-fashioned kerosene lantern was found satisfactory as a light source at night; its low intensity caused a minimum of disturbance but was adequate for locating specimens at close range.

These collections, supplemented by various laboratory observations, yielded a considerable body of life history information that is summarized in the following account. It deals principally with four species of the genus *Leiobunum: L. longipes, L. calcar, L. politum* and *L. vittatum,* these being generally the most abundant species taken. References to other species are made as appropriate.

ABUNDANCE AND BIOMASS

In the summer of 1958 collections of *Leiobunum longipes, L. vittatum, L. calcar,* and *L. politum* were taken from 1m x 10m quadrats studied at Grapevine Point. From June 11 to July 10, and from August 24 to August 26, samples consisted of one quadrat each; from July 11 to August 22, each sample included four quadrats. The numbers of individuals taken in these collections are shown in Table 1. These data are not sufficient to provide a

satisfactory measure of population changes but they indicate approximate relative abundances of the four species. *L. longipes* was the most abundant, contributing 77.4% of the total phalangids collected. *L. vittatum* and *L. calcar* were present at intermediate densities, accounting for 7.5% and 10.6% of the total, respectively. *L. politum* was encountered only from July 6 on, occurring at consistently low densities and contributing only 4.5% of the total. Over the entire collecting season, the phalangid population at Grapevine Point averaged 37.4 individuals per quadrat, a mean of 3.7 per square meter.

Biomass data were obtained from a few of the collections and are also presented in Table 1. They indicate average biomasses per square meter during the three sampling periods where data are available as follows: *L. longipes,* 89.9mg; *L. vittatum,* 13.4mg; *L. calcar,* 10.2mg; and *L. politum,* 2.8mg. Thus, the average total phalangid biomass of 116.3mg per square meter was composed of 77.3% *L. longipes,* 11.5% *L. vittatum,* 8.8% *L. calcar,* and 2.4% *L. politum.*

Both abundance and biomass figures point to the dominance of *L. longipes* in this phalangid assemblage. Because *L. calcar* tends to complete its life cycle relatively early in the season, this dominance of *L. longipes* becomes even more pronounced in the latter part of the summer.

DEVELOPMENT AND GROWTH

A major pattern of phalangid life history and development is found in the genus *Leiobunum,* exhibited by *L. longipes, L. calcar, L. politum* and *L. vittatum.* Each of these species hatches from eggs in the spring, passes through several body stages in the spring and summer, becomes sexually mature from midsummer to early fall, then mates and oviposits in the forest litter, where the eggs normally overwinter. A second pattern of development is seen in *L. ventricosum* and *L. nigripes:* the eggs are deposited earlier and hatch in the summer, the young grow to near-adults in the fall, over-winter in this condition, and then mature and mate in the following spring and early summer. A third type of life history is exemplified by *Phalangium opilio:* both eggs and young winter-over and two generations per year is the rule; the population includes individuals in several stages of development at any one time.

From a developmental standpoint, there seems to be no reason why eggs of most *Leiobunum* species, if oviposited in the fall, could not hatch before cold weather. Eggs laid by *L. longipes* developed and hatched in the laboratory without a cold diapause. The site and season of oviposition on Grapevine Point led to an interruption of development by the cold winter period. Whether development in these species must not proceed past a certain point in the fall in order to continue successfully in the spring is not known. Holm (1947) reported that *Opilio parietinus* develops no further than the blastoderm stage unless subjected to a cold period of two or three weeks. In his

TABLE 1

ABUNDANCE AND BIOMASS OF *Leiobunum* SPECIES AT GRAPEVINE POINT

Date of Coll. (1958)	Number of Individuals[1]					Biomass (mg. live wt.) [1]				
	L. l.	*L. v.*	*L. c.*	*L. p.*	Total	*L. l.*	*L. v.*	*L. c.*	*L. p.*	Total
6/11	63	1	10	0	74					
6/12	15	4	3	0	22					
6/13	12	0	0	0	12					
6/16	7	3	7	0	17					
6/18	33	7	7	0	47					
6/20	43	7	7	0	57					
6/25	7	3	0	0	10					
6/26	30	7	10	0	47					
6/27	70	0	27	0	97					
7/2	21	3	7	0	31					
7/6	28	4	1	2	35					
7/10	57	2	5	10	74					
7/11–12	110	18	33	11	172					
7/17–18	178	9	13	21	221					
7/24–25	100	18	14	9	141					
7/31–8/1	92	2	2	5	101	653.2	28.2	45.1	29.6	756.2
						28.4[2]	56.5	90.1	23.7	
8/7–8	76	14	4	4	98	672.6	210.6	91.1	25.2	999.5
						35.4	60.6	91.1	25.2	
8/14–15	132	9	7	5	153	1372.8	162.2	169.9	28.2	1733.2
						41.6	72.1	95.7	22.6	
8/21–22	58	0	2	0	60					
8/24	16	0	0	0	16					
8/25	7	1	0	0	8					
8/26	11	1	0	2	14					
Totals	1166	113	159	69	1507					
% of Total	77.4	7.5	10.6	4.5	100.0					

[1] From 6/11 to 7/10 and from 8/24 to 8/26, only 1 quadrat (1m x 10m) was examined on a given date; on other dates, 4 quadrats were used.

[2] Lower of 2 figures is mean biomass (mg. live wt.) of single specimens; N ranges from 4 to 18.

L. l., Leiobunum longipes; L. v., Leiobunum vittatum; L. c., Leiobunum calcar; L. p., Leiobunum politum.

study the percentage of hatch was increased if eggs were given a cold treatment of near 0°C for a short period.

EGGS.—Because the eggs of phalangids are very susceptible to attack by mold, litter in which they are oviposited should not be disturbed. On Grapevine Point, deer, forest rodents and a few birds caused considerable disruption of the leaves and twigs by forming paths and burrows, and by searching for food. In collecting from a variety of Michigan habitats, it was striking to note that *Leiobunum longipes, L. calcar, L. politum* and *L. vittatum* were absent or sparse in actively pastured woods which otherwise would be ex-

pected to house these species. Both eggs and egg cases, which are shed upon hatching, were collected in the Grapevine Point study area; some were moldy, partially embryonated eggs, indicating either that the female was not infallible in selection of oviposition site or that some disturbance had altered natural conditions.

Eggs were found in nature very infrequently. To study mating, oviposition and hatching, laboratory pairings of the four *Leiobunum* species were effected in observation chambers, 12 x 12 x 18 cm. Each was provided with Petri dish halves containing moist moss, leaf fragments or small pieces of decaying wood. The dishes were examined periodically and when eggs were found they were either transferred to another container or left undisturbed for incubation.

All four species at Grapevine Point oviposited predominantly in clusters. Eggs of *L. vittatum* and *L. calcar* were found only in clusters in cavities within the substratum, usually soil (Table 2). During egg laying, the ovipositor was observed to explore blindly and to deposit eggs in spaces as far removed from the surface as could be reached. Sometimes this was one centimeter, more than the length of the body. Apparently an undisturbed female will oviposit all the eggs available in the uterus. At the extreme end of its egg laying period, *Leiobunum calcar* has been observed to deposit eggs singly at intervals of several hours. Death of the animal usually followed shortly.

Leiobunum longipes and *L. politum* deposited eggs in a manner similar to the above, but frequently (Table 2) the female searched diligently for cracks and crevices within pieces of decaying wood. The spaces chosen were usually cylindrical and only large enough for the ovipositor to enter. These spaces were often completely filled with eggs; on one occasion eggs were so

TABLE 2
OVIPOSITION IN FOUR SPECIES OF *Leiobunum* ON GRAPEVINE POINT

		longipes	*vittatum*	*calcar*	*politum*
No. of females observed		29	6	6	7
No. of eggs per female		92.6	214	185.5	41
Dominant	Cluster	47	14	22	3
arrangement	Interstices	3	0	0	5
of eggs	Wood crevices	5	0	0	0
No. of eggs per cluster		45.4	92	54	28.7
No. of clusters per female		2.0	2.3	3.7	1.4
Maximum number of clusters by one female		4	3	5	2
Mean date of oviposition		8/25	9/6	8/13	8/22
Range of oviposition dates		8/7–9/25	8/15–10/15	7/31–[1]8/31	8/14–9/2

[1] Undoubtedly earlier since copulation was observed in the field as early as 7/2 and in the laboratory as early as 7/4.

closely packed that several had ruptured and the yolky material soaked into the adjoining wood. Occasionally *L. longipes* and *L. politum* oviposit eggs in a series of substratum interstices, each large enough to accommodate only a small number of eggs. The total of eggs in these several locations was considered as constituting one oviposition (Table 2). The species least selective of the egg deposition site is *L. calcar;* it is the only one of the four that places eggs between moist pieces of plastic sponge and glass.

Laboratory incubation of phalangid eggs thus far has been difficult to sustain. With the necessary moisture present for development, mold growth almost always overgrows the eggs before development is complete and hatching can occur. Two species have been hatched successfully: *L. longipes* and *Phalangium opilio.* The eggs of the latter appear to resist the attack of mold more strongly than the former; when eggs of the two species are maintained side by side in the same dish, *P. opilio* always survives longer than *L. longipes.* Todd (1949, and personal communication) found that brushing a substratum of moist plaster of paris weekly with a very dilute solution of copper sulfate prevented mold growth. Yuan and Edgar (unpublished) observed that eggs of *P. opilio* develop and hatch with greatest success when incubated in an atmosphere of 94 to 98% relative humidity. Eggs in drier air lost too much moisture to develop completely, and those in higher humidities were destroyed by mold. Attempts to retard mold growth by removal of mold spores from the eggs by rinses with weak solutions of detergent and various fungicides were generally unsuccessful. Hatching of *P. opilio* eggs was achieved by Klee and Butcher (1968) with a substratum of styrofoam provided with $\frac{1}{8}$ inch diameter holes approximately $\frac{3}{4}$ inch deep. A relative humidity of 75%–90% was maintained.

As development within the egg approaches the hatching stage, considerable anatomical detail may be seen through the nearly transparent egg case. The eye tubercle is most prominent and appears first. Later, the segments of the abdomen are visible. Legs III and IV are seen to extend posteromedially and then to bend anteromedially, terminating between the chelicerae and base of the palpi. Legs I and II traverse medially to the opposite side of the animal, extend dorsally and, in the case of the long second leg, completely encircle the girth of the animal and terminate just dorsal to its own trochanter. These leg positions are similar to those described for *Opilio parietinus* just before hatching (Holm, 1947). When emergence from the egg is imminent, movement within may be seen. The major movement is a slight anteroposterior contraction of the abdomen similar to that exhibited by adjoining segments of an earthworm as it inches forward. The dorsal portions of the segments relax before the ventral and cause a dorsal arching of the abdomen. The complete movement is cyclical and extends over a 5–6 second period. The uneven pressure of the contained fluid ultimately weakens the egg case and the fluid serves to lubricate the exit of the animal. The initial rupture of the egg membrane is done by a special "egg tooth" (Balbiani, 1872) which disappears with the first molt.

MOLTING.—The young, newly-hatched phalangid grows to maturity via a series of molts. Newly exposed chitin rapidly hardens to an inelastic but variably flexible coat and consequently restricts growth owing to stretching of this surface layer. This is particularly noticeable with leg length and less obvious with change in body size and proportions. Even though the outside coat of chitin cannot be stretched, the body may take on larger dimensions and greater mass by straightening out the infoldings and wrinkles. The recently molted animal with new, hard chitin consequently will have the leg length of the new stage and the body measurements of the old. With increase in time, the legs remain the same length but the body grows and fills out the "slack" in the outside body wall. For these reasons leg length rather than body size is used as a criterion of stage of development. Body size is useful to a limited extent, especially in sex determination, when eggs accumulate in the female and distend the abdomen to its greatest capacity.

There are seven molts, and consequently eight stages, after hatching, in the life history of the *Leiobunum* species studied on Grapevine Point (Table 3). A similar development is reported by Todd (1949) for *L. rotundum, Platybunus triangularis* and *Phalangium opilio* in England. The usual period between molts is 6–20 days with the exception of the casting of the first smooth skin at hatching. This first molt usually occurs within one or two hours of emergence.

Phalangids molt on tree trunks, small limbs, spider webs, undersides of leaves, windfall branches and twigs, and leaves in the litter. The surface used need have only two basic qualifications: (a) it should be positioned so that the animal can use the pull of gravity to its advantage in withdrawing the long legs, and (b) it must be rough enough for secure anchorage. Neither is an absolute essential, however, since on several occasions small immatures have completed the molt on the smooth floor of a Petri dish. For the larger bodied, longer-legged individuals the two above conditions must be met in some degree if a successful ecdysis is to occur.

All of the eight legs need not be attached to the substrate for the animal to molt perfectly. An anterior and posterior pair, usually I and IV, are the most commonly anchored. When the animal is suspended from a horizontal surface preparatory to shedding its chitinous case, the body is often held farther from the substrate than in a normal resting stance. In the latter, the body commonly is held less than one-third the distance from the supporting surface to the highest point of the arch of the longest leg. In preparation for molting the body is held almost pendulum-like, more than two-thirds of this distance from the surface.

When the phalangid takes the position it will maintain during the molt, it performs a series of spastic, jerking movements as if testing the strength of the attachment between the tarsi and the substratum. These movements probably sever internal connections between the old chitinous coat and the underlying chitin-producing epidermis. The external split and baring of the cephalothorax are initiated by this action.

TABLE 3
GROWTH STAGES OF FOUR SPECIES OF *Leiobunum* ON GRAPEVINE POINT

Length of leg IV (mm)

Stage	L. longipes			L. vittatum			L. calcar			L. politum		
	Range	x̄	N	Range	x̄	N	Range	x̄	N	Range	x̄	N
First		2.3	2									
Second		3.1	2									
Third	4.4–6.0	5.0	21									
Fourth	6.5–9.5	8.3	104		8.5	3					6.0	1
Fifth	9.8–17	13.8	92	12–15.5	14.0	24					9.5	1
Sixth	18–24	21.4	151	17.5–23	21.2	29	19–21.5	20.5	18	12.3–17	15.1	14
Seventh	26–38	32.0	156	28–34		40	28–35		37	20–26	23.0	33
	27–38	31.1	127	29–33		6				21–24	22.6	7
Total mean		32.0			31.1			31.2			22.9	
Eighth	45–63	54.3	106	43–56	45.8	23	42–49	45.9	60	32–36	34.0	12
	39–57	46.6	123	41–51	45.6	25	40–49	44.2	25	29–36	32.2	12
Total mean		50.1			45.7			45.7			33.0	

x̄, mean; N, number of individuals measured.

The initial rupture of the old skin occurs at the anterolateral margin of the cephalothorax so that the dorsum can peel backward over the eye tubercle and abdomen and the ventral portion can be pulled free of the mouth parts, chelicerae, palpi, abdomen, and walking legs, in that order. The last point of detachment of the animal from the old case is at the anal plate. Apparently, dorsal and ventral linings of a vestibule-like anus can be clamped together and held securely until the animal releases pressure and thus severs this last connection between itself and its exuvium.

The basic muscular contraction which gradually removes the animal from its case is abdominal, with assistance from the palpi and chelicerae. Also, muscles between the coxae and thorax are able to contract individually, thus slowly aiding in slipping off the case as one would remove a glove, unassisted, from one hand. When viewed from the side, the abdominal segments are seen to shorten along the longitudinal axis. Then, by relaxation of some muscles and contraction of their antagonists, the body may be flexed toward or arched away from the ventral surface.

Freeing the dorsum is accomplished quickly; extricating the long legs constitutes the arduous part of the whole task. A rhythmical pattern of: (a) flexing the abdomen to bring the chelicerae and palpi closer to the portions of the legs still in their cases; (b) grasping the legs by chelicerae and palpi; (c) arching the body away from the leg cases; (d) separating movements to prevent wet leg surfaces from adhering to one another during drying; (e) rest and then repetition of the above five activities, continues until all legs are free. The legs are pulled out of their encasements much as a person, with arms in sleeves tied to the fronts of his legs, would pull the arms ventrally and forward out of the sleeves. Even though the shorter legs are freed before the longer ones, they are still maintained in a bundle with the others and grasped by the chelicerae and palpi. These free legs do not grasp the others but rather, by contact friction, exert some pull on those still encased. When the legs are nearly free the animal will, by a disorganized type of walking movement, separate them as if to begin drying them. When the legs are entirely free, they are not immediately extended, but their distal ends are held in close proximity to the mouth parts and, one after the other, are threaded past them. This activity is necessary to remove all extracellular accumulations and liquids before they dry between the delicately connected articles of the tarsi. With this task finished, the animal allows the legs to hang partially extended and motionless while the new chitin solidifies. Often a series of strange, pulsing movements passes through all legs simultaneously as if, by intermittent internal fluid pressure, the legs were being gently forced to positions which would support the body in a normal, resting stance. This is the last chance for the legs to alter any dimensions or contour of joint articulation before the chitin hardens.

While the legs are hanging motionless the palpi go through a curious routine which suggests an exploration of the limit of all articulations. The segments seem to displace themselves spatially with each other and then

return to the original position. It looks as if it is a systematic double-jointed motion of getting out of joint and then snapping back at each palpal articulation.

During palpal activity the ovipositor of the female or penis of the male is gradually exerted to its full length, left exposed for a few seconds and then, very slowly, withdrawn a portion at a time. Several times the tip of the ovipositor is waggled in all directions just as one would test the flexible tip of a hose to make sure that it can move in right angles to the longitudinal axis and swing in a 360° arc.

Following the drying of the legs, the animal moves in a direction which brings it back to the same position it occupied when the case first began to split. As soon as the legs are secured the anal attachment is released and the animal is completely free of the old case for the first time. With a minimum of movement the animal moves backward the length of its body and buries its mouth parts in the wrinkled remains of the old body covering. Examined microscopically at this point, the old exuvium will be seen to be partially filled with a clear, viscous fluid. The purpose of returning to the case is to recover this fluid and use it to best advantage in replenishing body fluids and expanding the animal to its fullest size. A long period of inactivity by the animal in the nearby vicinity of the molt case completes the process of molting. The color of the new exterior is white in immature animals and pale gray or even bluish in adults or near-adults. As time passes, following molting, the coloration deepens in intensity and hue so that after a day or two one cannot be sure that a molt has recently taken place.

The time requirement for completion of various molts of a particular species increases as the size of the animal increases. Relative humidity, temperature, and air movement cause variation in these molting times. The most critical factor for a successful molt is relative humidity. If the surface of the molting animal dries too rapidly, the legs will be trapped within their old cases when the new, exposed chitin hardens. Resulting grotesque leg shapes usually make these appendages useless to the animal for locomotion or for any other activity except clumsy support.

Given an adequately high relative humidity, molting is not restricted to any particular period of the day or season. Since at any moment several body stages are usually present in a population of phalangids, molting is likely to occur at all times except in adverse moisture conditions. It is not uncommon to note, during a period of drought, an almost complete absence of molting activity. Within 24 hours of a rain following a prolonged dry period, nearly all the individuals of the population will have shed the old case. Thus, any graphic representation of leg lengths with time will not be a smooth line but rather a steplike one (for example, *L. calcar,* Fig. 1).

In the laboratory, phalangids frequently have difficulty in completing a perfect exuviation if temperature and relative humidity fluctuate. As temperature rises, for example, the relative humidity decreases, and since the animal cannot anticipate the thermostat or a strange set of environ-
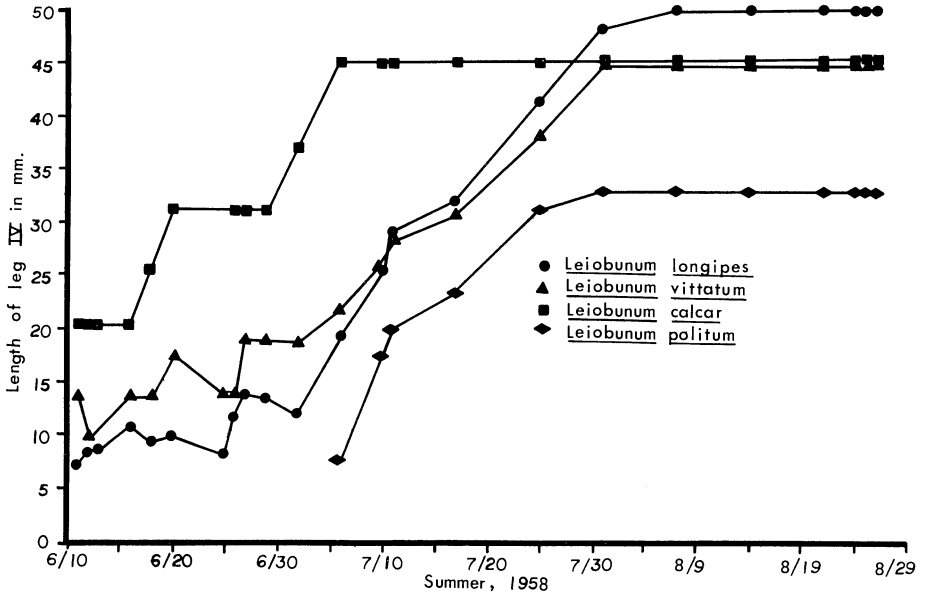
Fig. 1. Changes in length of leg IV in *Leiobunum* species studied at Grapevine Point.

mental conditions it is often caught with its legs only partially free. Usually the old case can be shed, but in taking an unusually long time to do so the chitin hardens with legs in grotesque, useless shapes. In nature, an individual is only very rarely seen with as much as the tip of one leg deformed. Correlating laboratory conditions with molting success suggests that the lowest R.H. at which the process is completed perfectly by near-adults at this latitide is about 60%. Infrequently, successful molts have been made at relative humidities as low as 57%, but more often leg deformation or failure results.

The length of the fourth walking leg was chosen as an index of body stage for two reasons. First, it is missing on both live and preserved specimens less often than the others. Second, since it is second only to leg II in length, accuracy in measurement is at least as high as it would be with the others. The leg proportions for the four pairs of legs remain constant; that is, if leg II is particularly long all others on that animal will be correspondingly longer than the mean for that leg, stage and species.

Comparative seasonal development of the four species of *Leiobunum* under consideration, as indicated by length of leg IV, may be seen in Figure 1. Unfortunately, collections are not available to complete the early part of the record; that is, stages of *L. longipes*, *L. vittatum* and *L. calcar* earlier than those with leg IV lengths of 7 mm, 14 mm and 21 mm, respectively, were not found in nature. None of the species was recovered in samples taken on April 11, 1958. Extensions of the curves for *L. longipes, L. vittatum*

and *L. calcar* to the points at which they might intersect the time axis suggest that eggs hatched sometime between May 20 and May 30.

At each molt, legs of all four species regularly increase in length very nearly one-half their previous length (Fig. 1 and Table 3). Only in stage eight can one be certain of the sex of all the individuals. Usually in stage seven the sex can be identified in *L longipes, L. politum,* and *L. vittatum.*

MATURATION AND LONGEVITY.—With experience one can distinguish the four species of the study area from the fifth stage onward. Previous to this, body-leg proportions are not diagnostic and a characteristic juvenile coloration prevades the four species of *Leiobunum. Leiobunum longipes* in the fourth stage exhibits a diagnostic white band at the distal end of tibia II. This band persists in later stages and provides a convenient field identification character. *Leiobunum politum* may be confused with it since most of the sections of all four pairs of its legs have lighter colored distal areas. The tarsi appear somewhat beaded with alternate dark and light brown in *L. politum* while in *L. longipes* the tarsi are uniformly darker brown. The femora of all legs early show a slightly heavier and darker spination in *L. politum* than in *L. longipes.* In the adult male of *L. longipes* this distinction does not hold. Usually the central dorsal pattern of *L. politum* is darker and its lateral margins more nearly parallel than that of *L. longipes.* Proximally the patella of the palpus narrows its attachment noticeably more in *L. politum* than in *L. longipes.* In the few stages prior to maturity the mean length of leg IV in *L. politum* is distinct from that of the other three species. The larger (not longer) legs of *L. vittatum* distinguish it quite readily from *L. longipes* and *L. politum.* It has no white spot on the distal portion of tibia II. The dorsal pattern becomes recognizable earlier than in *L. longipes;* the venter is a pasty gray. *Leiobunum calcar* is almost always larger bodied and temporally in a later stage of development than the other three species of *Leiobunum.* The coloration of the dorsum is characteristically patterned with more red and orange.

At the last molt the *L. vittatum* male exhibits a characteristically longer palpus than the female. It is an obvious character. Similarly, the palpi of the male *L. calcar* possesses a large spur on the femur. As growth proceeds there are abdominal size differences between male and female because females take on the task of egg production. The abdomens of the males are typically slender and pointed.

Sexes cannot be grossly distinguished with certainty in *L. calcar* and *L. vittatum* until the last body stages. With *L. longipes* and *L. politum,* body proportions and coloration indicate sexuality in stage seven. The central dorsal pattern of the female *L. longipes* is black, with a few puzzling exceptions, and brown in the male. The male abdomen remains truncate and rectangular while in the female it becomes expanded gradually and is bluntly pointed posteriorly. Similar distinctions apply to *L. politum* except that the male is a more uniform horn-tan in color while the female has a distinct, dark brown dorsal pattern and tan lateral margins.

Phalangids from the study area maintained and observed in the laboratory for several weeks displayed no obvious ill effects attributable to the unnatural surroundings. They fed readily, molted at comparable times, mated unhesitatingly, and presumably died after a normal life span. Table 4 records the mean and extremes for laboratory deaths of the four species from Grapevine Point.

BEHAVIOR

MATING.—Within a week after the first molts to stage eight have occurred in a population of *L. longipes,* the first signs of the approaching reproductive period appear. Small groups or clusters of 3–7 males and females are seen on tree trunks from three feet above the ground up to the lower

TABLE 4
DATES OF DEATHS OF FOUR SPECIES OF *Leiobunum* MAINTAINED IN THE LABORATORY

		L. longipes		*L. vittatum*		*L. calcar*		*L. politum*	
Sex		♂	♀	♂	♀	♂	♀	♂	♀
Mean		9/20	9/22	9/15	10/2	8/21	8/22	9/16	9/7
Range	♂	8/29–10/14		9/1–10/18		8/7–9/2		8/21–10/21	
	♀	8/29–11/1		9/2–11/27		8/4–9/2		9/2–9/11	
Number observed		30	28	19	11	8	4	10	4

branches. Since by this stage the animals have become large enough to be conspicuous on the litter, the trunks appear to provide a more suitable environment for these generally inactive gatherings. No apparent organization exists; males are not grouped together in one place and females in another, at least at first. Later on, males often appear at the periphery of the cluster. Clusters containing up to 58 individuals of *L. longipes* have been observed on Grapevine Point. Such clusters do not generally last for more than a few days: six days after the cluster of 58 was seen, only six male *L. longipes* remained at the same site.

Other than *L. longipes, L. vittatum* was the only species observed to form clusters. These were not associated with tree trunks. On August 6, 1958, three males and five females were found within six feet of the ground on leaves and branches of a beech tree. No activity was noted. Similarly, on July 11, 1959, clusters were observed on low broad-leaved herbs among sedges between the forest and shore line of Grapevine Point. One cluster of seven (three males and four females) occurred on the upper half of a plant about 20 inches high; the males were at the apex of the plant, two with legs in contact, while the females were within six inches of each other on the bases of nearby leaf blades. Other clusters of three each were seen in the same area.

Repeated observations of *L. longipes* clusters indicated that males eventually encounter females and attempt to copulate. The females vigorously resist this disturbance at first; when the frequency of copulation attempts increases they move away from the cluster, often farther up the tree, down to low vegetation, or to smaller trees where clusters do not ordinarily occur. Clusters, therefore, gradually disperse and disappear. The older males are the first to exhibit mating activity. As this activity increases, they wander more and more incessantly. Females are encountered more frequently and their resistance to mating eventually decreases, as resultant skirmishes become less intense.

Whether females of *L. longipes* leave isolated perches to wander over areas frequented by males is not known. Prior to 1958, when the collecting procedure had not yet included tree-shaking, I could not ascertain how many females survived the final molt or, when they did, to what portion of the habitat they retreated. Aggregations of both males and females were seen on trunks preparatory to mating; at this time, females were scarce in the litter and lower trunk populations. When collections from trunks and branches were kept separate from those from litter and low herbs, it was found that even during days of intense mating activity more females were collected on trees than elsewhere. Observations during the course of several mating seasons suggested that some females are entirely missed by males despite their continuous searching, and that others oviposit only a portion of their total egg production. Females which came from high in the branches consistently had abdomens more distended with eggs than those from the ground. If mating and oviposition are attained only via a sequence of trigger and release actions, the failure of some females to be mated and/or to oviposit is not surprising. On numerous occasions in the laboratory, unmated females have oviposited large clusters of eggs in a seemingly normal manner.

Mature males do not always limit their mating activities to females of their own species. The larger-bodied, more powerful males of *L. calcar* and *L. vittatum* occasionally try to copulate with any female phalangid encountered. Such attempts commonly result in conflict, and the male is often dragged and twisted by the female. He may try to face her and bring her close enough to effect a union, but she generally resists either by lowering her cephalothorax and raising her abdomen to avoid contact, or by turning away completely. Males that are conspecific with such a female do not interfere in these conflicts.

A peck-order of aggression exists among males of different species; it appears to depend upon relative body size and strength. *L. calcar* and *L. vittatum,* in that order, dominate *L. longipes* and *L. politum.* The latter two exhibit little antagonism toward each other or toward the two larger species. On one occasion, one male each of *L. calcar* and *L. vittatum* were placed in the same laboratory chamber. For two days the former continually harassed the latter, using both palpi and chelicerae to grasp legs, then

shaking and pulling. *L. vittatum* was strong enough to drag his antagonist around and eventually to escape from his clutches.

During the active mating period, *L. longipes* males exhibit one of two reactions to the presence of other males of the same species: (1) if a female *L. longipes* is present and the male has copulated with her, he will meet other males as intruders and try to fend them off; (2) if no female is near, males meet each other with indifference or mild avoidance. When two or more males encounter a female, the one which finally copulates with her has first to ward off the advances of the other males. Usually, the male closest to the female meets all challengers until no further advances are made. The victor may copulate ad libitum with the female but is always subject to further attack and displacement. When a group of males encounters a receptive female, as much as half an hour may be required to determine which one will serve as mate.

Struggles between males take the form of leg pulling contests. One will advance to an upper position, grasp a leg of the opponent with the chelicerae and palpi, and then violently jerk up and down or rapidly rotate the body. Rotation is in the dorsoventral plane and is clockwise when viewed from the animal's right side. One struggle lasted for 23 cycles of 3–5 revolutions each before the animal lower in position broke loose and fled. The objective appears to be to put so much shock stress on the leg that it is injured or broken from the body. Despite this, the upper male tries to put the other animal to flight. Often no consistent winner appears for some time. It has been observed that males which have successfully met a series of challengers have been those with all eight legs intact.

Repeated copulation with a female is the rule. In one series of laboratory observations, a male *L. longipes* was seen to attempt copulation at least 29 times over a period of two and one-half hours. If a male who has copulated with a female is challenged he must leave her briefly to repel the new threat. Occasionally a smaller male, who never directly challenges the reigning male, seizes the opportunity to mate with the unattended female while the defender is engaged with a third male. When the physically superior male returns to the female, he usually copulates again.

The act of copulation is rather simple. The male faces the female and grasps her by placing his palpi behind her second pair of legs close to the body. The second pair of legs of the male are poised at strategic places to detect interruption. The first legs are used to hold back the front legs of the female should she resist. The remaining legs apply support and direction to the body. At times, the female of *L. vittatum* has been observed to use her palpi and chelicerae to assist direction of the penis to her genital operculum. The copulation embrace may last for a period ranging from a few seconds to several minutes depending upon the quiescence of the female. She usually terminates the act by depressing the anterior part of her body which, if done vigorously and suddenly, almost always breaks the grip of the male.

Males other than the one escorting a female do not struggle with each

other when they meet. Either by sight, odor, or some tactile facility they recognize the male which must be defeated in order to copulate with the female. A dominating male often will not pursue its female out of the area in which it has fended off all comers. When the female strides unhindered out of this area the male reaches a point beyond which it will not follow. Other males show no further concern with fighting him, but establish another victor in the immediate vicinity of the female. The previous mate shows some effort to search his territory but no effort is made to re-acquire the lost mate outside the area of earlier mating activity.

Immediately after copulation the male forms an umbrella-like canopy over the body of the female with either the second or third pair of legs. If attention to the female is shown at any time, it occurs at this point, the male's legs gently stroking those of the female. In this manner the male practically prevents the escape of the female and shepherds her toward a stance of oviposition. Often it appears that if the male did not do this directing of the female she would simply walk away and fail to oviposit. Through the whole process of mating and oviposition, except as noted above, the female appears to take essentially no initiative.

Oviposition by *L. longipes* was observed in detail on one occasion. The ovipositor was exerted to its full length (13 mm) between the plastic sponge and glass wall of the watering tube in the chamber. The entire length of the tubular ovipositor was exposed to view through the glass. Generally, eggs arrived at intervals of 10–14 seconds, but occasionally two or three appeared in rapid succession 4–5 seconds apart. The ovipositor remained relatively inactive except at the terminal one-sixth portion. This region began vigorously twitching and waving back and forth two or three seconds after the last egg was discharged and continued until another appeared. The circular, lashing motion occurred rapidly (4–7 times per second) and may have aided in the peristaltic movement which carries the egg down the canal of the organ. As the egg passed along its path, no bulge in the diameter of the ovipositor was seen. Since the diameter of the egg was very nearly that of the ovipositor, the egg must have assumed an elongate shape. Eggs were placed on the glass or sponge singly by bringing the tip of the ovipositor close enough to touch the surface. When no surface was reached conveniently, the eggs accumulated in a string at the ovipositor tip. Approximately 120 eggs were placed in one particular cluster. After withdrawing the ovipositor, which was nearly twice the length of the body, the female spent 22 minutes at the waterer drinking and a shorter period feeding. By the time she had finished eating and drinking, her body outline was almost as distended and rotund as prior to oviposition.

Leiobunum vittatum does not exhibit so complex a pattern of mating activities as that of *L. longipes*. The male and female spend much time in inactivity quite close to each other. Sporadically the male pursues the female in a very vigorous manner. After copulation, the male ceases to attend the female or to shepherd her towards an oviposition site.

L. calcar mates repeatedly and for long periods. Usually the period is

20–50 minutes; the longest observed continuous copulation was for 125 minutes. No post-copulatory attention is shown by the male.

Reproductive activities in *L. politum* have been observed only a few times. Perhaps this species carries on most of its mating and ovipositing at night. The male approaches the female in much the same manner as does *L. longipes;* resistance of the female is either violent or relatively passive.

When males and females of *L. politum* and *L. longipes* are all present in the same restricted locality, both species carry on their respective activities without interference. Females of the two species may oviposit side by side in the same crevice or mound without dispute.

AGGREGATIONS.—At two different times in the life history of *L. longipes* there is an obvious discontinuous distribution of the population on the forest floor. One of these is associated with mating. In early August, during the reproductive period, one may predict with reasonable success where mating will occur. Among the irregularities in the typical forest floor contour are mounds topped by areas of moss, large fallen logs which are in late stages of decay, and stumps whose bases accumulate litter and moisture. Wherever an increase in the supply of moisture is apt to occur, phalangids will almost certainly center their mating and oviposition activity. Whether males come to these centers to search for females or whether the females congregate here and attract males is not known. On one occasion, 15–20 male *L. longipes* were seen wandering continuously over an oval ridge of soil containing windfall, a decayed log, moss, and some lichens. The animals avoided thickly tangled twigs and occasionally climbed a low maple seedling. When limits of the area were reached, males occasionally continued on out of the area, but more often they turned back and remained in the vicinity of the mound. One female *L. longipes* was also in the area, about one foot above the ground on the upper surface of a leaf of *Aralia nudicaulis*. After a period, I dislodged her to the litter surface. She "froze" for about one minute and then moved a few inches, whereupon a male touched her. She was recognized immediately but rapidly moved away about three feet. The aroused male was apparently unable to find her afterwards. When I placed her closer to the males, her alternate rapid striding and freezing behavior suggested a tendency to avoid detection.

The other time of aggregation is associated with the early stages of development. Upon hatching, the young move only very gradually away from the hatching site, and the centers of oviposition activity can still be detected as late as the next spring. After the third molt is completed, the animals frequently come to the surface litter and deploy rapidly to less populated areas.

ESCAPE AND CONCEALMENT.—If a phalangid is startled while resting or striding on a tree trunk it will usually spring away from the trunk and float to the forest floor. The long legs prevent too rapid a descent and maintain a horizontal orientation with the ground surface. Usually the descent of the

body is lost from sight in the dim light of the shaded habitat, and the animal frequently remains motionless at the spot where it lands. Unless one retains sight of the animal, he might as well wait patiently for it to move voluntarily; brushing the litter in an effort to flush it usually serves only to bury it deeper among the loose leaves. *Leiobunum politum* and the female *L. calcar* are especially successful in this method of escape. Others, especially *L. longipes,* escape by moving rapidly in an irregular course, casting very little shadow and blending well with the background litter coloration.

Phalangids frequently are found on a background substratum which seems to enhance concealment. The black, white, and gray *L. vittatum,* as well as *L. longipes,* frequently rest their bodies in insect scars or self-pruning irregularities of *Betula papyrifera* and *Populus.* Often the most rapid means of sighting individuals in these situations is to search the profile of the tree trunk for a leg held up away from the trunk surface or stretched across an area of contrasting bark. The body blends with the background or is almost out of sight. *Leiobunum calcar* and *L. politum,* both predominantly brown, usually remain in the curl of a fallen leaf or in the interstices formed by several pieces of litter. Curiously, as young phalangids increase in size and change coloration they shift from one substratum to another more concealing one. This is done by going to a somewhat larger trunk and shifting from *B. papyrifera* to the darker bark of maples. Even the health of the tree apparently is involved. Dead trees usually are avoided as are excessively rotted or discolored trunks of *Betula.* A factor involved may be the difference of relative humidity maintained in bark crevices or blemishes of living compared with dead trees.

AUTOTOMY.—Autotomy of legs is an effective means of escape for phalangids. Loss of an appendage is a simple matter and results only in decreased agility and the loss of a small droplet of blood. When one grasps an individual it is almost always by the legs since they are comparatively more accessible. If one leg or two adjacent ones are held and the animal can ply leverage on the autotomy planes with the others it often will break loose and may escape. It is not uncommon to see one or two legs of *L. longipes* tightly bound in a spider web; the phalangid survived apparently by the ability to release the entangled leg.

The question of whether or not a phalangid can rid itself of injured legs has received some discussion. Bishop (1949) cautiously suggests that phalangids lack the ability to rid themselves of damaged members. Observations to the contrary have been rare, but two situations suggest that under some conditions self-amputation occurs. On several occasions molts in the laboratory have been regular except for one leg, which was pulled free along only one-third of its length. The animal dried the remaining ones as usual and then proceeded to twist off the trapped appendage, leaving it twitching spasmodically, attached to the old exuvium.

The second observation was more conclusive. In handling a *L. longipes* the right leg II was broken in the middle of the tibia and remained attached

by only a thread of tissue. The animal grasped the dangling distal end with palpi and chelicerae and tugged on it until it was disengaged. For a short period it seemed to examine and fondle the piece and then proceeded to "thread" it past the mouth parts. When the broken piece was dropped accidentally to the leaf on which the animal was perched, it searched methodically over most of the surface of the leaf. Oddly, the first pair touched the disengaged piece several times but only a few times was it apparently recognized. When the animal recovered the disengaged piece it performed the typical threading operation as if nothing had happened. The broken stub was used as if the entire leg were intact. About 40 minutes after the broken distal portion was freed, the remaining proximal section was broken off. The actual release was not observed, but it occurred where there was no possibility of its getting entangled and breaking off accidentally.

MOVEMENTS AND VERTICAL MIGRATION.—When a phalangid is startled, the observer is often equally suprised to see as a response not flight but rather a strange pumping or bobbing up and down of the body while the legs remain in place. Velocity is gained with each cycle; following this, the animal usually strides away rapidly. It may remain stationary, however. This response occurs most frequently in cool weather or after the animal has been motionless for some time. Presumably this "pumping" up and down raises the temperature of the locomotory muscles. After the temperature reaches a certain level, the animal is able to travel faster. This activity has been observed in male phalangids just before attacking other males or seeking to copulate with females in the temporary care of other males. Wigglesworth (1950) explains the preliminary fluttering of large sphingid moths as necessary to warm the flight muscles above 30°C. If the moths are kept in an incubator at 34°C they are able to fly without initial fluttering. Perhaps the same mechanism operates in phalangids. Although greater speed of travel or activity may be attained in this manner, it may be hazardous to the animal when immediate escape is necessary for survival. Usually not more than one or two seconds are required to reach operating temperature.

In view of the body-to-legs proportions of this order of arthropods, the degree of agility is remarkable. With eyesight of questionable acuity, some species are able to move through a tangle of grass almost as fast as the collector can part the grass to follow them. The length of the legs enables opilionids to traverse terrain which would require circuitous detours by spiders, ants or other animals of comparable body size and speed. An interesting example of phalangid agility was observed in a laboratory chamber. The animal lost its footing while striding upside down on wire screen. Only one leg remained attached, and although it tried several times it did not have enough strength to bring the others to the screen above. It therefore grasped the anchored leg with the other legs and climbed it, as one would a rope, to the screen. All this was done in about 30 seconds.

Vertical migration in *L. longipes* appears to be more of a seasonal

phenomenon than a daily one. Animals hatch in the litter, remain there until they grow too large to occupy spaces between leaves and twigs, and then emerge to scamper over the surface litter in search of food. During inclement weather the animals ascend small-diameter tree trunks to varying heights where there is less likelihood of attack from spiders, birds and forest rodents. Gradually a larger proportion of the population moves from the forest floor to the tree trunks and branches (Fig. 2). Barring extremes in weather, *L. longipes* could presumably spend several weeks in the branches of trees without coming to the ground. Observations at Grapevine Point indicated that potential food was abundant in the canopy; small flies
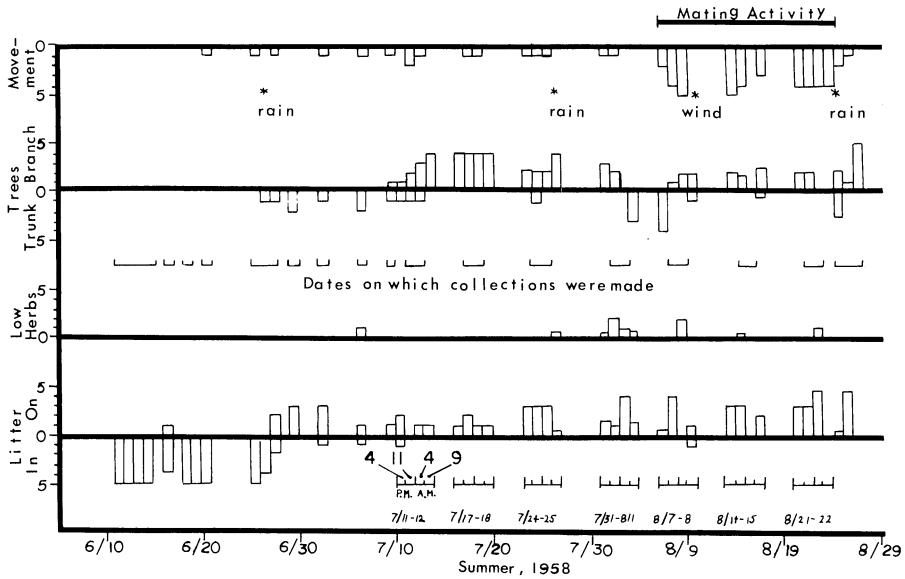

FIG. 2.   Stratal location and activity of *Leiobunum longipes* on Grapevine Point. The 0—5 scales on the ordinate indicate, in fifths of the collection, the proportion of *L. longipes* taken in particular strata of the habitat (in litter, on litter, on low herbs, on trunks, in branches) and while moving.

were numerous among the leaves, and the diurnal collections from the foliage contained many caddis flies, may flies, dipterans and small moths.

More activity occurs in the dark than in daylight (Edgar and Yuan, 1968). Greater nocturnal activity is to be expected, since the temperature is ordinarily lower and the relative humidity higher at night. The only time a majority of animals was found engaged in any activity in daylight was during the mating period (Fig. 2).

Searching activity is characterized by striding a few inches, nearly stopping to palpate the new territory with the second pair of legs, then moving ahead another few inches. Unusual objects or terrain are examined more cautiously. The phalangid's path is typically a meandering one, probably because the animal proceeds in such a halting manner.

ALERTNESS.—Phalangids spend a remarkably high proportion of their lives inactively, although this is not often apparent to the casual collector who is apt to startle the resting animals into activity before he observes them. Phalangids have been found in the laboratory to remain motionless for over 12 hours at a time. This behavior is protective to them in at least two respects: (1) movement may reveal their presence to a predator, and (2) if the humidity is low, or if water or food is difficult to obtain, the metabolic rate is lowered by inactivity and body reserves are conserved.

Several degrees of alertness may be exhibited. While the animal is motionless and resting, legs II are extended in the direction of the most probable approach of danger. At the slightest provocation they are raised and held motionless. If there is further disturbance each leg constantly roves in an arch approaching 180° laterally and 90° vertically. If the animal becomes greatly excited or injured it will flee with all speed or remain with an increased number of legs poised upward and outward from the body. On one occasion an excited animal was dropped several feet to the cement floor. Being a relatively heavy-bodied species it probably was slightly injured. It immediately stationed the longest leg pairs, II and IV, dorsolaterally from the body in a symmetrical manner. It was picked up but because of its vigorous efforts to escape was lost again to the floor. This time it balanced on three legs and waved five in the air. If the vision of the species were better perhaps it would have fled.

An animal ready to molt is clumsy and spends an unusually high proportion of time in protected seclusion and inactivity. After molting, as chitin hardens and new strength is acquired, the animal is most alert. The greatest perception of movement by L. longipes occurs a few days after the last exuviation.

LEG-THREADING.—A peculiar activity of these animals in all stages of development is that of "threading" or "mouthing" the tarsi. One leg at a time, the most proximal portion of the metatarsi will be brought to the mouth and slowly, aided by palpi and chelicerae, worked laterally until the terminal tarsi have passed across the fleshy lobes of the palpi and leg I endites. More time is spent on the terminal articles of the tarsi, and particularly on the tarsi of the second legs. Phalangids have been observed to keep the distal articles of the tarsi of the same leg in the region of the mouth for five minutes at a time. Phalangids keep themselves immaculately clean. In nature, their bodies seldom have debris adherent and ordinarily the legs glisten in pale sunlight.

Leg-threading is a corollary to phalangid activity. In the midst of mating or escape it is not uncommon for a phalangid to stop and spend several seconds mouthing a particular group of tarsal articles. Lyriform organs, single and grouped slit sensillae, and campaniform sensillae occur on phalangid legs. The function of the campaniform organs has been shown to be mechanoreceptive (Edgar, 1963). These organs seem to be highly sensitive and to permit the individual to recognize others of the same species and to

determine the sex in a rapid manner. Perhaps leg cleaning is necessary to preserve this high level of functioning.

FOOD HABITS AND TROPHIC INTERACTIONS

FEEDING AND DRINKING.—Feeding in nature is done where and when the animal finds food. There is some tendency, however, to carry food short distances to a point where disturbance is less likely. Phalangids have been seen carrying relatively large pieces (small moths or whole mayflies) for several feet and then climbing a short distance up a tree trunk before feeding. They often resist giving up food and will tug against the pull of another upon it. Feeding, as with mating, resting, and searching, often goes on for over an hour. Appendages used in feeding are palpi and chelicerae plus occasional assistance by one of the first pair of legs to manipulate food. The second pair is always raised and on guard against intrusion while the remaining legs furnish support. After feeding is finished phalangids are meticulous in cleaning palpi, tarsi, and the mouth region.

Living food is taken very timidly. If the phalangid detects movement but not aggressive behavior it will continue to feed, otherwise retreat occurs. The larger-bodied, stronger species, such as *L. calcar* and *L. vittatum,* feed more aggressively on living material than do *L. longipes* and *L. politum.*

Drinking is a simple operation and occupies periods of a few seconds up to four minutes depending upon thirst and availability of water. All that is needed is a capillary film of water. The muscular pharynx produces a rapid pumping motion which may take in water quite rapidly. An unusual opportunity to observe intake of water was afforded when one animal experienced serious difficulty in molting. The molt case was inextricably fast, with the animal dislodged from its molting site and lying upside down in the bottom of a petri dish. Observation with the microscope made it possible to note the change in contour of the film of water in the mouth area; it was seen that a pumping action of the pharynx, at the rate of 20–25 cycles per 10 seconds, brought water into the mouth.

FOOD ITEMS.—Disagreement exists in the literature on what constitutes the food of phalangids. Walker (1928) stated emphatically that "The food consists of fruit juices and other vegetable matter. Some authors believe that they eat animal food but I have never observed them eating anything except vegetable matter." Bishop (1949) has correctly assigned the feeding preferences and practices of phalangids. His observations are essentially the same as those reported here: a variety of foods, both plant and animal, are consumed by phalangids.

Harvestmen feed ravenously on mayflies, caddis flies and dipterans. Others, such as beetles, beetle larvae, snails, hymenopterans, some Hemiptera, pseudoscorpions, and mites are often too hard to be pierced. If by some other means the exoskeleton of these forms is fractured, phalangids accept them as food. Bristowe (1949) included living snails, bird droppings and occasionally fungi as food.

In the laboratory, phalangids from the study area have eaten Cercopidae (leafhoppers), Ephemeroptera (mayflies), Chrysopidae (lacewings), many kinds of Diptera, Apidae (honey bees), earthworms, spiders, moths and butterflies, cooked ham, raw hamburger, apple, marshmallow, and flavored gelatin. Some foods were taken only if nothing else was available: grass-hoppers, crickets, some snails, *Spirobolus* (millipede), cooked egg yolk, egg white, peanut butter, flour, and dry yeast. Most fresh beetles, including Cerambycidae, Elateridae, and Scarabaeidae, were refused even when mac-erated.

Phalangids undoubtedly use some plant material for food. However, only two observations in nature were made of phalangids eating anything but animal flesh, and one of these is questionable. In one instance, a female *L. vittatum* was seen feeding on a ripe wild red raspberry. Observation was close enough to see feeding movements of palpi and chelicerae. The other occasion occurred along a small stream. Here it was thought that either *L. longipes* or *L. politum* was feeding on the lichens and algae which cov-ered portions of an ironwood tree trunk. The dim light and alert animals made accurate observation impossible.

Dried and pulverized lean beef is most convenient as a food source for prolonged laboratory feeding of phalangids. It keeps well and needs to be prepared only infrequently. June beetles, grasshoppers and mayflies have been collected in quantity and prepared in a similar manner. While fresh June beetles and grasshoppers are not preferred food they are eaten without hesitation when dried and ground into small pieces.

Laboratory maintenance of most species of phalangids is usually simple and easy. A cubicle with side measurements roughly equal to twice the leg-spread of the adult is adequate for the long-legged species; a supply of dried food, and a small vial of water stoppered with a piece of plastic sponge are all that is necessary. Care is reduced to replenishing the water supply every 4–7 days and to infrequent feedings. The addition of freshly killed small insects like *Drosophila* is recommended

Todd (1949) used both animal and vegetable matter as laboratory food for phalangids. A mixture of dried egg, wholemeal flour and dry yeast was the basic food. Cultures of psocids and the larvae of the flour beetle, *Tri-bolium confusum,* were used to supplement the diet.

On one occasion, a *Phalangium opilio* oviposited a cluster of eggs in a Syracuse watch glass containing pieces of litter and shortly afterwards began eating them. Probably most species would eat their own eggs if they were easily accessible.

FOOD SUPPLIES.—To support phalangid populations at the densities ob-served on Grapevine Point (see p. 13), a considerable quantity of food must have been available, at least from late May until early September. To verify the magnitude of this supply of appropriate nutrition two kinds of samples were taken. In the first, the larger specimens found in the litter and on trees in a 1m x 10m quadrat were taken manually along with the phalangids used

to calculate abundance and biomass of *Leiobunum* shown in Table 1. The frequency of occurrence of non-phalangid invertebrates in the litter was derived from 43 collections taken from June 11 to August 26, 1958. Similarly, data for those in trees came from 28 collections made during July 11–August 15, 1958. In the second kind of sample, small inhabitants of the litter were obtained from a 0.5m x 0.5m plot within the quadrat and extracted with a Berlese funnel. Five of these collections were made, at the rate of one per week from July 11 to August, 1958. These Berlese samples included all litter material (excepting seedlings and green herbs) down to the root-permeated brown duff; the leafmold layer was generally not taken.

Table 5 lists the numbers and groups recovered by this procedure. The most abundant groups of invertebrates were collembolans, flies (these were under-represented because the method of collecting them in trees was extremely crude), mites, spiders, snails, pseudoscorpions, earthworms, and

TABLE 5
INVERTEBRATES (EXCEPT PHALANGIDS) COLLECTED IN LITTER AND ON
TREES ON GRAPEVINE POINT

Group	Density in Litter[1]	Percent Frequency of Occurrence	
		in Litter[2]	on Trees[3]
Mites	1,286[4]		
Spiders	1,096—64	86	96.4
Snails	968—8	39.5	
Pseudoscorpions	568		
Annelids	584	4.6	
Millipedes	80—16	16.3	
Centipedes	96—32	11.6	
Slugs		4.6	3.6
Insects:			
Collembola	12,376		
Diptera	3,848	55.8	53.6
Larvae	536—32	23.2	21.4
Coleoptera	82—53	37.2	32.1
Hymenoptera (mostly ants)	496	16.3	18
Lepidoptera	200—56	20.9	10.7
Homoptera (leaf hoppers)	160	2.3	14.3
Trichoptera (caddis flies)	53—72	11.5	25
Hemiptera	184	13.9	10.7
Neuroptera	8		3.6
Ephemeroptera		11.6	10.7
Mecoptera		2.3	7.2

[1] Numbers per 1m x 10m quadrat, based on Berlese samples from five 0.5m x 0.5m plots taken from July 11 to August 15, 1958.

[2] 43 quadrats, 1m x 10m, were collected manually over period of June 11 to August 26, 1958.

[3] 28 quadrats, 1m x 10m, were collected manually over period of July 11 to August 15, 1958.

[4] The left-hand figure is the number of specimens 5mm or less in length; the right-hand figure is the number of specimens more than 5mm in length.

ants. Millipedes, centipedes, beetles, caterpillars, leafhoppers, caddis flies, and hemipterans were also taken in considerable numbers. Most of these invertebrates were small—5mm or less in length. In view of the food habits reported above, these data suggest that a diverse and abundant food supply was indeed available.

CANNIBALISM.—Cannibalism among phalangids, especially immatures, is common. One species will attack its own kind or another species. A large proportion of all cannibalism and predation of phalangids occurs while the animals are molting and shortly thereafter, when new chitin is still soft and pliable. The molting animal has no defense during this period. Cannibalistic phalangids have been observed to suck fluids first from the body cavity and then, in the region of the coxae, drain each leg cavity. If the chitin is pliable the legs and body collapse under the slight negative pressure produced by the sucking phalangid pharynx. Cannibalism by *L. longipes, L. politum,* and *L. vittatum* has been observed. On one occasion two *L. longipes* attacked a third and fed at the same carcass until finished.

As the animal develops a harder exoskeleton and stronger body, cannibalism decreases markedly because of limited ability to invade and tear resistant tissue. The chelicerae are strong enough to crush animal matter for food but little penetration of a hard surface is possible.

PREDATORS.—Spiders are probably the most important group of predators on phalangids; a number of species either attack them directly or entangle them first in their webs. When a spider attacks a phalangid without the formality of web entanglement, it seizes the legs, forces them back out of the way, and then tears open the soft tissues of the cephalothorax, usually on the side dorsal to the coxae. Feeding is rapid as body juices are aspirated and imbibed. Both tree and litter spiders have eaten phalangids in the laboratory, where spider and phalangid were confined to a common chamber with water but no food. This predator-prey relationship has been observed repeatedly in nature.

Not all spiders are predaceous on phalangids; certain arboreal forms, as well as others, do not attack them. The fact that spiders were abundant at all strata in the habitat indicates that other invertebrates (Diptera, Trichoptera, Ephemeroptera, etc.), also present, may serve as food for both spiders and harvestmen.

Other invertebrates also serve as phalangid predators. On two occasions at Grapevine Point, an assassin bug (*Zelus* sp.) fed on phalangids. Centipedes have preyed on harvestmen in the laboratory. Even the large forest snail (*Triodopsis albolabris*) was seen to entangle the legs of two *L. longipes* in mucus and to consume all but parts of the legs.

Bristowe (1949) included fish, toads and shrews as predators on phalangids. Sankey (1949) has reported phalangids eaten by badger, fox and hedgehog. Surprisingly, they have not been reported from the stomach con-

tents of birds; it seems likely that their remains in bird stomachs have not been distinguished from those of spiders, which are frequently reported. At Grapevine Point, phalangids were observed being eaten by birds, frogs, and salamanders. A laboratory-caged Rose-breasted Grosbeak *(Pheucticus ludovicianus)* fed on both living and dead *L. longipes, L. vittatum* and *L. calcar,* and Golden-winged Warblers *(Vermivora chrysoptera)* have been seen to feed on phalangids and bring them to their young (L. E. Eyer, pers. comm.). Phalangids were also eaten in the laboratory by the Red-backed Salamander *(Plethodon cinereus)* and were recovered from stomachs of wild-caught specimens of this predator.

A presumed deterrent to certain predators is the secretion released when a phalangid is startled. The secretion is produced in so-called scent or repugnatorial glands in the cephalothorax and released through pores opening in the cephalothorax opposite the coxae of leg II. *L. vittatum* and *L. calcar* produce especially copious quantities, each with a distinctive volatile component. Frogs have been observed to take opilionids into their mouths only to expel them forcibly, almost immediately. Since phalangids have little or no means of inflicting physical damage, the scent gland secretion is probably the cause of such action. Attempts to demonstrate species differences in this fluid via paper and gas chromatographic separations thus far have been unsuccessful. A component of the secretion produced by *L. formosum* and *L. speciosum,* southeastern United States forms, is identical to that found in ants (Blum and Edgar, in press). Whether this secretion functions as a pheromone, as it does in ants, is as yet unknown.

A long list of animals that do not harm phalangids in the laboratory has been compiled. Of the many kinds of snails, insects (dipterans, hymenopterans, lepidopterans), millipedes, slugs, and mites (except one parasite form), none, with the exceptions noted above, has been observed to harm harvestmen.

PARASITES.—Phalangids have few external parasites. Small red mites (Erythraeidae) often are found attached to the bodies and legs of phalangids during the early adult life of the latter. Heavier infestations occur where ground vegetation is luxuriant and soil is moist to wet. In these situations in the southern part of the state, *L. politum* may have up to 20 mites riding along and feeding. On Grapevine Point, harvestmen seen carrying more than three mites each have been rare. Other arthropods, mostly insects, carried similar red mites during the same period.

A few other invertebrates have associations with phalangids which may or may not be of parasitic nature. Savory (1938) reported the presence of pseudoscorpions on *Opilio parietinus* in England but regarded them merely as phoretic travellers. On one occasion very small, immature mites and small oligochaetes were observed among a cluster of *L. longipes* eggs. Small nematodes have been seen among eggs in similar clusters but their presence was not correlated with damage.

LABORATORY STUDIES OF TOLERANCE AND SURVIVAL

Since the limits of tolerance or survival potential of a species are seldom evident and quantifiable in the natural environment, I attempted to determine in the laboratory certain optima and extremes for the species from the study area. Studies were made of temperature selection, performance in a relative humidity gradient, and survival time in dessication chambers.

TEMPERATURE TOLERANCE

A chamber approximately 140 cm x 17 cm x 14 cm was constructed so that a temperature gradient could be maintained within. To conduct heat into one end of the chamber and to assist in its removal at the other end, a steel bar 11 cm x 1.25 cm ran the entire length of the chamber, extending into a bath of boiling water at the high temperature end and into a bath of salt water and ice at the other end. Insulation was sufficient to maintain a temperature differential of 20°–22°C within the chamber. A copper screen floor separated the steel bar from the chamber proper. Five field thermometers, inserted at regularly spaced intervals into the cavity of the chamber, were used to indicate temperature points during experiments. Intermediate temperature values were obtained by interpolation. Glass containers filled with water were evenly spaced along the floor of the chamber to counteract the effects of a relative humidity gradient. Partial transverse partitions of screen were interposed alternately against the two walls of the chamber to discourage animals from moving too far along the temperature gradient at one time and to help prevent a moving animal from disturbing others.

Before admission to the temperature gradient chamber, each animal was placed in isolation for four hours, with abundant food and water. This helped to eliminate wandering to satisfy physical needs. After the phalangids were placed in the chamber through an opening in the glass top, it was closed and covered with tightly fitting cardboard so that possible orientation of the animals to light would be prevented. Each half hour the cardboard was removed and the position of each animal was noted.

Figure 3 records the temperature preference data for the four species of *Leiobunum* studied at Grapevine Point, as well as for *Phalangium opilio* and *Opilio parietinus,* which have been included for comparison because their natural habitats are different from those of the study area. Since the *Leiobunum* species shared a common habitat, it was expected that their temperature optima would not be widely divergent. This proved to be the case: mean temperature preference values ranged from 23.9°C for *L. longipes* to 24.2°C for *L. calcar* to 24.3°C for *L. politum* to 27.9°C for *L. vittatum.*

P. opilio exhibited a temperature preference (with a mean of 27.6°C) close to that of *L. vittatum.* In nature, *P. opilio* occurs in less protected areas than those preferred by most phalangids. Lawns, fence rows, and roadside grass, where this species abounds, often expose it to temperature extremes.
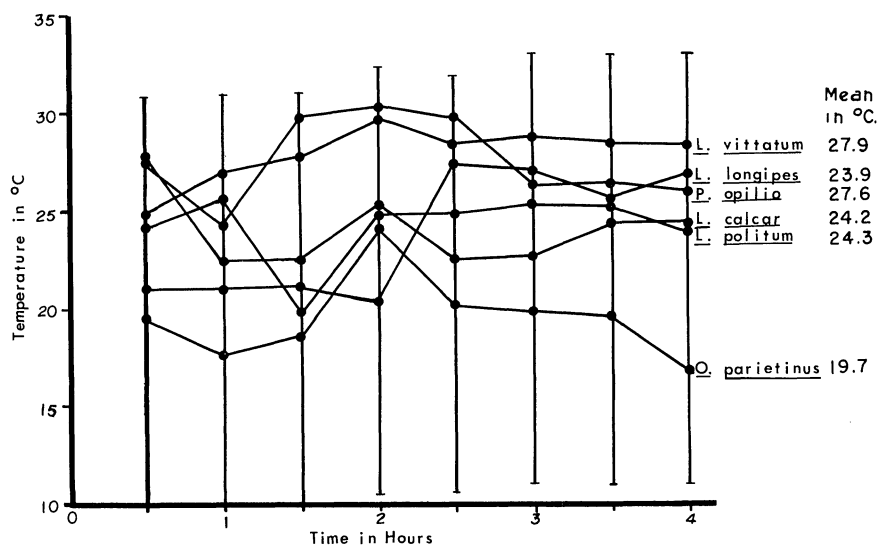
FIG. 3. Mean temperature preferences of six species of phalangids, based on location in a temperature gradient at successive half-hour intervals. Limits of gradient are indicated by cross lines at ends of time bars. Each point is the mean of 3—5 values.

Its comparatively high temperature preference suggests that it is well adapted to high summer temperatures.

In contrast, *O. parietinus* is often found on the shaded side of cement walls where the relative humidity is high and the substrate is usually cool. It is not surprising, therefore, that its mean temperature preference (19.7°C) in the laboratory proved to be comparatively low.

Thus the temperature preference data obtained in the laboratory appear to reflect conditions in the natural habitats of these species. They provide a basis for predicting, in the absence of knowledge about the typical habitat, the particular parts of a given diverse environment in which each of the species would be found.

RELATIVE HUMIDITY TOLERANCE

A relative humidity (R.H.) gradient chamber, similar to that used for temperature, was constructed to provide humidities from approximately 6.5% to 100%. Seven saturated salt solutions were chosen, along with distilled water, to produce a graded series of humidities: potassium nitrate, 94%; potassium chloride, 86%; sodium chloride, 77%; nickel chloride, 57%; magnesium bromide, 33%; lithium nitrate, 24%; and sodium hydroxide, 6.5%. Fingerbowls containing the salt solutions were placed in the bottom of the chamber and separated by wooden partitions which were slightly higher than the height of the fingerbowls. Copper window screen separated the glass containers, chemicals, and partitions from the animals. Prior to use, the chamber was sealed for several days. With as little disturb-

ance of the air in the chamber as possible, animals were admitted to the gradient through the top by carefully sliding a panel of glass toward one end and replacing it afterward. A cardboard cover over the glass top produced near-darkness within.

To calibrate the R. H. gradient produced by the salt solutions, concentrations of sulfuric acid ranging from 10% to 36% were placed in short lengths of capillary tubing, the liquid completely filling the cavity of the tube. Series of these tubes were placed on the screens directly over the various salt solutions and left for 12 hours. Depending on the concentration of the acid, such a tube will undergo a change in volume in equilibrating with the surrounding air: a 22% solution of concentrated sulfuric acid in distilled water will give up water to the atmosphere and the contents of the tube will shrink, if the R. H. of the air is below 85%; if the R. H. is above 85%, the tube will absorb water and will overflow. Thus, the tube of each series which did not change in volume indicated the R. H. at that point in the gradient.

Animals were prepared for use by depriving them of food and water for 6 hours. Following this, they were given unlimited food and water for 4 hours. Since the animals were left in the chamber until death, significant differences in survival might be expected to occur if the animals were initially in different physiological states. As many as 8 individuals were placed in the chamber at one time.

Observations were usually made every two hours, except during the early morning period. Occasionally, animals would be moving when an observation was made: either the individual was wandering before the cardboard cover was removed or it was disturbed by light or vibration at that time. In these cases, the position at the time the animal was first seen was recorded and a note was made that it was moving.

Mean R. H. preference values at successive intervals after placement in the gradient are shown in Figure 4. When the animals were concentrated at the high humidity end of the gradient, removal of the cardboard cover often caused some individuals to move to positions of lower R. H. This displacement resulted in lower mean values than would have otherwise been recorded.

Any statement of optimum R. H. must be qualified by some indication of the animal's physiological state. Figure 4 indicates that these animals did not require so high an R. H. immediately after feeding and drinking as they did one or two days later. As the individual approaches death from lack of water, it becomes progressively more sensitive to the drying effect of the surrounding air and consequently spends increasingly more time in the region of the higher humidities. Thus, the choice of humidity seems largely dependent on the hydration conditions of the body at the moment. This progressive shift in the optimum humidity of a species was not taken into consideration by Todd (1949), whose observations on phalangids in an R. H. gradient did not extend beyond 80 minutes. Under environmental conditions in nature, an animal probably does not often lack a supply of water
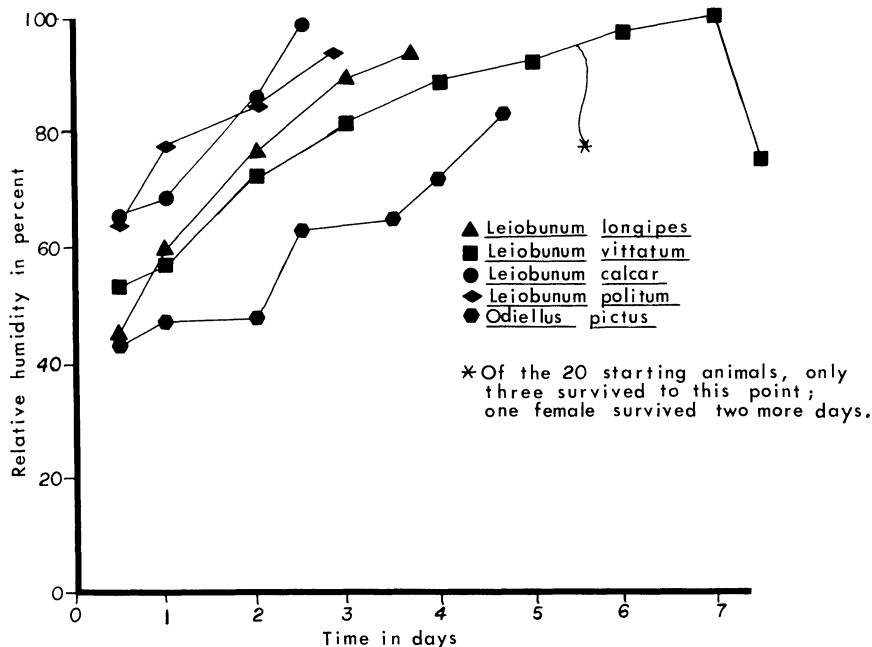
FIG. 4. Mean preferences of five species of phalangids at intervals from initial exposure in relative humidity gradient until death. Number of animals used ranged from 6 to 24.

for more than 18 hours at a time, and therefore it would not exhibit behavior characteristic of that during a drought period. However, in periods of consecutive hot, dry days and dewless nights, the entire population may be required to endure considerable fluid stress.

If a species can survive only a moderately short period of two or three days without water intake, it will be restricted to an environment which does not exceed that limit. All specimens of *Leiobunum longipes*, *L. calcar* and *L. politum* from the study area were dead after four days in the humidity gradient (Fig. 4). In contrast, *L. vittatum*, the species found in the greatest diversity of habitats in Michigan, exhibited marked survival reserve in the face of water shortage. It survived up to 7 days and is clearly a more hardy animal than its three congeners.

The relative humidity data for *Odiellus pictus* were included in Figure 4 to provide an example of a forest species which is found in areas with much less vegetational shelter and which exhibits a preference for comparatively low humidities. Probably more important than the ability of *O. pictus* to live a relatively long time without water is its characteristic of extreme inactivity. This species remains in the litter or occasionally ascends trunks a short distance to sun itself, but it never exercises except perhaps at night to forage for food.

The humidity gradient experiments showed that few species of harvest-men have consistent need for any particular R. H. within 12–15 hours of feeding and drinking. By the end of the first day, the more sensitive ones (*L. politum* and *L. calcar,* and a bit later, *L. longipes*) avoided the drier air of the gradient and confined themselves to humidities above 60%. From this time on, there was a gradual increase in the restriction to higher humidities (Fig. 4), although there were sporadic forays to all parts of the chamber in search of water or an escape route. When death was approaching, the animals would perch stolidly at, or very near, the moister end of the gradient and occasionally would make nervous, wandering sorties for vary-ing distances toward the drier end, only to return to their original site. Walking became halting and difficult. Quite often the animals' last efforts were to make one more search for water. This was the case with one *L. vit-tatum* which survived for seven and a half days (Fig. 4)—she left her position on the end piece of the chamber and reached the 70% point before expiring.

SURVIVAL IN DESSICATION CHAMBERS

Dessication chambers were made by placing calcium chloride under screen at the bottom of petri dishes 100 mm in diameter and 80 mm deep. To each of these containers was added a phalangid that had been fed and watered previously as already described and that had been carefully weighed. The animals remained undisturbed in the containers until they could no longer move their legs in response to prodding, the criterion used to indicate death. After death they were again weighed and their period in the dry-air chamber calculated.

These data yielded three measures of ability to withstand dessication: (1) hours of survival before death, (2) percent loss of body weight, and (3) rate of loss in body weight. The relative humidity experiments also gave a measure of survival time, but the data on body weight loss provided an additional line of evidence to explain why some species tolerate more rigor-ous environmental conditions.

Table 6 indicates the ability to withstand dessication for the four species of *Leiobunum* found on Grapevine Point and for *Phalangium opilio.* Sur-vival time in dry air closely paralleled that in the humidity gradient cham-ber; in dry air, *L. vittatum* survived longer than any of the other *Leiobunum* species, which died within ten hours of each other.

The animals selected for the dessication experiment were adults, and there was usually a size and body weight difference between males and females. Mean adult weights (in mg) of the two sexes were as follows: *L. longipes*—female 48.0, male 24.2; *L. calcar*—female 117.7, male 66.5; *L. vit-tatum*—female 80.6, male 43.1; *L. politum*—female 33.9, male 14.6; *P. opilio*—female 75.0, male 41.6. In all cases the female of the species outlived the male in dry air (Table 6); in *L. calcar,* the heaviest species, the female lived 46% longer then the male, and females of *L. longipes* and *L. vittatum* survived more than twice as long as the males. The percentage loss in body

TABLE 6

SPECIES RESPONSES IN DESSICATION CHAMBERS

Species	Survival time (hrs.)		Body wt. loss[1] (per cent)		Rate of body wt. loss (%/hr.)	
	♂	♀	♂	♀	♂	♀
L. longipes	25.1	59.1	36.7	38.1	1.67	0.83
L. vittatum	56.4	116.1	43.7	48.9	0.81	0.48
L. calcar	37.0	47.5	43.5	45.6	1.33	1.0
L. politum	18.4	38.6	40.0	44.6	2.76	1.36
P. opilio	75.6	120.0	48.3	57.6	0.72	0.52

[1] Calculated at time of death.

weight before death ensued was higher in females than in males, but because of their longer survival females lost weight at a lower rate. It is possible that females were able to make use of water present in eggs or egg materials stored within their bodies.

The physiology involved in this rate of loss of body weight is of basic importance in determining the success or failure of a species in invading and adapting to a wide variety of habitats. *Leiobunum vittatum,* for example, occupies many kinds of habitats in large part because of its ability to retain body fluids more efficiently than companion species.

HABITAT ANALYSIS OF MICHIGAN PHALANGIDS

ANALYTICAL METHODS

At each of the sites at which I collected phalangids, habitat data were also obtained. Measurements were made of the relative humidity in the habitat and in the nearby open area where vegetational influence was at a minimum and exposure was maximal. Primary emphasis, however, was placed on recording the structural and compositional characteristics of the vegetation. Ordinarily, three well-defined strata were present: a canopy or tree layer, an understory or shrub layer, and a ground layer (up to about three feet above the soil surface). In each stratum the extent of the plant cover was estimated visually according to the following scale: 1, cover none to sparse; 2, cover moderately sparse; 3, cover moderate; 4, cover moderately dense; 5, cover dense to complete. In woodland habitats the species of dominant or co-dominant trees were noted, and estimates of the basal area of all trees greater than 1 inch in diameter were obtained by the Bitterlich technique (Grosenbaugh, 1952). Mean values of these habitat parameters are presented in Table 7 for almost all of the phalangid species found in Michigan.

A measure of habitat use, which relates phalangid abundance to vegetational cover and which will be referred to as an *abundance-cover profile,*

TABLE 7

SUMMARY OF MEAN VALUES OF HABITAT MEASUREMENTS MADE IN STATE-WIDE COLLECTIONS

Species	Basal Area Estimates[1]	R. H. (Differ.) [2]	Mean density of cover			
			Upper	Under	Lower	Total
Leiobunum longipes	13.4	16.0	4.1	2.7	3.4	10.2
L. calcar	12.0	13.2	3.7	2.8	3.4	9.9
L. politum	11.9	17.2	3.5	2.9	3.3	9.7
L. vittatum	11.9	15.5	3.5	2.7	3.6	9.8
L. nigropalpi	14.3	12.5	4.1	2.7	3.2	10.0
L. ventricosum	11.1	11.5*	4.0	3.0	3.5	10.5
L. verrucosum	12.3	16.1	3.8	2.6	3.6	10.0
L. serratipalpe	12.8	26.4*	3.5	3.2	3.8	10.6
Caddo agilis	16.3	8.3*	4.0	3.2	3.2	10.4
Odiellus pictus	10.7	13.9	3.9	2.8	3.2	9.9
O. argentus	11.7	22.3	3.4	3.4	4.1	10.9
Phalangium opilio	—	15.7	2.4	1.2	3.5	7.1
Leiobunum nigripes	—	34.0*	1.0*	1.0*	4.5*	6.5*
Hadrobunus maculosus	7.5*	—	2.5	2.2	3.8	7.5
Opilio parietinus	11.0*	24.7	1.8	1.2	4.2	7.2
Leiobunum lineatum	8.0*	33.5*	2.5*	1.5*	4.5*	8.5*
Sabacon crassipalpe	15.0*	—	4.0*	2.0*	3.0*	9.0*

[1] Basal area estimates are in terms of sq. ft. of trunk cross-sectional area per acre at 4.5 ft. above the ground.
[2] Difference in relative humidity, in percent, at time of collections, between collection site and nearby open area where influence from vegetation is minimal.
* Fewer than 4 values.

was devised as follows. At every collecting site, the relative density of each phalangid species was evaluated according to a 5-level scale, from very rare (level 1) to very common (level 5), as judged by the number of individuals which could be collected over a given period of time. (Rates of collection and therefore density evaluations, differed from species to species: a value of 5 indicated a collection rate of at least 100 per hour for *Leiobunum longipes* but a rate of only 15–20 per hour for *Odiellus pictus*.) For each category of plant cover, the phalangid density was multiplied by its frequency of occurrence (in the total number of collections) to give a measure of relative abundance. The abundance values were then summed and the proportions attributable to each cover category were calculated. The complete profile was obtained by repeating this procedure for each vegetational stratum of the phalangid's habitat.

Table 8 shows the calculation of these values as illustrated by the occurrence of *Leiobunum vittatum* in the canopy stratum. This species was collected at 80 sites having a tree canopy, in which it had a total abundance value of 197. It was most abundant in conditions of moderate canopy cover— 39.6% of the total abundance value was attributable to cover category 4, and 21.8% to category 3—and was rarely encountered in sparse cover—only 3.1% of the total abundance value was attributable to cover category 1.

TABLE 8

CALCULATION OF THE ABUNDANCE-COVER PROFILE FOR *Leiobunum vittatum*
IN THE CANOPY STRATUM

Level of phalangid density (x)	Canopy cover category										Total no. of collections
	1		2		3		4		5		
	Phalangid frequency (f) and abundance (fx)										
	f	fx	f	fx	f	fx	f	fx	f	fx	
5	0	0	1	5	0	0	1	5	1	5	
4	0	0	3	12	3	12	6	24	2	8	
3	2	6	3	9	4	12	10	30	2	6	
2	0	0	3	6	6	12	6	12	6	12	
1	0	0	4	4	7	7	7	7	3	3	
Σf	2		14		20		30		14		80
Σfx		6		36		43		78		34	$197 = \Sigma\Sigma fx$
$\Sigma fx/\Sigma\Sigma fx(\%)$	3.1		18.3		21.8		39.6		17.2		100.0

f—The number of times *L. vittatum* was collected, at a given phalangid density and canopy density.

fx—The abundance, estimated by the product of a given phalangid density (x), and the number of times *L. vittatum* was collected at that density.

Σf—Total number of collections of *L. vittatum* at a given canopy density.

Σfx—Sum of abundance at a given canopy density.

$\Sigma fx/\Sigma\Sigma fx$—The proportion of abundance values attributable to a given canopy density, expressed as a percentage.

Phalangid habitats in woodland and forest were also assigned to groups on the basis of their dominant or co-dominant tree species, since these provided a convenient means of recognizing major habitat types. The following groups were recognized: maple *(Acer)*, aspen *(Populus)*, elm *(Ulmus)*, oak *(Quercus)*, white cedar *(Thuja)*, white birch *(Betula)*, and a "miscellaneous" group (all others). For each phalangid species, the mean abundance (measured as described above and illustrated in Table 8) at the sites belonging to a particular group were compared with the mean abundance at all sites. The deviations of each group mean from the overall mean provided an indication of the relative importance of each group as a habitat type. For example, populations of *L. vittatum* were of higher than average density at sites dominated by elm and white birch, and lower than average at sites dominated by oak and white cedar (Fig. 5b).

The percent of the total number of collections of each phalangid species that were made in each habitat type was also calculated (Fig. 5b). Although each type of habitat was not visited an equal number of times and there was therefore some bias in the frequency of representation in the total number of collections, these data provide some indication of habitat occupancy. They
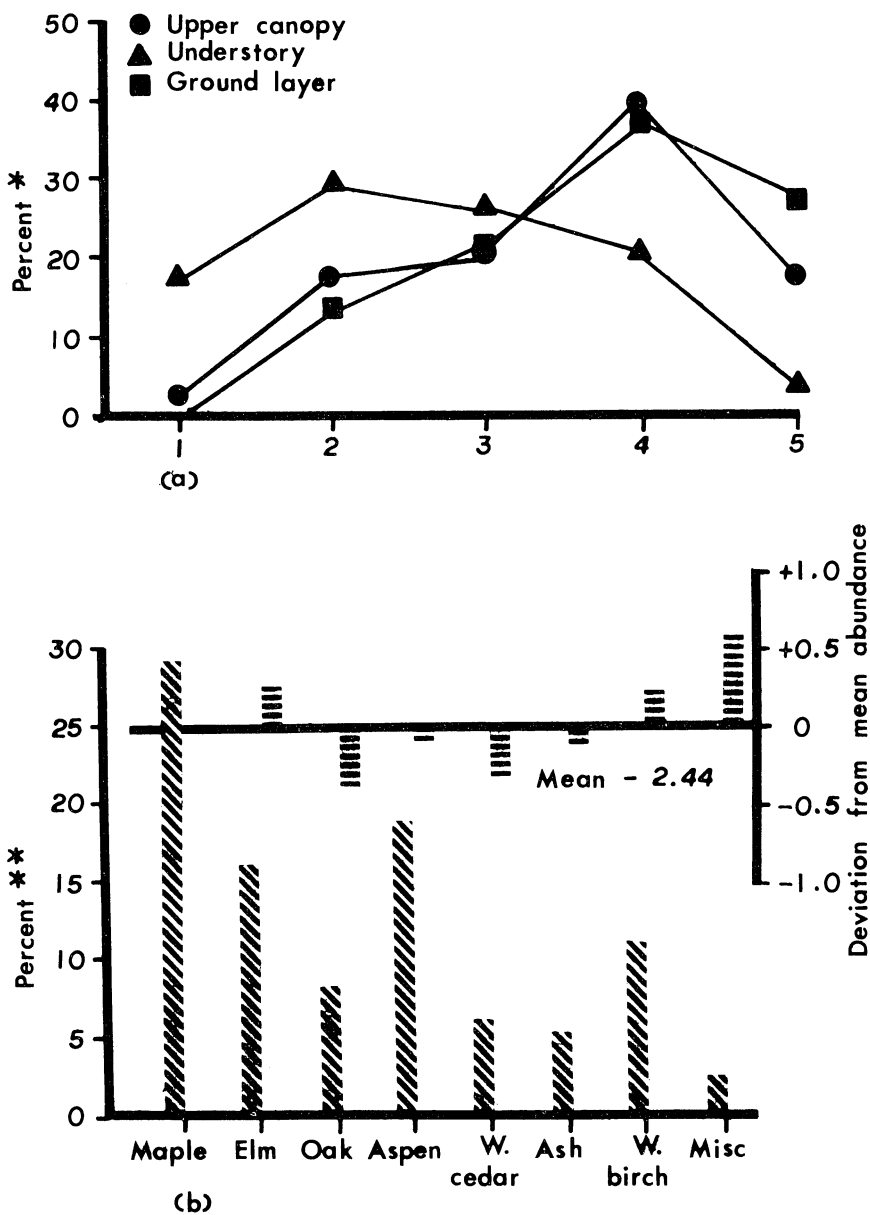
FIG. 5. (a) Abundance-cover profile and (b) Relative occurrence and abundance of
Leiobunum vittatum in the major canopy groups.*, proportion of abundance values at-
tributable to given vegetational cover, expressed as percentage. **, percent of collection
sites.

can be used in connection with the deviations from the mean abundance values to describe the range of habitat preference shown by a species.

HABITATS OF COMMON SPECIES

Leiobunum vittatum.—Collected in 65 of Michigan's 83 counties, this species undoubtedly occurs throughout the state. It is probably the most widely distributed phalangid in the northeastern United States. The spectrum of environments in which it has been found in Michigan ranges from the trunks of *Populus* growing in the shifting sands of Sleeping Bear Sand Dune in Leelanau County to the edge of a quaking bog mat in Cheboygan County. It apparently adapts readily to new conditions and tolerates severe physical extremes.

As has been shown in the previous section, this species is capable of surviving longer periods of dryness than any other species associated with it. In dry periods, it has been observed to move to openings and edges of wooded areas to imbibe dew and to forage. Its abundance-cover profile (Fig. 5a) indicates a considerable tolerance of low-density cover in the canopy and understory strata but a preference for greater cover in the ground layer. This suggests that the species tolerates drying conditions from exposure to wind and sun quite well but requires denser vegetation at ground level.

Figure 5b shows the mean abundance of this species in the "miscellaneous" habitat group to be considerably in excess of the mean. In this case, the dominant canopy species were white pine *(Pinus)* and balsam *(Abies),* willows *(Salix)* and box elder *(Acer),* and black locust *(Robinia). L. vittatum* apparently has a wide habitat tolerance.

Leiobunum longipes.—This species was most abundant in vegetation with a moderate to dense canopy and ground layer and a correspondingly less dense understory (Fig. 6a). The animal flourishes best in a situation characterized by protection from the drying effects of the sun, by an atmosphere of high relative humidity, and by protection from sudden and severe changes in other aspects of the physical environment.

L. longipes is frequently taken in ecotones between a very dense canopy or forest floor layer and relatively open area (roadside, meadow or clearing). In such instances, it is likely that humidity or shade in excess of optimum is nearby. Laboratory experiments showed that, in general, phalangids do not stay in 100% R. H. unless there is a shortage of available moisture elsewhere. In fact, very few species are found abundantly in woods with an extremely dense canopy.

This species was found in almost all types of habitat in which collections were made, but it was relatively more abundant in the maple-dominated group than in any other, and least abundant in the aspen-dominated group (Fig. 6b). A maple or maple-codominant environment generally possesses a protective, moderately dense canopy, with variable shrub-zone density and ground herbage, whereas an aspen-dominated environment provides com-
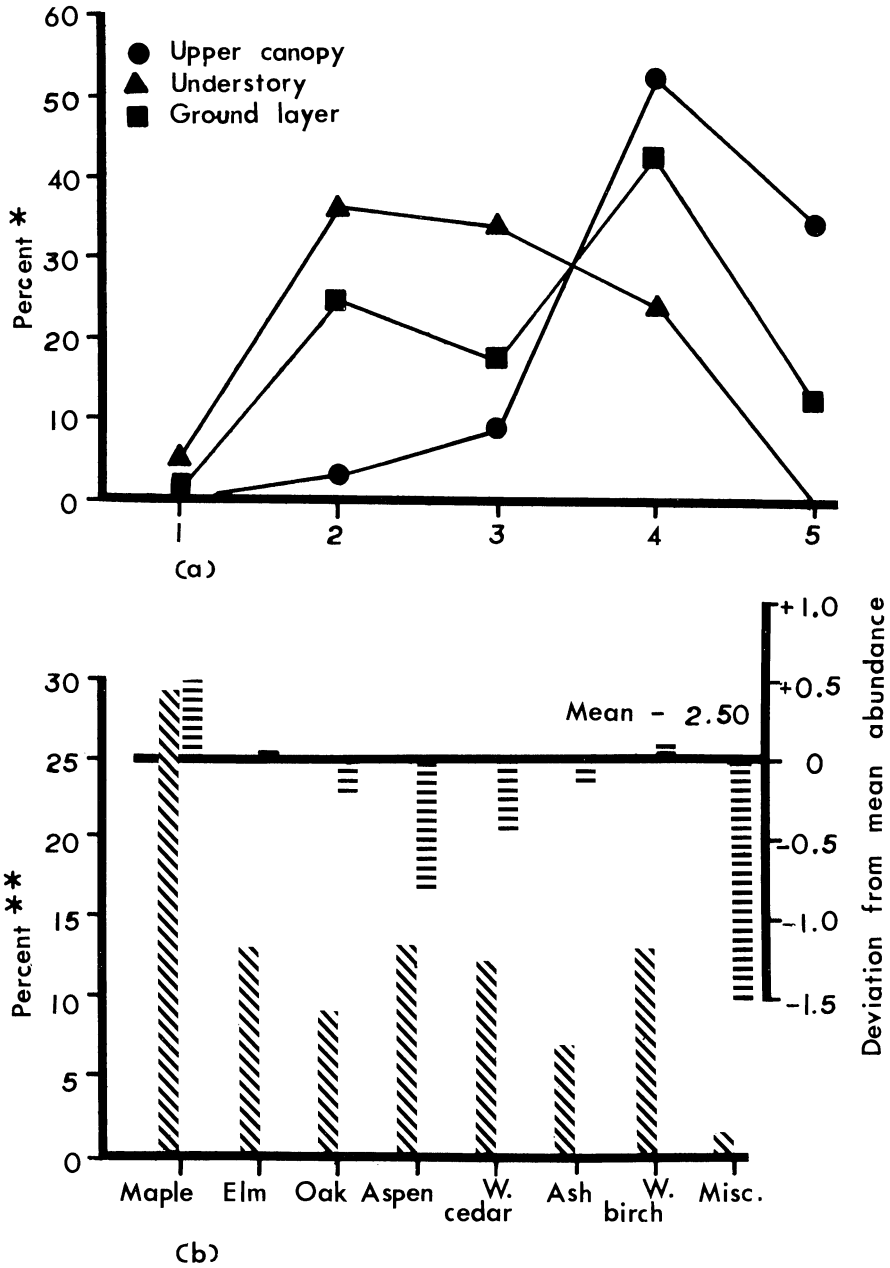
FIG. 6.   (a) Abundance-cover profile and (b) Relative occurrence and abundance of
Leiobunum longipes in the major canopy groups. See Figure 5 for key to ordinate symbols.

paratively little protection and is subject to considerably greater rates of moisture loss. The rarity of *L. longipes* in white cedar habitats, where moisture and R. H. were relatively high, may have been due to the widespread occurrence of conditions unsuitable for oviposition—a wet, acidic substrate, matted evergreen leaves, and sparse ground layer herbage.

Leiobunum calcar.—This large-bodied species was found over a fairly wide range of habitats. It was most abundant under conditions of medium to low cover in the canopy and ground layers, and of moderate density in the understory (Fig. 7a). Lower than average abundance values were recorded for *L. calcar* in habitats dominated by maple, elm, aspen and white cedar (Fig. 7b). Maple and elm usually furnish a high dense canopy that seems to be unfavorable for this species. Aspen, with its dry sandy soil, sparse canopy, and small accumulation of litter, and white cedar, with its highly saturated, acidic substrate and dense canopy, appear to represent opposite extremes of tolerance for *L. calcar*.

With its potential capacity to withstand wide fluctuations in insolation, temperature and moisture, *L. calcar* might be expected to be one of the very hardy species able to tolerate extremes of physical conditions. As a matter of fact, this species was the only one collected from a dry, open, sandy, jackpine—scrub oak association. Laboratory experiments, however, showed that *L. calcar* died very rapidly when placed in a low humidity chamber. Its survival in the dry habitat proved, on further investigation, to have been favored by the condensation of dew, which was formed in considerable quantities at times when moisture was not available under dense canopy. Whenever *L. calcar* was taken in such harsh conditions, the habitat was always characterized by openings in the canopy that would allow dew to form.

Dew or rain is not the only source of water available to phalangids, however. Fresh insects, spiders, and other invertebrates could supply a large amount of the needed water. *L. calcar* is probably the most voracious hunter and eater of the Michigan phalangids and undoubtedly supplements body water from its food. Bishop (1949) corroborates this observation by the statement: "During the daylight hours, when temperature and humidity permit, it forages openly and will attack and eat anything it can overcome. In the field it was found with bits of earthworm and well-chewed ants and other insects in its jaws." Only under conditions of moderate temperature and rather high humidity does this species become mobile. Its daytime activity in the more exposed environments under hot or dry conditions is characterized by extremely long periods of inactivity in a sheltered location.

Leiobunum politum.—This species was collected in Michigan more often than any other phalangid. It shows a strong preference for mesic conditions where there is a relatively constant source of moisture, and this type of habitat may have been investigated with greater than average frequency. Had collecting sites been chosen strictly at random, *L. politum* would probably have been represented less often, though still in large numbers at times.
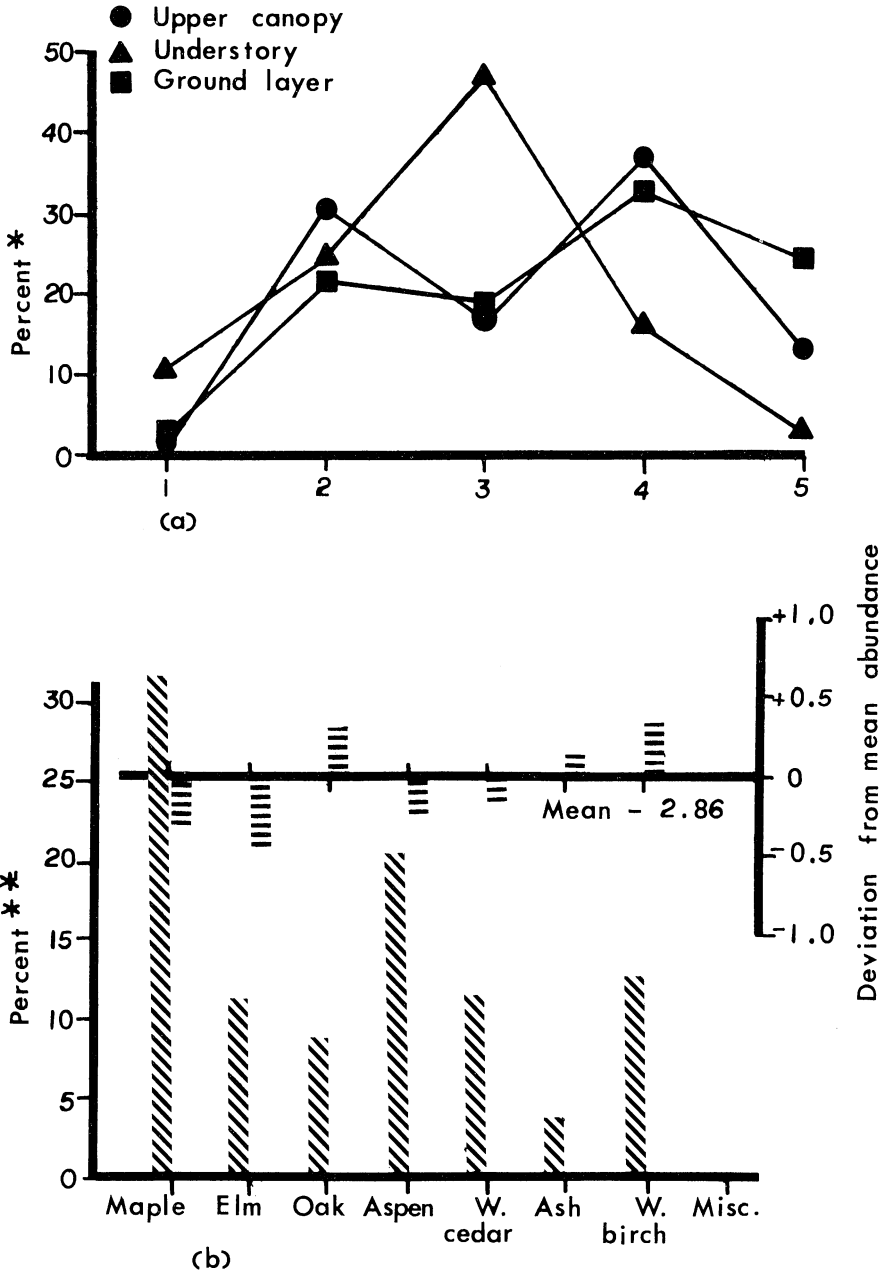
FIG. 7. (a) Abundance-cover profile and (b) Relative occurrence and abundance of
L. calcar in the major canopy groups. See Figure 5 for key to ordinate symbols.

It has been found both by itself and in association with almost all other species of phalangids. It is most abundant where the ground vegetation is luxuriant, thick, and often waist high. Frequently the soil is mucky and soft underfoot. Roadside seepage areas at the edge of low woods in the southern portion of the Lower Peninsula usually support high populations of this species. It often wanders upon reaching sexual maturity in late summer and will frequently be found far afield from the habitat characteristic of its egg and immature stages. The adult appears in church or school yards, cemeteries, in fence rows near woods, and in the interior of forests.

The abundance-cover profile of *L. politum* (Fig. 8a) indicates a preference for a habitat in which the canopy layer is moderately dense and the understory component varies from moderate to relatively sparse. This affords opportunity for profuse ground herbage where moisture is abundant. These conditions are characteristic of stands of ash *(Fraxinus)*, oak and elm along stream beds and on well-drained but moist soils. Usually the canopy is discontinuous so that the ground and shrub layers are not depressed by deep shade and can grow according to available moisture. *L. politum* is abundant in these habitats (Fig. 8b). White cedar stands, on the other hand, do not support this species at any but low levels of abundance, and its density was also well below average in the "miscellaneous" group of habitats, dominated by hickory–hawthorn *(Carya–Crataegus)*, willow–box elder, locust–ironwood *(Robinia–Ostrya)*, and locust alone.

SPECIES COMPARISONS.—The four *Leiobunum* species considered thus far occur together more commonly and consistently than any other species encountered. In relatively undisturbed forest environments containing ecotones from edges and openings in the canopy, one may quite accurately describe optimum microhabitats for each of the four species. Since the stratum which has greatest influence in determining microhabitat conditions is the canopy, it can be predicted that *L. longipes* will occur in highest abundance under dense canopy, that *L. politum* will be most abundant where the canopy is more moderate, and that *L. calcar* and *L. vittatum* will be found most often in close proximity to openings and vegetation borders.

Table 9 compares various habitat characteristics and the laboratory-determined tolerances of the four *Leiobunum* species. With its relatively high temperature preference and survival time in dry air, and its relatively low rate of loss of body weight under dessication, *L. vittatum* stands out as a species capable of living in relatively harsh conditions. By comparison, the three other species are fastidious animals with less latitude in those characteristics that are important for survival. *L. longipes,* which prefers the shelter of forest habitats, has the record with highest basal area and canopy cover values, together with the lowest temperature preference. Since both *L. politum* and *L. calcar* succumb to death by dessication quite rapidly, it is interesting to note the similarity in their basal area and cover values. *L. politum* ranges up from the forest litter to a greater extent than *L. calcar* but occupies sites where the relative humidity is high. In a dry air chamber, when
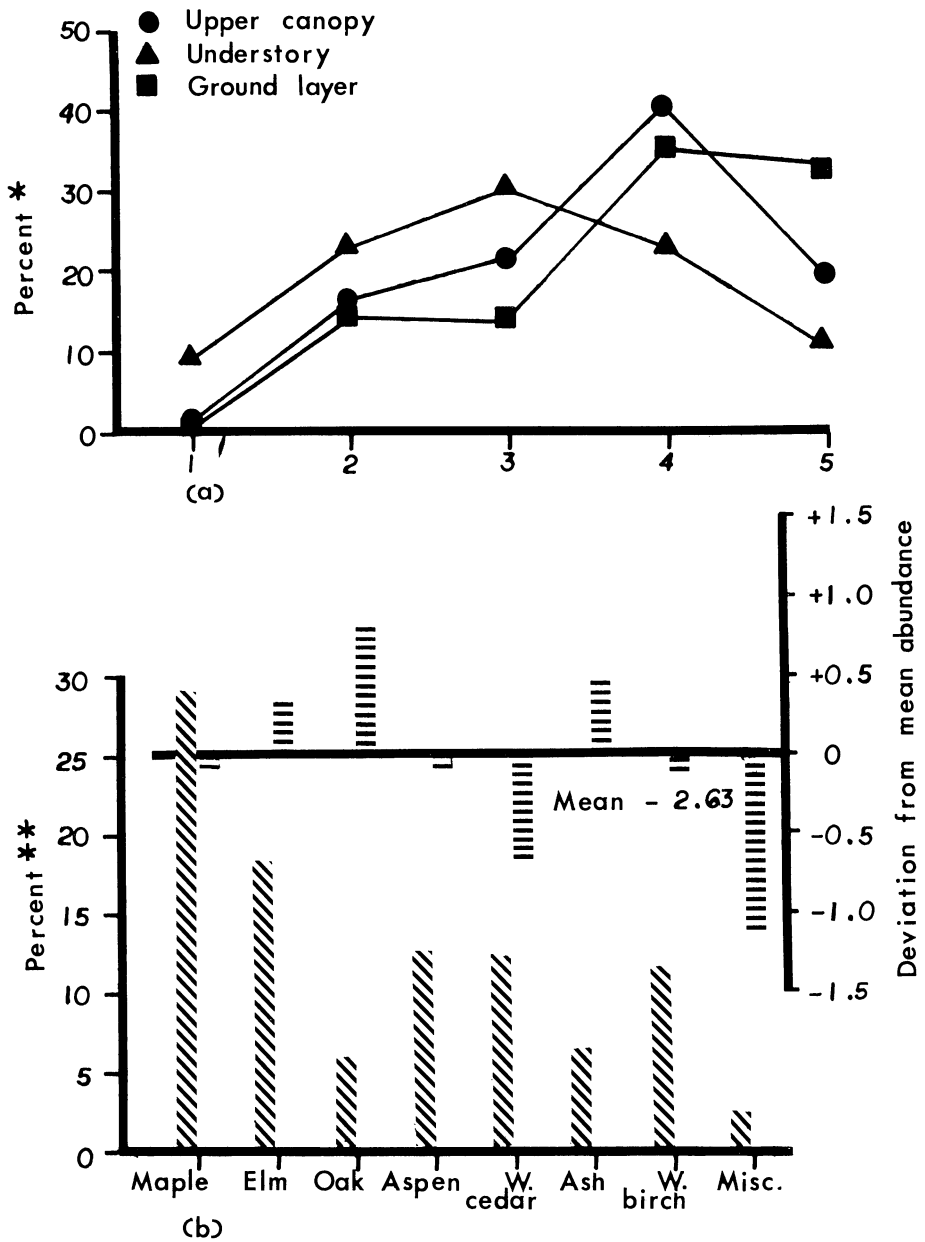
FIG. 8. (a) Abundance-cover profile and (b) Relative occurrence and abundance of *L. politum* in the major canopy groups. See Figure 5 for key to ordinate symbols.

TABLE 9

Comparison of Habitat Characteristics and Laboratory Performance
of Four Species of *Leiobunum*

	L. longipes	*L. vittatum*	*L. calcar*	*L. politum*
Basal area values[1]	13.44	11.90	11.98	11.90
Canopy cover estimation	4.15	3.54	3.66	3.51
Relative humidity preference between site and free air	15.0	13.7	14.7	15.9
Temperature preference in °C	23.9	27.9	24.2	24.3
Relative humidity preference during first 24 hours (%)	59.5	56.5	68.7	77.7
Hours survival in dry air	42.1	86.2	39.7	28.5
Per cent weight lost per hour under dessication	1.25	0.65	1.17	1.81

[1] Basal area values are in terms of sq. ft. of trunk cross-sectional area per acre at 4.5 ft. above the ground.

there is no possibility of avoiding dessication, *L. politum* loses body weight rapidly and expires very quickly.

These laboratory findings accord with habitat preferences of the different species. *L. calcar,* which is short-lived in a humidity gradient, avoids direct sunlight by seeking shelter in the litter; it occurs most often in woodland openings and ecotonal conditions that are likely to permit rain and dew to reach the forest floor. *L. politum,* also relatively vulnerable to low humidity, departs only rarely from the shelter of litter; it occurs in greatest abundance in seepage areas where ground vegetation is luxurious, surface water is plentiful, and openings in the canopy admit precipitation. *L. longipes,* which had a survival time intermediate between that of *L. vittatum* and those of the other two *Leiobunum* species, is most abundant when the dense canopy produces cool shade, the shrub layer is sparse, and there is a moderately constant supply of moisture.

HABITATS OF THE LESS COMMON SPECIES

Leiobunum nigropalpi.—This species is most abundant in habitats associated with the high, rather dense canopy of older stands of trees, in which the average basal area estimates are comparatively high (Table 7). Such stands often have openings in the canopy from collapse or disease of old trees; young climax trees found here account for a portion of the understory profile. The typical habitat within these stands is one with a moderate to sparse understory and ground layer (Fig. 9a). Stands dominated by ash and white birch yielded higher than average abundance values for *L. nigro-*
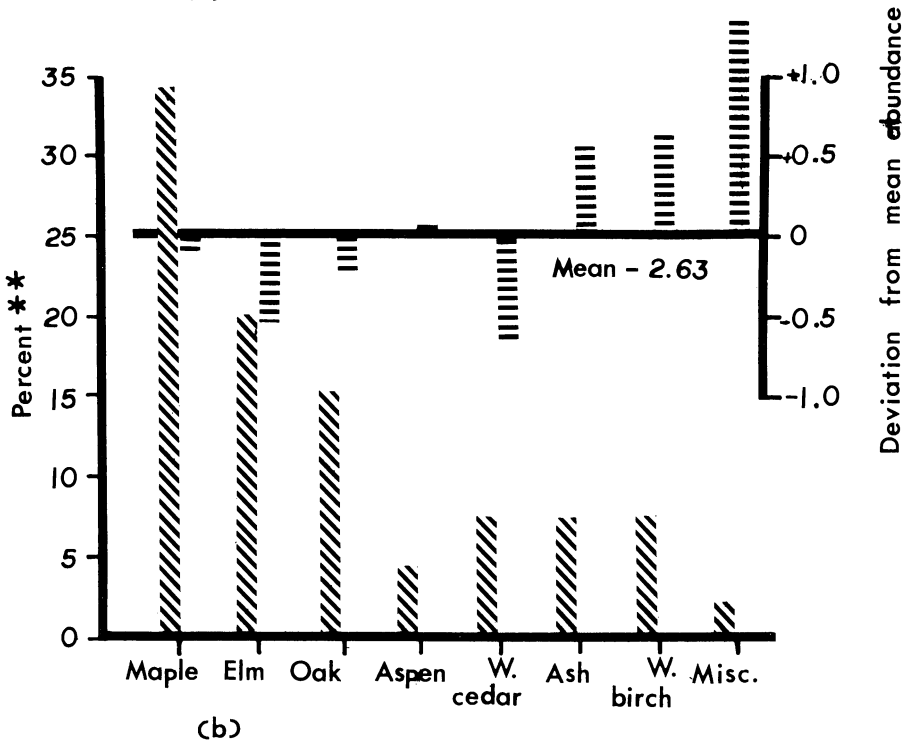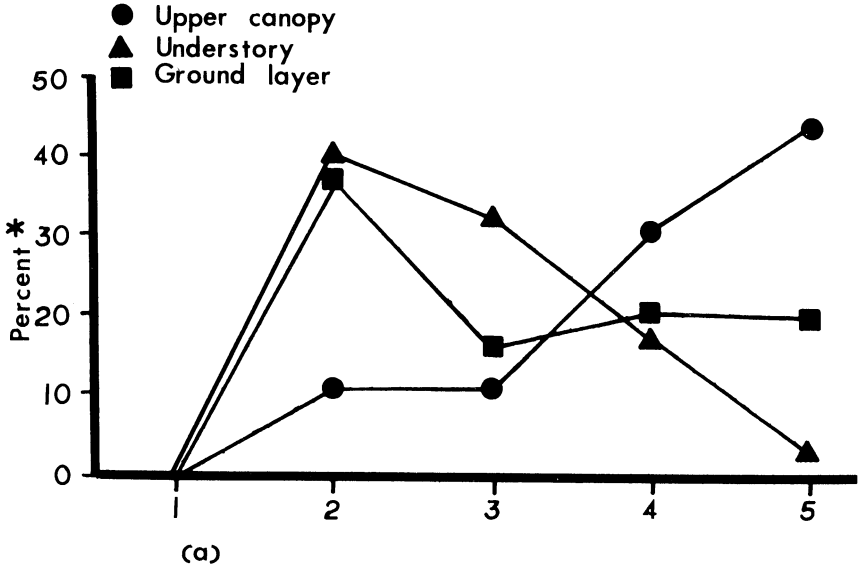
FIG. 9. (a) Abundance-cover profile and (b) Relative occurrence and abundance of
L. nigropalpi in major canopy groups. See Figure 5 for key to ordinate symbols.

palpi, while those dominated by maple, elm, oak and white cedar gave low values (Fig. 9b). This species was not collected consistently enough to determine whether it frequented clearings or edges in dry weather, nor was it subjected to laboratory experimentation to determine optimum R. H. and comparative survival in a dry atmosphere, but I would expect its performance to lie somewhere between that of *L. longipes* and that of *L. vittatum.*

Leiobunum ventricosum.—This species was not always distinguishable from *L. calcar* in the field, and cover-abundance data for it are available from only 9 samples. It overwinters as a subadult, and its relatively early maturation undoubtedly reduced its appearance in the collections, most of which were taken later in the summer.

The cover-abundance profile (Fig. 10a) indicates, in general, a habitat with fairly dense canopy and ground layer cover but with a moderate to sparse understory. Higher than average abundance values were recorded where ash and maple were dominant, lower than average values in oak and aspen (Fig. 10b). Several collections were made in the immediate vicinity of stinging nettles *(Urtica),* thorn apples, goldenrod *(Solidago),* May apples *(Podophyllum),* and poison ivy *(Rhus).* Wet spots and succulent, tangled vegetation with considerable windfall as well as mossy areas seemed to be the microhabitats supporting greatest densities.

Leiobunum verrucosum.—In Michigan, this species has been collected only from the southern half of the Lower Peninsula. It is considered a southern species by Bishop (1949) and probably finds its northern limits in the Lower Peninsula. It was taken 19 times in areas characterized by moist to saturated soils supporting dense luxuriant ground vegetation. Its cover-abundance profile indicates a preference for variable to moderately dense canopy (Fig. 11a). Higher than average abundance values were recorded only in aspen habitats; stands dominated by maple and oak gave much lower mean values (Fig. 11b).

Leiobunum serratipalpe.—This species was most abundant in moderate to dense cover in all vegetational strata (Fig. 12a). Higher than average abundance values were found in maple and oak habitats, lower than average in elm and maple. Immediate environments included low roadside areas, a swampy lake flats area, and a mesophytic forest floor.

Caddo agilis.—One of the species of phalangids which exhibits a particularly narrow range of environmental tolerance in Michigan is *C. agilis.* It occurs in habitats of moderate to dense canopy cover but is most abundant where the shrub and ground layers are sparse (Fig. 13a). The high mean basal area estimate of 16.3 recorded for habitats of this species (Table 7) indicates its preference for stands of comparatively large trees. Most of the specimens were taken in stands of white cedar, which in many cases was co-dominant with maple or white birch. Highest abundance values were recorded from habitats in the maple group (Fig. 13b). Optimal conditions for high abundance usually included one or more of the following: the presence of white cedar or other conifer; a conifer along with maple or white birch; a dense
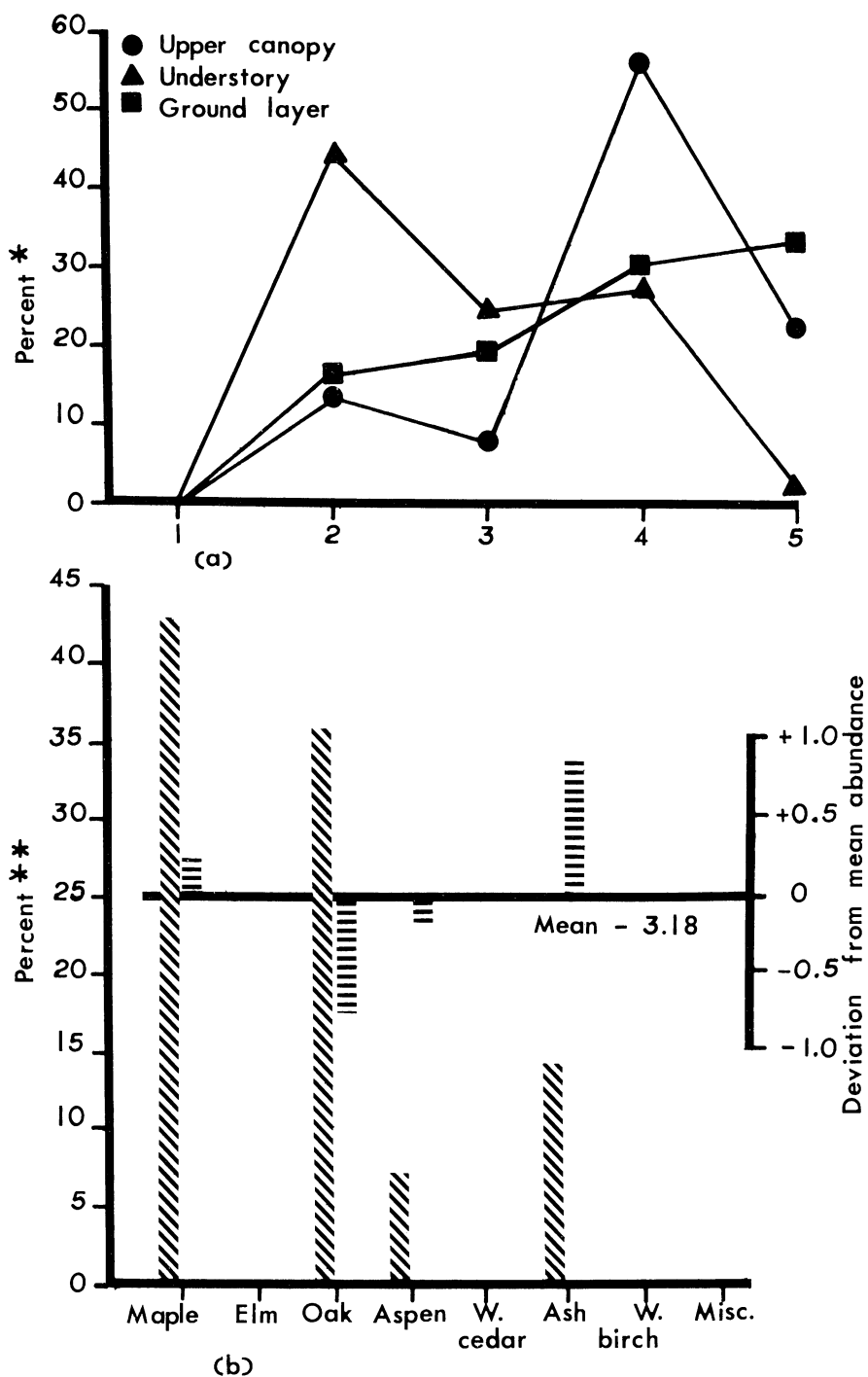
FIG. 10. (a) Abundance-cover profile and (b) Relative occurrence and abundance of *L. ventricosum* in the major canopy groups. See Figure 5 for key to ordinate symbols.
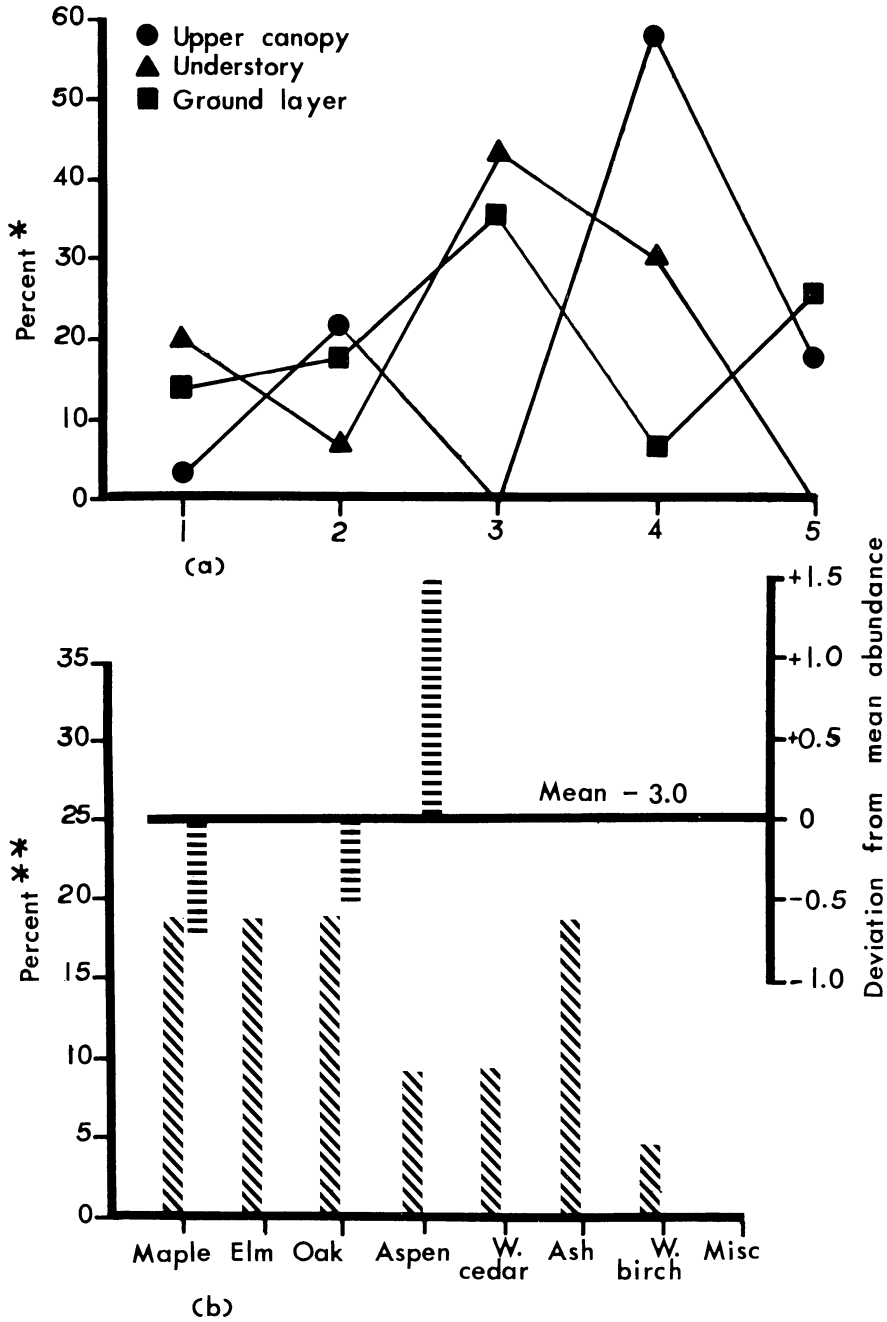
FIG. 11. (a) Abundance-cover profile and (b) Relative occurrence and abundance of *L. verrucosum* in the major canopy groups. See Figure 5 for key to ordinate symbols.
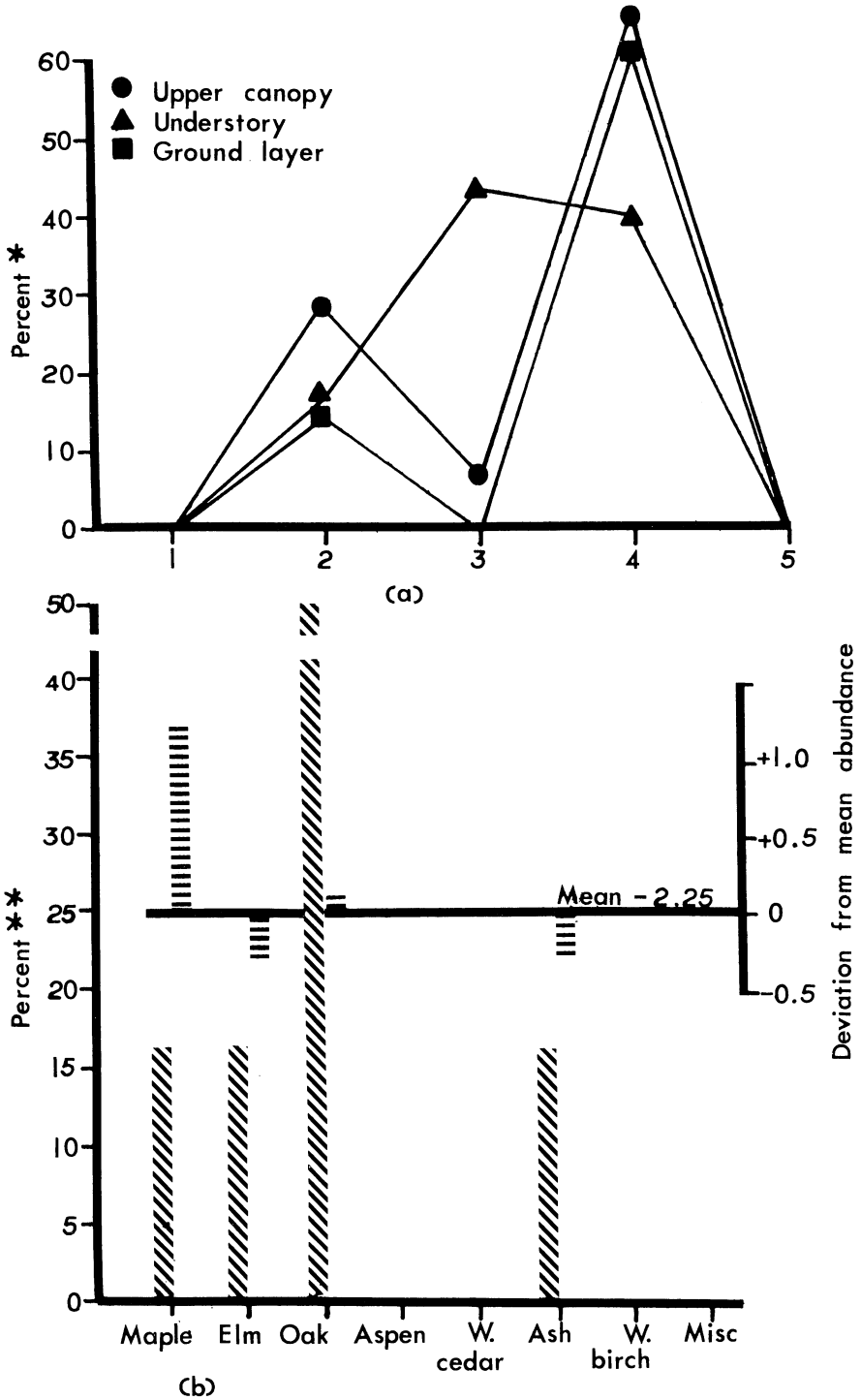
FIG. 12. (a) Abundance-cover profile and (b) Relative occurrence and abundance of
L. *serratipalpe* in the major canopy groups. See Figure 5 for key to ordinate symbols.
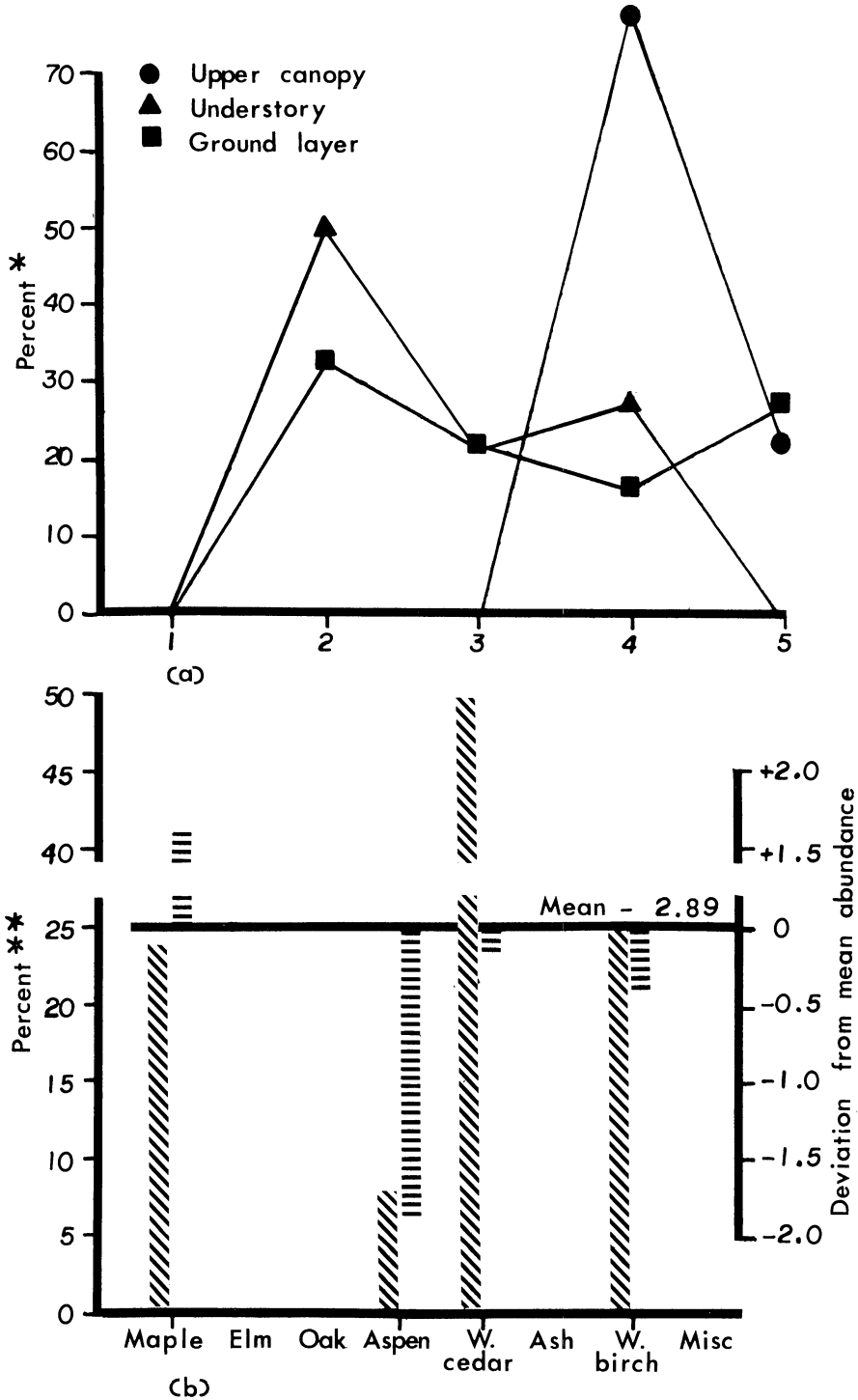
FIG. 13. (a) Abundance-cover profile and (b) Relative occurrence and abundance of *Caddo agilis* in the major canopy groups. See Figure 5 for key to ordinate symbols.

but not necessarily high canopy; sufficient ground moisture to support large patches of moss at tree bases; and a relatively bare ground layer.

Oddly enough, *C. agilis* may occur in the immediate vicinity of aspen. Low kettle holes with a constant seepage of water occur occasionally in an aspen association. Under these conditions a rather sharp ecotone between the comparatively xeric floor of the aspen stand and the wet, mossy substrate of the kettle provides a suitable habitat. An area such as this, about 40 yards at its widest, was encountered in Lake County. From the access via the highway, no other suitable areas were seen for several miles, but this limited situation yielded *C. agilis* along with *Leiobunum longipes*, *L. politum*, and *L. nigropalpi*.

Odiellus pictus.—Two forms of *Odiellus* were recognized in this study. They were originally designated (Edgar, 1966) as subspecies of *O. pictus*— *O. p. pictus* and *O. p. argentus*—but a re-evaluation of the evidence suggests that they should be given species rank, and they are referred to as such in this paper. They are distinguishable in details of external coloration as well as of habitat. They often occur together in the same general environment, but appear to occupy different portions of it.

O. pictus ordinarily occurs most abundantly under moderately dense canopy, where the understory and ground layers are somewhat sparse (Fig. 14a). Individuals are frequently found at the edges of heavily wooded areas, in grass or on tree trunks up to 5 feet above the ground. The largest collections per area were taken in habitats with scrubby, open canopy, few shrubs, and sod-forming, tangled grass. Higher than average abundance values were recorded at sites dominated by ash, aspen and white cedar (Fig. 14b).

O. argentus also reaches its highest abundance under moderately dense canopy, but in places where the understory and ground layers form thick cover (Fig. 15a). Higher than average abundance values for this species were found at sites dominated by maple and white cedar (Fig. 15b).

The higher mean basal area estimates and R. H. values recorded for *O. argentus* (Table 7) are also indicative of its preference for situations of greater vegetational protection than those occupied by *O. pictus*. Typical field notes on the habitats of the latter included such comments as "grassy edge of forest, scrubby area," "on sparsely weeded, grassy ridge," and "open, breezy, on small hill near level plain," whereas those for *O. argentus* referred to "dense undercover, ground soft from seepage," or "moss common, wet under foot, dense vegetation in narrow cut in woods."

Phalangium opilio.—The species discussed thus far have not been closely associated with man and his environs; their typical habitats are not sites of vegetational disturbance. *P. opilio* differs from these species in that it is not regularly collected away from man's habitations and disturbances. Gardens, lawns, hedges and other planted shrubbery, foundations of buildings, roadsides, and board piles are the usual habitats for this species. The difficulty of visually assessing the cover provided by buildings and building foundations prompted me to assign an arbitrary value of 1 for the cover density afforded
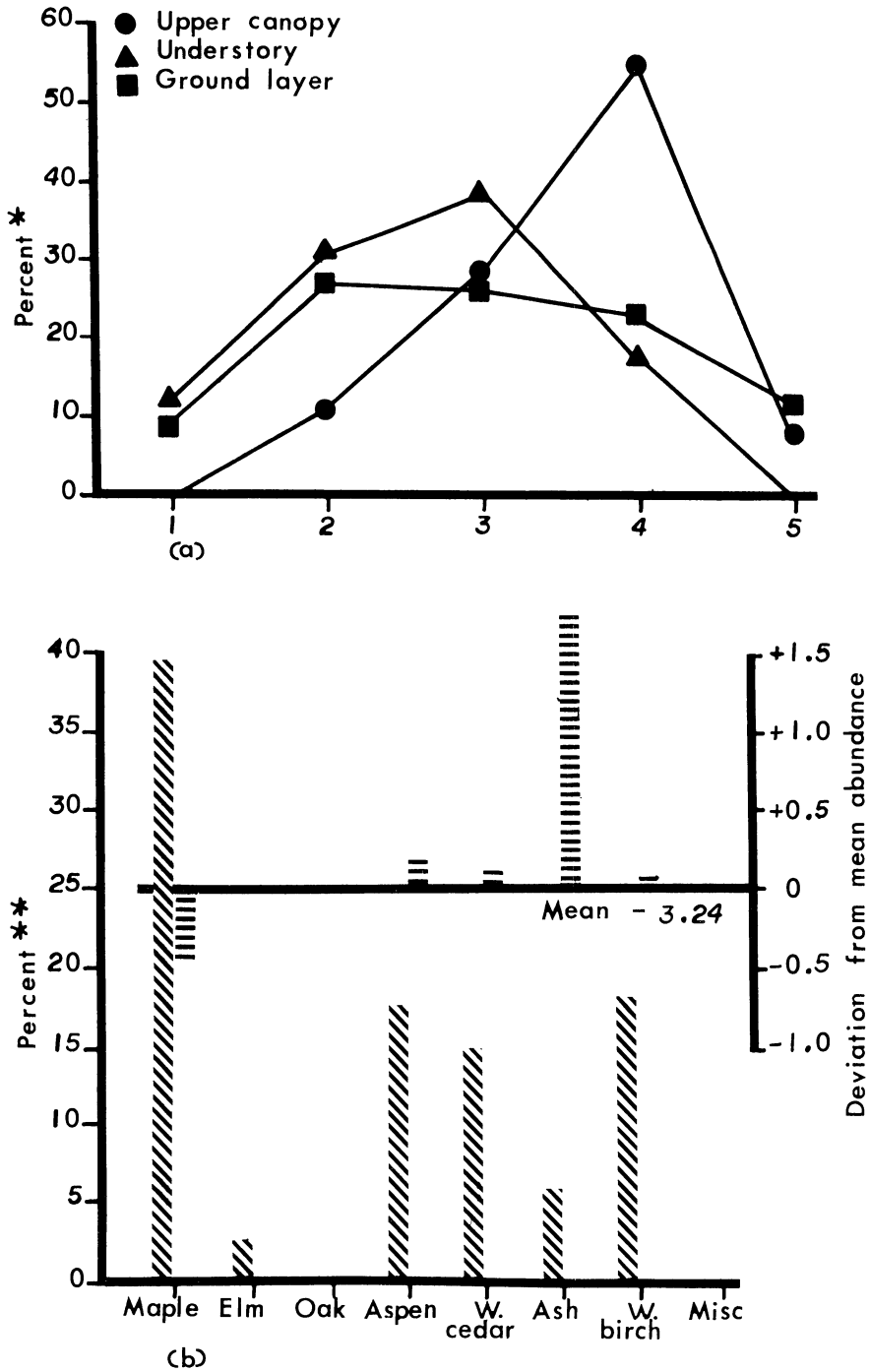
FIG. 14. (a) Abundance-cover profile and (b) Relative occurrence and abundance of *Odiellus pictus* in the major canopy groups. See Figure 5 for key to ordinate symbols.
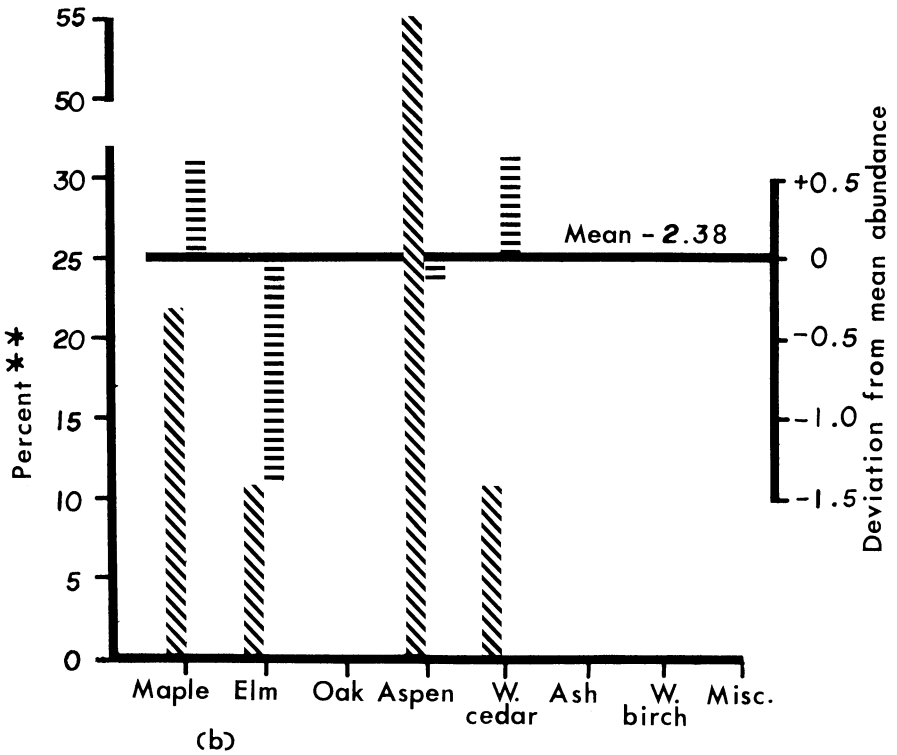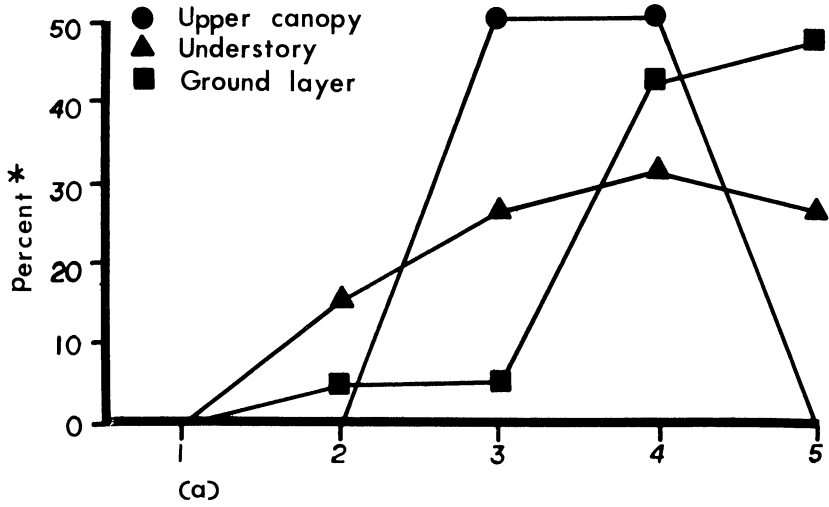
FIG. 15. (a) Abundance-cover profile and (b) Relative occurrence and abundance of
Odiellus argentus in the major canopy groups. See Figure 5 for key to ordinate symbols.

by building foundations (Fig. 16a). It was further assumed that such cover was most appropriately associated with the understory stratum of the vegetation. The canopy analysis (Fig. 16b) includes data from collections involving buildings and grass. The latter two items are added to the canopy groups in this instance only. Higher than average abundance values were recorded in these edificarian habitats and also in stands of aspen (Fig. 16b), which afford comparatively sparse understory cover.

Laboratory data indicate that this species is able to survive longer periods of dry atmosphere without food or water than any other species tested, except *Leiobunum vittatum*. The unprotected, often dry conditions of habitat occupied by *P. opilio* would seem to require such an ability. Indeed, it often seems to disregard exposure to drying. For example, the fence rows of a certain farm lane in Cheboygan County support a high population of *P. opilio,* and on nearly every cedar post on a hot, dry, windy July day one to several adults can be found running about, mating, feeding, and carrying on other normal activities. Fifteen adults were collected from one post.

Leiobunum nigripes.—This species was collected only in Macomb and Ottawa Counties. It is more widely distributed than these records indicate, however. Like *L. ventricosum,* it winters over as an immature. It matures, reproduces and dies before most of the other *Leiobunum* species of the area, and consequently was almost completely overlooked. When sought in moist decaying deciduous litter along margins of mud flats in streams, and in protected places near permanent sources of water in the late spring and early summer, *L. nigripes* is likely to be found in considerable abundance.

Hadrobunus maculosus.—Collection sites of this large-bodied species were in most instances in stands of grass and goldenrod. The environment was either dry, in which case the individuals were found in a board pile, or with scattered, small wet areas. Several *H. maculosus* were found among rocks in a talus slope between a limestone outcrop and the Ocqueoc Falls in Presque Isle County. The species is probably more widely distributed than its collections indicate (see Appendix). Its habitat seems less restricted than that of *P. opilio* and it has been recovered in association with ten other species of phalangids.

Opilio parietinus.—This species is world-wide in distribution but has been taken only a few times in Michigan. Four collections were associated with buildings, either from a north wall or from vegetation at the base of a north wall. One collection was from a stream bank with dense high grass and weeds, in an area of relatively open exposure.

Sabacon crassipalpe.—*S. crassipalpe* has been collected in Michigan in but two locations (see Appendix). It was sought and found for the first time in the State in a habitat which was described by Bishop (1949) as typical in New York. A single specimen was found in litter on a slight, north-facing slope under bracken ferns and a canopy of white pine, aspen, and red pine. This site was in Cheboygan County, at the east end of Hogback Road on
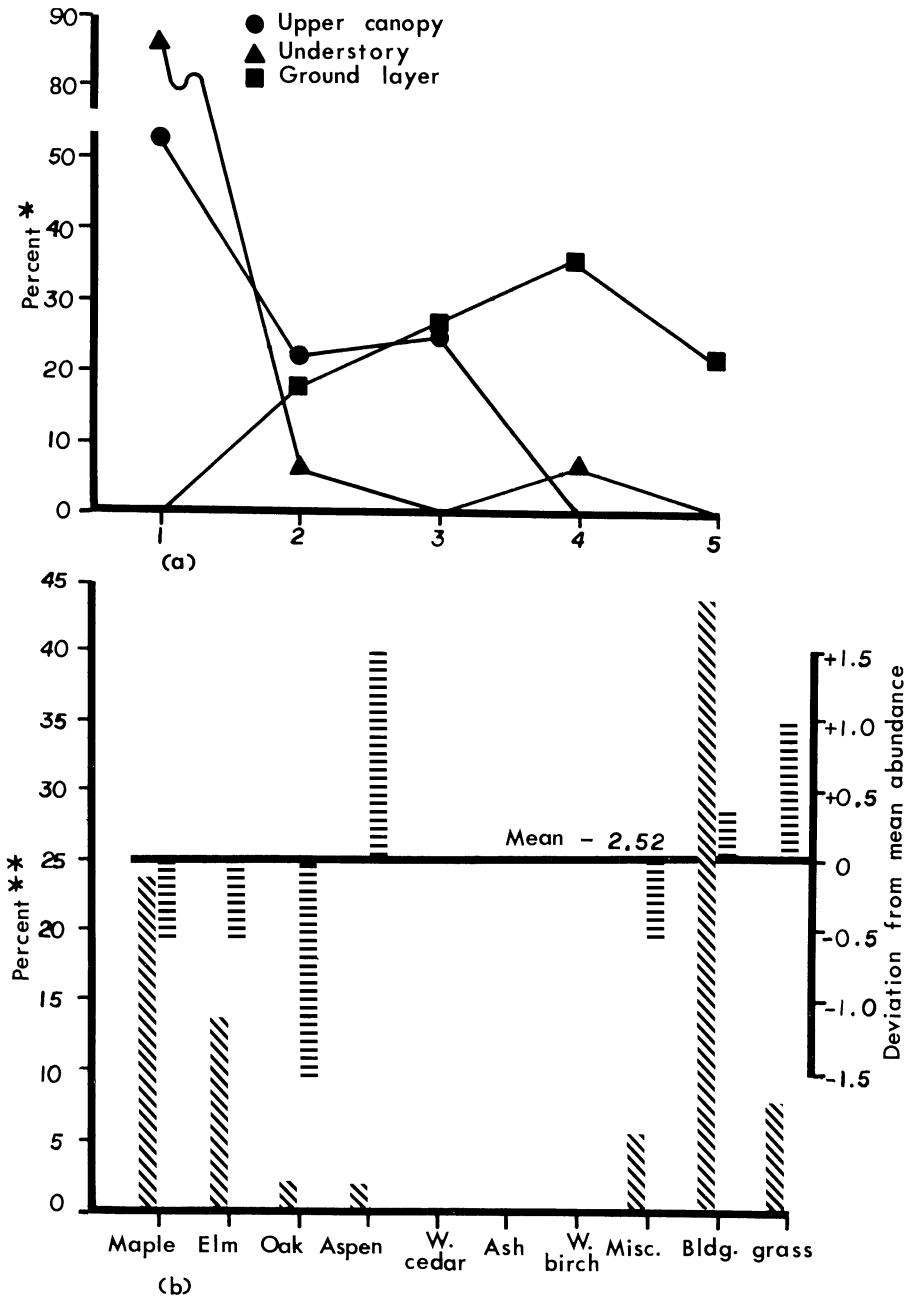
FIG. 16. (a) Abundance-cover profile and (b) Relative occurrence and abundance of *Phalangium opilio* in the major canopy groups. See Figure 5 for key to ordinate symbols. Understory cover, when associated with buildings, was assigned a value of 1.

the north side of Burt Lake (T. 36N, R. 3W, Sec. 3), in an irregularly rolling area of predominantly aspen (both *Populus grandidentata* and *P. tremuloides)* association. The second collection site was also in Cheboygan County (T. 39W, T. 3W, P.C. 334), only a meter or two away from the water's edge of Mill Creek. Individuals were perched on the under side of moss-covered pieces of limestone and decaying logs in an area of constant moisture and moderately dense shade.

Crosbycus dasycnemus.—I have collected only one specimen of this species—in a beech-maple-white birch-aspen complex northwest of the University of Michigan Biological Station laboratory area on Grapevine Point, an area that has been studied intensively for several years. It was taken in a litter sample and recovered from a Berlese funnel. The adult measures up to 1 mm in length and might easily pass unnoticed or be mistaken for a small spider, mite or insect. George Klee found several specimens in Berlese-sorted material taken from oak upland woods in Clinton County.

Leiobunum lineatum.—This recently described (Edgar, 1962) species was collected from three sites in the southern half of the Lower Peninsula of Michigan. The collection sites were relatively unprotected by canopy, one being southwest of the edge of a relatively mature maple woods, another in an unused school yard, and a third amongst willow and sedges along a stream bank. Understory was sparse at each site. Ground vegetation, however, was dense, bushy, and about two feet high.

APPENDIX

NEW COLLECTION RECORDS OF PHALANGIDS IN MICHIGAN

Species are arranged alphabetically by genus and, within genus, by species. With one exception *(Caddo boöpis)*, each species was collected in more than one county and/or more than once in the same county. Although the only collection information tabulated here is county and a range of collection dates, I have compiled and will make available to those who request it, specific tier-range-section designations and dates for 741 new phalangid collection records. Collectors and the number of their collections (in parentheses) in this list are: Robert R. Dreisbach (68), Arlan L. Edgar (651), George M. Klee (9), Julie H. Klee (2), Gary Manley (3), John Maki (1), J. Shaddy (1) and Frederick H. Test (6). UP refers to Upper Peninsula, NLP to Northern Lower Peninsula, and SLP to Southern Lower Peninsula.

Caddo agilis. UP: Baraga; Aug. 2. NLP: Alcona, Charlevoix, Cheboygan, Lake, Montmorency, Ogemaw; July 14–28.

Caddo boöpis. NLP: Montmorency; Aug. 10–20.

Crosbycus dasycnemus. NLP: Alpena, Cheboygan, Emmet, Presque Isle; July 16–Nov. 20. SLP: Clinton, Monroe; Apr. 15–Oct. 13.

Hadrobunus maculosus. NLP: Wexford; Aug. 1. SLP: Cass, Clinton, Ingham, Ionia, Kent, Livingston, Monroe, Shiawassee; June 23–July 21.

Leiobunum calcar. UP: Chippewa, Delta, Iron, Luce, Mackinaw, Menominee, Schoolcraft; July 26–Aug. 22. NLP: Alpena, Antrim, Arenac, Benzie, Charlevoix, Cheboygan, Clare, Crawford, Emmet, Iosco, Kalkaska, Lake, Leelanau, Manistee, Mecosta, Midland, Missaukee, Montmorency, Newaygo, Oceana, Oscoda, Otsego, Presque Isle, Wexford; June 15–Aug. 6. SLP: Berrien, Calhoun, Clinton, Eaton, Jackson, Kalamazoo, Livingston, Monroe, Saginaw, St. Joseph, Washtenaw; June 5–July 26.

Leiobunum flavum. NLP: Midland; July 1. SLP: Huron; July 30.

Leiobunum lineatum. SLP: Eaton, Gratiot, Sanilac; July 20–Sept. 24.

Leiobunum longipes. NLP: Alcona, Alpena, Bay, Benzie, Charlevoix, Cheboygan, Clare, Crawford, Emmet, Isabella, Iosco, Kalkaska, Lake, Leelanau, Manistee, Mason, Mecosta, Midland, Missaukee, Montmorency, Muskegon, Newaygo, Oceana, Ogemaw, Osceola, Oscoda, Otsego, Roscommon, Wexford; June 15–Sept. 1. SLP: Barry, Berrien, Branch, Calhoun, Cass, Eaton, Genesee, Gratiot, Hillsdale, Ingham, Jackson, Kalamazoo, Kent, Lapeer, Lenawee, Livingston, Montcalm, Saginaw, St. Clair, St. Joseph, Tuscola, Van Buren, Washtenaw; June 15–Aug. 15.

Leiobunum nigripes. NLP: Gratiot; June 1–July 15. SLP: Macomb, Ottawa; June 9–July 26.

Leiobunum nigropalpi. UP: Dickinson, Iron, Ontonagon; July 1–Aug. 12. NLP: Alcona, Arenac, Benzie, Gladwin, Grand Traverse, Iosco, Isabella, Kalkaska, Lake, Manistee, Mecosta, Midland, Missaukee, Muskegon, Newaygo, Oceana, Ogemaw, Osceola, Roscommon, Wexford; July 19–30. SLP: Clinton, Eaton, Gratiot, Ingham, Kent, Lapeer, Lenawee, Livingston, Oakland, St. Joseph, Tuscola, Washtenaw; July 19–Sept. 7.

Leiobunum politum. UP: Alger, Delta, Dickinson, Gogebic, Iron, Luce, Mackinaw, Marquette, Menominee, Schoolcraft; July 29–Aug. 3. NLP: Alcona, Alpena, Antrim, Arenac, Bay, Benzie, Charlevoix, Cheboygan, Clare, Crawford, Emmet, Grand Traverse, Isabella, Kalkaska, Lake, Leelanau, Manistee, Mason, Mecosta, Midland, Missaukee, Muskegon, Newaygo, Ogemaw, Osceola, Oscoda, Otsego, Wexford; July 20–Aug. 14. SLP: Allegan, Barry, Berrien, Branch, Calhoun, Cass, Clinton, Eaton, Genesee, Gratiot, Hillsdale, Huron, Ingham, Ionia, Jackson, Kalamazoo, Kent, Lapeer, Lenawee, Livingston, Macomb, Monroe, Montcalm, Oakland, Ottawa, Saginaw, Sanilac, Shiawassee, St. Clair, St. Joseph, Tuscola, Van Buren, Washtenaw, Wayne; (all counties) July 19–Aug. 2.

Leiobunum serratipalpi. SLP: Clinton, Hillsdale, Ingham, Lapeer, Monroe, Washtenaw; July 19–Sept. 21.

Leiobunum ventricosum. NLP: Alcona, Alpena, Cheboygan, Emmet, Grand Traverse, Iosco, Isabella, Manistee, Mecosta, Midland, Missaukee, Muskegon, Presque Isle; June 25–Aug. 3. SLP: Gratiot, Huron, Jackson, St. Joseph; July 19–27.

Leiobunum verrucosum. NLP: Bay, Mackinaw, Manistee, Mecosta, Midland, Muskegon, Newaygo, Wexford; June 15–Aug. 17. SLP: Calhoun, Cass, Clinton, Eaton, Gratiot, Hillsdale, Jackson, Kalamazoo, Kent, Lenawee, Livingston, St. Joseph, Washtenaw; June 13–July 26.

Leiobunum vittatum. UP: Alger, Baraga, Delta, Gogebic, Luce, Mackinaw, Menominee, Schoolcraft; July 20–Aug. 3. NLP: Alpena, Antrim, Arenac, Bay, Benzie, Charlevoix, Cheboygan, Clare, Crawford, Emmet, Gladwin, Grand Traverse, Iosco, Isabella, Kalkaska, Lake, Leelenau, Mecosta, Midland, Osceola, Oscoda, Otsego, Presque Isle, Roscommon, Wexford; July 5–Sept. 14. SLP: Barry, Berrien, Branch, Cass, Eaton, Genesee, Gratiot, Hillsdale, Huron, Ionia, Jackson, Kalamazoo, Kent, Lapeer, Lenawee, Livingston, Macomb, Monroe, Montcalm, Ottawa, Saginaw, Sanilac, Shiawassee, St. Clair, St. Joseph, Tuscola, Washtenaw, Wayne; July 19–Sept. 17.

Odiellus pictus. UP: Alger, Baraga, Chippewa, Luce, Mackinaw, Schoolcraft; July 27–Aug. 3. NLP: Alcona, Alpena, Charlevoix, Cheboygan, Crawford, Emmet, Kalkaska, Lake, Leelanau, Ogemaw, Oscoda, Otsego, Presque Isle, Roscommon; July 21–Aug. 14. SLP: Gratiot, Lenawee, Livingston, Sanilac, Shiawassee, Washtenaw; July 21–Nov. 24.

Odiellus argentus. UP: Alger, Chippewa, Iron, Marquette, Ontonagon; Aug. 2–3. NLP: Newaygo; July 20. SLP: Huron, Livingston, Tuscola; July 26–27.

Opilio parietinus. NLP: Arenac, Cheboygan, Wexford; June 30–Aug. 21. SLP: Ingham, Macomb, Saginaw, Sanilac; July 18–Sept. 24.

Phalangium opilio. UP: Alger, Chippewa, Delta, Dickinson, Gogebic, Houghton, Iron, Keweenaw, Luce, Mackinaw, Marquette, Menominee, Ontonagon, Schoolcraft; Aug. 2–3. NLP: Bay, Benzie, Charlevoix, Cheboygan, Emmet, Grand Traverse, Kalkaska, Manistee, Mason, Mecosta, Missaukee, Oceana; May 24–Aug. 10. SLP: Allegan, Barry, Calhoun, Cass,

Clinton, Eaton, Genesee, Gratiot, Huron, Ingham, Ionia, Kalamazoo, Lenawee, Livingston, Monroe, Montcalm, Oakland, Ottawa, Shiawassee, St. Clair, Tuscola, Van Buren, Washtenaw, Wayne: May 26–Sept. 1.

Sabacon crassipalpe. NLP: Cheboygan; July 19, 36N3W3; July 22–26, 39N3WPC334.

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This paper is based on a dissertation accepted in 1960 for the Doctor of Philosophy degree in Zoology at The University of Michigan.