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Distribution, Abundance, and Behavior of the Inquiline Ant *Leptothorax diversipilosus*[1,2]

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ABSTRACT

A field survey of the distribution of *Leptothorax diversipilosus* Smith in Washington was conducted from June 1970 to August 1971. Laboratory studies were conducted from October to January in 1969, 1970, and 1971. *L. diversipilosus* was previously considered a rare ant guest in the nest of its only known host, *Formica obscuripes* Forel. *F. obscuripes* nests were collected from the eight major physiographic areas in Washington and sorted in the laboratory. The inquiline was found in 30% of the nests sampled, and *F. haemorrhoidalis* Emery was established as a new host record. Only northwestern Washington yielded negative results, although 30 *F. obscuripes* nests were collected from this area. Throughout the remainder of the State, *L. diversipilosus* maintained the same range as its host, and it occurred under a wide variety of vegetative, climatic, altitudinal, and soil conditions.

Laboratory studies indicated that *L. diversipilosus* is a xenobiont in the nest of *F. obscuripes*. *L. diversipilosus* was never found living alone and was unable to survive without its host. Brood was reared separately from the host brood, although the adults moved freely throughout the host nest. *F. obscuripes* usually treats the inquiline with indifference and occasionally with slight hostility. However, observations indicated *L. diversipilosus* can obtain regurgitated food from their hosts either directly from a worker or more often from two workers as they exchanged food. Mating, transportation of adults and larvae, trophallaxis, grooming, and aggressive behavior are described.

Marion R. Smith (1939) described the inquiline ant *Leptothorax diversipilosus* Smith from 2 workers and an ergatogyne female collected by Falconer Smith at Fort Lewis, Wash. They were found in a nest of the western thatching ant, *Formica obscuripes* Forel. On Aug. 3, 1940 W. W. Baker found 2 colonies of *L. diversipilosus* at Spanaway, Wash. One was within a nest of *F. obscuripes,* and the other was an independent nest in some decayed wood near a colony of *F. obscuripes*. Individuals were sent to Smith who subsequently described the ergatoid male and the dealate female (Smith 1956). According to Smith, the inquiline ant *Formicoxenus nitidulus* (Nylander) of Europe and Asia is similar in habitat, morphology, and biology to *L. diversipilosus*. Both species have the same castes and intermediate forms; both live within nests of *Formica* sp. and have almost identical habits. Smith believed that *F. nitidulus* is the more highly specialized, because of a prominent spine beneath the postpetiole. Wheeler (1910) and Wilson (1971) gave a detailed account of the biology of *F. nitidulus*.

According to Snelling (1965) another rare inquiline ant, *Leptothorax hirticornis* Emery, is basically similar to *L. diversipilosus* in habitat, structure, and biology, and is also recorded from nests of *F. obscuripes*. Snelling established *F. intergroides intergroides* Emery as a new host for *L. hirticornis,* and he described the female and ergatoid male. There is no detailed account of the biology of *L. hirticornis* or *L. diversipilosus*. However, the distribution, life history, and ecology of the host ant, *F. obscuripes,* was worked out in detail by Weber (1935).

During 1964 several colonies of *L. diversipilosus* were found in eastern Washington near Pullman. Additional investigations showed *L. diversipilosus* to be quite common in nests of *F. obscuripes* in this area. This discovery indicated the inquiline ant might be widely distributed, and in 1970 a distributional study was conducted to determine host specificity, abundance with respect to host frequency, and the relationship of these to environmental parameters. Colonies of *L. diversipilosus* are composed of workers, females, forms intermediate between workers and females, and workerlike wingless males. We attempted to detail the life history, habits, and population data for these different castes, and to determine the nature of the relationship of *L. diversipilosus* to *F. obscuripes*. Laboratory nests provided information concerning food habits, biology, and behavior.

MATERIALS AND METHODS

This study was conducted July 1969 to March 1972. The survey of Washington was from June to September 1970, and from February to August 1971. Most of the laboratory studies were conducted during the months of October to January.

Survey Methods.—Washington has been divided into 8 major physiographic areas on the basis of soil, vegetation, climate, and geography (Highsmith 1962, Franklin and Dyrness 1969) (Fig. 1). The distribution of *L. diversipilosus* was determined by locating nests of its host, *F. obscuripes,* within these areas. Depending on abundance, up to 10 *F. obscuripes* nests were collected during each trip to an area. If the inquiline was found during laboratory sorting, no further collections of *F. obscuripes* were made from that area. Otherwise, further sampling was conducted until either *L. diversipilosus* was found or until 3 trips to the area were negative. Three negative trips was also the criterion used in limiting the search for *F. obscuripes* if they were not found in an area.

Typically, *F. obscuripes* constructs a prominent conical thatchwork mound, characteristically made of small twigs and grasses (Weber 1935) (Fig. 2).

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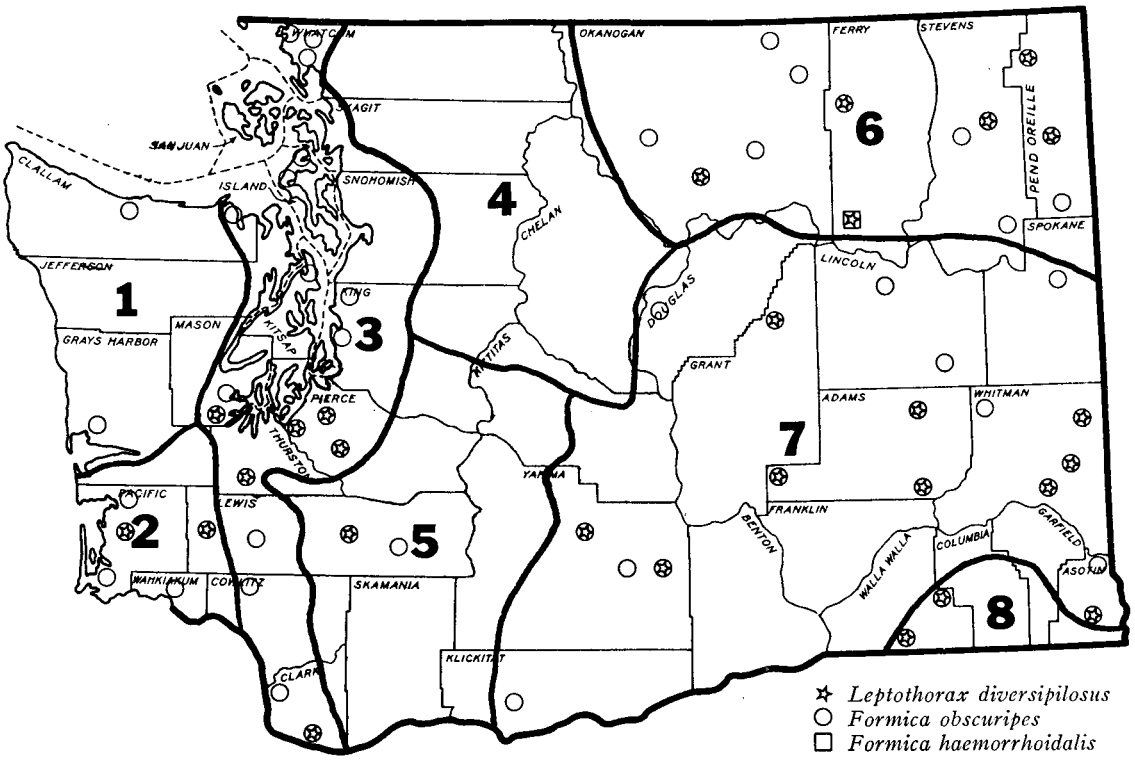

FIG. 1.—Known distribution of *L. diversipilosus* in Washington. 1, Olympic Peninsula; 2, Coast Ranges; 3, Puget Trough; 4, Northern Cascades; 5, Southern Washington Cascades; 6, Okanogan Highlands; 7, Columbia Basin; and 8, Blue Mountains. Modified from Franklin and Dyrness (1969).

Other species of *Formica* build mounds, and occasionally these were collected and sorted to see if *L. diversipilosus* was host specific. Three techniques were used to locate *F. obscuripes* nests. First, areas on the edge of fields, in open meadows, and along railroad beds were searched. A more effective technique was to question the local inhabitants of the location of large ant mounds. The best method was to sight nests along the roadside while driving. During late winter and early spring large *Formica* mounds were easily seen due to lack of concealing vegetation. Later, the taller, greener, thicker grass, which characteristically surrounds the nest, was a very distinctive indicator.

Field Collections.—Locality, date, weather, local vegetation, soil, terrain, and nest parameters were recorded upon locating a *Formica* nest. The top of the nest and the immediate area were searched for inquilines and associated arthropods.

The nest was shoveled into 25×61-cm polyethelene bags. The bags were numbered consecutively as filled, so the top part of the nest was in the 1st bag, and the bottom part of the nest was in the last. Each bag was sealed, and the colony number was recorded. Although it was often difficult to excavate the entire nest, the brood chambers, thatch mound, and most of the workers were always collected. If 2 mounds were situated close together, both were excavated to increase the probability of finding *L. diversipilosus*. The bags of nest material were then transported to the laboratory for sorting.

Since more bags were brought back to the laboratory than could be sorted during a short time, they were temporarily stored at 1°C. All bags remained sealed until sorted, and incompletely sorted bags were resealed and returned to the cold room. Records were kept of the cold-storage time for each bag.

Each bag was sorted by pouring some of the ants and nest material into a 25×40×4-cm pan. A 75-w light bulb was placed immediately above the pan to aid vision and to stimulate movement of ants and other arthropods in the pan. *L. diversipilosus* was readily detected because of its smaller size and slower movements. Small hollow twigs were broken open, and clumps of roots and twigs were pulled apart in search of *L. diversipilosus* colonies. A wet camel's hair brush was used to remove brood and adults unharmed from the sorting pan.

Host ants and *L. diversipilosus* not used in laboratory studies were preserved in either Kahle's solution or in 70% alcohol. Many adult and immature arthropods collected during sorting were preserved for later identification. Observations on the host ants, on *L. diversipilosus,* and on associated arthropods were recorded with the appropriate bag number. Later this information was correlated with the approximate depth within the *Formica* nests. A Berlese funnel was

not used because of potential brood damage and loss of behavioral and nest data.

Laboratory Studies.—A key was constructed to identify the castes and intermediates present in a *L. diversipilosus* colony. *L. diversipilosus* has ergatogynes or morphological intermediates forming a graded series between the worker and queen castes. Males are ergatomorphic with normal genitalia and a wingless, highly workerlike body. Population data for *L. diversipilosus,* including abundance and colony composition, were determined from all specimens including those used in the laboratory studies.

Several types of artificial nests were used to maintain and observe ants in this study. Clear 26×9-cm plastic containers with tight-fitting lids and a screened hole to prevent 100% humidity were often used. A ring of Vasoline® applied near the top of the container prevented ants from escaping when the lid was removed. All nests were kept at room temperature under an 18-h photoperiod. Distilled water was added to pieces of plaster-of-paris to retain moisture inside the container. A vertical nest was used when *F. obscuripes* and *L. diversipilosus* were placed together.

Most observations were through a Bausch & Lomb Stereozoom dissecting microscope mounted on a Bausch & Lomb Stereozoom stand with a rotatable arm. This method provided continuous 360° rotation and made it possible to follow a single ant under high power. Red sheets of 0.2-mm Plexiglass and red light bulbs were used to reduce disturbance to the ants from illumination. When the brood was concealed from view by nest material, 2 techniques permitted observation through a microscope from beneath. Dual prisms were set up under the container allowing observations of a limited area. Often the microscope was inverted on its stand and pulled under the container so that observations could be made from a supine position. Observations and experiments were conducted during different hours of the day for varying lengths of time for a total of over 200 h of observations during a 19-month period.

L. diversipilosus was usually maintained in a container separate from *F. obscuripes* to facilitate manipulation and observation. A large variety of food was periodically introduced, and corresponding behavior was observed. Interactions with *F. obscuripes,* including food transfer and nest relationships, were observed. Colonies of *L. muscorum* (Nylander) and *L. diversipilosus* collected from the same *F. obscuripes* nest were placed in a container together. Aggression, territoriality, and other interspecific interactions were observed.

RESULTS AND DISCUSSION

Distribution of F. obscuripes *and* L. diversipilosus. —From 8 physiographic areas of Washington (Fig. 1), 101 *F. obscuripes* nests were collected. No nests were collected from the Northern Cascades, and only a few were collected from the Olympic Peninsula and the Southern Washington Cascades. The higher elevations in these areas were inaccessible. The greatest number of nests per area, based on number located and searching time per nest, occurred in the Okanogan Highlands, Columbia Basin, and the southern portion of the Puget Trough.

F. obscuripes nests were found under a wide variety of soil, vegetation, and climatic conditions. They were usually situated on flat terrain (86%) and in areas exposed to the sun (94%). Most nests were surrounded by tall grass and were on the edge of fields or along roadsides. Nest altitude averaged 1400 ft (range 50–3700 ft). The average dimension of all the nests was 22 cm high, 45 cm diam above ground, 38 cm deep, and 37 cm diam below ground.

Out of 101 of the *F. obscuripes* nests sampled in Washington, 30 contained at least one adult *L. diversipilosus* (Fig. 1). The inquiline was found in every physiographic area except the Olympic Peninsula and the Northern Cascades areas in which only 2 *F. obscuripes* nests were found. In only 1 area of high host density, the northern portion of the Puget Trough, was *L. diversipilosus* not found.

On June 19, 1971, 3 ♂, 1 winged female, and 6 workers of *L. diversipilosus* were collected 1 mile N of Keller, 2500 ft, Ferry County, Wash., from a mound nest of *Formica haemorrhoidalis* Emery. Although a new host record, *F. haemorrhoidalis* is closely related to *F. obscuripes* and builds similar mounds of thatch (Gregg 1963). Both *L. hirticornis* and *F. nitidulus* have been collected from nests of more than one host species of *Formica.* A search through nests of related mound building species of *Formica* would probably establish additional host records for *L. diversipilosus.*

The distribution of *L. diversipilosus* was approximately the same as that of its principal host, *F. obscuripes.* Nests which contained the inquiline did not significantly differ from other *F. obscuripes* nests regarding exposure to sun, altitude, or nest size.

Colony units of *L. diversipilosus* were usually found just below the dry thatchwork mound and above the soil-nest interface of the host nest. They were found within 2 major types of nests. Large colony units, including all castes in addition to brood, were found within clumps of roots and smaller twigs mixed with soil (Fig. 3, 4). Some of these nests were also mixed with considerable amounts of decayed leaves and other vegetation. A typical nest clump was 24×24×12 (Fig. 3). Older larvae were scattered throughout the clump, while eggs and young larvae were often found together in the lower part of the nest (Fig. 4, 6). Many similar clumps unoccupied by ants occurred within the host nest, and it is assumed that *L. diversipilosus* only had to modify them as nests. Smaller colony units of *L. diversipilosus* were found within small hollow twigs about 48 mm long (Fig. 5). These twigs were occasionally part of the *F. obscuripes* thatch mound and were often part of the many twigs found within the host's brood chamber. Adults were observed scraping the inside surface of these twigs with their mandibles, but it is doubtful that they excavate entire twigs since many hollow, unoccupied twigs were found.

Many colony units, defined as separate nest clumps

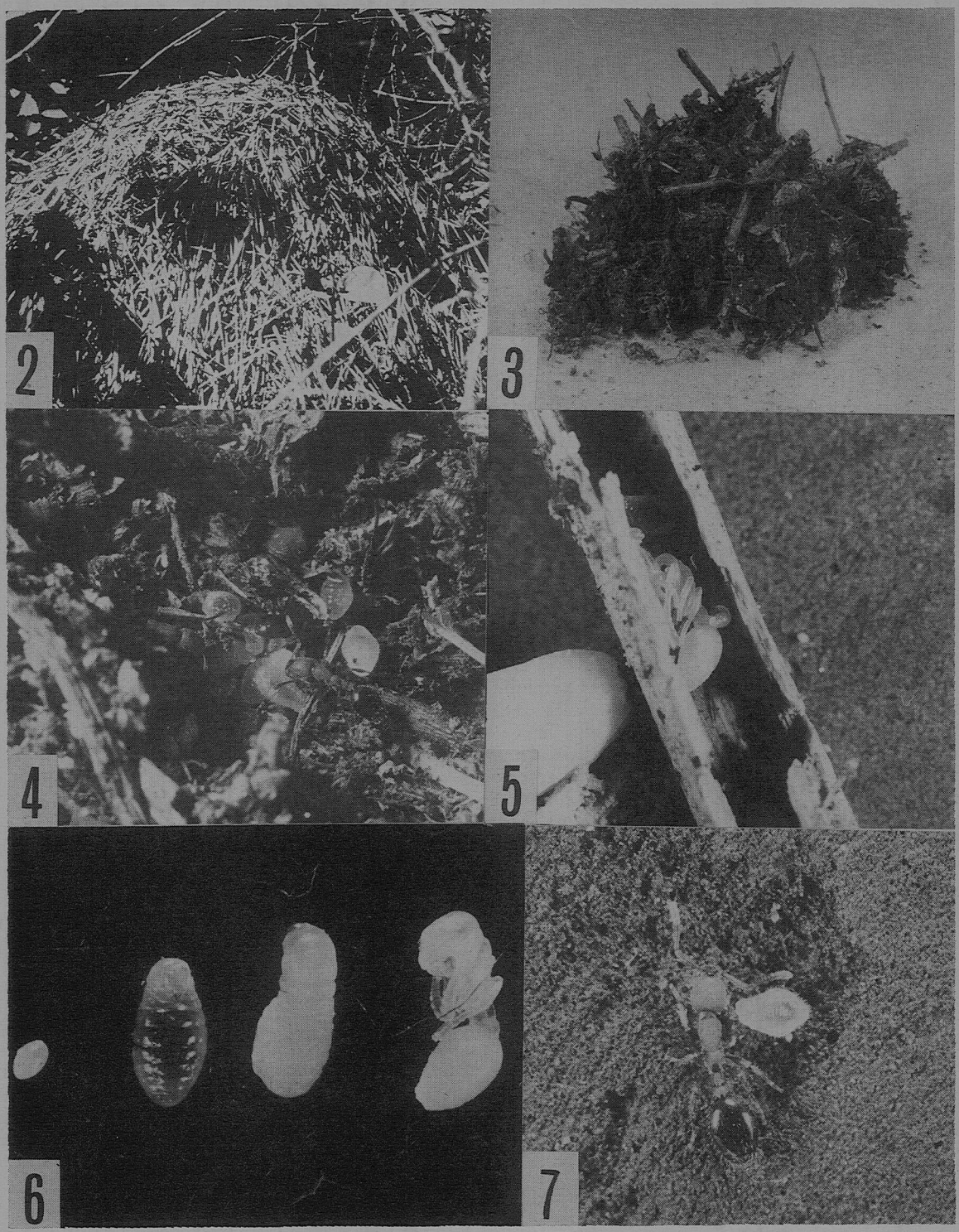

FIG. 2.—Nest of *F. obscuripes* with prominent thatchwork mound of twigs and grasses.
FIG. 3.—Typical nest clump of *L. diversipilosus* comprised of twigs, roots, and soil.
FIG. 4.—Nest clump opened exposing *L. diversipilosus* adults and brood.
FIG. 5.—Hollow twig which was split exposing *L. diversipilosus* brood.
FIG. 6.—Egg, young larva, mature larva, pupa of *L. diversipilosus*.
FIG. 7.—Adult *L. diversipilosus* with larva.

or hollow twig nests containing brood, were found within the larger host nests. The larger clumps containing brood may have been comprised of even smaller units. One such clump, observed for 5 months in the laboratory, consisted of 3 separate brood chambers, and little interaction was observed between adults from these separate chambers. During laboratory sorting mixing occurred within many of these separate clumps, so analysis of smaller colony units could not be made.

Adult *L. diversipilosus* were collected from every part of the host nest (Fig. 7). Winged females and males were most often found near the surface of the host nest, while the queens, ergatogyne females, and workers were found with their brood deeper in the nest. Often the nest clumps containing brood and adult *L. diversipilosus* were covered with *F. obscuripes* adults. These host ants were even found within the larger nest clumps, especially when they were near the host brood chamber. Inquiline brood was isolated, however, by the small galleries separating it from the host ants.

Colony Composition.—An attempt was made to determine colony composition based on individuals collected during laboratory sorting. It was difficult to collect the entire *L. diversipilosus* colony or all colony units for each host nest and often only a few adults were found. For this reason most of the data selected for discussion are from the nests containing large numbers of *L. diversipilosus*.

The following key to castes of *L. diversipilosus* based on original descriptions by Smith (1939, 1956) was used to determine colony composition:

1. Antennae 11-segmented 2
   Antennae 12-segmented; mandibles greatly reduced; genitalia concealed; vertex with small indistinct ocelli; 2.5–2.75 mm .....*ergatomorphic male*
2. Vertex with ocelli 3
   Vertex without ocelli; eyes rather small; base of gaster dark brown; 2.6–2.8 mm .....*worker*
3. Vertex with three small ocelli; body dark; gaster almost entirely black; 3.1 mm ...*ergatogyne female*
   Vertex with 3 distinct ocelli; eye larger and more convex; thorax queenlike; a distinct constriction on each side of the body anterior to the insertion point of the front pair of wings; wings absent; 3–3.5 mm .....*dealate female*
   Same as foregoing, wings present .....*virgin female*

Fluctuations in colony composition which may be regulated by seasonal influences are known for 7 months, February–August (Fig. 8). Total *L. diversipilosus* per *F. obscuripes* nest ranged from 1 to 3649; $\bar{x} = 190$ (Table 1). A total of 6455 adults and brood was found during this study; 86% were adults and 13% were larvae. Among the adults, 76% were workers, 18% ergatogyne females, 2.5% dealate females, 1.5% winged females, and 2% ♂. The total number of individuals was comprised of many separate colony units inhabiting the host nest. When these colony units were well defined, they were analyzed, and their adult ratios were similar to the total for the nest. However, the ratio of brood to adults was much higher with some units containing 79% brood. In the largest nest sorted, there were at least 10 colony units within clumps of twigs and roots and 10 separate colony units within hollow twigs. The average colony unit within these clumps contained 35 adults and 26 larvae. The hollow-twig nest had lower averages of 15 adults and 11 larvae.

Life Cycle.—Colonies of *L. diversipilosus* were found the year around within host nests. Adult castes except for males and virgin females overwintered and did not become active until early spring. During the spring and summer many teneral workers and ergatogyne females were found in the nests. Some of these adults were maintained in the laboratory for 202 days. Males were short lived; 27 were collected June 23, 1970, and survived for 1 week. Winged females usually shed their wings within 2 days of being placed in a laboratory nest and could no longer be readily identified, limiting further observations of this caste. Larvae of small to medium size overwintered, but it was not determined whether larvae from additional eggs laid during the spring developed into males and virgin females by early summer.

Three separate nest clumps containing *L. diversipilosus* adults and brood were maintained in the laboratory beginning Aug. 27, 1970, and colony development and decline were observed for 5 months. The 3 nests contained a combined total of 7 eggs, 11 larvae, 1 pupa, and 38 adults when first observed. Eggs were laid in clumps of 2–5 during the first 2 weeks, and most hatched into larvae 2 weeks later. The older larvae grew rapidly at first, and a few pupated, but inadequate food or other conditions caused a slow colony decline after the first 3 weeks. The duration of the pupal stage was 9–16 days. Pupae were separated from the larvae, although they were still kept within the brood chamber. As the colony began to decline, adults consumed larvae, and the surviving larvae developed more slowly. Some larvae managed to survive for 110 days before they were eaten, usually just prior to pupation.

No mating in the field was observed, but winged females and males were collected near the surface of host nests in June. Since the males are apterous, mating among members of the same colony probably takes place in or near the nest at this time. The inseminated winged queens then either disperse in search of new host colonies, or else they return to the same nest. According to Wilson (1963) intracolonial mating eliminates loss of virgin reproductives that normally occurs during dispersal and insures that queens will be mated. Colonies contained 1–55 queens, comprising 2.5% of all adults collected. Because of the occurrence of multiple queens within a host nest, the progeny of several queens probably breed, reducing the amount of inbreeding.

Intraspecific Behavior.—*L. diversipilosus* adults preferred darkness. They always concealed their brood and quickly moved them to dark moist areas when exposed to light. A thriving colony remained almost entirely within the confines of its clump or twig nest. Only occasionally were adults observed outside their nests. The brood chamber was beneath the adults in the nest clumps and could be viewed from below

through the plastic container. When too much light disturbed the brood chamber, the adults blocked the light with small particles of soil which they stuck together. When the colony declined, individuals ran about the bottom of the container. *L. diversipilosus* never left *F. obscuripes* host nests, and their sensitivity to temperature and humidity indicates a low survival rate if they were to do so. Mortality was very high in the laboratory except at 20–28°C.

Mating occurred when winged females and males from many colony units within 1 nest were placed together. The male climbed on top of the female with his pronotal legs resting on her metanotum. Its gaster was curved over the female's gaster to the right to contact the genitalia. When the female ran, the male was carried along. Mating usually lasted 2–3 min. Males tried to copulate with ergatogyne females and workers, but no eggs were found, and it is not known whether there was sperm transfer.

When a colony was first established in the laboratory much time was spent by adults in exploratory behavior. The entire nest container was searched, and much energy was spent in ants' attempted escapes. When brood was present, however, most adults remained in the brood chamber and constantly groomed and attended the larvae. While resting in the brood chamber, 4 or 5 adults congregated and begin grooming themselves and one another. Although several types of interactions were observed, *L. diversipilosus* appeared timid, preferred moist concealed conditions, and remained relatively inactive.

Workers often transported other workers about in a characteristic position. One worker clasped another by the mandibles just behind the head. The worker became inactive after arching its abdomen over the dorsal surface of the carrier ant. After being carried for several minutes and then being released, the worker moved away apparently unharmed. Both workers and ergatogyne females transported small and medium larvae between their mandibles.

Several attempts were made to determine the diet of *L. diversipilosus*. A large variety of foods and media was introduced in the laboratory with limited success. On many occasions both workers and ergatogyne females fed on unstrained honey and diluted table sugar. When feeding, their abdomens vibrated vertically 140 vibrations/min. On one occasion 7 workers ate together upon one piece of sugar while about 20 workers remained in the vicinity. One queen also was observed feeding on the sugar. Several workers fed on malt extract agar and agar agar, spending from 5 to 16 min vigorously brushing their mouth parts against the agar.

L. diversipilosus avoided host tissue, host larvae, other ant larvae, dead insects, and artificial media containing amino acids. However, when a colony began to decline, they readily attacked and devoured their own brood. Over 20 workers of one declining colony attempted to eat a single larva at the same time. A large larva was suspected of devouring some smaller nearby larvae when tissue from a partially eaten larva was observed in its mandibles. This larva was still feeding the next day. Essential nutrients for a thriving colony were not discovered, and gradually most of the adults and larvae in laboratory nests starved.

When sorting through a host nest, a clump of dead adult *L. diversipilosus* was found in a section of dirt which appeared to be a refuse area. Over 30 dead ants in various stages of decay were found. The dead were stuck together by a fungus and were partially

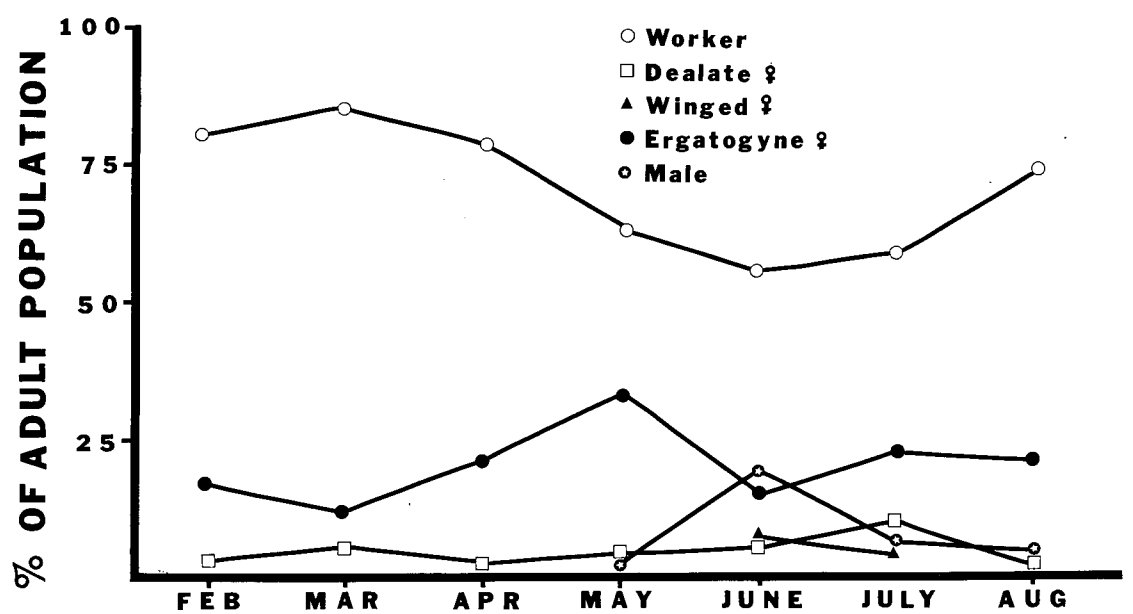

FIG. 8.—Fluctuations in ratio of castes in *L. diversipilosus* colonies. (Data from largest colony collected each month.)

Table 1.—Composition of the 14 largest colonies of *Leptothorax diversipilosus* collected in Washington.

Date	Worker	Ergato-gyne female	Dealate female	Winged female	Ergatoid male	Total brood	Total in colony
3-7-69	94	36	15	7	8	0	160
27-8-69	152	43	6	0	6	0	207
23-6-70	1	2	3	0	27	0	33
27-8-70	38	4	2	0	0	0	44
20-2-71	2353	492	55	7	4	738	3649
6-3-71	452	61	0	25	0	3	541
27-3-71	116	39	1	0	0	0	156
11-4-71	638	175	13	1	0	135	962
11-4-71	30	13	3	0	0	0	46
11-4-71	45	4	0	0	0	0	49
13-5-71	64	35	3	0	2	0	104
13-5-71	42	2	0	0	0	0	44
19-6-71	151	40	14	17	54	1	277
4-7-71	11	9	16	32	8	0	76
Total	4187	955	131	89	109	877	6348

buried in the clump of dirt. In the same area another group of more than 15 dead larvae was found in various stages of decay. The host nest contained over 3600 *L. diversipilosus,* and it is possible that injured and dead members were removed to this area.

Trophallaxis occurred between adults after feeding on diluted table sugar and honey. One worker tapped the other with its antennae, and a liquid exchange soon followed. Methylene blue dye was added to the honey as an aid in observing food transfer. Later, several larvae had darkened meconia, but no dissections were made to determine if they had taken in honey. Adults were observed "licking" the entire body of the larvae, and they may have obtained an attractive liquid in the process. The food fed to the larvae by adults was not determined, although the larger larvae were fed frequently.

L. diversipilosus, when placed with adults from other colonies of the same species, was seldom aggressive. Adults from each colony unit remained close to their own brood chambers and usually avoided interaction with one another. Occasionally a worker was attacked by one or more other workers and driven or dragged from the area and then released apparently unharmed. The attacked worker was usually dragged by its pedicel and one or both antennae.

Interspecific Behavior.—L. muscorum was collected from the same *F. obscuripes* nests as *L. diversipilosus.* Brown (1955) gave an account of the ecology of *L. muscorum,* which is abundant in the area of Pullman, and it nests in hollow twigs within *F. obscuripes* nests. For 3 months observations were made of a container containing colonies of both *L. diversipilosus* and *L. muscorum.* At first *L. muscorum* completely avoided contact with *L. diversipilosus* and quickly retreated whenever the latter approached. Although both species of *Leptothorax* could survive in a *F. obscuripes* nest, *L. diversipilosus* removed from its host began to slowly decline while colonies of *L. muscorum* thrived. Gradually the inquiline adults weakened and were attacked by *L. muscorum.* Three *L. muscorum* workers were observed killing a *L. diversipilosus* worker. No workers aided the dying ant, although some were in the area. Many dead inquiline workers were found with parts of their antennae missing, so the 2 species had to be separated. *L. diversipilosus* showed no territorial behavior and did not prevent *L. muscorum* from entering any area except the brood chamber.

In a vertical nest, about 50 *L. diversipilosus* were placed with about 40 *F. obscuripes* adults and brood. *F. obscuripes* was constantly reshaping the tunnels, causing the inquiline to move its brood and occupy new sites. Finally 4 small colony units of *L. diversipilosus* with separate brood chambers became established. *L. diversipilosus* kept their brood in areas where the host ants had not excavated, and they made small tunnels in the loose soil to the main host tunnels.

When an individual of *L. diversipilosus* was approached by the larger *F. obscuripes,* it quickly stopped and lowered itself to the substrate. The *F. obscuripes* would stop also, touch the inquiline with its antennae, and quickly pass on. The inquiline would then raise itself and continue in another direction. Occasionally the host workers made an aggressive or threatening move toward the inquiline. One host worker grabbed an inquiline by the pedicel and carried it about the nest. Eventually the inquiline was released, and the next day it was found dead in the container. *L. diversipilosus* traveled slower than its host and was easily overtaken. Often by merely halting when a host worker was near, the inquiline avoided a confrontation.

One *L. diversipilosus* worker fed on liquid food that was being regurgitated between 2 *F. obscuripes* workers. The worker had been concealed next to a group of *F. obscuripes* workers. Honey was added to the nest, and many host workers fed on it and exchanged this food with others. *L. diversipilosus* quickly darted out among 2 workers who were in the process of exchanging honey. The inquiline crawled over the abdomen of 1 worker and came up from under the same worker eventually positioning itself right below the mouth parts of its hosts. During this time the 2 workers continued to exchange

honey without appearing to be disturbed by the inquiline. The latter quickly touched the 2 workers with its antennae and fed from the exchanged liquid for about 3–4 sec, then it quickly darted back to the safety of some nearby twigs. The same *L. diversipilosus* worker fed twice more for about 2 sec while different host workers were exchanging food close by.

Periodically, *L. diversipilosus* approached a host worker and touched it on the abdomen with its antennae. If the worker turned around, the inquiline quickly retreated. One *L. diversipilosus* worker was fed directly from the mouth parts of a host worker. *L. diversipilosus* remained in the same area near a group of host workers for over ½ hr. Whenever 2 workers began to exchange food close by, the inquiline darted out from concealment and attempted to feed. The next day two inquiline workers found the source of honey and began to feed directly. Thus even though *L. diversipilosus* feeds on regurgitated food it is also capable of feeding directly on honey. In the field, essential proteins and other nutrients are probably obtained from the *Formica* hosts which are predaceous on other insects, providing liquid food which *L. diversipilosus* would have great difficulty in acquiring independently.

L. diversipilosus is a xenobiont, specialized for life inside the mound nests of *F. obscuripes*. These guest ants keep their brood strictly separated from the host ants, yet they move freely among their hosts as adults, obtaining food from them by regurgitation. *L. diversipilosus* appears to be dependent upon its host for survival, obtaining both food and protection from the environment. This form of symbiosis does not appear to be beneficial or harmful to colonies of *F. obscuripes*.

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REFERENCES CITED

Brown, W. L., Jr. 1955. The ant *Leptothorax muscorum* (Nylander) in North America. Entomol. News 66: 43–50.

Franklin, J. F., and C. T. Dyrness. 1969. Vegetation of Oregon and Washington. USDA Forest Service Research Paper PNW-80. USDA Pacific Northwest Forest and Range Exp. Sta., Portland. 216 p.

Gregg, R. E. 1963. The Ants of Colorado. University of Colorado Press, Boulder. 792 p.

Highsmith, R. M., Jr. [ed.]. 1962. Atlas of the Pacific Northwest. 3rd Ed. Oregon State University Press, Corvallis. 168 p.

Smith, M. R. 1939. Notes on *Leptothorax (Mycothorax) hirticornis* Emery, and description of a related new species. Proc. Entomol. Soc. Wash. 41: 176–80.

1956. A further contribution to the taxonomy and biology of the inquiline ant, *Leptothorax diversipilosus* Smith. Ibid. 58: 271–5.

Snelling, R. R. 1965. Studies on California ants. 1. *Leptothorax hirticornis* Emery, a new host and descriptions of the female and ergatoid male (Hymenoptera:Formicidae). Bull. S. Calif. Acad. Sci. 64: 16–21.

Weber, N. A. 1935. The biology of the thatching ant, *Formica rufa obscuripes* Forel, in North Dakota. Ecol. Monogr. 5: 165–206.

Wheeler, W. M. 1910. Ants: Their Structure, Development and Behavior. Columbia University Press, New York. 663 p.

Wilson, E. O. 1963. Social modifications related to rareness in ant species. Evolution 17: 249–53.

1971. The Insect Societies. The Belknap Press of Harvard University Press, Cambridge, Mass. 548 p.

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