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OVERWINTERING AGGREGATIONS OF *LEIOBUNUM PAESSLERI* IN CAVES AND MINES (ARACHNIDA, OPILIONES)

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ABSTRACT

In the forested mountain areas of southwestern Canada, *Leiobunum paessleri* (Roewer) form overwintering aggregations in the twilight regions of moist caves and mines. Each aggregation consists of adults of both sexes and may contain as many as one or two thousand individuals. The opilionids congregate from August to October and disperse from April to May. Colder temperatures seem to increase the density of the aggregations. When dense aggregations are formed (up to 2.6 individuals per cm^2), the opilionids hang by their pedipalps with their legs extended straight down from their bodies. Explanations of the aggregation phenomenon include: optimal temperatures and humidities, reduced desiccation, heat production, increased mating success, and reduced predation. Overwintering mortality factors potentially include cold, desiccation, starvation, predation and disease.

INTRODUCTION

Aestivation and hibernation are mechanisms commonly used by organisms to help them survive seasonally adverse conditions. What is particularly interesting about certain opilionids is that the resting individuals often form aggregations. In arid regions of Mexico, such aggregations are formed in the branches of candelabra cacti (*Leiobunum cactorum*[3]), along the banks of water channels (*Prionostemma wagneri* Goodnight and

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[3] Wagner (1954) listed Roewer as the authority for *Leiobunum cactorum* but searches by C. and M. Goodnight, J. Cokendolpher and ourselves have not found a published description of the species. It is probably a *nomen nudum*.

Goodnight, *Leiobunum desertum* Goodnight and Goodnight, undetermined species) and in hollow lava tubes (undetermined species) (Wagner 1954). In Texas, *Leiobunum townsendi* Weed form aggregations on and in buildings (McAlister 1962) and in cave entrances (Mitchell and Reddell 1971). In central Europe, *Amilenus aurantiacus* (Simon) and other species spend the winter in aggregations in caves (Martens 1978). In this paper we describe the overwintering aggregations formed by *Leiobunum paessleri* Roewer in caves and mines of southwestern Canada and discuss why these aggregations may form.

MATERIALS AND METHODS

Leiobunum paessleri was described by Roewer in 1910 from a male collected in Washington state. Since then it also has been recorded from Alaska, British Columbia, Oregon, California, Alberta, Montana and, possibly, Wyoming (Davis 1934, Kauri 1966, Levi and Levi 1951, 1955, Lindroth and Ball 1969). Recently Cokendolpher (1982) synonomized *L. oregonense* Goodnight and Goodnight with this species.

In 1934 L. J. L. first observed overwintering aggregations of opilionids while prospecting in various mines in British Columbia. However it was not until 1980 that we were able to initiate more formal investigations. Since then we have located several overwintering sites for *L. paessleri* in the mountainous areas of southern British Columbia and Alberta. The characteristics, locations, elevation of entrances (to nearest 50 m) and major tree species of these sites are given below.

Kuskonook Mine.—This abandoned mine (49°21′N-116°44′W) is located on Highway 3A about 6 km north of Kuskonook, British Columbia at an elevation of 600 m. The mine was probably made about 1890 and consists of a single 28 m horizontal tunnel. The entrance is 1.7 m wide by 1.5 m high and is located less than 5 m off the east side of a highway. Because of its accessibility, this mine served as our main study site. Trees near the entrance of the mine consist mainly of Ponderosa Pine along with some Douglas-Fir, Western Larch, Western Red Cedar, Trembling Aspen and Black Cottonwood. (Tree nomenclature follows Hosie 1979.) Overwintering aggregations were first observed in the mine in 1964. During 1981-83 we visited the site 12 times.

Cody's Cave.—This cave is located within Cody Caves Provincial Park, west of Ainsworth Hot Springs, British Columbia. The cave's entrance is 1.2 x 5.0 m at an elevation of 1450 m. The cave passages extend over 100 m into the rock (Hronek 1970). Near the parking area at the beginning of the trail to the cave is a small horizontal tunnel (less than 5 m deep) that also contained *L. paessleri.* The forest in the vicinity of the cave consists mostly of Amabilis Fir with some Douglas-Fir, Western Red Cedar and Western Larch.

North Star Mine.—This mine is at an elevation of 1200 m on the northeast face of North Star Hill—just southwest of Kimberly, British Columbia. The mine was dug prior to 1900 and consists of a single 16 m horizontal tunnel. The entrance is 1.2 x 1.6 m. The trees in the immediate area are almost entirely Lodgepole Pine.

Crowsnest Cave.—This cave is located on the north side of Crowsnest Lake, Alberta at an elevation of 1350 m. The lower opening has a perennial stream that discharges into the lake only a few meters away. When visited, the upper opening, about 2 x 0.5 m, extended only 5 m before the passage was blocked by water. The passage floods in spring. There is little vegetation in the immediate area – mostly bare rock.

Horne Lake Caves.—This group of three caves is located in Horne Lake Caves Provincial Park on Vancouver Island at an elevation of 200 m. The trees in the area are mainly Douglas-Fir, Western Hemlock and Western Red Cedar with some Red Alder.

Slesse Creek and Chipmunk Caves.–These caves are found in close proximity in the Chilliwack Valley of British Columbia. They are described in Thompson (1976). We did not visit these sites, but P. D. and M. P. Bragg collected *L. paessleri* in them on several occasions.

Densities (opilionids per cm^2) of overwintering aggregations were calculated by measuring the size of small aggregations and then brushing them into plastic bags for later counting, and by counting individuals on enlarged photographs. Populations (opilionids per site) were estimated by counting and measuring the number of "loose" and "dense" aggregations (see below). Movement of individuals was determined by painting their cephalothoraces or legs with enamel and observing the marked individuals on subsequent visits.

During the winter of 1980-81, four samples, each of 25 to 36 live individuals, were taken at intervals from the overwintering population in the Kuskonook mine. The specimens were individually weighed and then dissected to determine their sex. Means of the male and female weights were used to determine the regression equation that best described the weight loss of the population over the winter.

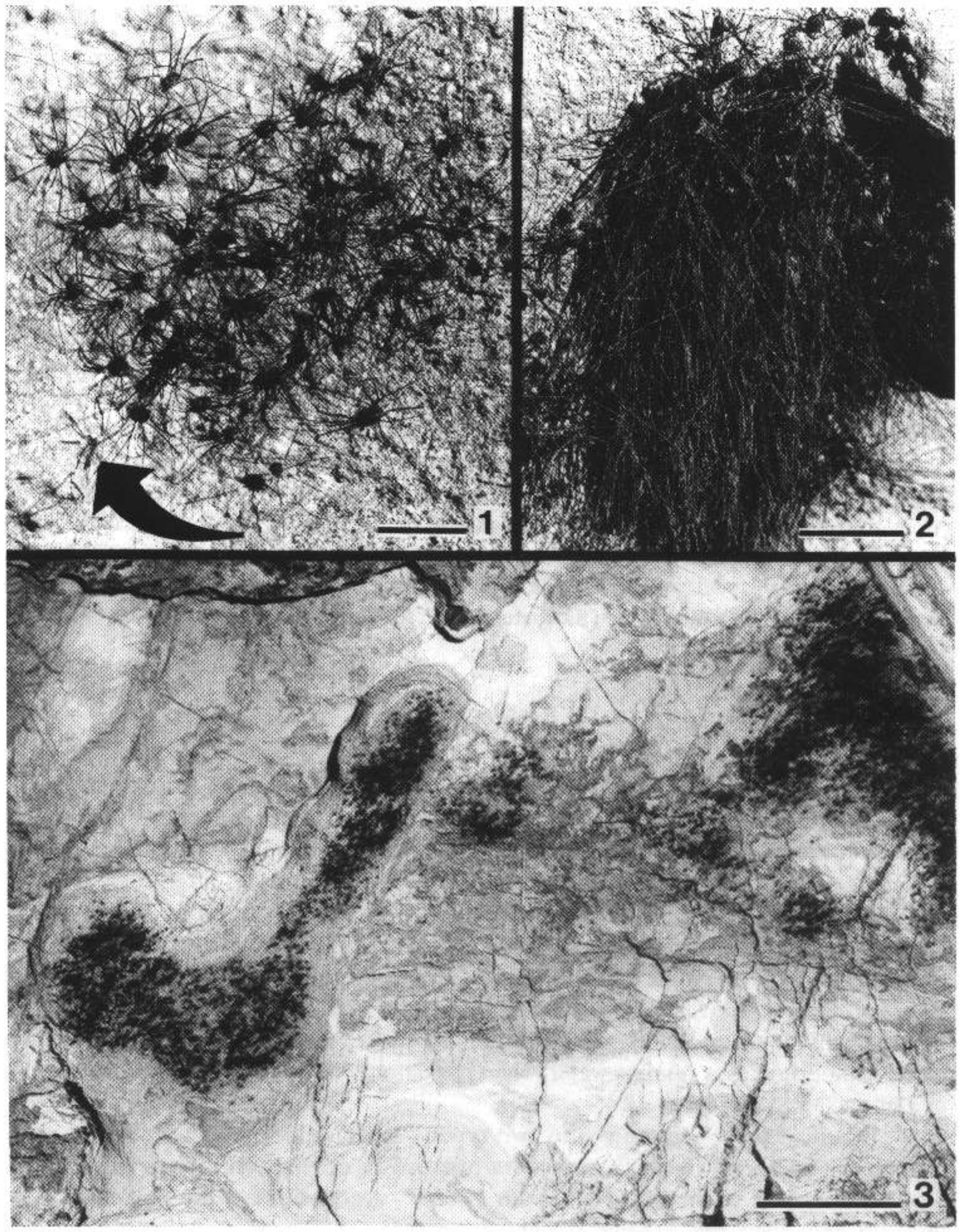
To investigate the lower lethal temperatures for *L. paessleri*, we placed 20 adults (collected 13 November 1981 at Kuskonook and tested 14 November) along with wet paper towels into cages that were in turn placed in unlit environmental chambers for 50 hours. The temperatures of the chambers were: -20, -10, -5, -3, 0.5, 5, and 10°C ± 10%.

Representative specimens form the overwintering sites have been deposited in the Canadian National Collection (Biosystematics Research Institute, Ottawa, Ontario, Canada K1A 0C6).

RESULTS

Aggregation Formation.–We found overwintering aggregations of *L. paessleri* on the walls and ceilings of a series of seven caves and abandoned mines at about 49°N between 114° and 124°W. Overwintering sites ranged in elevation from 200 to 1450 m and occupied four biogeoclimatic zones (i.e., Interior Western Hemlock, Interior Douglas-Fir, Subalpine Englemann Spruce-Subalpine Fir, and Coastal Douglas-Fir; Farley 1979). Though the habitats surrounding the sites ranged from fairly dry (e.g., Lodgepole Pine forest at the mine on North Star Hill receives about 660 mm of precipitation per year) to wet (e.g., Douglas-Fir forest at the Horne Lake Caves with about 2000 mm; Atmospheric Environment Services 1982), all sites had high relative humidities and considerable amounts of dripping or running water. The aggregations consisted of about equal numbers of adult males and females.

We classified the aggregations into two types: "loose" and "dense". In "loose" aggregations the bodies of the opilionids were oriented in different directions with the legs held outstretched or flexed (Fig. 1). In "dense" aggregations, most opilionids faced upwards with their legs hanging straight down (Fig. 2). The "dense" aggregations consisted of several layers of opilionids. The innermost layer clung to the substrate mainly by the claws of their pedipalps. Some also used their chelicerae. In outer layers pedipalps and legs were used by the opilionids to attach themselves to those underneath. In this way densities of up to 2.6 individuals per cm^2 were formed. "Dense" aggregations were restricted to nearly vertical surfaces.



Figs. 1-2.–Overwintering aggregations of *L. paessleri* in a mine near Kuskonook, British Columbia. Bars = 25 mm. Fig. 1. "Loose" aggregation; arrow indicates individual embedded in mineral deposits. Fig. 2. "Dense" aggregation with legs hanging down. Fig. 3. Aggregations in Cody's Cave, British Columbia. Bar = 25 cm. Note how one of the aggregations, containing about 1520 individuals, has formed in a "J" shaped cavity in the ceiling of the cave.

Aggregations often formed in crevices and hollows and took the shape of these spaces (Fig. 3). In more uniform areas, they were often circular or rectangular. The largest "loose" aggregations that we found occupied about 1 m^2 and consisted of one to two thousand individuals.

Our most detailed field observations were made at the Kuskonook Mine during the 1980-81 season. In mid-August 1980, there were about 30 subadults and adult *L. paessleri* in the mine (Fig. 4). By October there were about 7000 adults (calculated by using estimates of 2.5 opilionids per cm^2 for "dense" aggregations and 1.1 for "loose" aggregations). Throughout the winter, the "dense" aggregations tended to be located nearer the entrance than the "loose" aggregations. In December and February, the aggregations moved deeper into the mine and by March, individuals started to move outside. By mid-April, 8 months after aggregations started to accumulate, only a few hundred individuals were left. By 1 May there were no opilionids in the mine. Though some aggregations tended to occupy the same positions month after month, others broke up when their individuals moved to other or formed new aggregations.

The climate in the Kuskonook area (based on data from Creston; Atmospheric Environment Service 1982) is warm temperate and moderated by Kootenay Lake. The mean annual temperature is 7.8°C; precipitation, 568.9 mm. Mean minimum temperatures are below 0°C between mid-October and mid-March and though it may snow in any month between October and May, rain is present every month. The coldest month is January with a mean daily minimum of -6.4°C. In August 1980, it was cooler and wetter than usual but the winter was warmer with more rain. Spring was also warmer than normal but precipitation was less in March. Hours of daylight reached a maximum of 16.1 h in June and a minimum of 8.1 h in December. Immigration into the mine started when day length was greater than 14 h; emigration, before the vernal equinox.

With slight variations, similar observations on aggregations were made at other overwintering sites. In Cody's Cave no opilionids were present on 20 August 1980, but by 12 October there were at least 20,000–the largest population that we encountered. In this cave most aggregations were found within 15 m from the entrance, but some individuals were found as far back as 40 m–about the extent of the twilight zone of this cave. The mine on North Star Hill held a few hundred *L. paessleri* when it was visited on 11 October 1980. The cave on Crowsnest Lake held a few dozen on 1 November 1980. The Horne Lake Caves had several hundred on 16 February 1982, although in other years there were fewer specimens (R. A. Avis, personal communication). The Slesse Creek and Chipmunk Caves had less than 30 individuals in the winter of 1980-81.

Weight loss of the population that overwintered in the Kuskonook Mine in 1980-81 is shown in Fig. 5. The weight loss was greatest between October and December and then declined more slowly during the rest of the winter. Of six equations tested, the one that best described the data was the power equation.

Individual Behavior.–When individual *L. paessleri* were disturbed by light, touch or human breath, they often moved their bodies up and down in a "bobbing" behavior. The movement occurred in the legs mainly at the junction of the patella and tibia. If an aggregation was disturbed, some individuals would start "bobbing" and the group would quickly break up with individuals moving away from the disturbance or dropping to the floor. When members of an aggregation were disturbed, they joined other aggregations both toward and away from the entrance. Physical contact usually elicited release of scent gland secretions. When individuals encountered a pool of water, their tarsi did not break the surface tension. Thus they could move readily about on the water's surface. This resistance to wetting was not complete, and individuals at high relative humidities usually had water droplets on their legs and specimens in captivity often drowned.

Potential Predators.—In the overwintering sites we found various animals that could potentially prey on *L. paessleri.* In the Kuskonook Mine these included: spiders (*Pimoa haden* Chamberlin and Ivie), centipedes [*Tomotaenia epleptica* (Wood)], camel crickets (Gryllacrididae), frogs (*Hyla regilla* Baird and Girard), salamanders (*Plethodon vandykei* Van Denburg) and bats. In Cody's Cave there was evidence of wood rats, *Neotoma cinerea* (Ord). In the North Star mine there were several *P. haden.* In the Crowsnest cave, there was odor of a skunk, *Mephitis mephitis* (Schreber). Camel crickets (*Tropidischia xanthostoma* Scudder) were present in the Horne Lake Caves.

A few of the potential predators (i.e., crickets, frogs, salamanders) were collected and their guts examined for opilionid remains. Some did contain arthropod fragments but there was no evidence that they had fed on opilionids. The only direct evidence that *L. paessleri* were preyed upon in the overwintering sites were piles of hundreds of opilionid legs found in the Horne Lake Caves.

Other Cave Occupants.—We also observed other animals in the caves and mines that were unlikely predators but possible food sources for the opilionids or their potential predators. The most common were fungus gnats (Mycetophilidae, including species of

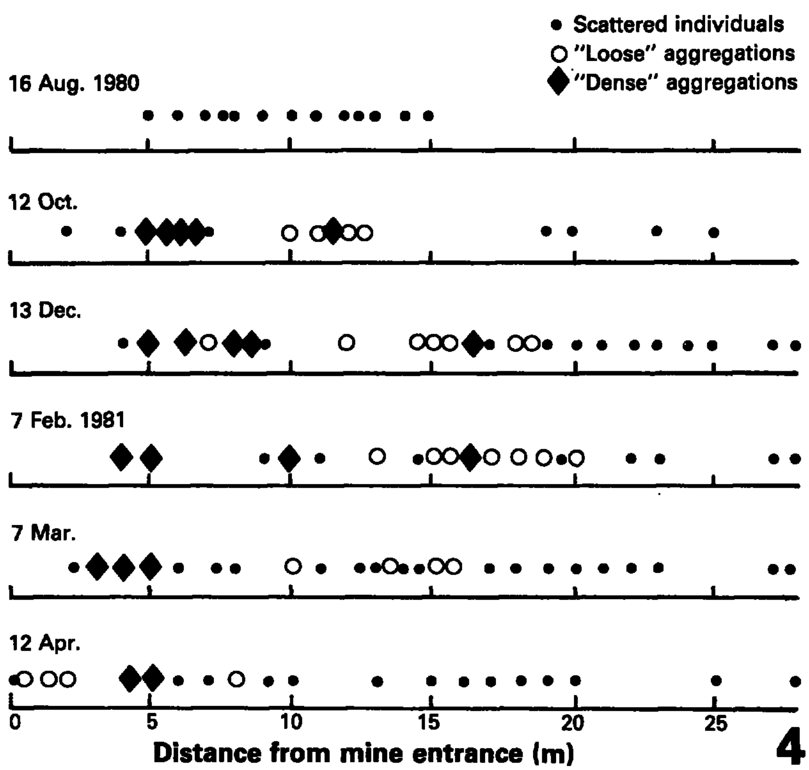


Fig. 4.—Types and relative locations of aggregations of *L. paessleri* in the Kuskonook mine during the 1980-81 season.

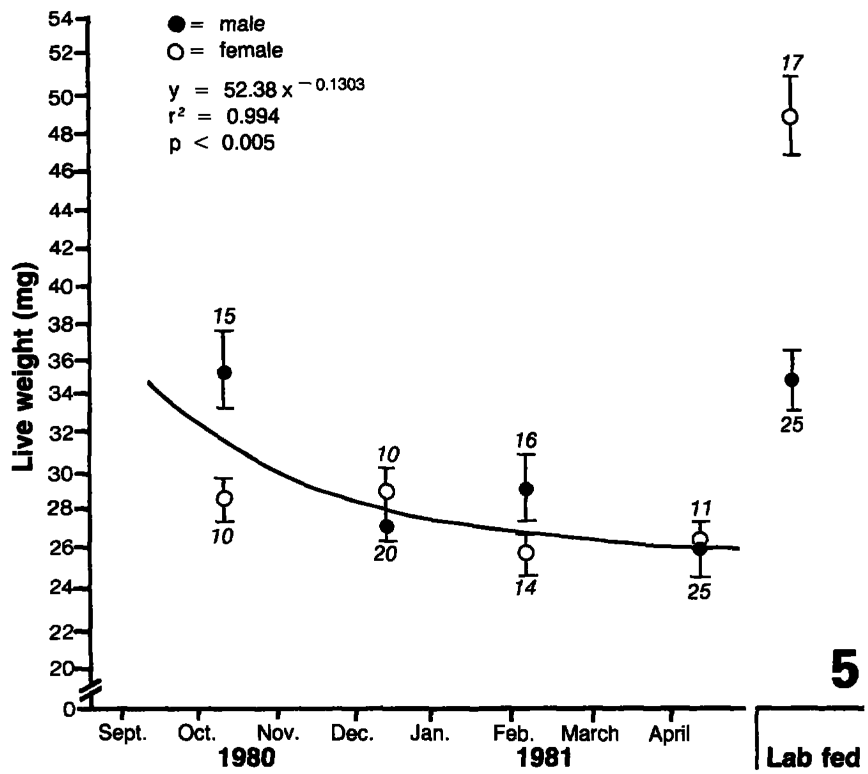


Fig. 5.—Mean weight losses of the 1980 population of *L. paessleri* that overwintered in the Kuskonook mine as well as maximum weights reached by adults fed in the laboratory. Vertical bars indicate standard errors; numbers, the total number of individuals of each sex used to determine the means.

Exechiopsis and *Mycetophila*), but there were also various moths (including Geometridae and Noctuidae), crane flies (Tipulidae) and sowbugs (Isopoda).

Miscellaneous Field Observations.—In April 1981 there were several dead *L. paessleri* in the Kuskonook mine that had fungal hyphae emerging from their bodies and leg joints. They were similar in appearance to an unknown species of opilionid illustrated by Griffiths (1978). The mine also had several dead opilionids that had become embedded in travertine deposits (Fig. 1).

Miscellaneous Laboratory Observations.—In the laboratory, specimens readily fed on freeze-dried tubifex worms (sold as fish food), slices of fresh apple, banana, bread and cut up larvae of the beetle *Tenebrio molitor* L., as well as moribund or dead members of their own species. The latter was common only under dry conditions. On average, adult males from the Kuskonook mine reached a maximum weight of 35.2 mg; females 49.2 mg (Fig. 5). The weight of "fed" males was not significantly different from those collected in early fall i.e., 35.2 vs. 35.8 mg). Specimens kept in light and fed showed considerable darkening in color.

Mating behavior, observed in specimens collected in mid-winter and kept at room temperatures for several weeks, was typical of other Palpatores i.e., "face-to-face" with no detectable courtship. We were unsuccessful in eliciting oviposition. Substrates tried were: moist sand, potting soil, cotton and various mosses. In the temperature trials, we found no survival below -10°C, 20% for -5, 32% for -3, 100% for +0.5, +5 and +10.

DISCUSSION

Why Aggregations?—Though warmer temperatures and shelter from wind and snow are undoubtedly the main reasons why *L. paessleri* and other opilionids overwinter in caves and similar habitats, the question remains—why should they not space themselves evenly or randomly throughout the site rather than in aggregations? There are five possible explanations.

One, aggregations are formed because preferred temperatures and humidities are found only in certain microhabitats within the overwintering sites. As all organisms tend to seek optimal environmental conditions, this explanation probably applies to some extent to all aggregations—especially to such as those that formed in the cavities in the ceiling of Cody's Cave. However this explanation is not adequate to explain why several discrete aggregations are often formed side by side or why aggregations are formed in very different locations within one cave.

Two, the intertwining of the opilionids' legs decreases air movement and hence evaporation and desiccation. Under arid conditions this is a likely hypothesis, but the overwintering sites that we found had high humidities and supplies of free water.

Three, aggregations could trap heat produced by body metabolism. Though overwintering *L. paessleri* can lose 20% of their weight by spring, the amount of heat that this would generate is probably insufficient to raise the temperature of an aggregation substantially over an entire winter. It is possible that *L. paessleri* supplement their energy reserves by feeding on other organisms that live in the overwintering sites or by cannibalism. However neither of these alternatives would favor aggregation formation.

Four, aggregations may improve mating success by providing an abundance of potential mates within a small area. We consider that this is also unlikely because the opilionids could mate at the (restricted) entrances of the overwintering sites as the aggregations accumulated or dispersed without needing to form such long term aggregations.

Five, the combined action of many opilionids' scent glands are more effective at repelling predators than an individual's effort. Along with the seeking of optimal temperatures and humidities, we think this is the most likely reason why *L. paessleri* form aggregations. Though these opilionids have several lines of defense against predators, such as camouflage coloration and escape behavior, the effectiveness of most defense mechanisms would be reduced in these circumstances because the opilionids would be slowed down by the cold and because the predators probably would be adapted to the dark and confined environments.

The size of aggregations may be determined by a combination of substrate and microclimate suitability as well as by chance additions of incoming individuals. The density of aggregations are probably determined primarily by temperature with some influence by light intensity. As most *L. paessleri* overwintered relatively near the entrances of caves and mines, it seems that optimal temperatures are relatively low—a behavioral mechanism that would reduce metabolism and hence extend food reserves.

Life Cycle of *L. paessleri*.—In our study area, *L. paessleri* overwinters only as adults. Other North American *Leiobunum* overwinter as eggs or young (Edgar 1971). We speculate that *L. paessleri* are stimulated into dispersing from their overwintering sites by the increasing temperatures and day lengths of April and May. Mating probably takes place the spring, rather than the fall, because both males and females survive until spring. The eggs are laid outside of the overwintering sites and the resulting young reach maturity in late summer (P. D. Bragg and R. G. H. unpublished data). From August to October subadults and adults begin to accumulate in potential overwintering sites. The subadults molt into adults before winter and the annual cycle continues.

Mortality Factors.—There are several factors that affect the survival of overwintering aggregations and hence the geographic range of *L. paessleri.* Though *L. paessleri* can survive in several diverse forest types, it does not seem to be able to cope with temperature much colder than -5°C and so low temperatures are probably a major limiting factor. Caves and mines allow the species to inhabit areas they would otherwise not be able to populate. Desiccation due to low moisture levels is another mortality factor. Prolonged overwintering periods that lead to death by starvation is a third factor. As masses of opilionids are a considerable potential food supply to predators, predation is also likely important. Caves and mines that harbor substantial numbers of vertebrate predators could eliminate overwintering populations. This is possibly the reason why one cave we visited was devoid of *L. paessleri.* Though the surrounding area should be able to support the species, the cave (Sawatsky 1978) does have a year round population of bats, and bats are quite capable of eating opilionids (Wagner et al. 1977). Disease is another potential threat. However the fungus that we observed on dead *L. paessleri* in the spring in the Kuskonook mine may have been saprophytic rather than pathogenic. It is unlikely that the travertine mineral deposits trapped live opilionids but rather embedded only dead specimens.

Other Opilionids That May Form Aggregations.—Nearly all opilionids that have been found to form aggregations belong in the subfamilies Leiobuninae (e.g., *Leiobunum*), Gyantinae (e.g., *Amilenus*), or Gagrellinae (e.g., *Prionostemma*) of the Phalangiidae (Martens 1978, Wagner 1954). As the biology of these animals is studied, it is likely that aggregation behavior will prove to be a common trait and that several more species will be found to avoid environmental extremes by using caves and similar habitats.

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