TERRITORIAL BEHAVIOR IN THE ANT PRENOLEPIS IMPARIS (SAY)

by

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INTRODUCTION

The writer has long been interested in ecological and bionomical relationships of organisms, primarily insects with especial regard to the activities and behavior of ants. One of the main aspects of this behavioral interest includes territoriality in ants. Territoriality may be briefly defined as the maintenance and active defense of certain areas and/or objects.

In the fall of 1953 ants were observed traveling from certain colonies located on the grounds of Insectary Number One at Kansas State College. These ants appeared to keep within the limits of rather clearly demarked areas.

This study was undertaken in order to determine whether these ants maintained a definite territory which they utilized for the upkeep of the colony or whether they kept within a definite foraging area which, because of circumstances, was not entered upon by workers from other colonies.

Observations were begun in the fall of 1953 and continued through until May of 1954.

MATERIALS AND METHODS

Manhattan, like the greater part of the United States, experienced a dry year in 1953. The total precipitation was 18.10 inches, 9.93 inches below normal. The total precipitation at the time the observations were begun was 13.19 inches, 5.20 inches below normal. At the time this study was

undertaken, the ground at the insectary yard was dry and powdery for more than a foot in depth. Except for some small plots which had been planted to sorghum and beans, there was little vegetation on the area. The vegetative covering of the alleyways between the plots were bare for the most part, with only a few weeds such as dandelion, velvet weed, wild mustard, and scattered patches of blue grass with some foxtail, fescue, and others mixed in. Insect activity was at a low ebb. The most common insect observed was the differential grasshopper, Melanoplus differentialis (Thomas). No ants were noticed although a few rather deserted-looking mounds were present. On the 28th of September the grounds south of the insectary were watered for one and a half hours. Another soaking was given to the yard on September 30, this time of four hours duration. Subsequently, the faunal activity in the area had greatly increased. Crickets, bees, wasps, flies, ground beetles, leafhoppers, spiders, and some birds were attracted to the area. The yard was watered again on the morning of October 2 and in the afternoon activity of the formicid fauna was noted for the first time since observations had been started on these grounds. The numbers and activity of the ants increased daily until, on the 14th of October, the colonies as shown on Plate I were located. With the ants available for study, observations were begun on their behavior.

The principal ant used in this study was Prenolepis imparis (Say). Crematogaster (Acrocoelia) lineolata (Say), Cremato-

EXPLANATION OF PLATE I

Ant colonies are marked as follows:

2, 3, 4, 5, 7 *Prenolepis imparis* (Say)

A, B *Leptothorax pergandei* Emery

C *Crematogaster minutissima missouriensis* Emery

D *Crematogaster lineolata* (Say)

++++ Main trails of *P. imparis* (Say)

---- Main trails of *L. pergandei* Emery

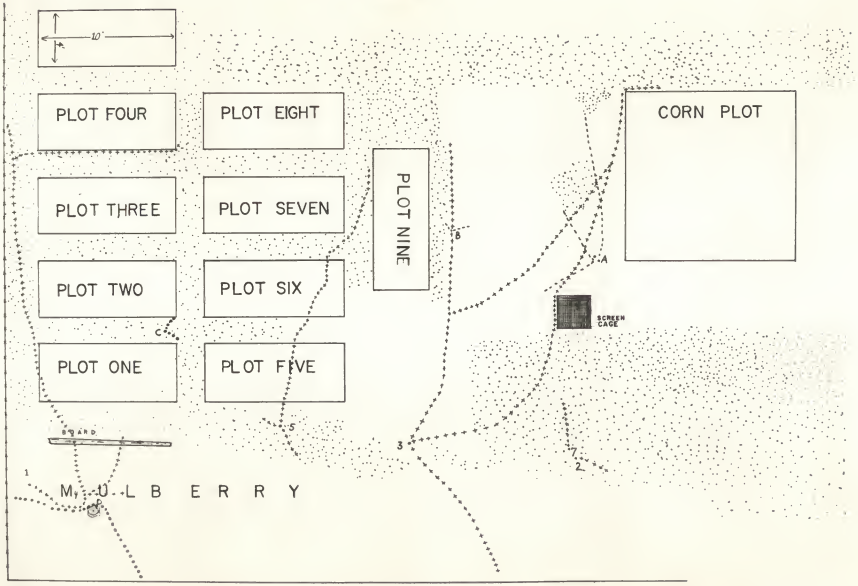
oooo Main trails of *C. lineolata* and *minutissima missouriensis* Emery

Foraging workers radiated out from main trails. Only main trails are shown. These trails represent the center points of the territories. Boundaries of the territories lie between the main foraging trails of the different colonies.

Stippled area represents weeds and grassy areas. Unstippled area represents barren or sparsely vegetated area. MULBERRY represents area along south of insectary grounds shaded by mulberry bushes.

Plots one to nine are four by ten feet plots planted to sorghum or garden beans in the fall of 1953 and left bare in the spring of 1954. The screen cage is 27 inches to a side. It remained in the position indicated throughout the entire time the studies were conducted but was associated with this study.

PLATE I


10'
PLOT FOUR
PLOT EIGHT
PLOT THREE
PLOT SEVEN
PLOT TWO
PLOT SIX
PLOT ONE
PLOT FIVE
PLOT NINE
CORN PLOT
SCREEN CAGE
BOARD
MULBERRY
10 FEET

gaster (Orthocrema) minutissima missouriensis Emery, Leptothorax (Dicothorax) pergandei Emery, and Solenopsis (Diplorhoptrum) molesta (Say) were also observed in regard to their interactions with P. imparis. The colonies of P. imparis used were located along the south end of the insectary grounds, (Plate I). This area remained shaded by the north wall of a house adjacent to the insectary property. In addition to this shade, the area was further protected from the direct rays of the sun by a row of volunteer mulberry sprouts growing approximately two yards from the house, but casting their shade over a four yard swath and extending for four yards along the south edge. This strip seldom received the direct rays of the sun.

The colonies were located by trailing individual ants to their nests. This was difficult because these ants usually did not build a conspicuous mound, but tended to locate the entrance where it was protected, under sheltering plants, boards, etc. Another difficulty encountered in attempting to locate the nest openings was that these ants tended to congregate in sheltered places along their trails. Thus, when a board was overturned, there might be a large number of ants gathered there giving the appearance of a nest site. In these instances, the covering material was removed and the trail followed the next day past this spot. As an aid in drawing out the ants, vials filled with sugar or pollen were placed at various spots around the grounds. After each colony was located, it was marked with a stake.

In order to facilitate trailing the ants, the trails were marked with pins, toothpicks, stakes and strings. By placing these behind the ants as they traveled, or placing them at each site where an ant had been observed, the trail usually became apparent in a short time. In measuring the distances the trails extended, a string was laid along the marked-out trail and then measured.

Marsh T-6 Yellow Marker Ink was used to mark the ants. This ink was applied directly to the gasters of the ants by means of a small camel's hair brush. In this way, individual ants could be observed and their actions followed more closely. A five-inch Bausch and Lomb reading glass was found to be a valuable aid in making observations.

Climatological data were taken by means of soil and air thermometers and, at a later date, a soil and air recording thermograph was used. The latter proved more useful because it kept a constant record of both soil and air temperatures. A soil auger was used to make a hole in which the soil thermometers and the soil element of the thermograph could be placed.

A useful method for determining the origin or home nest of the ants where the trail home was difficult to follow was found in the use of sugar vials. These were vials of varying sizes partially filled with sugar. The procedure involved allowing the vial to remain in a location for a period of time until it became filled with ants attracted to it. Then this vial filled with ants was placed at the entrances of the nests

nearby. When placed at their home nests the ants caused little excitement and quickly ran into the nest. However, when placed at the entrance of a strange nest, the intruders were immediately set upon by the home ants.

Observations usually were made daily from September to November 11, and from March 7 to May 28. The majority of the daily observations were made about six o'clock in the evening. During the winter months of December, January and February, sporadic observations were made on mild days but there was little activity and usually it was confined to the nests. Forms such as Plate II were used in recording the observations. On these forms information as to the weather, notes on the behavior of the ants, and records of experimentations were kept. The trails of the ants were sketched on these forms and the area each colony controlled was plotted.

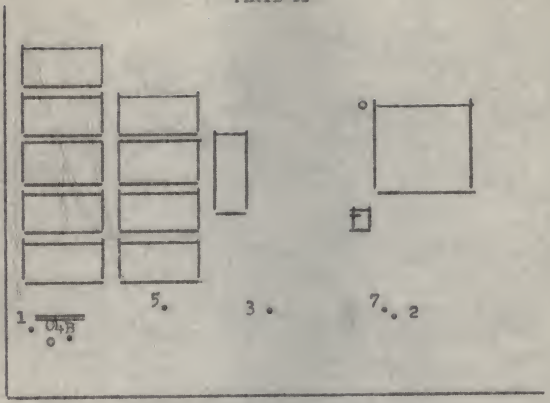
REVIEW OF LITERATURE

Territorial Behavior

Territoriality is a phenomenon which has been shown to exist in many animals and can assume many forms. In order to clarify the following work, the term territoriality should be defined.

According to Odum (1953), p.162, "Individuals, pairs, or family groups of vertebrates and the higher invertebrates commonly restrict their activities to a definite area called the home range. If this area is actively defended, it is called a territory." Dice (1952), p. 235, says, "The actual

PLATE II



Date_____ Time _____
Air Temperature ____ Type of day_____
Soil Temperature____

Activity_____

Remarks

Form used for recording daily observations.

existence of territorial behavior, however, can only be considered proved when it has been shown that the presumed holder of a territory actually defends its boundaries against trespassers." Howard (1948), p. 15, stated, "There cannot be territories without boundaries of some description, there cannot well be boundaries without disputes arising as to those boundaries."

Thus the modern view delimits a territory as an area actively defended against trespassers, which are mainly competitors. This definition serves to separate the idea of territory from that of the home range. Dice (1952), p. 231, described the home range as "The area over which an individual animal habitually travels while engaged in his usual daily activities..., p. 247. The home range also includes all the feeding sites, breeding sites, and places of refuge habitually used by the individual, and all other areas regularly traversed by him...Among the features of a home range that may be defended by various kinds of animals may be mentioned : (1) the nest, homesite or roosting place, (2) the feeding area, (3) the food itself, (4) the mating site, (5) the mate or mates, (6) the eggs or young, (7) the area around the individual itself, (8) the area around the mate or around the social group."

There has been considerable work done in describing the types of territories exhibited by many animals other than insects. Nice (1941), p. 468, stated that "...territory seems to be largely a vertebrate characteristic." She covered the lit-

erature of bird territories quite well and included references to the literature on territorial behavior of other vertebrates, including fishes, amphibians, reptiles, and mammals. P. 468, "Territorial behavior occurs widely throughout the vertebrate series. It is based primarily on a positive reaction to a particular place and a negative reaction to other individuals." P. 470, "The chief function of a territory is defense--defense of the individual, the pair, the nest, and the young. In many cases it also serves to bring the pair together and to strengthen the bond between them." In his studies of the House Wren, Kendeigh (1941) notes that although the wrens maintained and defended their territories vigorously, their boundaries were rarely static and frequently in a state of flux. Apparently, territory size fluctuates with population density and food supply. Hinde (1952) found that the Great Tit's territory is neither rigid nor clearly defined. Howard (1948) demonstrated how territories are fitted to the specific needs of the birds in respect to size and inclusiveness. He stated, p. 16, "Securing a territory is then part of a process which has for its goal the successful raising of offspring." Heape (1931) made this general statement concerning territoriality:

> There can, I think, be no question that territorial rights are established rights among the majority of species of animals. There can be no doubt that the desire for acquisition of a definite territorial area, the determination to hold it by fighting if necessary, and the recognition of individual as well as of tribal territorial rights by others, are dominant in all animals. In fact, It may be held that the recognition of territorial rights, one of the most significant attributes of civilization, was not evolved by man, but has been an inherent factor in the history of all animals.

Investigations concerning invertebrate territorial behavior have not been as extensive as those covering the vertebrate field. One of the basic differences encountered in invertebrate territorial behavior, or at least that of the ants, is the lack of reproduction defense. That is, there is no defended mating site, no defense of the mates as such, and little, if any, attempt at reducing the intraspecific competition in mating. In fact, the male ant, and most invertebrate males, unlike their showy, aggressive vertebrate counterparts, are in general small, weak, short-lived, and tolerated only so long as is necessary for them to perform their life's functions.

Pearse (1939), p. 222, stated, "Various spiders, insects, and crabs defend their territorial rights", and again, p. 556, "Crustaceans, insects, birds, mammals, and some other animals defend territories." Odum (1953) reiterated these same views, but did not elaborate on them.

It can be readily demonstrated that ants exhibit territoriality, at least to the extent that they will defend the nest, or homesite, and young. Wheeler (1910), Forel (1929), and Talbot and Kennedy (1940) described some of the defensive behavior shown by ants during an attack by slave-making ants. The writer (1953) in a previously unpublished report observed that among incipient colonies reared in the laboratory, the ants were quick to attack an intruder and/or hurry to carry the immature stages to safely. These intruders included various insects and objects manipulated by the observer. Anyone who has incurred the

wrath of an aroused colony of ants will readily appreciate the fact that they are quick to defend their property. Of course, the violence and pugnacity of the ants in their attack is dependent upon the nature of the ant itself and also upon the size and ferocity of the intruder. Also, ants tend to defend aphid colonies against the majority of intruders.

However, the greatest danger to a species comes not so much from the inroads of parasites and predators, but from competitors. Usually, the greatest competition to an individual or unit of a species comes from other individuals or units of the same or closely allied species. Therefore, it is against this group that the main aim of territorial behavior is directed.

The bulk of the past literature dealing with "territories" among ants has dealt with the home range or foraging area. Pickles (1937, 1946), Headley (1941), Carey and Diver (1937), and others, in referring to ant "territories" gave descriptions of areas that more properly should be called the home range or foraging area.

Pickles (1946a) described a situation wherein the normal pathways of different colonies of Camponotus aethiops Lati. were disrupted by the pitching of tents in a vineyard. The tent ropes served to connect trails used by two colonies. He described the prolonged battles between these two colonies and said, p. 222, "...by 10 a.m. the battle had stopped and the ants from nest A were traveling over the ridge of tent no. 4, having apparently won that extra territory." However, he went on to

point out that there was continued fighting until finally the "...ants seemed to avoid the stretch of rope that joined the two tents." In describing observations of Formica rufa L. in a bird sanctuary Elton (1932) found that there were no connections among the trackways of neighboring nests. Each colony maintained "...independent food territories, trees, and nests." In conclusion he stated that normally there was not hostility among nests, neither were there common tracks or food supply. He also described the destruction of a small colony which lay close to the areas utilized by two larger colonies. One of the large colonies raided and destroyed the small colony. This attack occurred during a year with a late, cold spring, when the food supplies were rather short.

Morisita (1939) gave an excellent portrayal of battles between different species of ants. He showed that ants held territories and defended them and also would attack another ant in order to gain its territory. "It is suggested that such attacks of Tetramorium seem to be made in order to enlarge their territory for the purpose of supplying their increasing population with sufficient food in summer."

Talbot (1943), p. 44, working with Prenolepis imparis in an orchard found that "...no colony maintained a territory of ground which it defended against invasion from other colonies ...however, bits of fruit were strictly 'private property' for a colony and were defended with fighting if necessary."

The Ant Prenolepis imparis (Say)

This species of ant was first described in 1836 by Thomas Say as Formica imparis, but was placed in the genus Prenolepis Mayr by Emery in 1893. Wheeler (1930) expressed interest in this ant because of its great similarity to Prenolepis henschei Mayr, an extinct species that once flourished in the amber forests of the Lower Oligocene Tertiary of northern Europe. He considered P. imparis to be little more than a variety of the extinct henschei.

The distribution of this ant is very wide. Wheeler (1930) defined the range as extending from the latitude 19° to 46° in North America, covering nearly the whole of the United States, a portion of Ontario and south to the states of Vera Cruz and Colina in Mexico. In all, the nine varieties cover a large portion of the temperate zone. Smith (1947) named seven varieties, one or more of which are thought to occur in every state.

There are many records in the literature attesting to the fact that P. imparis is a "cold weather ant". Wheeler (1930) recorded the unpublished notes of A. C. Burrill who states that in Massachusetts, workers were observed to come to the surface of the soil nearly every week all winter. The lowest temperature at which he recorded activity was 6° F. one morning in February of 1928. Talbot (1943a), p. 252, observed that "Prenolepis imparis is a cold weather ant, beginning activity above ground at temperatures just above freezing and reaching its peaks of foraging at temperatures between 45° and 60° F. Above

60° there is a decrease in numbers of ants above ground which progresses steadily with rising temperatures until, above 75° F., almost no ants are found above ground...during favorable temperatures, (the ants) reached peaks of activity at humidities of 80-100%." Smith (1947), p. 612, observed, "These ants (P. imparis) apparently can withstand more cold than any other species in the United States."

Nests of this ant are usually built in shady, moist locations and more often in clay soils. Wheeler (1930) found them most often near oak trees. Dennis (1941), p. 86, said that while they are often found near oaks, "Any large plant or tree infested with aphids or coccids seems to be sufficient for the maintenance of a colony of these ants." Talbot (1943), p. 44, described 88 colonies in an orchard "...most numerous near the fruit bearing trees in cut lawn and were scarce or absent where trees were lacking or where there was a heavy matting of uncut grass."

The food of Prenolepis imparis (Say) consists of liquids, mainly "honey-dew", plant saps, insect juices, etc. This has been reported by Smith (1924, 1947), Wheeler (1930), Dennis (1941), and Talbot (1943). The writer has also observed them feeding upon a dead, newly-hatched nestling bird which had fallen near one of their nests.

OBSERVATIONS IN THE FALL 1953

During the fall of 1953 the main part of the work was directed towards locating, marking, and observing the colonies of ants upon which these studies were to be conducted. As has been mentioned previously under METHODS, as the result of the hot dry summer and fall, the ants in the insectary yard were not active during September and were observed only after they had been induced to become active again by watering the insectary grounds. By the 14th of October the colonies as shown in Plate I were located and the observations were started regarding the range of their activity. Ants were followed to and from the nest and food gathering sites. Vials filled with sugar were placed at various locations throughout the area and the colony which utilized each one was noted. By these means, it could be seen that the ants tended to stay within certain areas and utilize food within those areas, but did not appear to travel far from them. These areas are shown in Plate I. These could not at this stage be called territories but only foraging areas since it was not known whether the areas were defended, nor whether they would be maintained for any length of time.

Daily observations were discontinued November 15 because of the dryness and oncoming cold weather. Observations were made on mild days during the winter months and especially at those times when there was abundant moisture due to either rain or melting snow.

OBSERVATIONS DURING THE SPRING 1954

During the winter and early spring the observations were made at intervals to determine the condition of the study area and to observe ants as they appeared. The early months of 1954 were dry and cold. The average temperature for January was 24.9° F., for February 42.5° F., and for March 39.3° F. and the total precipitation for this period was 2.69 inches. No ants were observed above ground until the 10th of March.

Observations were begun on March 7th and continued daily through May with the exception of a few days. The majority of the observations were made in the evening around six o'clock but supplemental observations were made at other times during the day. The chronological data for the spring are included to summarize the daily activity of the ants.

March 7, 1954

The air temperature was 64° F. and the day was warm and sunny. No ants were observed. Sugar vials were placed out to determine whether ants could be attracted to them.

March 8, 1954

Cooler today with the temperature at 52° F.; no ants had as yet appeared above ground.

March 9, 1954

Temperature 60° F.; sunny and warm, but no ants were observed.

March 10, 1954

Ants were observed for the first time this spring. Air temperature 59.5° F.; the soil temperature at the surface was 47.5° F. and at one foot below the surface was 39° F. A few ants were seen at the sugar vials. They were moving slowly and no definite trails could be followed.

March 11, 1954

Activity had increased over that of March 10. Some trails were marked with pins in order to follow them later. The soil temperature at the one foot level had risen to 42° F.

March 12, 1954

The weather on this day was similar to that of the day before. No noticeable increase in activity could be detected.

March 13, 1954

The temperature took a sudden drop below freezing. A few lethargic workers could still be seen moving slowly above ground.

March 14 to 17, 1954

During this time the temperatures were mainly below or just above freezing. Ant activity apparently had stopped. No ants were noticed moving above ground, but a few could still be found in a somewhat dormant stage lying under leaves near the nest sites.

The remainder of March was generally cold and dry. The average maximum temperature was 52.1° F. and the average minimum was 26.4° F., with an average of 39.3° F. Total precipitation for March was 0.58 inches coming from a rain of 0.53 inches and a trace of snowfall. In general these conditions were not favorable to the ants and although they were sporadically active on a few warm days, there was no prolonged activity and no important happenings.

April 5, 1954

Temperature on this day was 65° F. Nest A had opened up and there was much activity excavating and building up the mound. A few ants were observed to go out foraging. The ants at nest 5 were the only other ones that appeared to be active on this day.

April 6, 1954

There had been a rain of 0.13 inches the night before and the temperature during the day rose to 80° F. The ants were quite active. There were many ants working around the mound and moving to and from nest site A. The ants at colony 3 had started foraging, but appeared to have shifted their trails somewhat from that of last fall. Those at nest 5, however, appeared to be using about the same area that they did last fall. Many ants from nest 4 were gathered about sugar vials placed in plot 1.

In the afternoon the P. imparis were swarming. The

reproductive forms tended to restrict their activities both in the air and on the ground to the shaded south portions of the yard. Many more males than females were noticed. The ratio appeared to be around 100 to 1. As the light shifted, the ants withdrew more and more towards the south end to keep in the shade. A female on the ground was pursued by three males even though the female was in coitu at the time.

April 7, 1954

The warm weather continued with the temperature at 83° F. No females were seen but a few male P. imparis were running around on the ground. Most of them, however, were caught and carried into the nests by P. imparis workers.

April 8, 1954

The day was cooler, 63° F., and the ants were very active. The foraging trails now extended eight feet or more into the insectary yard. In contrast to last year, the main direction appeared to be straight north instead of an easterly slant.

April 10, 1954

There was a strong wind blowing near the surface of the ground. The ants were inactive and gathered in sheltered places. Those ants along the more exposed part of the trails were being blown off the trails. One male P. imparis was seen still crawling over the

ground.

April 11, 1954

Weather turned cooler with the temperature around 45° F. The soil had become dry again and ant activity had greatly diminished.

April 12, 1954

This day was little different from April 11. Only a few workers could be seen.

April 13, 1954

The insectary grounds were watered. Before watering little activity was observed, but after watering all of the P. imparis colonies had resumed their foraging.

April 15, 1954

A colony of Crematogaster lineolata (Say) was located. The nest was in an old stump about one foot back of colony 4. Large numbers of Crematogaster could be seen following a trail leading towards the house in the south.

April 17, 1954

The dry weather continued. P. imparis activity was curtailed. Workers were seen to travel only one or two feet from the nest although the temperature was a favorable 65° F. The other species of ants in the yard were more active.

April 19, 1954

There had been a trace of rain during the night and the ants were more active than they had been on the

preceding days. Still there were no ants observed traveling more than two or three feet from the nests. The Crematogaster were engaged tending aphids on a mulberry bush near the nest. A large sugar vial and two small pollen filled vials were placed between colony 4 and the Crematogaster colony to see whether there would be any competition.

April 20, 1954

At 8:00 a.m. the ants were quite active. The large sugar vial was full of ants from colony 4. Although the pollen vials were closer to the nest, only one or two ants at a time were visiting these vials. No Crematogaster were seen at the vials. Some of the workers from colony 4 were carrying in Wild Mustard seeds.

The ants were still active in the evening. P. imparis and C. lineolata were noticed crawling on the same shrub but on different branches. These two species appeared to have completely different modes of travel. P. imparis tended to remain concealed under sticks, stones, matted grass, etc., while C. lineolata moved rapidly along on top of such objects, and utilized twigs as pathways to carry them over the impediments below.

April 21, 1954

Rain had fallen during the early morning and at six

o'clock in the evening the ground was still moist. More rain fell later on in the evening to bring the day's total to 0.39 inches. The P. imparis were all actively foraging.

April 22, 1954

The temperature was 62° F., and the ground still moist and the relative humidity high. The ants were quite active with long foraging columns extending from all the P. imparis colonies far out into the yard. An experiment was performed with ants from nest 4. Soil was carefully taken from the sides of the trail until at this point the strip of soil was only three inches wide. Then this section was undercut and a rake slipped underneath it. After this the two ends of the strip were severed and the whole section rotated 90° with the aid of the rake. Ants accumulated at both ends of the excavation where the section of the trail had been severed. From time to time one or two ants wandered into this excavation but returned again without crossing it. At the end of one half hour they had not succeeded in establishing a path across the chasm. Then the section of trail was rotated back 90° to its original position. A little time was required for the ants to find their way across the loose soil at the point where the section was joined to the main trail, but soon the ants were streaming

across the old trail.

April 24, 1954

It was extremely warm during the day with the temperatures reaching the 90's. However, the temperature dropped rapidly toward sundown and the ants began foraging farther from the nest as the weather conditions became more favorable. There appeared to be a distinct tendency to remain as much as possible in the shade. The trails for the most part remained within the shade of plants, in small depressions and micro-valleys.

April 26, 1954

The activity appeared to be the same as the two preceding days. Ants from the different colonies were placed at various points within the territories of other colonies. When ants were placed at or near the nest opening of another colony, they were immediately set upon and killed or driven away. If ants were placed farther away from the nest opening along a foraging trail, they were able to run away without much difficulty. However, they were pursued and sometimes caught and killed. Pugnacity appeared to be more prevalent near the nest.

April 28, 1954

The day was cloudy and overcast with temperature reading 65° F. In the afternoon the sky cleared and the sun shone brightly. Some fighting between workers of

P. imparis was noticed near the fence at the west side of the grounds. Only two or three individuals were involved. Between P. imparis and C. lineolata there was some antagonism when they met. There was never any actual fighting, but only a sort of "nudging" each other and then backing away. Ants from colony 7 were transferred within a pollen vial and placed at nest 3 and 4. In both cases this transfer caused fierce fighting among the workers.

April 29, 1954

This day was also cool and cloudy with the temperature in the 60's. A dead nestling bird was noticed lying on the ground between nests 5 and 3. The Crematogaster from the nest in the stump were actively feeding upon the bird. Their trail to the bird crossed the trail of P. imparis from colony 5, but there was no antagonism.

May 1, 1954

There was little change from the previous days. The ants appeared to be keeping within restricted areas and did not stray from them.

May 3, 1954

P. imparis was observed carrying in seeds, various immature homopterans, and also tending aphids which were scattered about in the weeds.

May 5, 1954

For the first time a colony of P. imparis was noticed

near colony 7. This was numbered 2. It lay 18 inches southeast of colony 7 and at the top of a small ridge which put this colony about two inches higher than 7. The new colony appeared to be a small one, and the nest opening was not conspicuous. The small dead bird which C. lineolata had been feeding upon had been washed away from its original position by a heavy rain. P. imparis from nest 5 were feeding upon it, and the C. lineolata apparently had either lost or abandoned the bird. There were a few Crematogaster near the spot where the bird originally lay, but none of them went over to the new resting place.

May 6, 1954

Thirteen vials filled with sugar were placed between nests 2 and 7 (Plate III fig. 1). This was done in order to determine the vial each colony would utilize and where a boundary was drawn between the two nests. P. imparis from 5 were still feeding on the dead bird. A few C. lineolata were seen near the bird, but there was no antagonism between these two species.

May 7, 1954

Colony 2 had apparently taken over all the vials lying between it and number 7. Some of the ants in the vials were marked in order to trace their movement and they all returned to nest 2. One of the vials was placed on the mound of colony 7 and allowed to fill

EXPLANATION OF PLATE III

In Fig. 1, 2 and 3:

---- indicates the main trails of colony 2 across the area.

.... indicates the main trails of colony 7 across the area.

XXXX indicates workers from colony 2.

0000 indicates workers from colony 7.

Stippled vials are those containing sugar; unstippled vials represent those which once contained sugar.

Fig. 1. Position of ants and ant trails (May 15, 1954) at the time fighting first broke out between the two colonies near colony 7.

Fig. 2. Position of ants and ant trails on the morning of May 16, 1954. Colony 7 had pushed colony 3 past vial C and there was fighting at this point and also near vial H.

Fig. 3. Position of the ants and ant trails after hostilities had ceased between the two colonies. The arrows mark the furthest point to which colony 7 had driven and the point to which they had been pushed back by colony 2. Exact position of vials shifted slightly during this time as the result of washing by rain, wind, etc. However, none of the vials was shifted more than one inch from its original position.

PLATE III

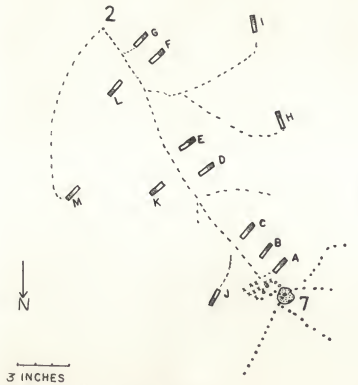


Figure 1

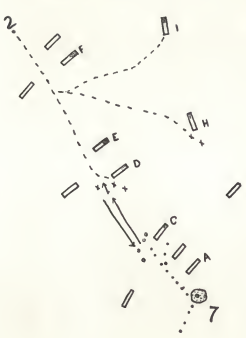


Figure 3

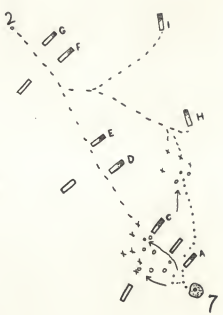


Figure 2

with ants there. When the vial was replaced in its original position, the ants in it were attacked by workers coming from colony 2.

May 8, 1954

There was no noticeable change from the preceding day. Colony 2 still held control of all of the vials between it and 7. There were several Wild Mustard seeds scattered around the mound of nest 7, but the workers going in and out paid no attention to them.

May 9, 1954

Colony 2 still held all the vials, so eight more vials were placed in a ring about three to four feet from 7 to see which way its territory extended (Plate IV, fig. 1).

It had been noted that when ants were placed on the trails of areas used by another colony they appeared lost and ran off at full speed, but when removed to another place in the trail or area used by their own colony, they wandered around, slowly, tapping their antennae to the ground.

May 10, 1954

Colony 7 was feeding at three of the eight vials placed ringing it. Colony 2 was using one of them, and colony 3 had one. The rest had not, at that time, been visited by ants. (Plate IV, fig. 1) Two ants were noticed fighting near the mound of colony 7.

EXPLANATION OF PLATE IV

Fig. 1. Position of colonies 3, 7 and 2, and the vials which had been placed in the area. Dotted lines from vials to colonies indicate colony that utilized vial. Vials are drawn out of proportion.

Fig. 2. Position of colonies 5 and 3, and vials placed between them. X indicates fighting among ants. Fan shaped spread of ants is depicted east of vials X and Y.

PLATE IV

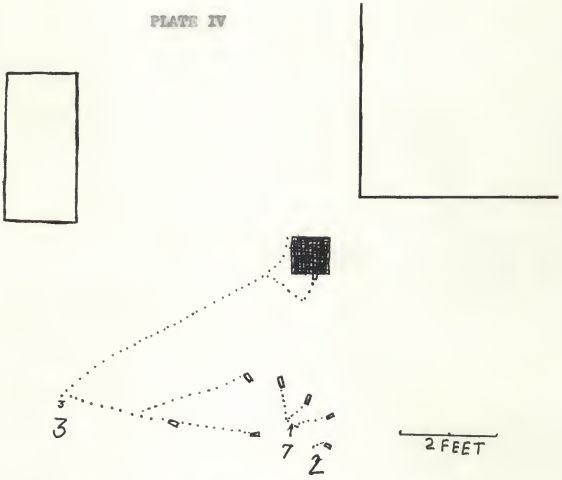


Figure 1

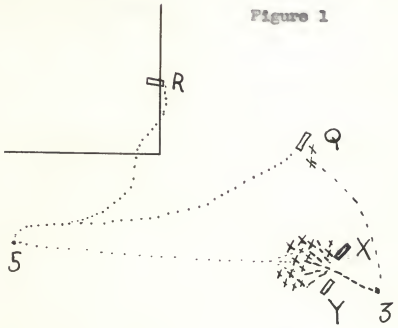


Figure 2

May 11, 1954

There was no significant change in activity noticeable. The colonies appeared to remain within the areas they had been using.

May 12, 1954

The temperature was 69° F., but the sun was shining brightly even at six o'clock and the ants were keeping within the shade but there were a few ants traveling over the trails extending across the bare, unshaded areas.

May 13, 1954

Activity was about the same as it had been on the preceding days. Colony 4 had its trail running parallel to one used by C. lineolata. The C. lineolata were traveling along the top of an exposed root, while the P. imparis were moving along the side of the root on the ground. Occasionally, some of the ants from the two different colonies would meet, but there was no fighting. Usually they would touch antennae for a moment, and then both would back off and go on their way.

May 14, 1954

There was a 0.78 inch rain on the preceding night. Relative humidity was high and the activity was about the same.

May 15, 1954

This day was cloudy and overcast with the temperature

at 75° F. At three o'clock in the afternoon rather fierce fighting was noted at vial A near colony 7. A stream of workers from colony 2 were coming down and forming a line in front of the vials. Only a few workers were coming over from colony 7 (Plate III, fig. 1).

May 16, 1954

This day was cloudy and overcast, and the temperature in the morning was 55° F. At eight o'clock in the morning a battle was still raging between colonies 7 and 2. It appeared that 7 was attempting to gain some of the sugar vials. Vial A had been taken by colony 7, and workers from that colony were feeding on the sugar. Vial B was empty and there was a great fight going on around vial C. It appeared that 7 was the agressor and also the stronger. Many ants from both sides were engaged in fighting. Some of the fights were one to one, some two to one, three to two, etc. Workers were seen carrying off dead ants and many injured ants littered the area. By nine o'clock vial C fell to colony 7. After fighting past it, they rushed in and dragged out two workers from colony 2 which were still in the vial (Plate III, fig. 2). While all this fighting was going on, the workers from both sides continued to visit the vials and to do work bringing up soil from within the nest and

placing it around the nest openings.

May 17, 1954

The fighting had stopped except for a few scattered individuals. Colony 7 held vials A, B, and C, while colony 2 held the remainder. There appeared to be a neutral area between vials C and D where no ants were observed. Colony 3 now held most of the vials ringing 7 (Plate IV, fig. 1).

May 18, 1954

There was no fighting between colonies 2 and 7, and the area between vials C and D was not traversed by any of the ants. Colony 4 was tending two large aphid colonies located about a foot east of its nest site. The other trails this colony had been using appeared to be abandoned. Colony 3 appeared to be sending more workers along a trail leading to the house on the south and fewer out across the barren, sunny areas. Some sugar vials were placed to check on the territorial limits between colonies 3 and 5.

May 19, 1954

Fighting had resumed between colonies 2 and 7. Workers from colony 7 were fighting around vial D. After a time workers from 2 pushed those from 7 back to vial C. Later workers from 7 fought back to D and past it to E and appeared to be winning. The sugar was gone by this time in vial A so that of all the

vials controlled by colony 7, only C contained sugar and that supply was running low (Plate III, fig. 3). Colony 5 had taken over all of the vials that had been placed between it and colony 3 except one (Plate IV, fig. 2). Two of the vials were moved closer to colony 3. At 4:30 p.m. a few skirmishes between workers from the two colonies were noted near vial Q. This vial had been held by colony 5 and they had a large number of workers traveling to and from it while there were only a few stragglers from colony 3. The two vials X and Y which had been moved were not noticed by the ants.

May 20, 1954

All fighting had stopped on this day. Vials A, B, and C were empty and colony 2 had held on to the rest of the vials so that colony 7 had no food supply in the area. Colony 3 was feeding at vials X and Y, and colony 5 was visiting the rest. There was no antagonism noted between these colonies. The majority of the workers from colony 4 are engaged in tending the aphid colonies and few could be seen along its old foraging trails.

May 21, 1954

There was little change in activity on this day. The weather was warm and sunny with the temperature at two o'clock 80° F. Few ants were noticed out in the

bright sun. Many were congregated in shady areas along the trails.

May 22, 1954

The day was hot and dry; temperature rose to 85° F. and the ants were not active except close to their nests.

May 24, 1954

It was cool and overcast on this day. All the vials between colonies 7 and 2 were empty and there were few ants in this area. A fierce battle was raging between workers from colonies 3 and 5 near vials X and Y. Colony 3 had formed a line in front of the vials and the fighting was very fierce (Plate IV, fig. 2).

May 25, 1954

The fighting had stopped between colonies 3 and 5. Colony 3 still held X and Y, and 5 held Q. One or two ants could still be seen fighting in the area between colonies 7 and 2. Inasmuch as the sugar was all gone from the vials between these two colonies, a large vial filled with pollen was placed between them in the space where vials C and D had been.

May 26, 1954

No fighting was observed on this day. Each colony appeared to be holding to what they had and were keeping within their boundaries.

May 27, 1954

Colony 7 had taken over the pollen vial and no ants from colony 2 were seen near it. Vial X was empty and there was much fighting around vial Y. Workers from colony 5 were fighting with workers from colony 3 and those from 3 appeared to be successful in warding off colony 5.

May 28, 1954

There was still fighting near vial Y. Large numbers of ants were moving toward it from colony 3 and 5. Colony 3 held vial Y and was feeding upon it while the fighting was going on. Colony 7 still held the pollen vial. Colony 2 did not appear to be active.

The taking of chronological data was discontinued on the 29th of May. At this time the territories of the ants stood, for the most part, as they were when the studies were begun in the fall of 1953. The main differences noted were the fluctuations of the boundaries and slight shiftings of the foraging trails throughout the year.

CONCLUSIONS AND DISCUSSION

Evidences of Territoriality

It appears that in the cases observed the ants did maintain a territory. Each colony of Prenolepis imparis studied maintained and defended a certain area which it used for food supply. This area was defended from the inroads of ants from

different colonies of the same species, but different species were tolerated. This tolerance was probably based on the differences in behavior and food habits of the ants. The ants Leptothorax pergandi appeared to be mainly carnivorous and were not attracted to sugar or other sweets. The Crematogaster appeared to be somewhat separated from the P. imparis by the differences in their foraging behavior, that was, their tendency to remain in the open on top of rocks, twigs, etc. Solenopsis molesta (Say), a tiny ant, did not wander in the open far from its nest. Its small size enabled it to remain unmolested as it tended to keep to places too small for the larger ants to enter. All of these species of ants reached their foraging peaks under different climatic conditions than P. imparis. Thus P. imparis and the other species studied were not stimulated to a high degree of activity at the same time and thereby tended not to interfere with each other.

These territories varied in size and there appeared to be constant shifting along the borders as the different colonies encroached upon each other. The main foraging trails of the colonies appeared to remain about the same throughout the year, however, and no attempts to take over control of an established food source well within the confines of one territory were noted. Around the outer edges between two territories occasional, but fairly constant, fighting between individual ants could be observed. It is quite probable that individual scouting workers continually crossed over into different territories but met with resistance as they encountered workers from the colony that held

the area. The center points and main sections of the territories could be easily determined, but the actual demarcation between the center points of two different territories was not readily demonstrable. There are probably no clear cut or distinct boundaries to these territories, but they fade into each other and constantly shift back and forth. The main points defended within these areas were the food sources such as the aphid colonies, sources of plant exudates, seed bearing plants, sweets, animal material, etc. However, the fighting was not necessarily confined to the food material itself, but has also been observed to occur along a defense perimeter of ants gathered blocking the trail of a colony towards a source of food (Plate IV, fig. 2). Also when a group of ants were transferred out of their territory to near the nest site of another colony, the invaded colony would vigorously defend their nest site and kill or drive off the invaders. In such cases as this there was no food material involved, only transgression. In no cases were the trails of different P. imparis colonies observed to cross. In all cases the trails led directly to the food material from the nest site and any other ants from different colonies were quickly set upon and repulsed or killed, unless at times the attackers succeeded in taking over the site.

Types of Fighting or Antagonistic Behaviors of the Ants

Several types of fighting or antagonistic behaviors were noted among the ants. They are briefly described below:

"Nudging." This type usually occurred between ants of two different species. In this type the ants, after a preliminary tapping of their antennae, met with their heads opposing and pushed back and forth for a few moments. After that usually one or both of them backed off and ran away. In these cases the mandibles were not used and there was no other effort than pushing with the head.

"Snapping." This was usually observed between ants of the same species, but from different colonies, although it was sometimes noted with different species after a few moments of "nudging", or among the members of the same colony. In these cases the ants normally stood opposing each other anteriorly with the mandibles spread wide and the head aligned parallel to the ground. The ants would be separated from each other by a small distance and would spring forward and snap with their mandibles at each other. Between these snapping movements there would often be a period of antennae tapping. There seemed to be no effort to catch hold or get a grip on the opponent. The ants themselves moved very little while engaged in this. After a period of time the ants would back up and move away from each other. Sometimes one ant would move away and leave the other one standing there with the threatening attitude with mandibles spread.

"Riding." This was observed only a few times. In this type one ant would hold on to some portion of another with its mandibles; usually this was on the legs. No attempt at bringing the abdomen around for squirting formic acid was made. The one ant simply held on, and the other ant made a few attempts to dislodge it but usually went to no great effort and walked on, dragging the one ant.

"All-out fighting." This was the case in the fierce battles between colonies. The ants would grab hold of a vantage point on their opponent and bring the abdomen under and forward to eject formic acid on the opponent. While the ants were engaged in this, they would often roll around on the ground and tumble about quite vigorously. Many times the ants fought two against one, three against two, or even, two or three against the same number.

Normally this fighting went on until one or often both of the fighters (or more, depending upon the number fighting) were killed or maimed so that it was incapable of offering further resistance. Then the dead or dying ant was usually carried somewhere by the victor. These ants were not carried back to the nests, but apparently were carried into the grass for some distance and then left while the victor either went back to the nest or returned to re-enter the fray. On two occasions it was observed that one ant would flee from another and that the other ant would pursue the fleeing one for some distance, capture and kill it. Normally, however, if an ant succeeded in escaping

from the grasp of another, there was no pursuit.

Favorable Climatic Conditions

After observing the ants over a long period of time and noting their behavior under different climatic conditions, their "shade-loving, cold weather" preferences could be noted.

The nests were found only in the shaded areas of the insectary yard. All the nests on the south side were located in areas well shaded by mulberry bushes and protected from the sun's rays by being along the north wall of a house.

The ants themselves tended to stay in the shade as much as possible. Wherever it seemed possible, the trails were stretched through grass or weed patches and avoided the barren sunny stretches. However, their trails did extend for long distances across these places. Generally in these cases, activity was greatest in the early morning, late evening, or on cloudy days when the direct rays of the sun did not strike on the ground. Quite often there were shaded "resting places" along the trails. At various points along the trails large numbers of ants could be found clustered under small piles of leaves, in rank growths of weeds or grass, under boards and rocks, or in shaded depressions. Both those ants coming from and returning to the nest stopped at these places. It could not be determined whether all the ants stopped in these places, or which segment of the workers did, if only portions of them did.

The temperatures that appeared to be most favorable for

stimulating the ants to their greatest activity were on the low side as has been reported in the literature. Workers were observed moving about on days when the air temperature was 30° F. and the soil at the surface was just above freezing. The most favorable temperature seemed to be between 65° and 75° F. A high relative humidity also favored the ants' activity. The greatest activity could be observed on cloudy, overcast days with the temperature around 70° F. On days when there were intermittent showers, they would cease activity soon after the raindrops started hitting the ground, but return almost immediately after the rain had stopped. On days when there was heavy rain, they would remain in the nests for a longer period.

Foraging Behavior

In foraging, P. imparis seemed to move mainly along established routes or trails in large numbers. Apparently individual ants strayed for short distances from these main trails in search of food. These trails extended for great distances. One was traced for a distance of 58 feet from the nest site. Another was extended 63 feet. These trails were in general the shortest distance between two points except for the tendency of the ants to stay within shaded areas.

Under favorable conditions the ants moved swiftly along their routes. The ants appeared to travel in small groups of three or four, with a short distance between groups. The movement along the trails was in short spurts followed by a period

of standing still, or of irregular movement, and much movement and tapping of the antennae. Usually the ants stopped and exchanged antennal tappings or movements upon meeting fellow workers coming from the opposite direction.

The trails appeared to be narrow and the ants were seldom seen traveling side by side, but rather one behind the other and in exact "follow-the-leader" style. There appeared to be alternate branches and approaches to objects, but this was a matter of two or more choices and not a wide pathway permitting random movement over it. An exception to this traveling along trails occurred when ants were moving up to join battle. They seemed to spread out as they approached the scene of the battle. (Plate III, fig. 1; Plate IV, fig. 2)

Food Materials

These ants were seen to carry in many types of food materials. Sweets, such as sugar and pollen, were very attractive to them and they eagerly carried off any and all they found. Workers could be seen visiting the various flowers, mostly dandelions, and obtaining nectar from them. Plant sap exuding from bruises or cuts on the plants or their fruit was also gathered. A few ants were observed carrying mustard seeds, but it is not known that they utilized them as there were many scattered around the nest site as though they had been dropped there. Ants coming in and out of the opening paid no attention to the seeds.

Dead insects, if small enough, were carried bodily into the nest, or if too large then the workers gathered about it and brought it in in pieces. The ants were also observed feeding on a small, dead nestling bird. Aphids, leaf hoppers, male ants, and other small live insects were carried bodily into the nest by the ants. Aphids were tended to a large extent. In some cases individual ants visited aphids scattered about on different plants and in other cases a very large aphid colony concentrated on two or three plants close to each other was visited by a stream of ants to and from the nest.

SUMMARY

Although there is a considerable amount of literature pertaining to territorial behavior among the vertebrates, and especially among the birds, the literature on invertebrate territorial behavior is not extensive.

Observations were made on colonies of Prenolepis imparis (Say) to study their territorial behavior. Other species of ants studied as to their interactions with P. imparis were Leptothorax pergandei Emery, Crematogaster lineolata (Say), C. minutissima missouriensis Emery, and Solenopsis molesta (Say).

Daily observations were made during the fall of 1953 and the spring of 1954. During the winter months observations were made only on a few of the mild days.

It appeared that each colony of P. imparis (Say) studied

maintained a territory. The boundaries of these territories were not rigid and distinct but faded into each other and shifted. Territories were determined by placing vials containing sugar at various localities within the area of study. The main foraging trails and nest sites of the P. imparis remained constant and were vigorously defended against the attacks or intrusions of other colonies of P. imparis. Trails of P. imparis were not observed to cross. Other species of ants were tolerated, probably the result of differences in food habits and behavior.

Different types of fighting or antagonistic behavior of the ants were noted. These ranged from simple pushing or "nudging", through "snapping", "riding", to all-out-fighting.

P. imparis was most active on cool, cloudy, or humid days, and activity was increasingly apparent when two or three of these climatic conditions occurred in combination. Temperatures around 65° to 75° F. appeared to be the most stimulating and a high relative humidity, especially after a rain, greatly increased activity. The direct rays of the sun were avoided by the ants as much as possible. Foraging peaks of P. imparis occurred at a distinctly lower temperature than those of the other species studied.

When traveling along the main foraging trails the workers of P. imparis appeared to move in small groups of three or four. These groups always followed one behind the other and the ants within the groups were not observed traveling side by side.

P. imparis utilized a large variety of food materials.

The workers were observed feeding upon or carrying into the nests sugar, pollen, nectar, plant saps, seeds, live and dead insects, a small nestling bird, and aphid secretions.

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TERRITORIAL BEHAVIOR IN THE ANT PREMOLEPIS IMPARIS (SAY)

by

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AN ABSTRACT OF

A THESIS

submitted in partial fulfillment of the

requirements for the degree

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Department of Entomology

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OF AGRICULTURE AND APPLIED SCIENCE

1954

This study was undertaken to determine whether ants, and in particular Prenolepis imparis (Say), exhibits territoriality and to what extent has their territorial behavior developed.

Although the literature pertaining to territorial behavior among the vertebrates, and especially the birds, is quite extensive, very little data have been published concerning invertebrate territorial behavior.

Observations were made on five colonies of Prenolepis imparis (Say) along with two colonies of Leptothorax (Dicothorax) nerrandei Emery, two colonies of Solenopsis (Diplorhoptrum) molesta (Say) and single colonies of Crematogaster (Acrocoelia) lineolata (Say) and Crematogaster (Orthocrema) minutissima missouriensis Emery. P. imparis was the species studied and the other species were observed to determine their interactions with P. imparis. The study was conducted on the southern portion of the grounds of Insectary Number One. All of the colonies were located in this area and the P. imparis colonies were all situated so that they received the shade from a house adjacent to the south. This area was further shaded by a row of volunteer mulberry sprouts along the south edge of the property.

Because of the hot, dry summer and early fall the ants were not active but were stimulated into activity by the application of water to the insectary grounds for a period of

three days. The ants were observed for the first time that fall on the third day of watering. Devices such as pins, thoothpicks, stakes, strings, and colored ink were used to mark the ants and their trails so that their activity and behavior might be more easily studied and recorded. Vials filled with sugar were placed at various locations throughout the area and records were kept as to which colony utilized each vial and the location of each vial in regard to the colony utilizing it and to the other colonies close by. These vials were also used to collect ants which were then transferred to locations within the areas utilized by other colonies, especially to the nest sites of those colonies. These vials were also placed among the nest sites of the varbus colonies in order to induce them to cross into the territory of another colony in search of food.

Climatological data were recorded in order to determine the influence of the weather factors upon the activity and behavior of the ants.

With the exception of a few days, observations were made daily during September, October, first two weeks of November, last three weeks of March, April, and May. During the winter months observations were made mainly on the mild days. These observations were recorded and the foraging trails, locations of vials, areas utilized by the ants, locations of areas and objects visited by the ants, and other data were recorded on forms made for this purpose.

It appeared that in the cases observed the ants did maintain a territory. Each colony of P. imparis studied maintained and defended a certain area which they used for food supply. This area was defended against ants of other colonies of the same species but ants of different species were tolerated. This tolerance appeared to be based upon differences in food habits and behavior patterns of the various species. There are probally no clear-cut of distinct boundaries between these territories but rather that they merge into each other and shift from time to time. The nest sites and the main foraging trails constituted the center points of these territories. The boundaries lay in areas between the main foraging trails and nest sites of the colonies.

The most favorable conditions at which P. imparis reached its peak of foraging activity were low temperature, 65-75°F.; high humidity ; and cloudy or overcast skies.

The workers of P. imparis tended to keep within the shade, and the main foraging trails followed shaded routes as much as possible. When traveling, the workers went under leaves, boards, in small depressions, etc., and they congregated in such places along the trails.

Fighting among the ants was noted on several occasions. Battles were observed around vials of sugar placed among the colonies. The fighting or antagonistic behavior varied in degrees of ferocity.