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BEHAVIORAL ASPECTS
OF SOUTHWEST MICHIGAN OPILIONIDS

by

Wolfgang C. Schroeter

A Thesis
Submitted to the
Faculty of The Graduate College
in partial fulfillment
of the
Degree of Master of Arts

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Wolfgang C. Schroeter

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INTRODUCTION

Opilionids (Arachnida: Opiliones) are arachnids that have such descriptive common names as harvestmen or daddy longlegs. In the summer and early autumn opilionids become a conspicuous component of the invertebrate fauna; however, as common as these animals are, little attention has been paid to their behavior. Most published research on opilionids deals with their taxonomy.

The intraspecific interactions of opilionids is a significant area of ethology that needs careful examination. Intraspecific interactions fall into three categories: reproductive, aggressive, and cooperative behaviors. A knowledge of the reproductive behavior of opilionids is essential for a complete picture of the evolution of behavior among arachnids. Aggression is so poorly understood, that any study that includes a description of aggressive behavior is an important contribution in this area. Cooperative behavior is of interest because of its intimate relationship to social organization.

This study is an effort to observe and describe the behavior of several species of opilionids found in a mesic forest habitat. The location of the study is a wooded area near the south side of Wolf Lake in Van Buren County, Michigan. Opilionids encountered and included in the study are Leiobunum longipes, L. politum, L. vittatum, and Odiellus pictus.

LITERATURE SURVEY

The behavior of an organism is closely related to its physiology. The late Kaestner has written extensively on opilionids in various zoology books. These works contain some of the very few descriptions of opilionid physiology. Kaestner's recent work (Kaestner, 1965) has been translated into English.

The opilionids have two simple eyes located in an elevated tubercle which is found in the center of the anterior portion of the body. It has been stated that it is unlikely that opilionids are able to distinguish more than the difference between light and dark (Savory, 1962; Kaestner, 1965). However, it appears that there are differences in the structure of the eye between species and these differences may be related to the habitats of these individual species (Curtis, 1970). This would indicate that it is possible that vision may be an important and better developed sense in certain species.

Savory stated: "The study of harvestmen is the study of legs." (Savory, 1938, 1962). This is an accurate description since in most common species the legs are the most conspicuous part of the anatomy. This is even more descriptive when the importance of the legs and other appendages is assessed. Opilionids move through the world with their long second pair of legs tapping out the area in front of them (Savory, 1938, 1962). The legs are covered with many tactile hairs and also with a complex set of proprioceptors. These aid in keeping the animal informed on its orientation (Edgar, 1963). The second pair of legs evidently has a chemoreceptive function. When these legs are removed

the animal has an increased difficulty in locating food (Savory, 1938, 1962). However, no chemoreceptive system in the second leg has been identified neurophysiologically (Edgar, 1963).

Any experience of trying to capture opilionids will demonstrate the fragile nature of the bond between the body and the legs. Through the process of autotomy the opilionids are easily able to cast off legs that have been captured by a predator or entrapped. These cast off legs will continue to twitch for some time and, consequently, offer a diversion while the rest of the animal escapes. Unlike many spiders, opilionids are unable to regenerate lost legs. Although all opilionids have eight legs when they hatch, only a minority will have a full complement at the end of the breeding season (Savory, 1938, 1962).

In addition to the legs, opilionids also possess two sets of anterior appendages: the pedipalps and the chelicerae. These appendages are mainly associated with feeding. The chelicerae and pedipalps appear to be sites of tactile sensors and chemoreceptors. They may also be sites for receptors responding to humidity levels (Wyllie, 1963).

Most descriptions of the reproductive behavior of opilionids claim that there is no courtship prior to copulation (Savory, 1938, 1962; Edgar, 1960, 1971; Cloudsley-Thompson, 1958). Males are able to detect females, possibly through pheromone secretions (Edgar, 1971). The male will advance toward the female. The female, which is usually larger than the male, may reject the advances of the male, or she may allow copulation to take place. Mating is achieved by the partners standing, facing each other. The male grasps the female with his pedipalps. There is a special structure on the pedipalp of the male Leiobunum

calcar that allows the male to grasp the female more securely during mating (Bishop, 1949). The penis of the male may be guided to the genital opening of the female by the chelicerae of the female.

In the European trogulid genus Ischyropsalis, which prey on snails, there are fields of hairs on the chelicerae of the males. These short hairs are the site of secretions (pheromones) that are presented to the female for acceptance. This constitutes one of the first descriptions of courtship displays in opilionids. These fields of hairs are also significant in the taxonomy of this genus (Martens, 1967, 1969a, 1969b).

Pheromones are believed to be an important factor in the behavior of opilionids. Pheromones appear to be necessary for the identification of conspecifics and members of the opposite sex (Edgar, 1971). However, the cheliceral secretions of the European trogulids are the only presumed pheromone that has been described (Martens, 1967). Opilionids have secretory glands between the coxae of the first and second legs (Savory, 1938, 1962; Kaestner, 1965). The coxal gland secretions are believed to have a defensive function and produce the characteristic fetid smell in recently captured opilionids (Savory, 1962). The secretions also appear to have a tranquilizing effect on the opilionids themselves. Opilionids that are captured and confined to a jar scramble around the sides of the jar at first, but then become sluggish and eventually motionless. This torpid state is quickly relieved when the opilionids are released from the jar and given a chance to revive in fresh air (Savory, 1938, 1962). The opilionid Vonones sayi is able to release a quinonoid secretion from its coxal glands and apply these

secretions directly onto predators with its legs (Eisner et al., 1971).

Aggressive behavior has been observed among male opilionids. A male will grasp an opponent's leg with the chelicerae and pedipalps. While rotating the body the male will shake the leg of the opponent violently. This, apparently, is an attempt to injure or possibly remove the opponent's leg (Edgar, 1971). Bloodless encounters observed among male opilionids in Great Britain possibly result from erroneous mating attempts caused by mistakes in recognizing the sex of a prospective partner (Cloudsley-Thompson, 1958).

The body of most opilionids is not heavily sclerotized and it is susceptible to dessication. Consequently, opilionids are confined to areas of high relative humidity. Many species have limited periods of activity which may include the night time or early morning. These activity periods are dependent on the environmental conditions found in the habitat (Fowler and Goodnight, 1966). Particular species are limited to particular habitats (Todd, 1949). Dessication tolerance varies among species and this gives an excellent indication of where certain species may be found (Edgar, 1960, 1971).

The most common genus of opilionids in the north central United States is Leiobunum. There have been a few descriptions of Leiobunum behavior. Newman (1917) was the first to report Leiobunum aggregations and a synchronous "bobbing" behavior within the aggregation. Aggregations of Leiobunum longipes have been reported that are almost entirely male. These aggregations have also been observed demonstrating synchronous behavior, in this case called "pumping" or "dancing" (C. J. Goodnight, personal communications; Edgar, 1960, 1971). In

Mexico Leiobunum cactorum aggregations containing many thousand individuals have been reported in the forks of candelabra cacti. These aggregations are believed to be initiated by pheromone secretions. This is a cooperative behavior that minimizes water loss within the aggregation under arid conditions (Wagner, 1954).

METHODS AND MATERIALS

Observations of opilionid behavior were made in the field and in the laboratory. The field observations were made at the Wolf Lake location. The laboratory observations were made at Western Michigan University on specimens collected at the Wolf Lake site.

The study area at Wolf Lake is a mesic wooded area west of the public access road extending to the lake shore. The canopy layer of the forest is mostly beech with maple and oak. In the forest (shown in Figure 1) ground vegetation is sparse. Soft bodied dipteran insects were numerous at all times that opilionids were found.

Field observations were made 12 times at either dusk or dawn during August, 1975. At first a flashlight was used to aid in observations; but this seemed to disturb the opilionids. Edgar (1971) had found a kerosene lantern to be adequate, so subsequent observations were made by this light and proved more satisfactory.

The laboratory observations were done at facilities at Western Michigan University during the summers of 1975 and 1976. Study specimens were collected at Wolf Lake chiefly by sweeping shrubs and trees with a sweep net. The sweep net is the most effective method of collecting opilionids, because there are more opilionids present that may be seen.

Identifications of specimens were made either by C. J. Goodnight or from keys written by Davis (1934) and Edgar (1966).

The specimens were kept in two 30 X 12 X 12 inch terraria with ventilated plastic film covers. The floors of the terraria were covered



Figure 1. Study area at Wolf Lake

with sand and moss, moisture was maintained by regularly spraying with distilled water. The specimens were fed a mixture of bananas, sugar, corn starch, gelatin, and yeast. This was eaten readily by the opilionids. Insects that were captured in the sweep net were occasionally given as supplement to the regular feed. A drinking dish was filled with distilled water at all times.

The laboratory observations were of two types: qualitative and quantitative observations. The qualitative observations were done by placing opilionids randomly in a terrarium and noting their behavior. Eight conspecifics were placed in a terrarium in the order of their capture. Consequently, conspecifics of both sexes were observed together and the sex ratio in the terrarium was dependent on the frequency of the sexes encountered in the field.

Feeding preferences were examined by offering the opilionids a choice of food materials. The first group of three choices consisted of sugar in water, corn starch in water, and unflavored gelatin in water. The opilionids were also offered a choice between soft bodied dipterans (e.g. mosquitoes, midges and crane flies), harder bodied dipterans (e.g. house flies), and woolly caterpillars. The insects were freshly captured and killed by freezing. The responses of the opilionids were noted.

Quantitative behavior was observed by placing an individual animal among an established group of eight conspecifics. The group of eight animals were all of the same sex while the introduced animals were alternately males and females. Three species were examined: Leiobunum longipes, L. vittatum, and L. politum. Six encounters for each sex

were observed for a total of 72 observations. Behavior of the introduced individuals was observed and recorded manually on a six-channel polygraph produced by Ralph Gerbrands Co. Observations were made until the introduced individual became dormant.

Each of the six channels on the polygraph was activated by a switch on a key board. Each of the switches represented a behavior type, the proper switch would be turned on by the observer as long as the particular behavior lasted. If the observed animal was inactive no switch would be turned on.

Switch one represented walking or climbing.

Switch two represented grooming. Notes were made describing which appendages were being groomed.

Switch three represented contact. This switch was turned on during the time an individual was in contact with another animal.

Switch four represented displaying (pumping behavior).

Switch five represented attempts at mating.

Switch six represented agonistic behavior.

The collected data formed linear records of behavior. The different cases were compared to each other.

Fernald (1973) showed that orientation analysis could be used to infer behavioral states in animals. Therefore, orientation studies are a useful tool in ethological research.

To observe orientation patterns, eight opilionids, all conspecifics of the same sex, were placed in a terrarium. The floor of the terrarium was sectioned by a coordinate grid. The 30 inch terrarium length was divided into ten sections; the 12 inch width was divided into four.

Consequently, the floor had a coordinate system containing 40 three by three inches squares. The columns (ordinate) were numbered from one to ten, and the rows (abscissa) were lettered A, B, C, and D. Each animal was assigned to the square that contained its body. The animals' positions were recorded every 15 minutes for a two hour observation period. Observation periods were either from 8:00 to 10:00 A.M. or from 8:00 to 10:00 P.M.

The data collected were analyzed for distribution preferences of the animals. A modification of the nearest neighbor analysis (Clark and Evans, 1954) was used to examine individual distances. The number of animals observed n varied since animals would climb on the walls of the terrarium.

The expected $\bar{r}_x = \sqrt{\left(\frac{12}{n}\right)^2 + \left(\frac{4}{n}\right)^2}$

The observed $\bar{r}_o = \frac{\sum_{i=1}^n \sqrt{(x_1 - x_2)^2 + (y_1 - y_2)^2}}{n}$

x_1, y_1 are the coordinates of the observed animal.

x_2, y_2 are the coordinates of its nearest neighbor.

$R = \frac{\bar{r}_o}{\bar{r}_x}$ R of approximately 1 represents a random distribution.

R greater than 1 represents dispersion.

R less than 1 represents clumping.

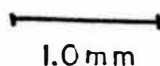
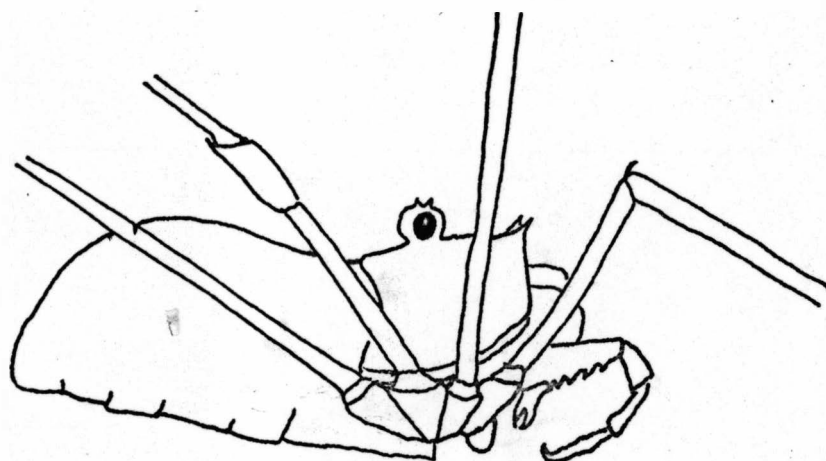
RESULTS

The most common species of opilionid found in the forest was Leiobunum longipes which is most numerous during midsummer. Leiobunum vittatum survived longer than the other species, consequently, it became the dominant species in the late summer. Leiobunum politum was quite common during the summer of 1976, but it was not seen in 1975. Leiobunum nigripes was once found in the forest during the midsummer, but it was usually associated with a neighboring field. Odiellus pictus was found rather infrequently from midsummer to early autumn.

L. vittatum was the first species to appear in the adult stage in the forest. By the beginning of July some L. longipes were found in the adult stage, and by late July L. longipes had become the dominant species in the forest. At the same time L. politum became very numerous closer to the lake where the ground cover was heavier. The species included in the study are described and illustrated in Figures 2 through 8.

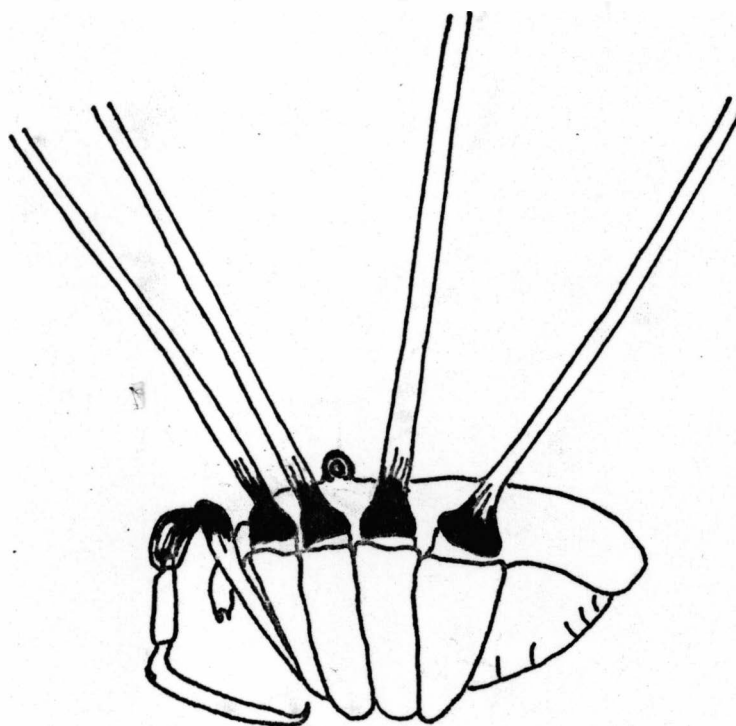
The study area had three distinct habitats: the forest edge, the forest, and the forested lake shore. The forest with its sparse ground cover was used by L. longipes and O. pictus. L. longipes was usually found within 50 m of the forest edge. Inside this area males were more frequently encountered than females. Beyond 50 m from the edge L. longipes was found to be rather scarce. The individuals that were observed in this area were always females.

In the forest edge which has rather dense shrub-sized vegetation all three species of Leiobunum were found. In this area L. vittatum



ODIELLUS PICTUS MALE

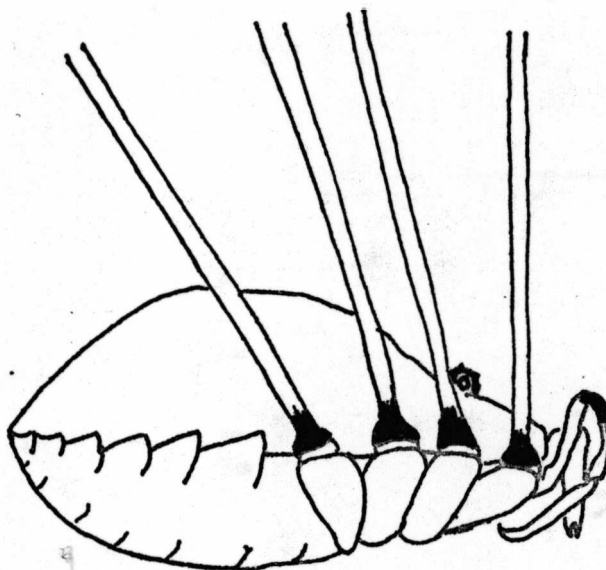
Figure 2. Odiellus pictus male 5.6 mm long; legs I-IV 13, 27, 13.5, 19.5 mm long. The genus is recognized by long spiny palpi and a trident of spines at the carapace edge in front of eye tubercle. (Edgar, 1966)



1.0 mm

LEIORBUNUM LONGIPES MALE

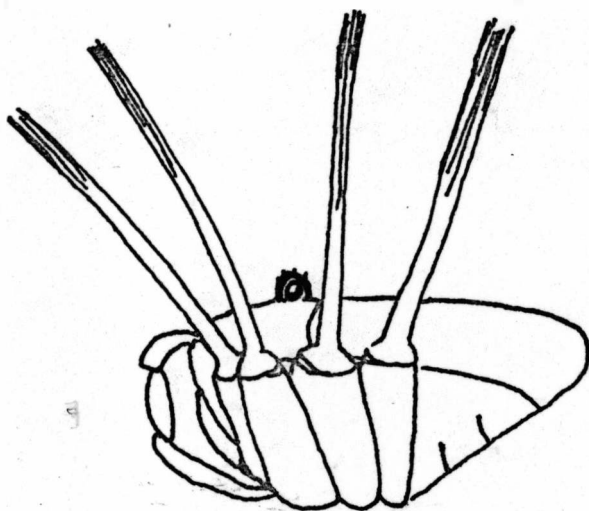
Figure 3. Leiorbunum longipes male 4 mm long; legs I-IV 43, 78, 43, 58 mm long. Dorsum has no distinct central figure. The distal part of tibia II has a white band. (Edgar, 1966)



1.0 mm

LEIOBUNUM LONGIPES FEMALE

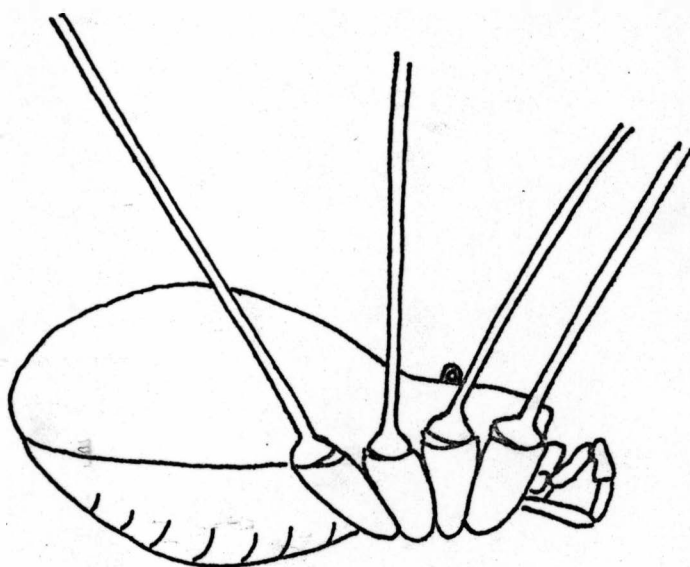
Figure 4. Leobunum longipes female 6 mm long; legs I-IV 37, 70, 37, 51 mm long. Dorsum has central figure. The distal portion of tibia II has a white band. (Edgar, 1966)



1.0 mm

LEIOROBUNUM POLITUM MALE

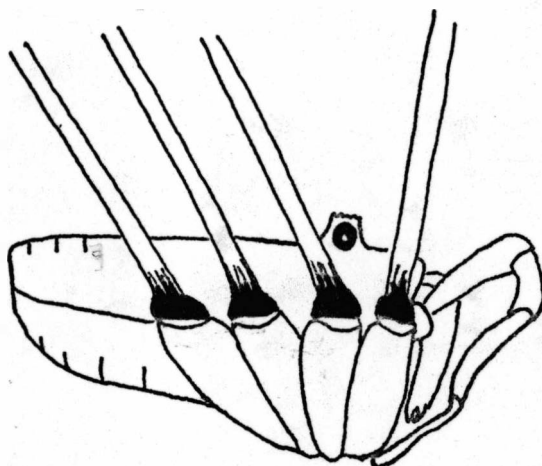
Figure 5. Leiorobunum politum male 4.5 mm long; legs I-IV 21, 44, 24, 35 mm long. Dorsum golden yellow, legs dark brown or black. (Edgar, 1966)



1.0 mm

LEIORHYNCHUS POLITUM FEMALE

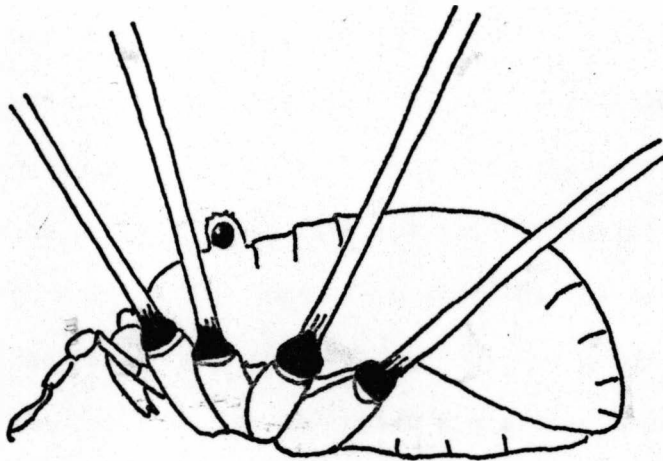
Figure 6. Leiorhynchus politum female 5.5 mm long; legs I-IV 20, 38, 21, 30 mm long. Dorsum usually has distinct central figure. Legs frequently have lighter bands at distal portion of tibia. (Edgar, 1966)



1.0 mm

LEIOBUNUM VITTATUM MALE

Figure 7. Leiobunum vittatum male 5-7 mm long; legs I-IV 31, 57, 31, 43 mm long. The leg length is extremely variable. Distinct central figure; coxae and trochanter contrasting (palpi of male longer than female's). (Edgar, 1966)



—
1.0 mm

LEIORHYNCHUS VITTATUS FEMALE

Figure 8. Leiorhynchus vittatus female 7-9 mm long; legs I-IV 34, 65, 34, 48 mm long. Dorsum has distinct central figure, coxae and trochanter contrasting. (Edgar, 1966)

was the most common in the area where the forest borders on the lake the ground cover becomes very dense. The three species of Leiobunum were all present in the vegetation. In this area the dominant species appeared to be L. politum.

L. vittatum was common in neighboring grassy areas and open fields while L. longipes and L. politum were limited to the study area. O. pictus was found only in the forest area. This species is cryptically colored and it is able to press its body into irregularities on the tree trunk, making it nearly impossible to find. The best time to collect this species was found to be during, or just after, a rain storm. At this time the trunks of the wet trees are glossy and the body of O. pictus, dull.

Behavioral observations were attempted on O. pictus; however, this species will remain quiescent for 24 hours at a time. Their lack of activity made them impractical for this study. O. pictus is apparently able to survive well into the autumn, and was the longest lived of the species in the study area.

L. longipes was the most active of the species. Daily movements began around sunset when the males moved from the foliage of the larger trees to the trunks. They were rarely found on the trunks of beech trees which are very smooth. The females remained in the foliage at this time. Consequently, for a brief time the sexes were separated. The females moved down the trunk after dark; at this time mating was frequently observed on the trunks. During the night both males and females could be found on the ground or on the tree trunks. At dawn the females moved back into the foliage. While the males remained on the tree trunks until midmorning.

Male L. longipes were frequently observed in groups of several individuals. There have been reports of L. longipes aggregations containing over a hundred individuals (Edgar, 1971). However, aggregations of that size were not seen during the study.

Pumping is a rhythmic movement of the body, perpendicular to the substrate while the legs remain secured to the substrate. Pumping was frequently observed among male L. longipes and L. politum. It occurred when these animals encountered a conspecific. Pumping also occurred sometimes when a male L. longipes was disturbed by the presence of the observer.

In the study area L. politum and L. vittatum inhabited areas where the foliage was quite dense. Consequently, it was impractical to study these species in the field.

In the laboratory all three species of Leiobunum demonstrated identical feeding preferences. They fed on soft bodied dipterans first. The harder bodied dipterans were also eaten. However, the woolly caterpillars were never even tried. The three species all preferred the water and sucrose to either water with starch or gelatin.

The adults of the three species could be maintained in the same terrarium without having them prey upon each other. However, L. flavum, which was captured in an adjoining field, preyed readily on other species of opilionids. Adults of the three Leiobunum species would prey on juveniles even of their own species, especially if the juveniles had just molted.

The mating behavior of the three species of Leiobunum is similar to that typically described for opilionids. The male and female stand

facing each other and the long penis of the male is extended and penetrates the genital opening of the female (Figure 9). There is a great difference between the species in regard to duration and frequency of copulation (Table I). The very few observations of L. vittatum demonstrates the relative infrequency of copulation in this species. On the other hand, L. longipes females were observed copulating many times in a single day. Apparently, L. politum females copulate once daily. Therefore, there seems to be an inverse relationship between copulation duration and copulation frequency. The matings of L. vittatum consist of several penetrations, each lasting for about a minute. L. longipes and L. politum each had a single penetration per mating.

Females of all three species would assume a "nonreceptive" position when they were unwilling to mate and being approached by a male. In the nonreceptive position the pedipalps are placed on the substrate and the body is held nearly perpendicular to the substrate (Figure 10). Consequently, mating becomes impossible and the male will eventually tire of the situation and retreat.

Aggressive encounters were observed between males in L. longipes and L. politum. These encounters appeared as if they were mistaken mating attempts (Figure 11).

The orientation data were examined by nearest neighbor analysis. The results are found on the graphs and statistical comparisons in Figures 12, 13, and 14. Note that the graphs of all the animals except that of L. longipes males have a nearest neighbor ratio of about one which indicates that the animals are randomly distributed in reference to each other. L. longipes males have a ratio greater than one and this



Figure 9. Leiobunum vittatum mating;
male (left) has penis extended

Table I
Duration of Mating Encounters

<u>L. vittatum</u>	<u>L. politum</u>	<u>L. longipes</u>
2347 seconds	656 seconds	75 seconds
3130	476	22
	367	50
	427	71
		22
		13
		25
		12
		21



Figure 10. *Leiobunum longipes* female (left) nonreceptive position; female holds body perpendicular to substrate to avoid the mating attempt of male (right)



Figure 11. *Leiobunum longipes* aggressive encounter between two males

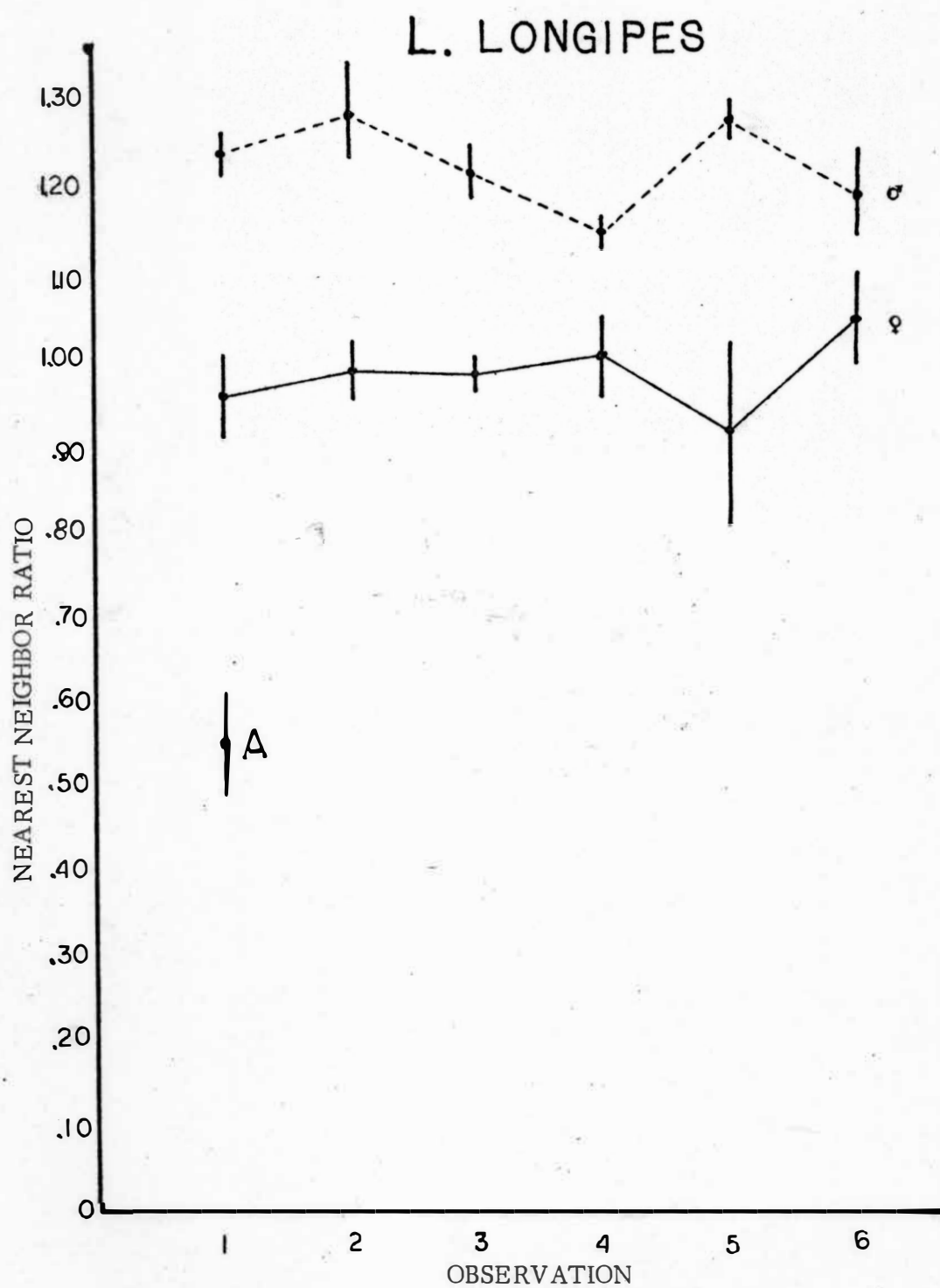


Figure 12. Nearest neighbor ratio L. longipes.
Point A represents freshly captured group of males.

L. POLITUM

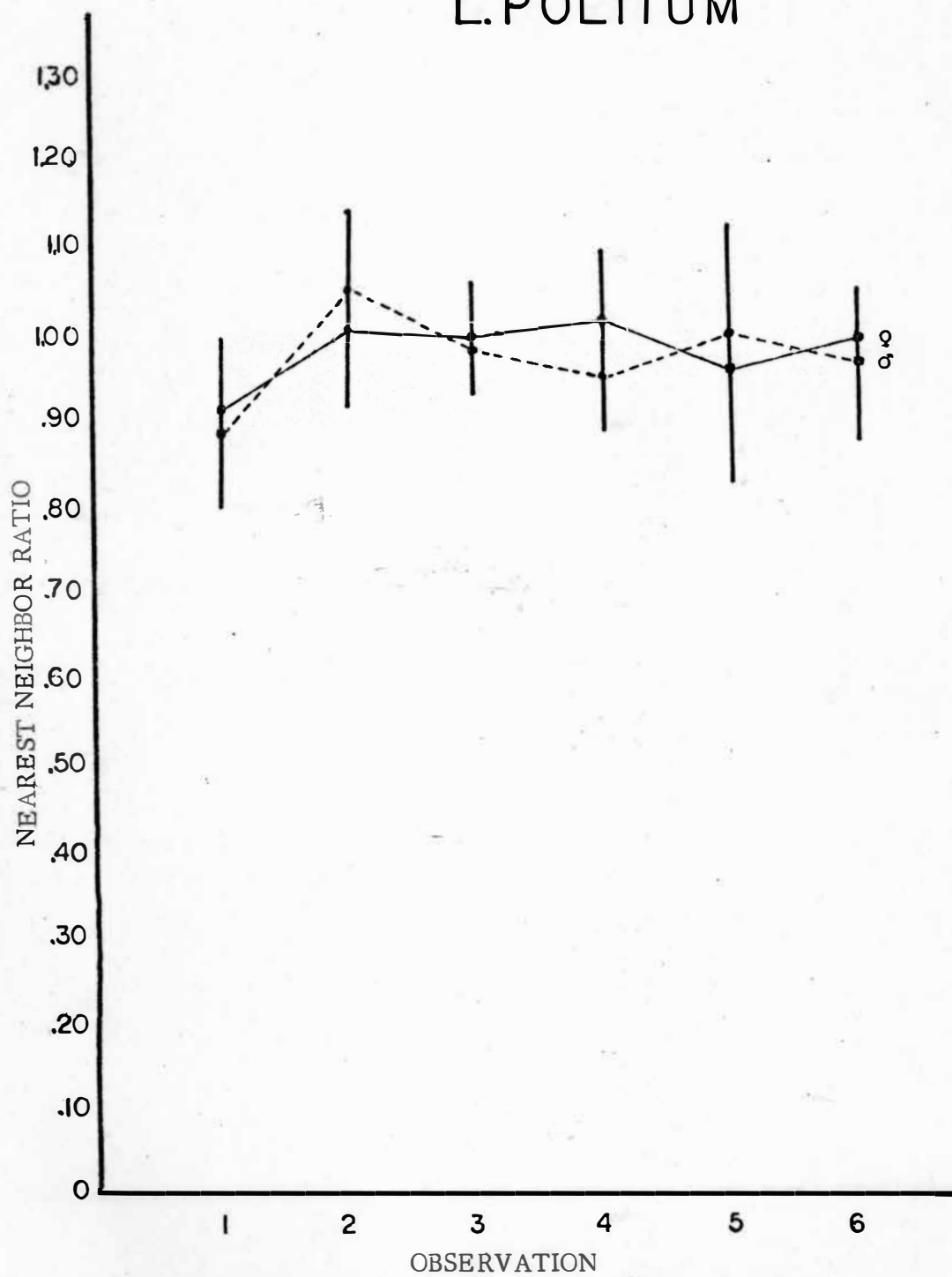
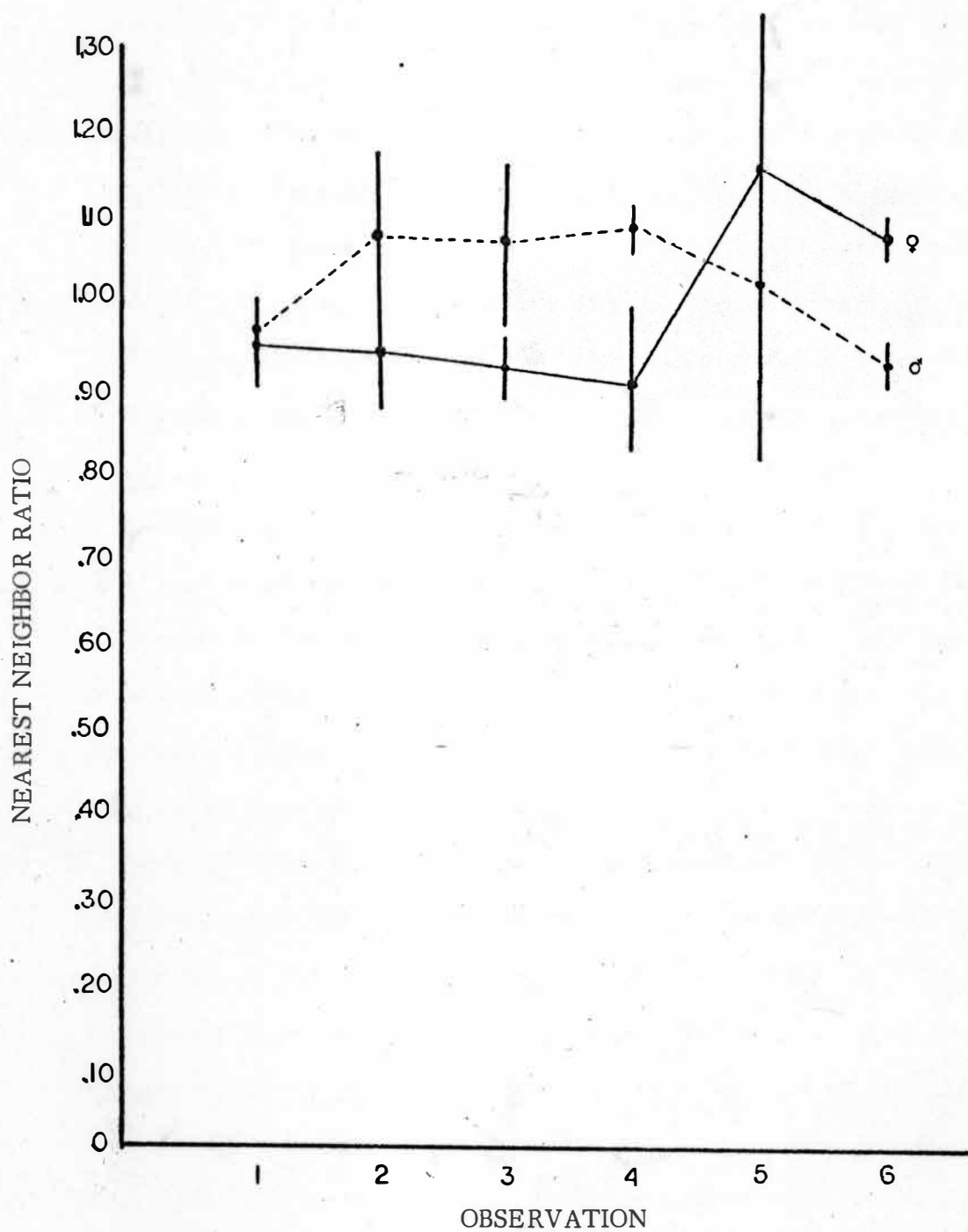


Figure 13. Nearest neighbor ratio L. politum.

L. VITTATUM

Figure 14. Nearest neighbor ratio L. vittatum.

indicates that the animals exhibit dispersion due to individual repulsion. Point A on the L. longipes graph represents a nearest neighbor analysis on a freshly captured group of males. Point A represents a ratio of less than one, which means that these animals exhibit a mutual attraction which caused clumping. After 24 hours in captivity these animals too demonstrated the typical male L. longipes dispersion.

Figure 15 represents the percentage of animals that were observed in the same grid square. It is interesting to note how infrequently male L. longipes were found in the same square. This should be contrasted with point A where the males were freshly captured and tended to form clumps.

The distribution, according to sex and species, of behavior patterns that involve or may be related to intraspecific interactions is plotted on Figure 16. Grooming and the pumping display are two behaviors that might be related to intraspecific interactions. Figures 17 and 18 were compiled to demonstrate any possible relationship between these behaviors and social interactions.

The pumping display does appear to be associated with an increase in contact time when male L. longipes and L. politum are with female conspecifics. The opposite appears to be true for male L. vittatum. A decrease in contact time for displaying female L. politum among males appears possible.

Grooming appears to occur more frequently in animals that are confined with conspecifics of the opposite sex than those confined with the same sex. It appears that grooming increases contact time between conspecifics of opposite sex.

PERCENT SHARING AN AREA

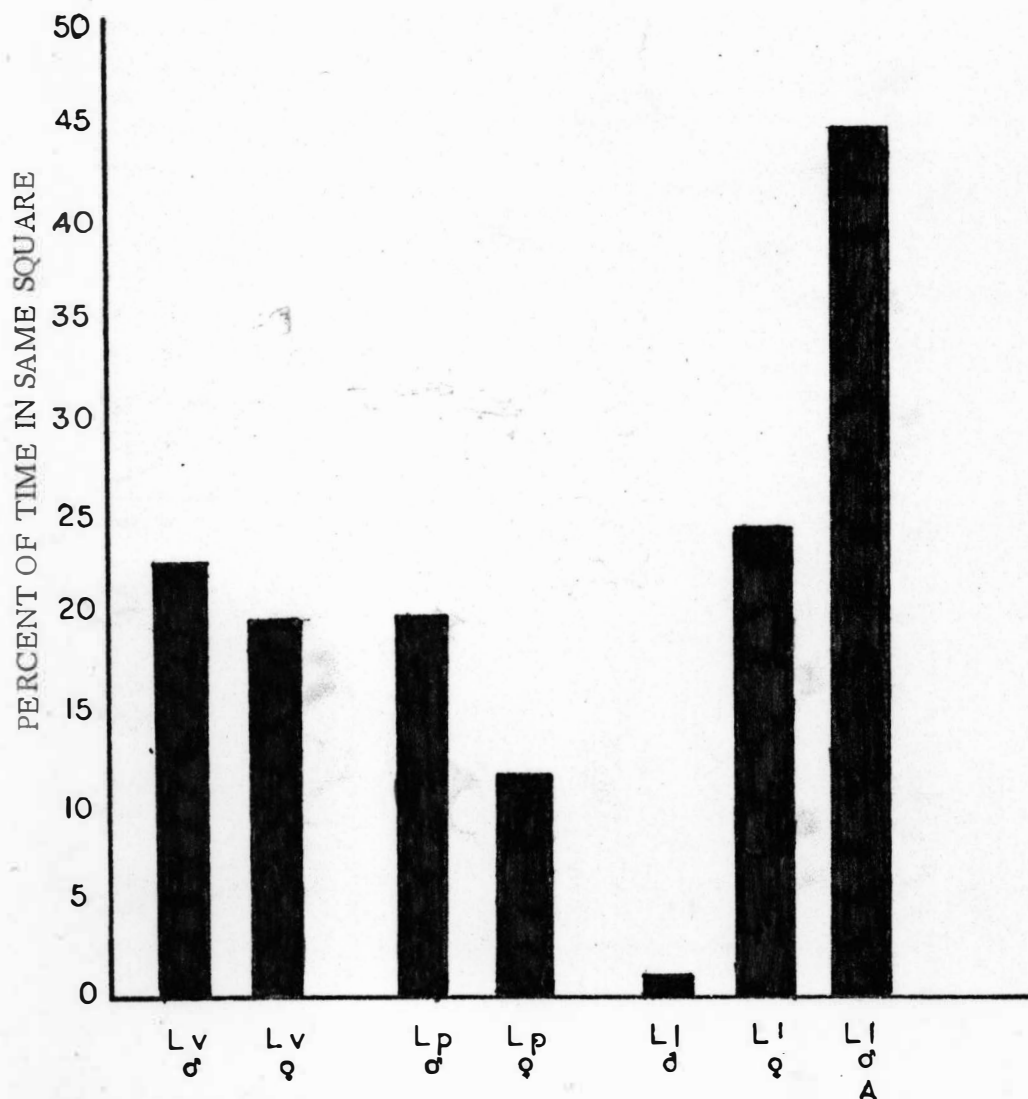


Figure 15. Spatial Distribution. Frequency of two individuals sharing the same grid square.

L l = L. longipes, L p = L. politum, L v = L. vittatum

Figure 16

Distribution of Behavior

Species	Behavior			
	Groom	Pump	Mate	Attack
<u>L. vittatum</u> male	*	*	*	
<u>L. vittatum</u> female	*		*	
<u>L. politum</u> male	*	*	*	*
<u>L. politum</u> female	*	*	*	
<u>L. longipes</u> male	*	*	*	*
<u>L. longipes</u> female	*		*	

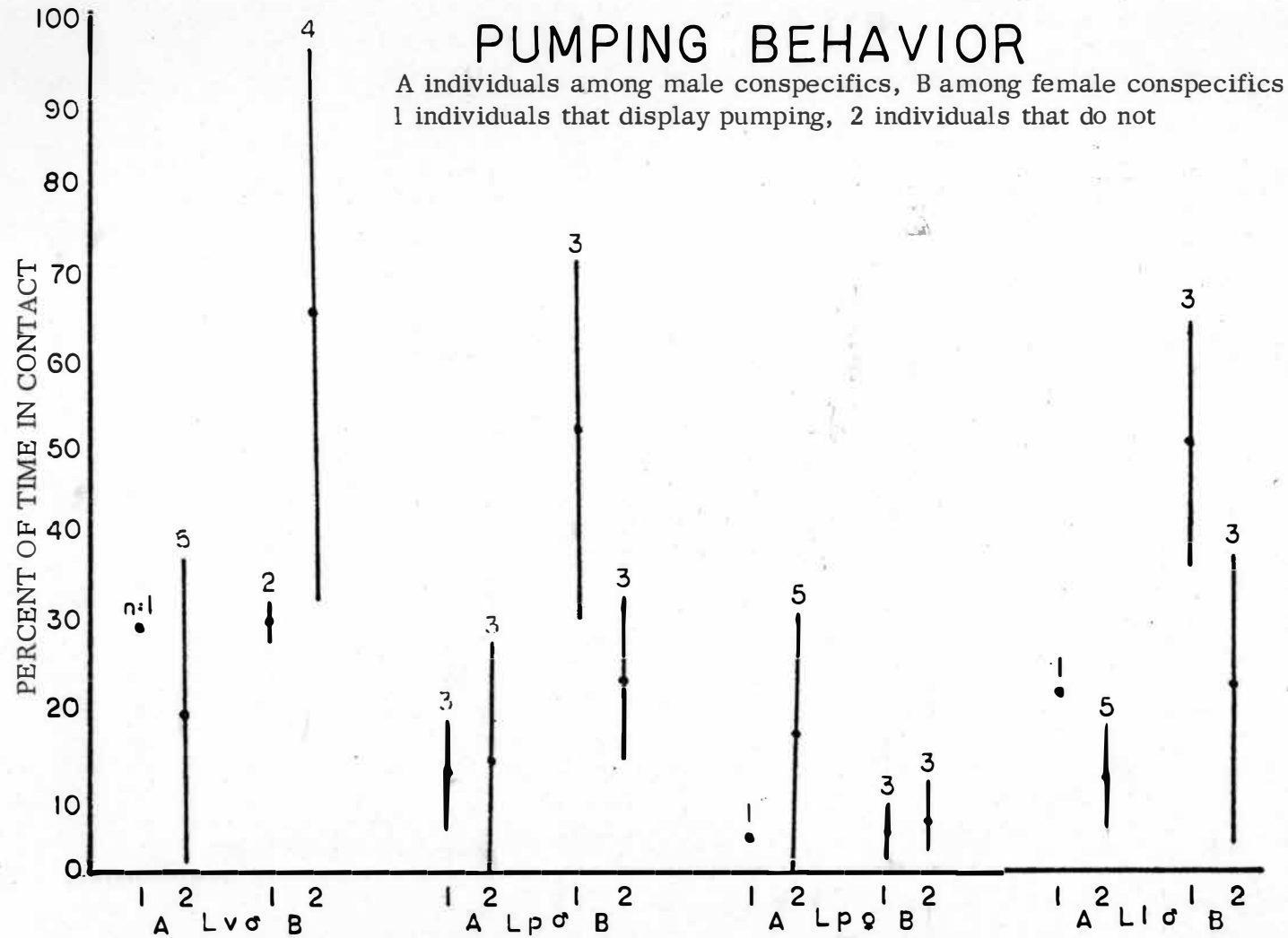


Figure 16. Percentage of time spent with conspecifics as a function of pumping display. Mean and sample variance are shown.

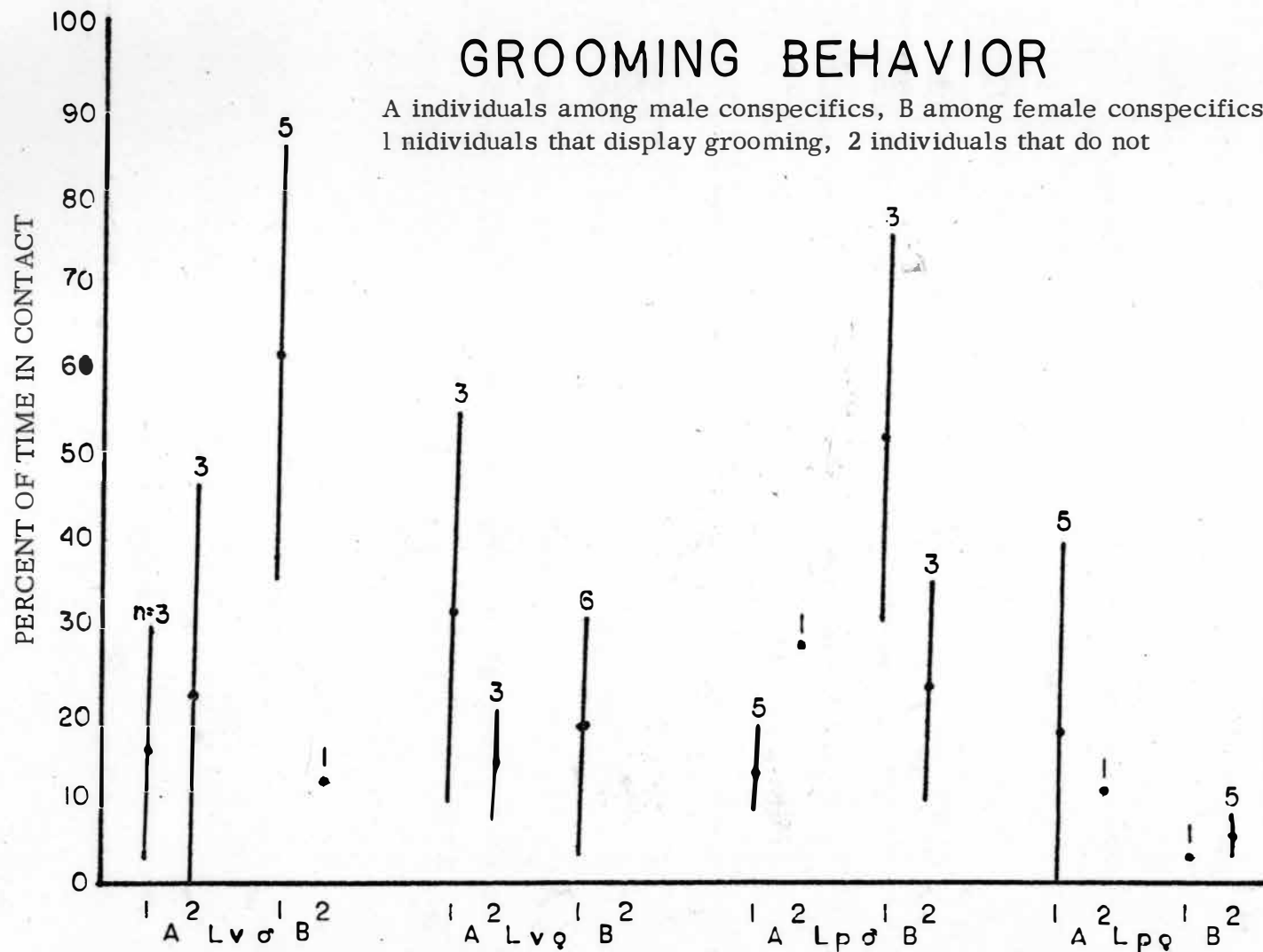


Figure 17. Percentage of time spent in contact with conspecifics as a function of grooming.

DISCUSSION

The three species of Leiobunum are quite different in appearance. It is interesting to note that L. vittatum lacks the degree of sexual dimorphism found in the other two species.

L. vittatum mates infrequently, a female may mate only once and apparently have her entire complement of eggs fertilized. The extended duration of copulation observed may be necessary to insure this.

How mate selection in L. vittatum works is not very apparent. It seems possible that chemical cues (pheromones) are necessary to recognize the proper species and sex. Whatever mechanism is used for mate selection, it appears adequate since males were never observed attempting to mate with other males.

The pumping display was occasionally observed among male L. vittatum. The pumping display did not seem to offer the animal any advantage. The behavior was elicited when the animal was placed in a novel situation or startled. The behavior could be a displacement activity that would benefit the animal through the generation of metabolic heat (Edgar, 1971).

The remaining two species of Leiobunum show distinct sexual dimorphism. In both cases the males are considerably smaller than the females. From appearance alone one may suspect that L. politum and L. longipes will have reproductive behavior differing from L. vittatum.

L. politum mate rather frequently, females have been observed mating at least once a day. Males may mate more frequently than that. Females do not always mate again with the same male.

L. politum select their mates through the use of pumping displays. The animal may be able to recognize conspecifics through pheromones. However, visual cues are apparently necessary to recognize the sex of a conspecific. Males were frequently observed attempting to mate with other males; this invariably led to an aggressive interaction. When a male locates a conspecific and he is physiologically ready to mate (motivated) he may perform the pumping display. If the conspecific also performs the pumping display in return, the male will not attempt to mate with it. But, if the conspecific does not display in return, the male may attempt to mate with it even if the conspecific is also a male.

The pumping display is usually much more common among males than among females; consequently, it is used as a means of identifying the sex of a conspecific. However, female L. politum will frequently perform a pumping-like display while depositing eggs. This appears to benefit the female by preventing male interference at this time.

L. longipes mate very frequently. Some females may mate several times in a single hour. As in L. politum, sexual identification in L. longipes is achieved through the pumping display. Female L. longipes were never observed performing the pumping display.

Among the male L. longipes, pumping took on another behavioral significance. When one male approached another and they both performed the pumping display, they would remain close together. The two males would, frequently, be joined by additional males all behaving similarly. Eventually an aggregation of males would be formed. Therefore, the pumping is not only important as a method of identifying sex in this

species, but it also clearly functions as a social releaser during the formation of aggregations (Eibel-Eibesfeldt, 1970).

The three species of Leiobunum all exhibit the pumping display. The display has little behavioral significance among males of L. vittatum. In this case the behavior could possibly be considered either a residual or a primitive behavior. L. longipes with its male aggregations could be viewed as having the behavior well developed. Therefore, it becomes evident that the pumping display is directly correlated to a high level of promiscuity in the species. In this case promiscuity refers to the simultaneous existence of polygyny and polyandry. It seems probable that the evolutionary benefits of the pumping display are closely related to the benefits of promiscuity.

Polyandry has the benefit of maximizing the genetic variance among the offspring of a female. Polygyny maximizes the genetic variance among offspring of a male. Promiscuity, therefore, would maximize the genetic variance of the entire population. The behavioral liability associated with promiscuity is reduced parental care. In this area opilionid parental care ends at the time that the eggs are deposited. Therefore, promiscuity would be maladaptive only when it interfered with a female depositing eggs (Trivers, 1972).

The female opilionids lay clusters of eggs, each cluster may contain 50 or more eggs. Promiscuity will greatly increase the genetic variance within each cluster. The selective advantage of this is not very clear. A high level of genetic variance in a cluster may be advantageous if there is a high probability of sibling-sibling mating. The variability would reduce the possible expression of deleterious recessive traits.

However, considering the mobility of the adult opilionids this does not seem as if it would have any great selective importance.

The major sources of mortality among adult opilionids are predation, dessication, and adverse weather. The major loss in the potential population of opilionids occurs during the egg stage. Egg losses are due to several factors including: dessication, predation, and fungal infestation. A high egg loss due to fungal infestation is common in animals that have reproduced in captivity (Edgar, 1971). A high level of fungal infestation is probably also common in natural populations. It may be possible that under certain conditions the fungi could restrict the range of a species. A high genetic variance in the population may make it possible for some eggs to survive certain types of fungal infestations, producing a plasticity of resistance within the population. A species that has this plasticity would be able to occupy a greater variety of habitats than a species that does not have it.

The pumping display is a behavior that evolved from, most likely, a displacement activity to a behavioral releaser. Grooming frequently appears as a displacement activity among many groups of animals, in some animals it even has the function of a releaser (Lorenz, 1941). Grooming was very frequently observed among introduced animals. Grooming of the pedipalps was most frequent, it is probably closely related to the reception of the sensory systems located there. In the three species of Leiobunum the observed grooming may be beneficial by maximizing sensory reception when animals are in novel situations. It may be possible that in other species of Leiobunum grooming has a signalling (releaser) function.

The pumping display in L. longipes and L. politum appears to be very important in intraspecific communication. The pumping display is generally found only in male animals; however, female L. politum that are depositing eggs will exhibit pumping-like behavior. This apparently will limit the amount of attention that a male will pay her, since she has identified herself to him as a male. The female will only produce this "deceiving" display while depositing eggs. At other times when a female L. politum is approached by a male and is unwilling to mate, she will assume the typical nonreceptive posture. This posture has been observed among all three species of Lejobunum. The pumping like display of L. politum females does not appear to be derived from a displacement activity, but, rather, it is actually related to the searching pattern for locating egg deposit sites. The pumping displacement activity took on the function of sexual identifier and releaser since it seems to have occurred at different rates in the two sexes.

L. longipes, the most common species in the forest, is behaviorally the most complex. The most intriguing part of their behavior is the formation of male aggregations.

The aggregations seem to be groups of males cooperating in mating. This could be termed semi-sociality since it would be cooperation among individuals of like stage (Michener, 1969). The pumping display functions as a social releaser, easing the repulsion between male conspecifics. However, these aggregations are not permanent and may break-up when the proper stimuli are not present. The most important stimulus is the presence of females. A vertical display area, such as a tree trunk, may also have some importance. Without the proper stimuli

pumping seems to become more infrequent and this apparently results in indiscriminant mating attempts. In the absence of females, males will attempt mating with other males resulting in aggressive encounters. The agonistic behavior causes the repulsion between individuals that is demonstrated in the orientation data. In nature this type of repulsion would, most likely, result in migration to a more suitable area. The aggregations containing many individuals probably occur at times when few sites with suitable stimuli exist.

The apparently unusual distribution of females throughout the study area may be due to sedentary male L. longipes and very mobile females. The possible advantages of having the females wandering over a large range are: 1) females would have a low probability of mating with siblings, 2) females would mate with the maximum variety of males, 3) females would disperse their egg clusters and possibly expand the range of the species. The sedentary nature of the males could be important in the evolution of aggregations.

The benefit of the male L. longipes aggregations appears to be increased probability of encountering passing females and inseminating them. The liabilities of the system are that the aggregations expose themselves to increased predation, and individual males have reduced chances of mating. These two liabilities have to be out-weighted by the assets of the system. The second liability of some males suffering reduced genetic expression in the following generation can be considered genetic altruism.

Wynne-Edwards (1962) believes that evolution of a social order will always carry a genetic cost to some individuals and this cost is

balanced by the benefits to the entire population. Even though individual selection would be directed away from the formation of sociality, the total population would benefit greatly and, therefore, evolution proceeds towards the development of sociality (group selection).

Fisher (1958), on the other hand, states that the individual is the unit on which selection acts. Any altruism that may evolve is derived from behavior that originally only benefited closely related individuals, consequently, this altruism is in reality nepotism (Hamilton, 1964). The nepotistic behavior may diminish an individual's reproductive expression, but a portion of its genome would still exist in reproductively successful relatives. If the relatives of an altruistic individual benefit to a point where they out-reproduce other family groups, then the genetic material associated with altruism may be preserved through evolution as kin selection. Kin selection is closely related to individual selection since an individual's genome is never entirely lost as long as its relatives perpetuate themselves. In a trivial sense kin selection may be considered a type of group selection since selection acts on kin groups (West-Eberhard, 1975).

The female L. longipes lay their eggs in clusters. If the eggs survive and develop into adults, and the adults stay in the same area where they had originally hatched, then there would be a high probability that the individuals in the same area are related to each other as either sibling or half-sibling. If this were the case, then it would be of small genetic cost to the males to remain in the same area and help other males to secure mates since they are, most likely, aiding a sibling. It would be genetically beneficial for females to wander from

the area in which they had hatched since the males there are probably closely related to them. The polyandrous behavior of the females may benefit the population socially as well as genetically. The fact that the females mate frequently makes it possible for nearly all the males to have a chance to leave offspring and, consequently, reduce the cost of sociality.

More evidence for this might be demonstrated through marking experiments. However, it would be difficult to demonstrate relatedness in natural populations.

The habitats of L. vittatum (i.e. open fields, shrubs) do not have suitable areas for visual displays and, consequently, chemical cues would have an adaptive advantage. Without visual cues a high degree of sexual dimorphism would not be necessary. Body coloration patterns that are cryptic would be selected for. The male L. vittatum coloration pattern closely resembles that of the female; however, in the male there appears to be a greater variety in the background color. This may suggest that the male color has not yet reached selective equilibrium. The female colors are quite constant.

In the habitats of L. vittatum there are no apparent sites where conspecifics can readily meet; therefore, matings would occur at times of random encounters with the appropriate conspecifics. These encounters may be extremely rare in certain portions of the habitat. Under these conditions a female that could fertilize all her eggs during a single mating would have the selective advantage.

CONCLUSIONS

In the study area there were four species of opilionids: L. vittatum, L. politum, L. longipes, and O. pictus. The behavior of O. pictus evolved around extremely cryptic body coloration and structure. The most conspicuous behavioral adaptation of O. pictus is extremely reduced activity. Consequently, this study focuses on the three Leiobunum species. The behavior of the three related species is examined and their behavioral development is analyzed in terms of modern evolutionary theory.

Leiobunum vittatum

L. vittatum appears to be behaviorally the most parsimonious. Matings are very infrequent; it is possible that some female L. vittatum mate only once in their entire life. The mating behavior is direct, without any detectable visual cues. The low level of mating errors would indicate that there is an accurate sex and species identifier present. This identifier may be associated with pheromone secretions.

Pumping has been observed among male L. vittatum, but this is apparently a residual displacement activity. Sexual dimorphism is reduced in this species. The background color of the males is very inconsistent varying from deep red to a white background that is similar to that of the females. This may indicate that the loss of sexual dimorphism and development of cryptic coloration is a secondary evolutionary event.

L. vittatum is able to survive under drier conditions than either L. longipes or L. politum. L. vittatum also has the ability to survive longer at the end of the summer than the other two species.

Leiobunum politum

L. politum has more complex observable behavior patterns than L. vittatum. Mating appears relatively frequently; during the peak of the season female may mate daily. Prior to a mating attempt, a male may exhibit the pumping display. This appears to signal a male's sex and sexual motivation. If this display is directed at another male he will frequently respond with a similar display. After the pumping, one of the displaying males will usually leave the area. Occasionally, males do not display or return a display. This frequently results in an agonistic interaction between the two males. The agonistic behavior apparently stems from an inappropriate mating attempt. Animals that do not exhibit the pumping display are assumed to be females and become possible mating partners for the displaying males. Animals that pump in return, also identify themselves as males and are avoided as possible mating partners. Female L. politum exhibit a pumping-like display while they are depositing eggs.

Leiobunum longipes

L. longipes is the species that shows the greatest behavioral complexity. Males use the pumping display to identify their sex and sexual motivation. The pumping display also seems to function as a social releaser, making the observed male aggregations possible. The

aggregations are usually found on tree trunks where they form at dusk. The males and females spend the day in the foliage of the trees, moving down the trunks to the ground at night. The male aggregations are formed before the females move down the trunk. The aggregations appear to be males cooperating to intercept and inseminate females.

When females become scarce the pumping behavior becomes more infrequent. The decrease in displaying leads to an increase in erroneous mating attempts which end in aggressive encounters. This agonistic behavior leads to repulsion between the individual males causing them to disperse. The aggregations probably evolved from sibling groups, hatched from the same egg cluster, through natural selection on kin groups. The large aggregations that have been reported are possibly secondary groupings, occurring only after the original aggregation sites became inadequate.

The behavior of the female L. longipes is notable for two points: 1) they are extremely mobile, even wandering outside the range of the males, 2) they mate frequently, mating several times within an hour. Both of these behaviors may be related to the male aggregations. The wandering would reduce the chance of inbreeding, and the frequent matings would increase the possibility of matings for all the males in an aggregation.

General Remarks

The mating strategies that exist in the three species differ considerably. L. vittatum probably use chemical cues (pheromone) for mate attraction. In L. politum and L. longipes a visual cue in the

form of a pumping display as a method of male identification is utilized. The only females that frequently exhibit a similar display are those of L. politum, but this display originates from a different behavior than the display of the males. The female pumping-like display is part of the searching pattern for sites to deposit eggs. This is usually a time when the females are not sexually receptive. In the males the pumping is related to a displacement activity. It appears to have solely this function in L. vittatum males. In the L. longipes males, pumping takes on the added function of being a social releaser allowing the formation of cooperative mating groups.

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