To the Graduate Council:

I am submitting herewith a thesis written by James Cockerill entitled "Resource Partitioning by Forest Species of Harvestmen of the Genus Leiobunum (Arachnida, Phalangida)." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with major in Ecology.

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RESOURCE PARTITIONING BY FOREST SPECIES OF HARVESTMEN OF THE GENUS LEIOBUNUM (ARACHNIDA, PHALANGIDA)

A Thesis

Presented for the

Master of Science

Degree

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ABSTRACT

The temporal, spatial and functional niche of forest species of harvestmen (Arachnida, Phalangida) on a Southern Appalachian foothill is investigated in order to determine if the pattern of resource partitioning is consistent with strategies dictated by competition theory.

Three species, Leiobunum calcar, L. nigropalpi and L. longipes, share common life histories in that they overwinter as eggs, reach maturity in the late spring and early summer and reproduce soon thereafter. These species show a strong overlap in diel activity and in the type and size of food items scavenged for. There is some degree of spatial segregation, most apparent at night, when different proportions of the three populations forage in different forest strata and show a preference for forest patch type along a continuum of ground cover abundance and sparseness of the forest understory.

This habitat selection is discussed in view of the likelihood that it 1) reduces the potential for competition among the species, 2) is a product of the optimal functioning of the species to obtain preferred resources and/or 3) is part of a mechanism by which the populations remain reproductively isolated. I conclude that harvestmen densities are maintained below competitive levels by predation and that species differences in habitat associations may represent divergent adaptations to predation based on optimal functioning criteria.

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CHAPTER I

INTRODUCTION

Niche quantification through the analysis of variables believed to be associated with the temporal, spatial and functional dimensions of the niche has proved, for a wide variety of taxa, to be a successful means of demonstrating how resources are partitioned by closely related species (Pianka, 1976). The uniform spacing or overdispersion of species along one or more resource axes has typically been attributed to the effects of interspecific competition. However, it has been difficult to show experimentally that competition is, in reality, the structuring force. More often sympatric species are found under conditions of abundant food resources, breeding or nesting sites or other potentially limiting resources. This leads to the suspicion that other density-dependent phenomena are more important in structuring communities and account for the spacing out of its member species along gradients. Slobodkin (1964) and Paine (1966) demonstrated how predation can control species diversity. Selection for reproductive isolation has also been implicated in establishing ecological divergence among sympatric species (Watson, 1962). Community structure, as well, may be a result of optimal functioning on the part of species differentially adapted to microclimatic or microhabitat features or by species which differ in predatory behavior (Kronk, 1980; Wiens, 1977).

Observational studies of resource partitioning may have much relevance to establishing the role of competition; they may indicate indirectly whether or not it is, in fact, the reason for ecological separation. Schoener (1974) uses predictions from competition models

to examine the patterns of resource partitioning in studies ranging over a diversity of animal groups. Several trends are significant and readily explainable by competition theory. In the majority of cases reviewed by Schoener, partitioning along spatial dimensions of the niche has been shown to be more important than functional or temporal separation (though the analysis is biased due to the disproportionately large number of vertebrate cases). This trend can be explained in light of the theory of optimal foraging strategies (MacArthur and Pianka, 1966). Where optimal macrohabitat patches are continuously distributed and large, relative to the vagility of a species, or where a species is vagile enough to cross through unsuitable patches without considerable loss in hunting time, it is more efficient for it to specialize by patch type than to exclude from its diet those items which are preferred by its competitors. As a result spatial overlap with potential competitors is reduced.

Terrestrial arthropods appear to be a striking exception to this general trend; partitioning by food type or food size is a more common pattern. Partitioning along food dimensions might be expected where there is little overlap between populations of neighboring species in body size or size of feeding structures due to little variance in these variables within populations. This is frequently found in organisms having non-overlapping generations or those in which immature forms differ only slightly from adults or approach maturity rapidly.

Temporal partitioning is suggested as most important for predators, for whom prey is generally available only at certain times of day or season or for other organisms living in environments where

physical conditions exhibit marked cycles. Animals which incur severe risks from predators while processing food should also partition food temporally.

The nutritional mode of a group of species is often more closely associated with its manner of resource segregation. Several groups of terrestrial or semi-aquatic invertebrate species reviewed by Schoener which are primarily scavengers or detritivores exhibit differential use of habitat or microhabitat as an important way of partitioning resources.

The study of resource partitioning undertaken here for a cohort of three harvestman species of the genus Leiobunum (Arachnida, Phalangida) tries to assess the likelihood that competitive interactions, either ongoing or occurring in the recent past history of the community, are responsible for the differences in niche of the three species. Observed differences should be considered in light of morphology, behavior and role in the community. These highly vagile arthropod scavengers are widespread inhabitants of temperate forests. They spend most of their life cycles beneath the understory. The more common smaller forms have only one generation present within a year. The pattern of resource partitioning in this group is examined as an initial step toward a more comprehensive study of the mechanisms of resource utilization in the group and the forces underlying the ecological and morphological differences found among the several species.

CHAPTER II

LIFE HISTORY AND ECOLOGY OF THE SPECIES

There are few published works on the ecology of North American Leiobunum. The review given here is not intended to be comprehensive but will highlight what is known of the distribution, life history and niche of the three most abundant species found on the study site, L. calcar, L. longipes and L. nigropalpi. The bulk of the review comes from the work of Edgar and Yuan (1968) and Edgar (1971) done on Michigan populations of L. longipes and L. calcar and from Bishop's publication on the phalangids of New York (Bishop, 1949). The latter includes records of the distributions of these three species as well as observations of the feeding behavior, diet and activity of L. longipes and L. calcar.

Distribution

All three species occur widely throughout the eastern half of North America; they are found in forests and woodlands of the northeastern, southeastern and Great Lakes states and even occasionally in the south central states bordering the Mississippi River. Leiobunum longipes and L. calcar both have been taken in western Canada, but L. nigropalpi has no record west of the Mississippi. It does not appear among specimens from New England examined by Bishop (1949) and was not present in collections from northern Wisconsin reported in Levi and Levi (1952). Thus, it appears to be more restricted in its range than the other two species.

Physical Tolerances

Edgar (1971) investigated temperature and relative humidity preferences as well as rates of water loss in Michigan specimens of L. longipes and L. calcar. Under laboratory conditions both showed a temperature preference near 24° C. Of the four species of Leiobunum tested, L. longipes and L. calcar exhibited intermediate preferences in a humidity gradient (59.5% and 68.7%, respectively). A greater water loss rate for L. longipes is attributable to the higher dessication rate for males of this species. (The males of Leiobunum are generally smaller than females of the same species and L. longipes is the smallest of the three species encountered here.) Though L. nigropalpi was not tested, Edgar assumes, on the basis of the habitats within which it was collected, that it is probably slightly more tolerant of high temperatures and low humidities than the other two species.

Habitats

Using data from the Michigan populations, Edgar (1971) established abundance profiles based on the degree of cover provided by various layers of the forest. The three species discussed here differ in that L. calcar is most often found under a more sparse canopy than the others and L. nigropalpi is most abundant in forests where the ground cover is moderately sparse.

Activity Patterns

Edgar and Yuan (1968) investigated the daily locomotory behavior of the three species in pressure displacement chambers subject to normal photoperiodic conditions. Leiobunum calcar and L. nigropalpi exhibited identical patterns: a sudden burst of activity occurring at dusk and

continuing until dawn. At that time there was a gradual decline in activity, until finally, by noon, movement in the chambers became immeasurably small. Leiobunum longipes, particularly the females, had a strong diurnal component of activity but remained active well into the night. Similarly, Fowler and Goodnight (1974) found some populations of this species to exhibit a bimodal pattern, the peaks of activity occurring about twelve hours apart. Bishop (1949) reports that New York populations of L. longipes and L. calcar are diurnal. Such discrepancies among populations from different areas can most likely be explained by the modification of normal photoperiodic rhythms by factors such as humidity and temperature.

Diet and Feeding Behavior

There appears to be some confusion in the literature as to whether or not Leiobunum take live prey under natural conditions. Bishop (1949) relates accounts of predation for L. longipes and L. calcar. Sankey and Savory (1974) report that British members of the genus attack a wide variety of prey from among litter detritivores. In contrast to this, Walker (1928) believed that harvestmen eat only vegetable matter and Edgar (1971) observes that "living food is taken very timidly." Forster and Forster (1973) classify harvestmen primarily as scavengers, which take nearly all kinds of dead invertebrates. Bristowe (1949) expands the case for omnivority by adding fungi and bird droppings to the list of diet items.

Life Histories

According to Edgar females of L. longipes and L. nigropalpi both lay their eggs in early fall. The eggs overwinter and hatch

in spring. Michigan populations of L. longipes are known to mature in late June. Leiobunum calcar completes its adult stage earlier than either of these two.

Early instars of Leiobunum spend their time in or on the litter before migrating vertically into the shrub layer and onto tree trunks where they may be found during the day in crevices and irregularities of the bark. Edgar (1971) believes that the vertical migration continues throughout the season, with individuals returning to the ground in late summer only to mate and to lay eggs. Todd (1949) suspects this is true of two British members of the genus.

Two large species from the Eastern United States, L. ventricosum and L. nigripes, are known to lay eggs early in the summer. These hatch before fall, so that these species overwinter as subadults. Weed (1893) corroborates this with evidence for a Mississippi population of L. ventricosum.

CHAPTER III

MATERIALS AND METHODS

Description of the Study Site

During the summer of 1981 six Leiobunum species were collected from a Chestnut Oak-Scarlet Oak-Pitch Pine (Quercus prinus-Q. coccinea-Pinus rigida) community on an Appalachian foothill in Upper East Tennessee. The foothill adjoins the western boundary of the Cherokee National Forest near the Greene Co.-Cocke Co. line (latitude 35° 59' N). The study site on the foothill has a northwest-facing slope of approximately seven degrees at an elevation of 715 m above sea level. The understory of the forest was composed of red maple (Acer rubrum), black gum (Nyssa sylvatica) and sourwood (Oxydendrum arboreum). Mountain laurel (Kalmia latifolia), young black gums and flame azalea (Rhododendron calendulaceum) comprised the shrub layer. Galax aphylla and several species of Vaccinium dominated a generally sparse field layer. Part of this area had been grazed by a few cattle from nearby pastures as recently as 1978 and this accounts for some destruction of the understory in the form of bent trunks and broken branches. The area is relatively dry for a Southern Appalachian forest; there are no creeks or streams and the soil is well-drained.

During the winter of 1981 two 0.5 ha replicate plots (labelled A and B) were chosen on the site. Within each plot seven 2.0 m wide belt transects, running parallel, were randomly selected and marked with flagging at 5.0 m intervals. Because of the difficulty of sighting and identifying harvestmen high up on trees, the sample space was limited to

the lower 2.25 m of the forest. Only harvestmen within the 2.0 m wide belts were included in the sampling.

Transect Sampling

Three samples were taken on each plot between May 4 and August 30, 1981. Samples IA and IB were made in the spring, samples IIA and IIB in the early summer and samples IIIA and IIIB in the late summer. Within each sample eight 3 hour long subsamples were taken, each at a different time and on different days, so that after eight subsamples an entire 24 hour period of activity was surveyed on a plot.

Harvestmen were located by walking slowly along transects. The order in which transects were walked was randomly determined prior to the walk. In addition to transect walks, early instars were collected from litter bags and pitfall traps in areas immediately adjacent to the 0.5 ha plots. At least three of the six species found on the study area are known to overwinter in eggs which are usually laid near the ground in the late summer or early fall. Since the transect searches in the early spring were, then, likely to ignore the instars too young to have begun their vertical migration into the understory it was hoped that these two methods would complement transect data regarding seasonal changes in use of microhabitat and temporal activity.

In the first several subsamples it was sometimes necessary to capture individuals for identification under a dissecting microscope. When possible, individuals taken were returned the following day to the location at which they had been captured. The total number of harvestmen that were kept as voucher specimens, which died in captivity or were injured during field collections was less than 5% of the total number

of individuals sighted. Care was taken not to disturb the fauna or the habitat in any other way.

A 6-volt lamp, worn on a headband, was used from one hour before sunset until sunrise. Harvestmen did not appear to be affected by this bright light in any way; feeding, copulation or direction of movement was uninterrupted as long as the observer kept still. Individuals of all species were most sensitive to movements of the observer when they were in the resting position. These often jumped from their perches or scurried away as the observer approached and such behavior accounts for missing data regarding microhabitat, orientation and kind of activity. It was necessary to mark the location of such individuals immediately after sighting by attaching pins or adhesive markers to the nearby substrate.

Niche Measurements

Variables which would facilitate the simultaneous investigation of the temporal, spatial and functional dimensions of the niche of the species were selected and data were recorded for each.

Temporal niche

In order to examine both the daily and seasonal activity patterns and the effects of physical factors on activity the following information was gathered:

1. Date and time of sighting.
2. Type of activity or inactivity including feeding, foraging, preening, reproductive behavior and all interspecific interactions.

3. Orientation of the body and appendages with respect to the substrate.
4. Wet and dry bulb temperatures of the air measured just above the dorsal surface of the individual.
5. The amount of solar radiation, in cal/cm^2/min., striking the forest floor at a position on each plot that was moderately shaded (percent of leaf cover between 25% and 75%).

Harvestmen were identified to species and sex by carefully lowering an 8X Agfa magnifier over the individuals. Determinations were made using the keys provided in Bishop (1949), Comstock (1948) and Davis (1934). Wet and dry bulb measurements were taken using a probe-type hygrometer (Atkins Model F01-F10, Atkins Technic Inc., Gainesville, Fla.) Solar radiation was measured using a mechanical pyranograph (Model R401, Weathermeasure Corp., Sacramento, Cal.).

Spatial niche

The lower 2.25 m of the foothill forest as a macrohabitat for harvestmen was investigated in two ways. First, the habitat was considered as a number of vertical layers or strata through which harvestmen move on a daily basis and in which they spend time in various activities. The following features were deemed important:

1. Stratum of the forest occupied, either the litter surface, low foliage (herbs and shrubs) or tree trunks and tree branches.
2. Height above the ground at which the harvestman was first located by the observer.
3. Microhabitat associations (e.g., bark crevices, knots, branch axils).

Secondly, the habitat was perceived as a mosaic of patch types with regard to the type, frequency and size of the vegetation. The following data were recorded at each sighting:

4. The location of an individual along the transect.
5. Species of plant occupied.
6. Stem diameter of the plant in cm at breast height, taken for all shrubs and trees greater than 1.0 cm in diameter.
7. The number of individuals situated on or moving upon a single vegetational unit.

Food niche

When harvestmen were observed with food, the items were taken away immediately with forceps and placed into vials containing 70% ethyl alcohol. These were subsequently identified and measurements were taken of their lengths and widths. Frequently harvestmen were found with invertebrates which were missing one or more tagmata. In these cases the longest dimension of the food remnant was recorded. Both the time and location of feeding were noted.

CHAPTER IV

RESULTS AND INTERPRETATION

Life Cycle Phenomena

Density estimates from subsample counts

Total counts for the six species of Leiobunum found on transects between May 4 and August 30 appear in Table 1. Mean density was estimated using counts from those subsamples which contained only adults.

A total of 1112 harvestmen were sighted and identified. Leiobunum nigropalpi and L. longipes constituted 93.2% of the sample. These two species along with L. calcar, the third most abundant species, are reported to overwinter as eggs, while two of the three rare species, L. ventricosum and L. nigripes, overwinter as subadults (Edgar, 1971). Both L. nigripes and L. vittatum were more abundant in collections made outside the forest; L. vittatum appeared frequently in collections in a nearby residential area, while L. nigripes was sometimes found in cleared areas on the foothill below the study site. Because of the decidedly different life cycles of L. ventricosum and L. nigripes and the insufficient data for all three of the rarer species, I will exclude them from further discussion.

Density estimates, expressed as number of individuals per transect (138.88 m^2) are presented in Figure 1 for the three common species for each of 48 three hour subsamples. Low densities during May and early June can be explained by the difficulty of seeing instars in the litter where they spend much of their time prior to the initiation of a daily vertical migration.

Table 1. Total Counts and Mean Seasonal Density Estimate for Each Species of *Leiobunum*

Species	Total Nos. Found	Mean Seasonal Density Estimate (ind's/0.5 ha)	No. Sub-Samples	95% Confidence Limits of the Mean (ind's/0.5 ha)
L. nigropalpi	577	224.35	32	187.56 - 261.14
L. longipes	459	275.40	24	231.48 - 319.32
L. calcar	54	24.45	40	16.23 - 34.66
L. ventricosum	17	9.05	36	4.81 - 13.28
L. nigripes	3	-	3	-
L. vittatum	2	-	2	-

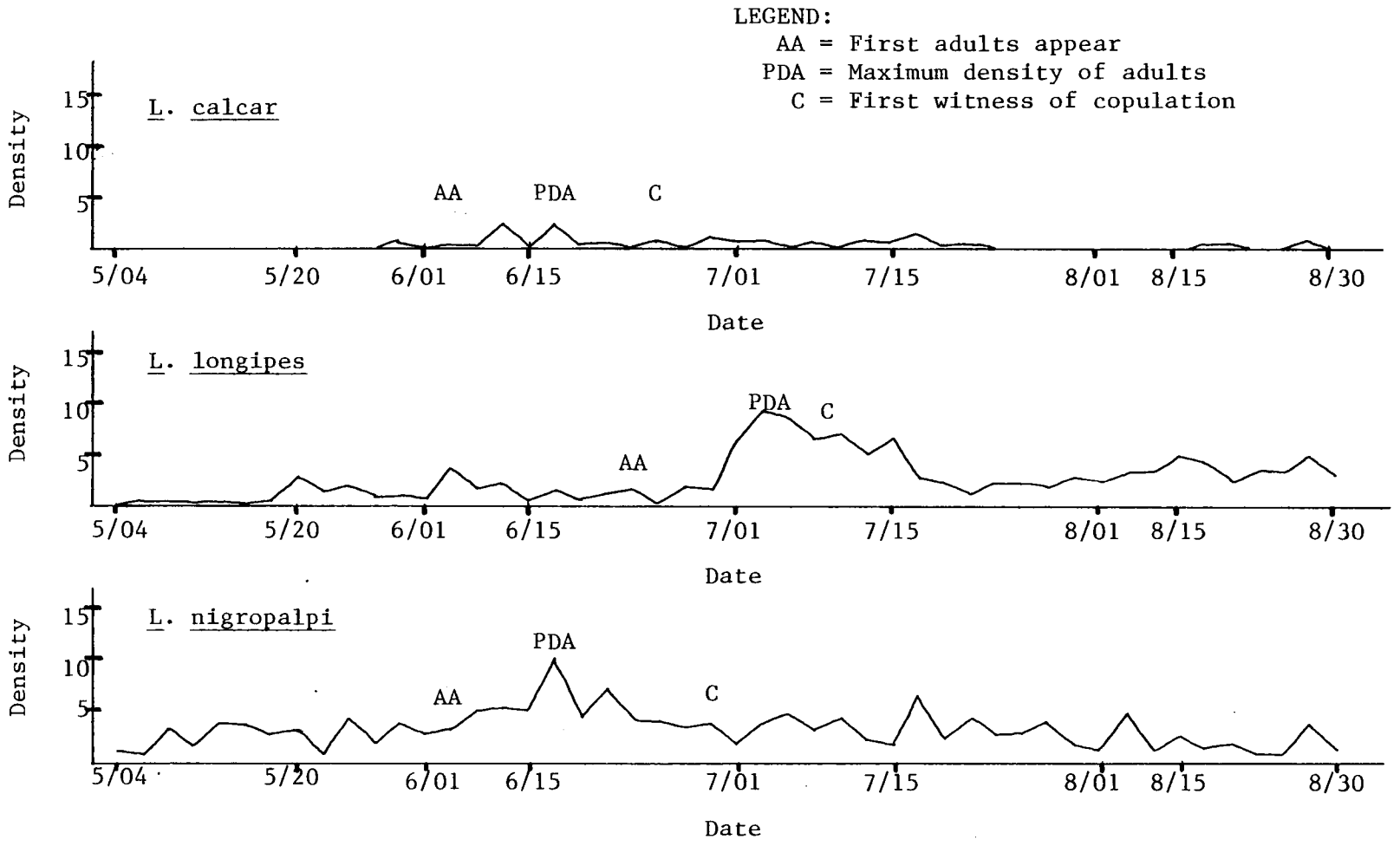


Fig. 1. Observed Densities of the Most Abundant Species of Leiobunum for all Subsamples (shown as number of harvestmen per transect)

Maturity and reproduction

Also included in Figure 1 is the time of onset of important events in the life cycle: the first appearance of adults, the time at which a maximum number of adults are present in the population and the first observation of attempted copulation. Oviposition was never observed, but the daily reappearance of a considerable fraction of the population on the litter during the daytime hours is most likely associated with mating and egg-laying. A significant increase in this fraction occurs in the sample following that in which copulation was first witnessed (Fig. 2). This sequence of life cycle events for L. longipes lags behind that of L. nigropalpi by about two weeks. Although this difference might be merely a one time occurrence, it would still indicate that the two species have different sensitivities to those environmental factors controlling development and that this might be associated with a mechanism for temporal segregation of the species.

The adult life cycle of L. calcar is compressed into a shorter period that may well precede events in the life cycles of the other two species. It was observed to copulate before either of the other two species, but there is an insufficient number of sightings of L. calcar to lend much support to this.

Mortality factors

In mid-July the densities of all three species on the study site showed a marked decline. I am not certain that such a decline can be attributed mainly to mortality. Observations of predation are limited to three incidents, all involving spiders. In two cases I witnessed feeding by cursorial spiders (Salticidae on L. longipes and Gnaphosidae on L. nigropalpi) which took place during the late afternoon on tree

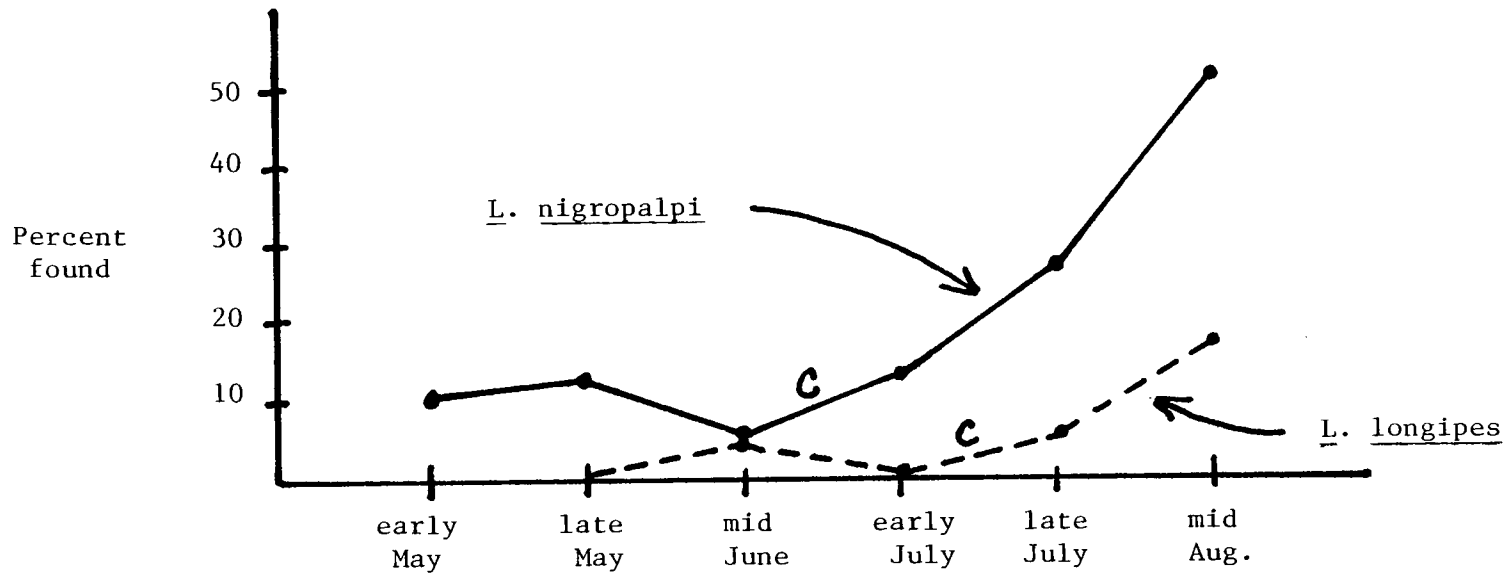


Fig. 2. Proportions of Leiobunum Sighted on the Litter between 0600 and 2100 Hours for each of the Six Samples

C Indicates the time at which copulation was first observed for the species.

trunks. A third harvestman was found on the abandoned web of a Theridiidae and was eaten beyond identification. Mites (Erythraeidae) were found in late June and early July attached to the femoral and metatarsal segments of the legs of all three species. In most cases the chelicerae of the mite had penetrated the cuticle. There were often several mites on a single leg and it was not uncommon to find harvestmen with ten or more of these attached. In a very few cases mites were found attached in the vicinity of the eye tubercle. Such heavy infestations have been observed elsewhere (Edgar, 1971) and may be a significant source of debilitation and/or mortality in early adult life.

A second explanation for the observed decrease in sightings is attributed to the reduced proportions of females in the populations. Sex ratios for L. nigropalpi and L. longipes are presented in Table 2 for samples made up primarily of adults. The pooled ratios do not fit a 1:1 ratio in either species (for L. nigropalpi, $G_H = 7.22$, $P < .01$; for L. longipes, $G_H = 27.54$, $P < .001$), nor is each a homogeneous set by a G-test of heterogeneity (for L. nigropalpi, $G_H = 6.46$, $P < .10$; for L. longipes, $G_H = 9.24$, $P < .01$). This scarcity of females, particularly in the last sample, may be related to egg-laying activities. Either females become cryptic for a period of time prior to or after oviposition, so that they were difficult to locate, or the stress associated with reproduction is a significant mortality factor. Edgar (1971) observed that L. calcar, at the end of its egg-laying period, dies shortly after laying its last few eggs.

Temporal Niche

To determine whether daily activity patterns of the species differ and the extent to which activity changes seasonally the number of

Table 2. Sex Ratios in Adult Populations of *L. longipes* and *L. nigropalpi*

	Species	
	L. longipes	*L. nigropalpi*
Samples	m:f	m:f
Early Summer Plot A	mostly immatures	61:62
Early Summer Plot B	79:64	48:40
Late Summer Plot A	53:27	65:38
Late Summer Plot B	89:33	37:19

individuals recorded as active during a subsample was taken as a fraction of all individuals found excluding those whose activity status could not be determined. This percent of activity per three hour time period is presented as a series of histograms (Fig. 3). Corresponding samples on the two plots were pooled because of missing data in one or more subsamples. Data for L. calcar is presented only for the early summer sampling because of the sparse number of sightings in the other samples. A three factor ANOVA (Samples X Time periods X Species; Table 3) was used to test for the significance of each possible source of variation in percent of activity including possible first order interactions (Time periods X Species, Samples X Time periods, and Samples X Species). The second order interaction (Samples X Time periods X Species) was required as an error term since the ANOVA is without replication. It was first necessary to transform data by the arcsin function since percent of individuals active within a population is not likely to be normally distributed. Leiobunum calcar was excluded from the analysis because of its low abundance in spring and late summer.

As can be seen from the histograms the differences in activity across time periods is the largest source of variation and can be interpreted to mean that both species are primarily nocturnal. A Duncan's Multiple Range test (Table 4) discloses that the means of activity by time period (pooled for species) fall into two sets, 2100 hours to 0600 hours and 0600 hours to 2100 hours. The added variation due to samples is accounted for by the difference in mean activity (pooled for species) between the late summer sample and the preceeding two samples (Duncan's Multiple Range test, see Table 5). This increase in percent activity for the two species is taken to be associated with

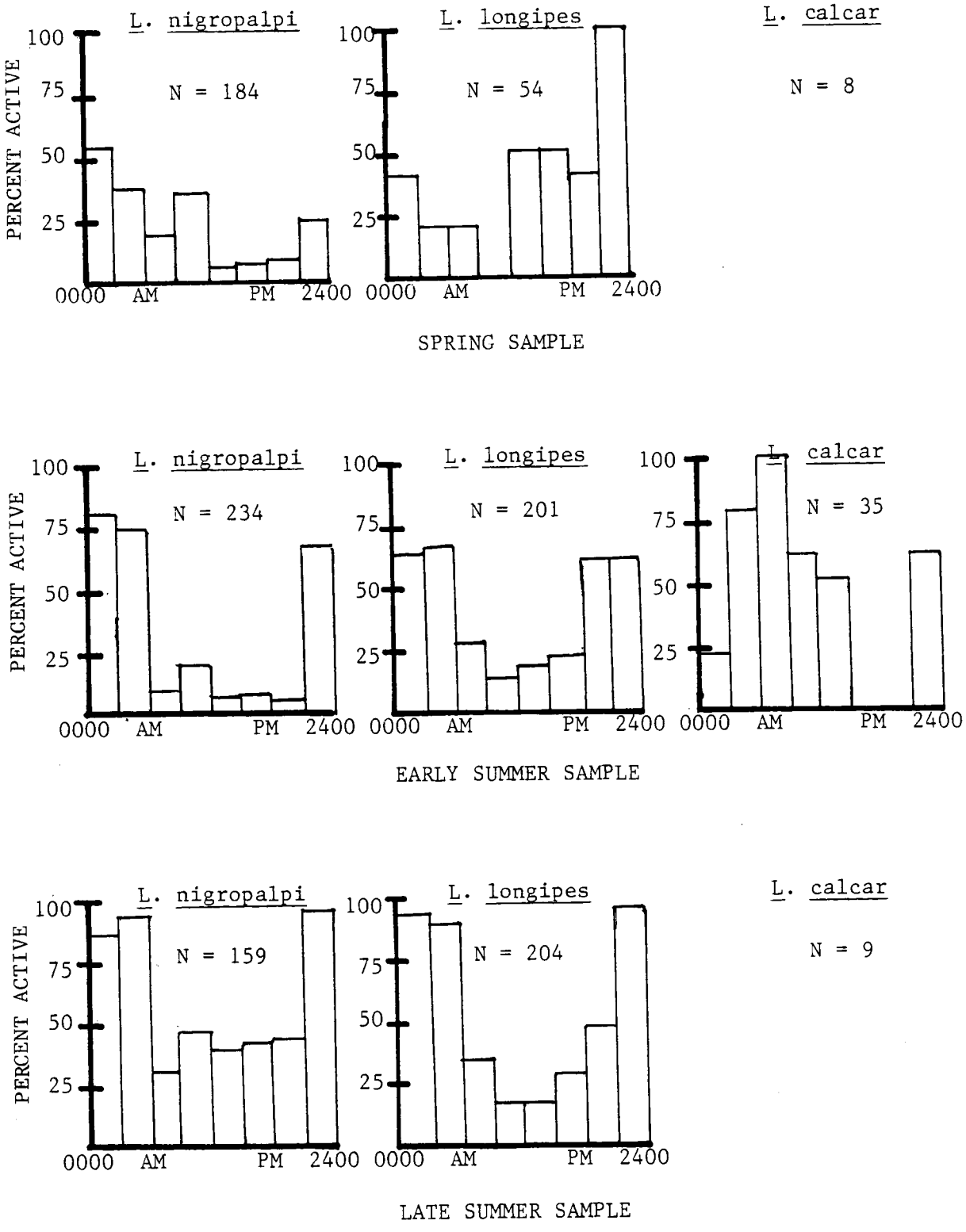


Fig. 3 Daily Activity Patterns of the Three Species of Leiobunum (plots A and B pooled for each sample)

Table 3. Three-Way ANOVA Results for Temporal Niche

Source of Variation	df	SS	MS	F
Samples	2	2244.92	1122.46	6.313*
Time periods	7	12693.44	1813.35	10.199***
Species	1	174.42	174.42	0.981^{ns}
Samples X Time periods	14	1946.89	139.06	0.782^{ns}
Samples X Species	2	349.55	174.78	0.983^{ns}
Time periods X Species	7	2070.25	295.75	1.663^{ns}
Samples X Time periods X Species (Error)	14	2489.14	177.80	

*Significant at $P < .001$.

***Significant at $P < .05$.

^{ns}Not significant.

Table 4. Means of Activity for Time Periods Compared by Duncan's Multiple Range Test (pooled data for L. nigropalpi and L. longipes)

Time period	Mean Activity (%)
0000-0300	74.1 c
0300-0600	74.7 c
0600-0900	24.7 d
0900-1200	17.3 d
1200-1500	19.9 d
1500-1800	25.4 d
1800-2100	30.2 d
2100-2400	84.1 c

Means with the same letter are not significantly different.

Table 5. Means of Activity for Samples Compared by Duncan's Multiple Range Test (pooled data for L. nigropalpi and L. longipes)

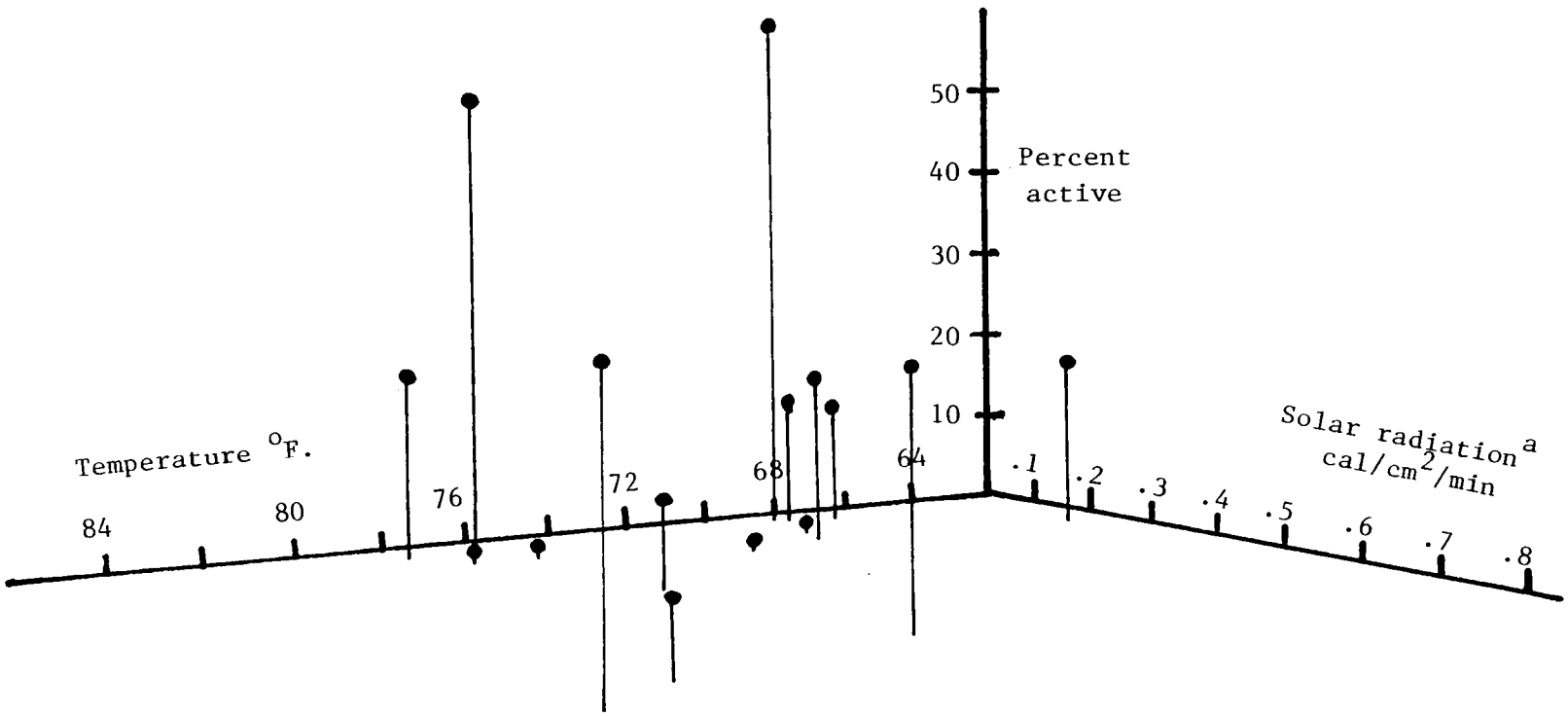
Sample	Mean Activity (%)
Spring	30.8 a
Early Summer	40.9 a
Late Summer	59.2 b

Means with the same letter are not significantly different.

mating and oviposition, although movement of males on the litter during the day makes an additional important contribution. The function of this behavior is not believed to be related to reproductive activities since males are not protective of females or their eggs once they have been oviposited. Of the ten attempts at copulation (for L. nigropalpi, N = 5; for L. longipes, N = 5) which were observed on the plots for the entire sampling period, none were recorded between 0505 and 1755 hours. No daylight feeding by males was ever observed.

The lack of a significant interaction effect, Time periods X Species, demonstrates that the daily activity rhythms of L. nigropalpi and L. longipes are not different. The strongest inference that can be made from the few observations for L. calcar is that there is a sufficient degree of temporal overlap to preclude partitioning of food resources or the minimizing of an interference type of competition based on the time dimension of the niche alone.

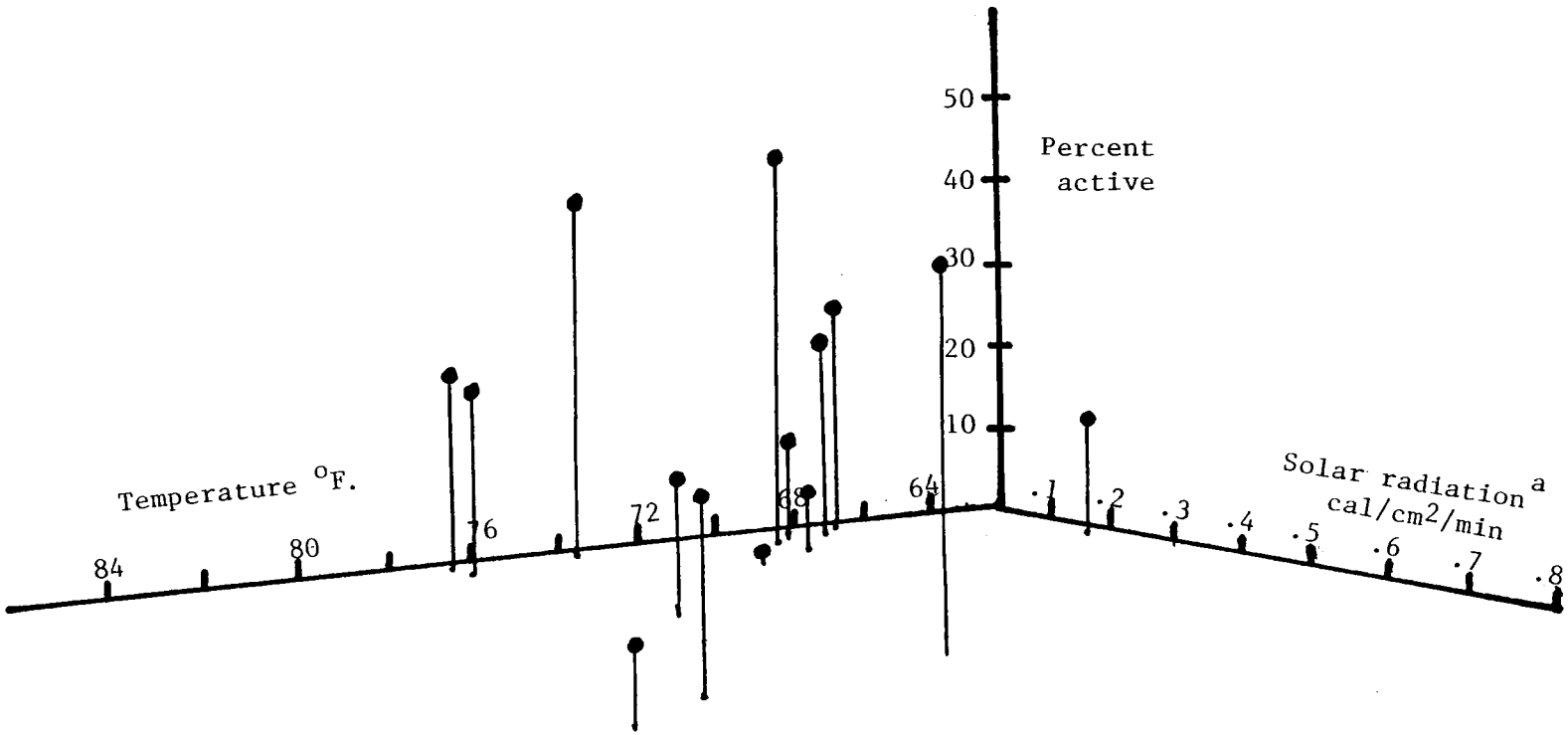
Figure 4 shows that harvestman activity during daylight hours is apparently unrelated to either temperature or conditions of light. A similar scatter of points was evident for nocturnal periods also. In the same way, relative humidity was not an indicator of activity. Figure 5 shows the proportion of all individuals sighted along transects which were active within a given humidity range. The mean relative humidity on the plots for the entire sampling period was 77.7% ($\pm$ 14.8%) during the day and 82.4% ($\pm$ 12.4%) at night. These are both higher than the preferences arrived at for L. longipes and L. calcar in a humidity gradient (Edgar, 1971) indicating that, in terms of vapor pressure of the ambient air, the environment on the foothill is generally favorable at all times of day and night for these species.



A. Leiobunum nigropalpi

Fig. 4. Percent of Individuals Sighted which were Active at Various Temperatures and Light Intensities

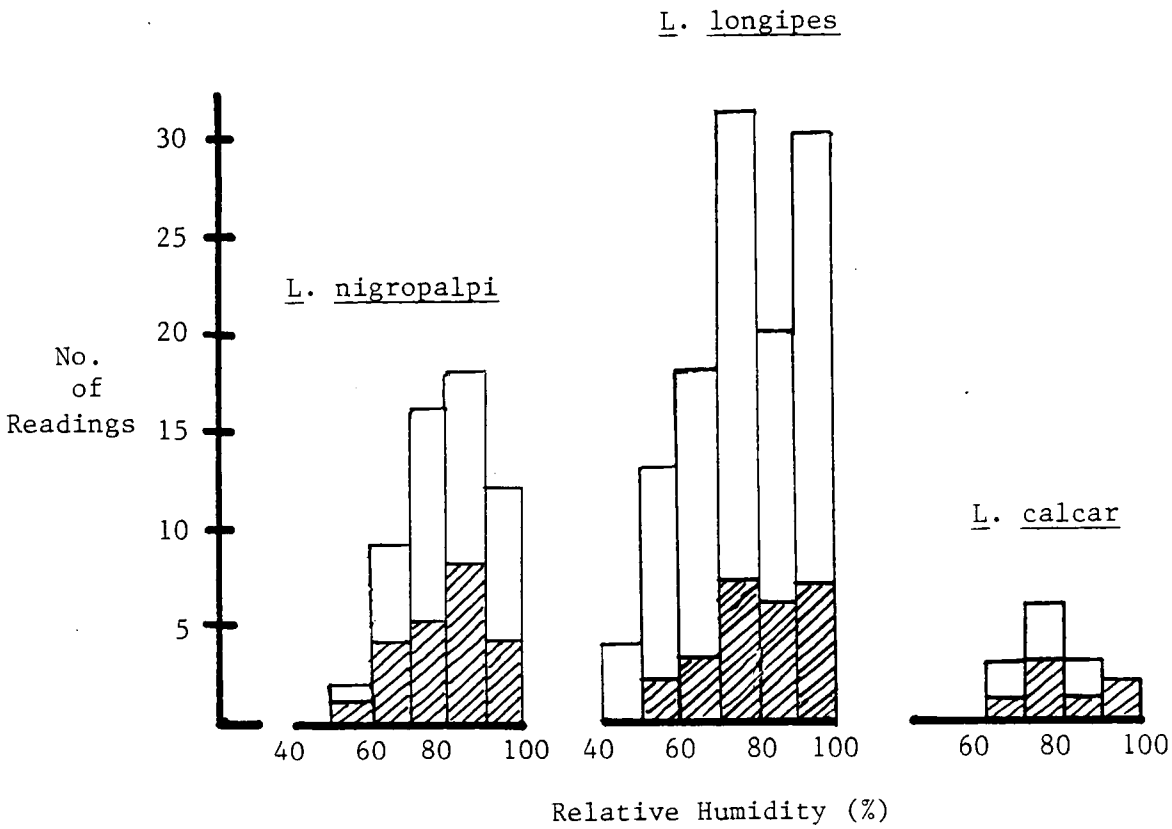
[a]Measured as the maximum amount received on the plot during a subsample.



B. Leiobunum longipes

Fig. 4. (continued)

[a]Measured as the maximum amount received on the plot during a subsample.



Shaded portions of the bars indicate the proportion of readings in which an individual was active.

Fig. 5. Percent of Individuals Active at Various Ranges of Relative Humidity

Spatial Niche

Resting perches

During the daylight hours (0600 to 1800) all three species can be found resting on tree trunks. Most often their bodies are tucked into some surface irregularity, e.g., fissures, cracked bark, knots or behind bark scales. This usually necessitates the protrusion of the legs well out from the surface of the trunk. It seems most likely, then, a means of concealing the body from the direct assault of a predator or from adverse physical conditions, i.e., direct sunlight or dry air, while maintaining a posture which enables a wide range of movement of the sensory apparati of the distal leg segments. Savory (1974) considers the arachnid capability of autotomy, or "the shedding of legs to allow the owner to escape from danger," to be a valuable form of self-defense in opilionids and in view of this the exposure of the legs beyond bark crevices does not incur additional risk of predation.

With regard to the importance of obtaining a crevice of optimal dimensions, the vertical distributions of L. nigropalpi and L. longipes on the trunks of various tree species is of interest (Table 6). Neither population can be said to occupy microhabitats on a given species of tree proportional to the occurrence of that species in the forest, if the proportions considered are calculated on the basis of relative trunk surface area[1] (for L. longipes, $\chi^2 = 12.075$, $P < .05$; for L.

---

[1]For the lower 2.25 m of trunk, it is assumed that the diameter was constant, so that the relative surface areas of several trees can be compared directly from their diameters at breast height.

Table 6. Frequency of Association of Adult Leiobunum with Tree Bark between 0600 and 2100 Hours

Height (cm)	Tree Species CHO	BLG	SCO	RMP	PINE	ALL
L. longipes (N = 188)						
< 200	1	1	2	1	3	8
151 - 200	7	5	0	5*	8	25
101 - 150	18*	10*	5	3	18*	56
51 - 100	9	18	7	1	24	60
0 - 50	3	5	4	1	6	17
Pct. of Total	20.2	20.7	10.1	5.9	31.4	100.0
L. nigropalpi (N = 154)						
< 200	7	5	3	4	4	23
151 - 200	8*	9	5	2	9	33
101 - 150	6	9*	4*	7*	7*	33
51 - 100	3	5	4	6	13	31
0 - 50	2	0	1	1	0	4
Pct. of Total	16.9	18.2	11.0	13.0	21.4	100.0
Tree Species Contribution[1]	18.8	15.2	13.0	8.3	37.0	

[1] As a percent of total bark surface.

*Indicates the class containing the mean height.

Key to Tree Species: CHO = Chestnut Oak BLG = Black Gum
SCO = Scarlet Oak RMP = Red Maple PINE = Pitch Pine

nigropalpi, $\chi^2 = 43.582$, $P < .001$). This inequitable distribution by plant species cannot be explained by a preference for trees with consistently deep crevices such as chestnut oak or pitch pine. Leiobunum nigropalpi is found more often than expected on red maple, which has smooth bark with very little cracking except at the base. Leiobunum longipes is found more often on black gum than predicted although this small tree has only shallow crevices at best which would leave most of the body of the harvestman exposed. Altogether 26.6% of L. longipes and 31.2% of L. nigropalpi perching on trunks occupied trees which offered few good sites for concealment. Both species tend to show a lack of preference for pitch pine, a tree with much surface irregularity. One explanation consistent with these data is that shade provided by the overhead canopy is as important as association with bark crevices. Red maple and black gum in this forest are small, understory trees with broad leafy crowns that offer protection from solar insolation. Their extensive leaf cover would additionally provide higher humidities than unprotected tree trunks. On the other hand, pitch pines growing on the foothill suffer from insect damage and have no needles on all but their uppermost branches. Because the distribution of perching heights by tree species is not explainable on the basis of availability of crevices alone, it would appear that harvestmen are able to exploit either of two strategies for locating a suitable diurnal refuge within the lower understory. It would also suggest that humidity and temperature considerations are more important to these species than the protection crevices might afford from predation.

Dispersion patterns

Harvestmen of two of the three Leiobunum species are not randomly dispersed on trees during the daylight hours. By a goodness-of-fit test to the Poisson distribution L. nigropalpi and L. longipes show significant aggregation (Table 7). That this clustering of individuals is not related to mating behavior is evident from the number of multiple occupancies of trees by single sexes versus mixed when compared with the expected frequencies from a binomial distribution assuming equal numbers of each sex. (The latter is true for the subsamples in question. See Table 2, p. 19.) For L. calcar there are too little data to reach a conclusion, but its density is so low on the transects that it is highly unlikely that it will show the aggregation characteristic of the other two species.

Vertical spatial niche

The vertical distribution of the three species for time of day and season is shown in Figure 6. The forest understory comprises three major strata to the harvestmen:

1. The litter, including fallen trees and branches.
2. Low foliage made up primarily of Galax aphylla, Vaccinium spp., shrubs and stump sprouts not exceeding 1.0 m in height above the forest floor.
3. Tree trunks and branches extending up to a height of 2.25 m.

Data from sample II is presented as a representative sample in Table 8 and histograms for the entire survey in Figure 6.

A four factor G-test of independence (Samples X Species X Habitats X Time periods) was done to determine if the use of the various

Table 7. Dispersion Pattern of *Leiobunum* on Trees between 0600 and 2100 Hours (selected samples)

	Frequency by Species		
	L. nigropalpi IIA	*L. longipes* IIB	*L. calcar* IIA&B
Number trees in the sample	434	437	871
Number trees unoccupied	375	356	864
Number trees occupied by:			
one individual	46	57	7
two individuals	8	16	0
three individuals	1	1	0
more than three individuals	1	1	0
Probability of random dispersion	<.005	<.001	-
(Goodness-of-fit to a Poisson Distribution)	$\chi^2 = 13.43$	$\chi^2 = 19.36$	
Percent of observed multiple occupancies which included mixed sexes.	46.2	54.5	-
Percent of multiple occupancies by mixed sexes expected from a binomial distribution (sexes 1:1)	60.6	57.4	-

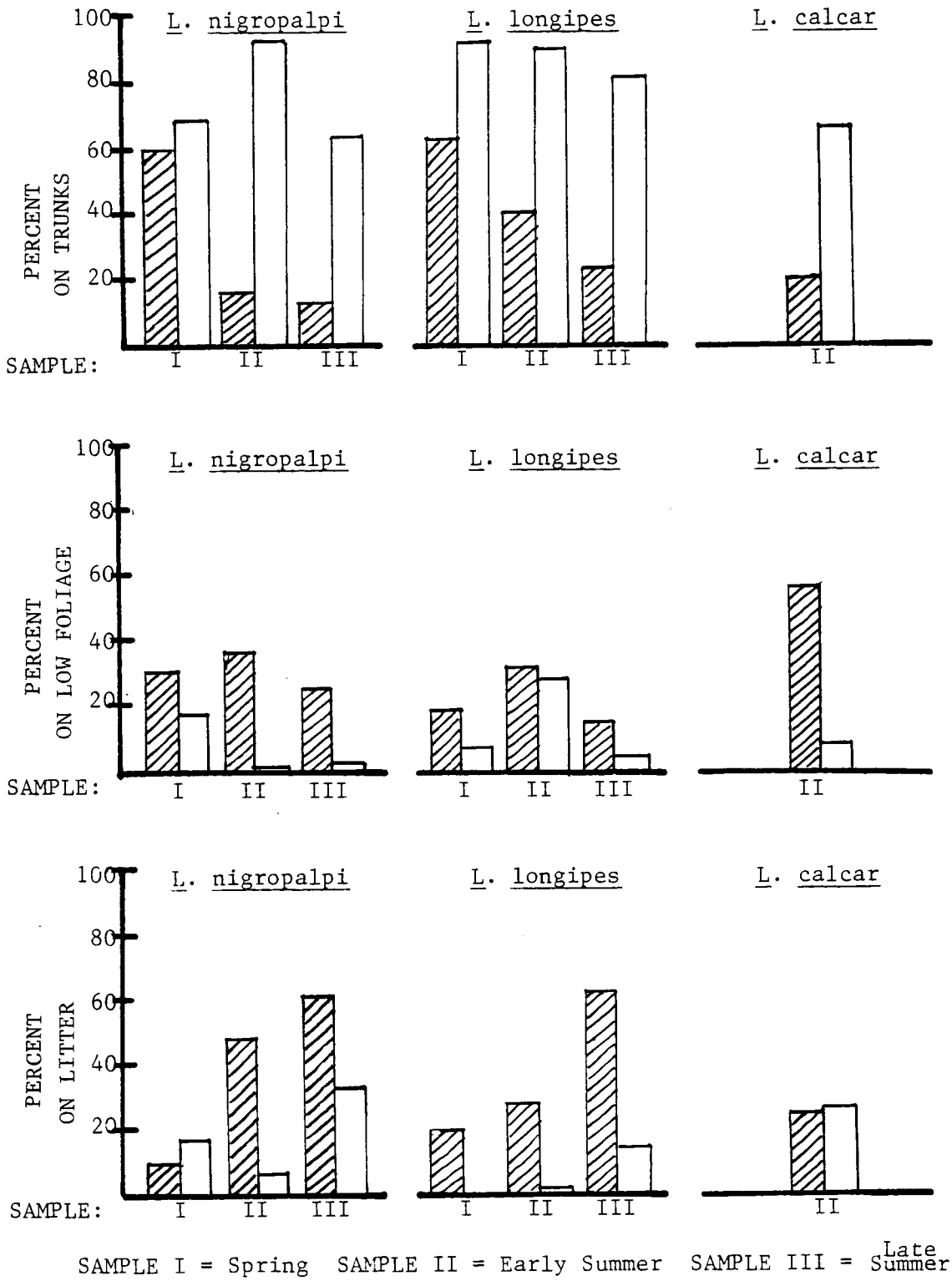


Fig. 6. Percent of each Species Found in Three Forest Strata by Night (Shaded Bars) and by Day (Unshaded Bars) for Time of Season Indicated

Table 8. Frequency Distribution of *Leiobunum* in Three Forest Strata by Time Period (early summer samples)

Time period	Species								
	L. nigropalpi			*L. longipes*			*L. calcar*		
	Low Foliage	Tree Trunks	Litter Surface	Low Foliage	Tree Trunks	Litter Surface	Low Foliage	Tree Trunks	Litter Surface
0000-0300	13 (43.3)[a]	4 (13.3)	13 (43.3)	10 (47.6)	6 (28.6)	5 (23.8)	4 (80.0)	1 (10.0)	0 (0.0)
0300-0600	9 (27.3)	6 (18.2)	18 (54.5)	3 (21.4)	5 (35.7)	6 (42.9)	5 (51.0)	3 (30.0)	2 (20.0)
0600-0900	1 (3.4)	27 (93.1)	1 (3.4)	4 (11.1)	32 (88.9)	0 (0.0)	0 (0.0)	0 (0.0)	3 (100.0)
0900-1200	0 (0.0)	26 (89.7)	3 (10.3)	0 (0.0)	25 (100.0)	0 (0.0)	0 (0.0)	5 (100.0)	0 (0.0)
1200-1500	1 (3.7)	23 (85.2)	3 (11.1)	1 (3.4)	28 (96.6)	0 (0.0)	0 (0.0)	1 (50.0)	1 (50.0)
1500-1800	0 (0.0)	25 (96.2)	1 (3.8)	3 (11.5)	22 (84.6)	1 (3.8)	1 (25.0)	3 (75.0)	0 (0.0)
1800-2100	1 (3.3)	29 (96.7)	0 (0.0)	4 (13.3)	25 (83.3)	1 (3.3)	0 (0.0)	1 (100.0)	0 (0.0)
2100-2400	11 (37.9)	5 (17.2)	13 (44.8)	4 (21.1)	11 (57.9)	4 (21.1)	2 (40.0)	0 (0.0)	3 (60.0)

[a]Figures within parentheses are percentages within time period for each species.

forest strata by L. nigropalpi differed from that of L. longipes. The overall result of the test, as indicated in Table 9, is that these four factors are not jointly independent. Both three-way tests involving species and habitat together (Samples X Species X Habitats and Species X Habitats X Time periods) also failed to demonstrate that harvestmen select habitat strata independent of the influence of all the variables considered. Partitioning of G for Species X Habitats X Time periods into nocturnal periods (T_n) and into diurnal periods (T_d) indicated that the differential use of the habitat by the species applies only during daylight hours. This is probably an artifact resulting from the difficulty of locating L. longipes on the litter during the spring, since it was immature and small at this time. A separate two-way G-test of Species X Habitats carried out using daytime sightings (from the two summer samples only) is significant ($G = 10.40$, $P < .01$) showing that adult L. nigropalpi and L. longipes are spatially separated during the day. This is accounted for primarily by the greater relative number of litter sightings for L. nigropalpi (33% vs. 14% for L. longipes) during the late summer samples.

If a similar G-test (Species X Habitats) is performed for nocturnal periods, G is again significant ($G = 31.56$, $P < .001$) indicating that vertical separation occurs among adults at night also, even though the original three-way test (Species X Habitats X Time periods (T_n)) indicated that individuals are located within the habitat independent of any of these factors. The abundance of both species on tree trunks at night during the spring sample produced a swamping effect, obscuring the actual differences that existed in the later samples between the species in their selection of habitat strata. These differences are

Table 9. Four-Way G Table for Vertical Habitat Separation of *L. longipes* and *L. nigropalpi*

Source of Variation	G	df
Samples X Species X Habitats X Time periods	334.34***	131
Samples X Species X Habitats	136.72***	12
Species X Habitats X Time periods	255.78***	37
T_n partition	15.34^{ns}	12
T_d partition	34.90*	22

***Significant at $P < .001$.

*Significant at $P < .05$.

^{ns}Not significant.

accounted for by the greater numbers of L. longipes moving about on tree trunks at night. This is somewhat reduced in late summer as L. longipes becomes more active on the litter. (Partitioning of Samples X Species X Habitats for nighttime observations, sample II vs. sample III, gives G = 31.56, P <.001.)

Data for L. calcar was analyzed in a three-way G-test of independence (Species X Habitats X Time periods (T_d vs. T_n)) for early summer sightings only, first against L. longipes and L. nigropalpi together and then separately against each. The multiway analysis is presented in Table 10. The three-way test shows a lack of joint independence in the distribution of the three species into habitats by time periods. The partitioning of Species X Habitats (L. calcar vs. L. longipes and and L. calcar vs. L. nigropalpi) is significant for both pairs of species. During the day L. calcar is found more often on the litter than either of the other two. Its numbers are consequently reduced on trunks. At night, L. calcar is less abundant on the litter than L. nigropalpi, less abundant on trunks than L. longipes and more abundant on the low foliage than either.

In terms of vertical separation beneath the understory the species differ primarily in two ways. The appearance of each species on the litter during the day is staggered seasonally. Leiobunum calcar is present first in greatest relative numbers, then L. nigropalpi, followed by L. longipes. This sequence is consistent with the first dates of copulation presented earlier, so that the movement of females on the litter during the day is probably associated with reproduction. Secondly, there is a separation according to stratum during the night at the time of year when the densities of all three species are

Table 10. Three-Way G Table for Vertical Habitat Separation of L. calcar, L. longipes and L. nigropalpi (early summer samples)

Source of Variation	G	df
Samples X Habitats X Time periods	262.10***	12
Species X Habitats	29.16***	4
Species X Habitats partitioning:		
L. calcar vs. L. longipes	18.32***	2
L. calcar vs. L. nigropalpi	7.90*	2

***Significant at $P < .001$.

*Significant at $P < .05$.

concurrently high (Fig. 1, p. 15). The largest proportion of L. nigropalpi is found on the litter, the largest proportion of L. longipes is found on tree trunks and in branches while the majority of L. calcar appears on the low foliage.

Patch utilization

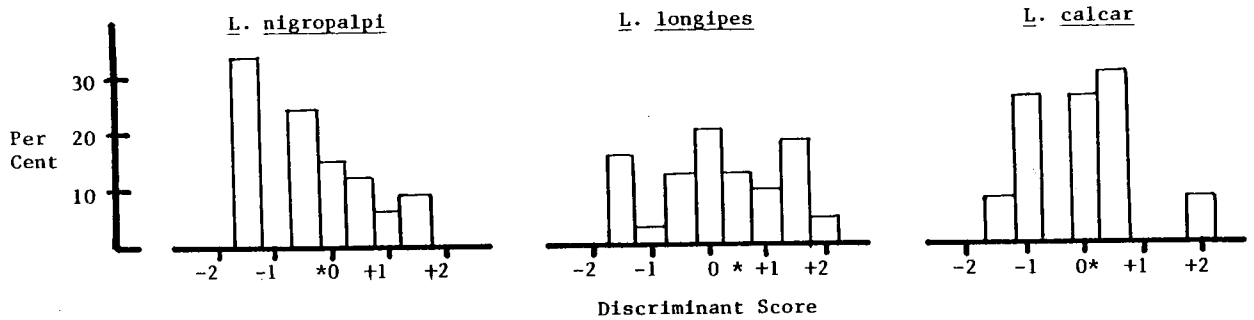
The use of forest patch types by the species was investigated by means of a discriminant function analysis which computes linear functions that best discriminate among the three species. The five discriminating variables used, the way in which each was measured and their relevance to the ecology of harvestmen appear in Table 11. Each of the observations used in the step-wise analysis is assigned a discriminant score on each function. These scores and the centroids for each species are plotted on the discriminant function axes. The standardized coefficients of the discriminant function which explains the greatest amount of variance (discriminant function I) are useful in showing the order of importance of the variables in distinguishing the species. The univariate statistics obtained in the analysis are expedient in comparing the species on each variable individually. Because harvestmen on the study site use different strata at different times of the day, I assumed that the habitat features used in the discriminant analyses would be viewed differently by the harvestmen during the day and at night. Therefore, two separate analyses were carried out: one for sightings between 0600 and 2100 hours (N = 691) and the other for sightings between 2100 and 0600 hours (N = 396).

Discriminant analysis of nocturnal observations. Only one discriminant function is reported (Fig. 7) since it explains 92% of

Table 11. Discriminating Variables Used in the Habitat Analysis

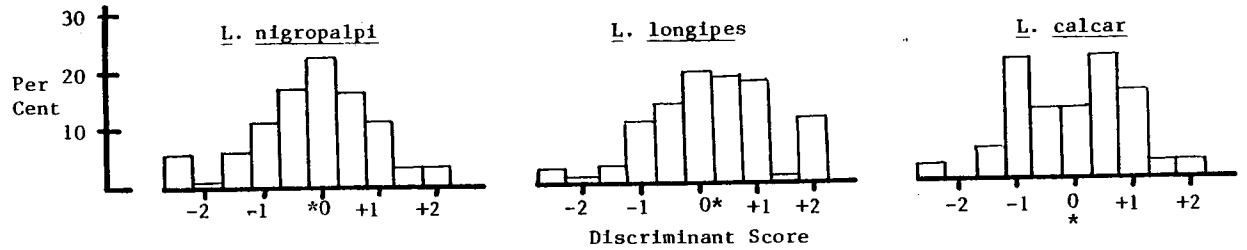
Variable	Measurement[1]	Relevance
Evergreenness of the Understory and Canopy (EVG)	Sum of the basal areas in sq. dm of all pine trees > 3.0 cm dbh.	Indicates a partially open canopy and exposure of harvestmen to sunlight.
Amount of Cover provided by the Understory (USC)	Sum of the basal areas of all trees > 1.5 cm dbh and < 8.5 cm dbh.	Indicates the amount of protection afforded from adverse physical factors.
Total Basal Area (BAC)	Sum of the basal areas of all trees > 2.0 cm dbh.	Serves as an index to the abundance of perching sites; provides relief from adverse physical factors.
Amount of Shrub Cover (SHC)	Scale assignment based on leaf cover (1 to 5, 1 = absent; 5 = very heavy).	Uncertain
Amount of Ground Cover (GRC)	Scale assignment as for shrub cover.	Increases spatial heterogeneity in the foraging habitat; offers suitable feeding sites; offers relief from adverse conditions for individuals active on the litter during the day.

[1]Measurements of all five variables were made in each 5 m interval of a transect in which a harvestman was sighted.



A. Observations between 2100 and 0600 hours.

D.F. I Y = 0.999GRC - 1.745USC - 1.983
(0.650) (0.587)



B. Observations between 0600 and 2100 hours.

D.F. I Y = 0.871GRC + 0.527SHC + 0.159EVG - 3.534
(0.604) (0.465) (0.423)

Standardized coefficients are indicated in parentheses below the unstandardized coefficients.

Fig. 7. Species Histograms of Discriminant Scores for Habitat Use

*Group centroid.

the total variation in habitat association among the species. The discriminant scores are therefore plotted as histograms. From the discriminant function in standardized form it can be seen that the variables ground cover and understory cover are useful in discriminating among the species. Table 12 shows that only the group centroids for L. nigropalpi and L. longipes are significantly different. From the positions of the centroids along the discriminant function axis (Fig. 7) it is clear that L. longipes forages in patches of the forest having more ground foliage and less basal area contributed by understory trees than does L. nigropalpi. Leiobunum calcar is intermediate to L. nigropalpi and L. longipes such that it is statistically indistinguishable. The univariate analysis provided in Table 13 confirms the result of the discriminant analysis. The only variables whose group means are significantly different at $P < .10$ are ground cover and understory cover. It is difficult to explain the ecological importance of the relative magnitudes of either of the two variables. Leiobunum longipes, for instance, forages more widely in a vertical dimension than the others, having the largest proportion of its nocturnal sightings made on trees. Less basal area within the understory vegetation would seem only to decrease its foraging area along this dimension. Harvestmen foraging more frequently in the litter (L. nigropalpi) and in the low foliage (L. calcar) would benefit more from a dense ground cover since this would provide a heterogeneous environment which offers numerous escape routes from cursorial spiders stalking the forest floor.

Discriminant analysis of diurnal observations. One discriminant function explains 97.5% of the total variance in habitat association and only it is reported (Fig. 7) along with the group histograms and

Table 12. F-test of Equality between Group Centroids for each Species Pair (nocturnal)

Species Pair	F[a]	P
L. nigropalpi and L. longipes	4.498	0.0117
L. nigropalpi and L. calcar	0.466	0.6281
L. longipes and L. calcar	1.122	0.3268

[a]Degrees of freedom = 2 and 392.

Table 13. Univariate Means and F-tests for Differences in Nocturnal Utilization of Forest Patches

Discriminating Variable	Group Means[1]			F	P
	nigropalpi	longipes	calcar		
Total Basal Area (BAC)	3.29	3.29	2.83	0.715	0.4897
Evergreenness (EVG)	1.22	1.42	1.33	0.475	0.6223
Ground Cover (GRC)	2.49[2]	2.67[2]	2.59[2]	3.256	0.0396
Shrub Cover (SHC)	1.73[2]	1.87[2]	1.69[2]	1.371	0.2552
Understory Cover (USC)	0.36	0.28	0.38	2.963	0.0528

[1]Means are given in sq. dm/10 m^2 unless otherwise indicated.

[2]Represents a mean of discrete scale values (see Table 11, p. 40).

group centroids. As in the nocturnal analysis only the centroids for L. nigropalpi and L. longipes are distinguishable (Table 14). Here, three variables are important in discriminating between these two species. Based on the magnitude of the standardized coefficients (Fig. 7), ground cover is most important while shrub cover and evergreenness of the canopy and understory are secondarily and equally important. Since the centroid for L. longipes lies to the right of that for L. nigropalpi its daytime patch preference can be interpreted as characterized by more ground cover, more shrub cover and more pine trees. The univariate analysis of Table 15 shows that all three variables considered individually are significant sources of variation among the species, with L. calcar intermediate to L. longipes and L. nigropalpi in its selection of forest patch types.

It is easier to explain diurnal habitat partitioning on the basis of the amount of evergreenness than on the basis of shrub cover or ground cover for individuals that are perched on trees between 1.0 and 2.0 m above the ground. Interpreted in this light L. longipes might be thought to be more tolerant of the generally drier conditions prevalent in canopy openings than the other species. Given that it is smaller in size than either L. nigropalpi or L. calcar while not distinctly different from either in body shape, this does not seem probable. Edgar (1971), as noted earlier, found higher water loss rates in L. longipes than in other Leiobunum species investigated. Perhaps, since individuals located within such patches are more often than not found perched on the bark of pines, this highly irregular substrate provides generally better protection from predators without a substantial sacrifice in microclimatic favorability.

Table 14. F-test of Equality between Group Centroids for each Species Pair (diurnal)

Species Pair	F[a]	P
L. nigropalpi and L. longipes	10.656	0.0001
L. nigropalpi and L. calcar	0.799	0.4945
L. longipes and L. calcar	0.466	0.7062

[a]Degrees of freedom = 2 and 687.

Table 15. Univariate Means and F-tests for Differences in Diurnal Utilization of Forest Patches

Discriminating Variable	Group Means[1]			F	P
	nigropalpi	longipes	calcar		
Total Basal Area (BAC)	4.13	4.05	3.53	0.526	0.5911
Evergreenness (EVG)	1.47	2.00	1.62	3.184	0.0420
Ground Cover (GRC)	2.51[2]	2.75[2]	2.74[2]	9.549	0.0001
Shrub Cover (SHC)	1.72[2]	2.02[2]	1.83[2]	9.278	0.0001
Understory Cover (USC)	0.28	0.27	0.25	0.243	0.7844

[1]Means are given in sq. dm/10 m^2 unless otherwise indicated.

[2]Represents a mean of dicrete scale values (see Table 11, p. 40).

Food Niche

Type and size of food

Ants comprise a substantial part of the diets of the Leiobunum species on the study site. Nine of twenty-eight items taken from feeding harvestmen were ants of various sizes (3 mm to 9 mm). Ants are eaten by all three species including immatures of L. nigropalpi. A complete list of food items is shown in Table 16. This list indicates that these harvestmen are consumers of a diversity of arthropod forms. Harvestmen also consume prey from a large size range from small ants to larger hymenopterans such as yellow-jackets. The mean length of item eaten by species and sex is presented in Table 17. (Leiobunum longipes males were never observed feeding.) Included is the mean body length of each group of harvestman measured from adult specimens in my collection. Some items, when taken, consisted only of appendages such as legs, wings, or antennae and are not included in the table. Where a partially eaten item included one or more of the major body divisions (i.e., abdomen, thorax or head) the length recorded for that item was the sum of lengths of such fragments. It seemed presumptious to estimate the overall size of an item based on the size of remnants because scavengers may partake of the remains of dead arthropods as well as whole items.

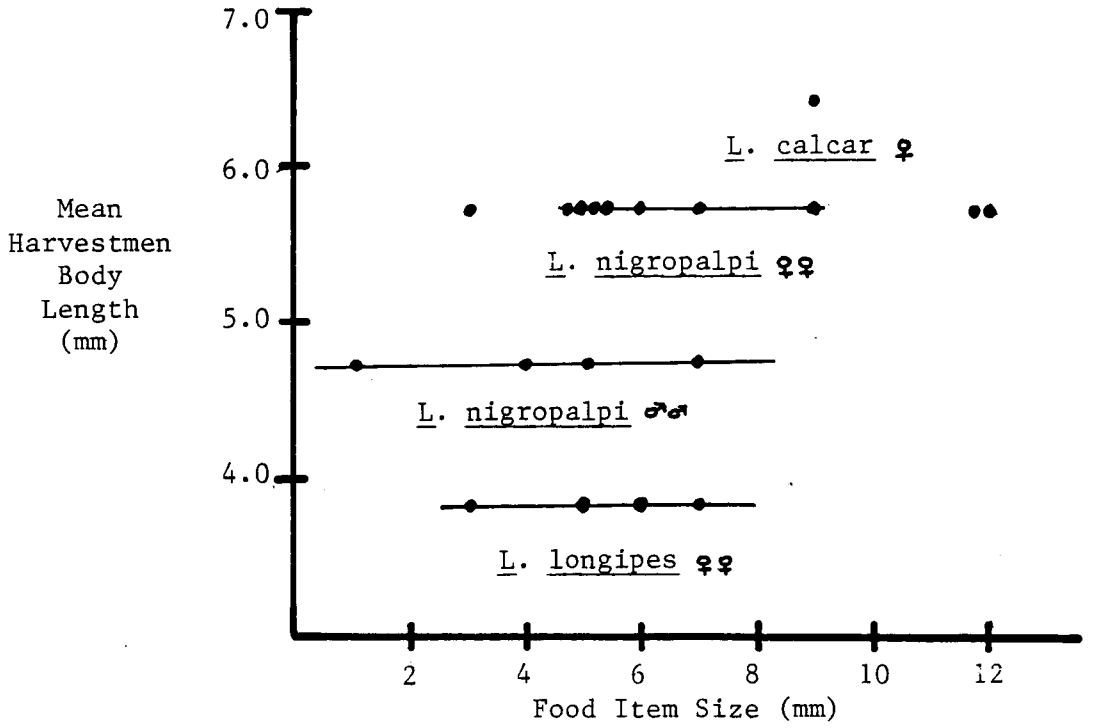
The means of food item lengths shown in the table for L. nigropalpi males, L. longipes females, and L. nigropalpi females are not significantly different (Student-Newman-Keuls test for comparison of means, LSR = 4.03, $P < .05$). As can be seen from a diagram of harvestman length vs. item size (Fig. 8) there is much more variation in the length of food items taken by a group than in the body length of the

Table 16. Items Eaten by Leiobunum on the Study Site

Food Item	Numbers Eaten
ants	9
spiders	3
other hymenopterans	3
dipterans	2
moths	1
crickets	1
roaches	1
beetle eggs	1
insect pupae	1
animal pellets	1
unidentifiable	4

Table 17. Mean Lengths and Standard Deviations of Items Eaten According to Species and Sex of Harvestmen

HARVESTMEN			FOOD ITEMS			
Species-Sex Groups	Mean Body Length (mm)	S.D.	No.	Largest (mm)	Mean Length (mm)	S.D.
L. nigropalpi immatures	4.0	-	2	4.0	3.0	1.4
L. nigropalpi males	4.7	0.15	4	7.0	4.3	2.5
L. longipes females	3.8	0.12	4	7.0	5.3	1.7
L. nigropalpi females	5.7	0.18	10	12.0	6.9	3.1
L. calcar females	6.4	-	1	(9.0)	-	-



Horizontal bars show the 95% confidence limits of the means.

Fig. 8. Overlap in Sizes of Food Items Taken by Various Species and Sexes of Leiobunum

group itself. Because of this variation and the small sample sizes involved, partitioning of food resources by size is not apparent in this study. In light of the feeding behavior of L. nigropalpi reported below there may be, in fact, some upper critical size of food items, different for different sized harvestmen, beyond which individuals cannot maneuver food to a safe feeding perch. The largest items taken within groups (Fig. 8 and Table 17), when compared to harvestmen proportions, support this notion, but more field observations of feeding, especially including L. longipes and L. calcar males, are necessary before a conclusion can be reached.

Location of feeding

Table 18 categorizes twenty-one feeding observations made between 2100 hours and 0600 hours according to one of three forest strata within which consumption of the item took place: litter, low foliage or tree trunks and branches. Perches within low foliage (either Galax aphylla or Vaccinium spp.) accounted for 57.1% of the observations, while only 27.5% of all harvestmen sighted between these hours were occupants of foliage in the field layer. This significant difference ($\chi^2 = 9.614$, $P < .01$) and the consideration that harvestmen appear to forage more often in the litter than on the other strata leads to the suspicion that this is a preferred perch for feeding.

To confirm this preference a feeding experiment was undertaken at night in the area of forest between the two survey plots. Freshly killed ants from 5 to 10 mm in length were placed on white plastic discs which had been randomly spread upon the leaf litter inside a 5.0 sq. m arena. Observations were made using the 6-volt headlamp. An attempt was made to follow each harvestmen that seized an ant from one

Table 18. Feeding Locations Occupied between 2100 Hours and 0600 Hours (all species)

Stratum	No. Feeding	Percent of Total
Litter	4	19.0
Low foliage	12	57.1
Tree trunks/branches	5	23.8

of the discs until it had consumed the item or abandoned it. The following observations (N = 12) were made and bear importance to the question of preferred feeding locations.

1. After taking the food harvestmen moved away from the disc a distance usually not more than 20 cm to a location within the leaf litter.
2. If disturbed by crawling or flying invertebrates (often a harvestman of the same species attempting to steal food) the individual would scurry away with its food and if encountering the stem or low-hanging leaf of a plant of the field layer would make its way upward into the top of the plant.
3. Harvestmen reaching such a perch were seldom molested from below even if the plant were Galax aphylla, which normally grows no higher than 10 cm above the forest floor. On several occasions I observed L. nigropalpi females to maintain a perch for over an hour and finish their meals completely undisturbed.

The experiment was successful in indicating that sites on low foliage are safer feeding locations than ones in the litter. This has an important consequence for the upper acceptable limit to food item size: the item must be of a size and weight that it can be easily maneuvered onto a feeding perch and be held in a suitable posture while feeding ensues. On one night during the feeding I found an L. nigropalpi female dragging a large dead spider (Latrodectus mactans, approximately 0.75 g in body weight) along the leaf litter. When attacked by two males of her species she tried unsuccessfully to move the spider onto

a Vaccinium leaf and subsequently was forced to share her catch with the intruding males.

Time of feeding

Twenty-three of 28 observations were made between 2100 hours and 0600 hours attesting to the primarily nocturnal activity of the species. On three occasions, females (one L. calcar, two L. nigropalpi) were observed with food during daylight hours. From a survey of feeding times of individual species there appears to be no temporal segregation with regard to foraging activity, at least for L. longipes and L. nigropalpi (Fig. 9). There is but one observation for L. calcar among the 28 and this coincides with its observed period of greatest activity, 0300 to 1200 hours.

Evidence for scavenging

The three most abundant Leiobunum species on this East Tennessee foothill study site appear to be strict scavengers based on three observations.

1. They are often found with food items of a size and kind (large spiders, flies and hymenopterans) which they are unlikely to have overcome had these been alive.
2. Whenever live prey were seized, they were quickly abandoned as soon as they began to struggle.
3. Harvestmen were not observed to pursue ants moving about beneath them although ants are a major diet item. Their response seems to be merely an attempt to avoid them.

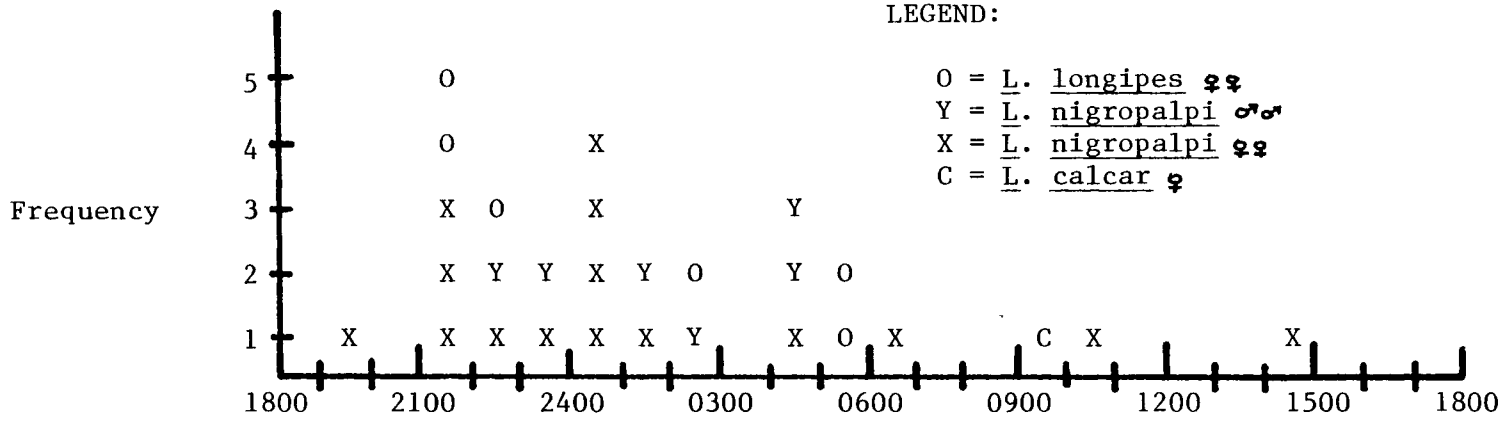


Fig. 9. Time of Day of Feeding by Species and Sex

CHAPTER V

DISCUSSION

The three most abundant species on the foothill, Leiobunum calcar, L. nigropalpi and L. longipes, have similar life cycles in that they overwinter as eggs, hatch after winter and mature to adulthood in late spring or early summer. However, L. calcar was observed to mate before the others and adults of this species were relatively abundant for a shorter period of the year than the other two species. Adults of L. nigropalpi appear about two weeks in advance of those of L. longipes and begin to mate about two to three weeks sooner. Given that demands for food resources during the reproductive phase are greater than at other times during the life cycle, this seasonal separation may serve as an opportunity for resource segregation.

The times of the year when the densities of all three species are highest (mid-June to mid-July) coincide and at this time there is a pronounced reduction in vertical habitat overlap during the time of day when the species are most active (2100 to 0600 hours). Leiobunum calcar can be found in midsummer primarily in the low foliage while L. nigropalpi forages to a greater degree upon the litter. Leiobunum longipes forages to a greater degree on tree trunks where it was observed on several occasions to feed on scraps of food in the unoccupied webs of spiders. This species is thought by Bishop (1949) to have the best developed visual acuity among Leiobunum. Given the relative scarcity of food remnants on tree trunks and in tree branches the possibility that it occasionally hunts for live food in this stratum by means of visual stimuli cannot be precluded. According to Edgar

(1971) it is adept at avoiding capture by spiralling around tree trunks, doing this in a haphazard fashion when disturbed. This would be adaptive for avoiding predators relying on vision. Leiobunum nigropalpi more often parachuted from its perch when approached by the observer.

Based on vegetational features of the habitat there is a somewhat patchy distribution of the species. At night, L. longipes is active beneath a more sparse understory and in slightly heavier ground cover than the other two species. During the day it can be found in patches of forest with a partly open canopy (resulting from occupation by pines) and where the ground and shrub cover is more dense.

Investigation of the functional niche of the species with regard to food type and size revealed little evidence for ecological separation in these ways. Ants are a major diet item for harvestmen on the foothill and all three species eat them. When grouped according to both species and sex, harvestmen are distinctly different in body length, a situation in which partitioning of food by size is considered likely. Instead, the groups exhibited extensive overlap in the sizes of items taken, although a small sample size may have been responsible for more variability than actually exists. There is, however, some indication that the ability to maneuver large items to safe feeding locations may be different among the groups and dependent on the size of the individual harvestmen.

Leiobunum nigropalpi and L. longipes are strongly nocturnal and do not partition resources on the basis of diel activity. Both species show overlap with L. calcar, though the latter appears to be more active during the early daylight hours. Because food resources for scavengers are continuously available throughout the day, one species

gains very little over another by searching for food at different times of day, particularly when the species do not engage in an interference type of competition (Schoener, 1974). Thus, by competition theory, temporal partitioning is unexpected for scavengers.

CHAPTER VI

CONCLUSION

The pattern of resource partitioning seen here is consistent with the pattern predicted by competition theory. Organisms which are able to process a wide variety of food items and sizes that are generally continuously available to them through the day should, according to optimal foraging strategies (MacArthur and Pianka, 1966) make use of habitat partitioning to avoid competition. This is provided that optimum patches within the habitat are continuously distributed or that a species is vagile enough to transgress the distance between optimum patches without a significant loss in search time. Harvestmen are highly vagile relative to the distance between strata in their vertical forest habitat. Leiobunum longipes, for instance, can rapidly descend trees, move across the litter and find another tree with little loss in searching time.

Although the observed pattern of partitioning would, then, indirectly implicate competition, there is no empirical evidence that the forest species of Leiobunum studied on the foothill routinely compete for resources; individuals of the different species were never seen engaged in conflict over food or space. There appears to be an abundance of good perches both for resting and for feeding. The availability of food was not assessed. Certainly Leiobunum must share their scavenging role with numerous species of ants and crickets active at night both on trees and on the forest floor. The frequent observations of L. nigropalpi males stealing food from females of their own species may indicate that, even if numerous dead arthropods may abound within

the litter, it may be difficult for the olfactory organs of harvestmen to detect them.

Before a conclusion can be reached regarding the importance of interspecific competitive effects in accounting for the ecological separation observed here, several other possibilities should be explored.

Could the differences among the species have been established and maintained for the purpose of reproductive isolation? The seasonal differences are hardly disparate enough to prevent hybridization, especially since copulations within L. longipes and L. nigropalpi continued up until the end of the sampling period (August 30). Given the vagility of these harvestmen and the fact that habitat overlap, though apparent in degree, is far from complete, it seems unlikely that spatial separation maintains sexual isolation. No interspecific sexual encounters were ever observed, supporting the idea that the species are already behaviorally isolated in this respect.

The extent to which predation limits competition by ensuring low densities should be investigated for these populations. Periods during which predator density is low might lead to changes in harvestmen density which encourage interspecific interactions. These may lead to further ecological divergence among the species or even the displacement of a species from the habitat.

Could habitat partitioning by these species result from optimal functioning for preferred resources? There is little specific preference for microclimatic conditions if temperature and relative humidity are considered important variables for harvestmen. There is also little reason to suspect that differential selective pressures exist for optimal use of the habitat in maintaining a constant availability of food.

These species scavenge widely for numerous kinds of food items whose distribution is not believed to be spatially variable. The possibility remains, however, that the species differ in their abilities to avoid detection or capture by predators while foraging and feeding. This is supported by the observed differences in escape behavior employed by L. longipes and L. nigropalpi. The different structural features of the strata in which these two species forage would imply the use of different strategies for avoiding predators. According to optimal functioning theory, habitat selection should be most accentuated at the life stage where demand for a resource is strongest (Kronk, 1980). In this regard, it is not known at what times predation acts most intensely on harvestmen.

If predation is the overriding selective force for these harvestmen, then relaxed predation over an extended period should 1) obscure the habitat differences among the species if optimal functioning explains these differences or 2) lead to further niche separation, perhaps along a second dimension, or to exclusion, if competition is important.

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VITA

James Cockerill was born in Baltimore, Maryland on March 27, 1947. He was graduated from Woodlawn High School in the Baltimore County school system in June, 1965. Shortly thereafter he entered the United States Navy to begin a four year tour of duty during the Vietnam War. After discharge he was employed in the Traffic departments of two major freight companies prior to entering the University of Houston, Texas where he received the Bachelor of Science degree in Biology in May, 1978. In September, 1979 Jim entered the Graduate Program in Ecology at the University of Tennessee, Knoxville. There, under the direction of Dr. Susan Riechert, he pursued the research reported in this thesis, earning for himself the Master of Science degree in Ecology.

Jim plans to continue the study of harvestmen both as a hobby and an independent research effort. He believes that, despite trends in government policies against funding economically unproductive curricula, today's generation of natural historians should continue in what is not only an American heritage but has also been a cultural mission throughout the history of Western civilization - the advancement of knowledge about the animal world merely for the enjoyment and edification of man.