Dispersal Related to Density in the Amphipods Hyalella azteca and Gammarus pseudolimnaeus

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Dispersal Related to Density in the Amphipods
Hyalella azteca and *Gammarus pseudolimnaeus*[3]

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Abstract. The relationship between population density and rate of dispersal and tendency to aggregate in two species of fresh-water amphipods, *Hyalella azteca* (Saussure) and *Gammarus pseudolimnaeus* Bousfield, was tested by laboratory experiment.

Populations of *H. azteca* showed an inverse relationship between initial density and dispersal rate; this relationship is a function of the tendency of populations of higher densities to form aggregations. The dispersal rate of *G. pseudolimnaeus* was not appreciably affected by changes in population density, and increased density did not result in aggregation. Both species aggregated around vegetation in preference to aggregation around other amphipods.

The non-aggressive behavior and pronounced thigmotaxis of both species contribute to their aggregation and dispersal behavior.

The widely held concept that animal populations are regulated by certain density-dependent factors (Allee et al. 1949, Lack 1954, Odum 1959) has been challenged recently by Andrewartha and Birch (1954). Partly in response to this challenge, Bovbjerg (1959, 1960) investigated the relationship between density and one possible density-dependent factor, the rate of dispersal, in laboratory populations of the crayfish *Cambarus alleni* Faxon, and the crab *Pachygrapsus crassipes* Randall. His results indicate a positive density-dispersal relationship, which he attributes to the intraspecific aggressive behavior characteristic of both crustacean species. Following these studies the question arose: What is the relation of population density to disperal rate in non-aggressive species which tend to aggregate in nature? In an attempt to answer this question, amphipod crustaceans displaying such characteristics were chosen for this laboratory study.

THE EXPERIMENTAL ANIMALS

Two species of fresh-water amphipods were used in separate but similar experiments. These were *Hyalella azteca* (Saussure) 1858 (*H. knickerbockeri* Bate) and *Gammarus pseudolimnaeus* Bousfield 1958[2] (Figure 1).

H. azteca is a small species (adults 4 to 8 mm long) and is "the most common and most widely distributed North American
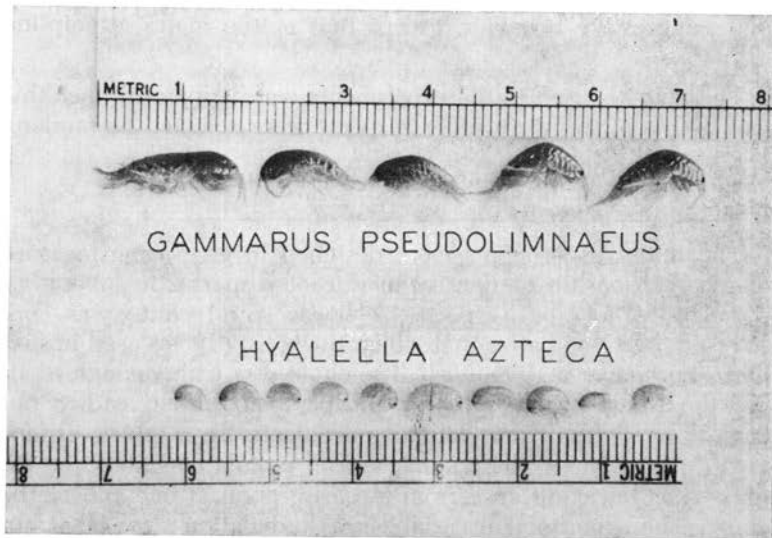

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Figure 1. Adult amphipods of the two species studied, showing their relative sizes.

fresh-water amphipod crustacean," being found from Mexico north to the tree line in Canada and Alaska (Bousfield 1958). It is found in abundance primarily in permanent fresh waters rich in vegetation and reaching a monthly mean summer temperature of more than 10° C (Weckel 1907, Jackson 1912, Gaylor 1921, Hubricht 1943, Pennak 1953, Bousfield 1958, Ward and Whipple 1959). Breeding is limited to the warmer months of the year, growth is rapid, and the reproductive potential is very high (Embody 1911, Jackson 1912, Gaylor 1921, Geisler 1944, Bovee 1950). *H. azteca* is the most abundant amphipod in the Lake Okoboji region of northwest Iowa, where I conducted the studies on this species at the Iowa Lakeside Laboratory.

G. pseudolimnaeus is a much larger animal (adults 10 to 17 mm long), widely distributed in the Mississippi drainage basin of east central United States and in the southwestern St. Lawrence system, being a species "of larger rivers and lakes that breeds in tributary streams and springs that are cool in summer"; it is "probably seasonally migratory" (Bousfield 1958). Ovigerous females are found mainly from April to July and the life span is about 16 months (Bousfield 1958). The animals used for these experiments were collected during the fall and winter seasons from the spring brook and water-cress beds of McLeod Spring, near Cedar Rapids, Iowa. I performed the experiments in Iowa City.

Two observations concerning these amphipods are particularly pertinent to this investigation. First, both species tend to aggregate under stones, in vegetation, or on other materials of the substratum of their natural habitats. Second, neither species dis-

plays aggressive behavior, except that of the males attempting to pair.

The animals used in the experiments were apparently healthy, well fed adults, and in other respects were selected at random.

EXPERIMENTAL PROCEDURE

Dispersal experiments.

The initial experiments were designed to give some measure of the relationship of density to rate of dispersal in laboratory populations. For each species, a linear spiral chute was constructed, patterned after that which Bovbjerg (1959) used in similar experiments with crayfish. The chute was wide enough to allow the animals to move freely and pass each other readily, but narrow enough to limit lateral movements. In a given experiment, movements of individuals and of populations could be expressed as linear distance from a release point at one end of the chute. The experimental variable was population size; other environmental factors were kept constant. During each experiment the locations of all animals were recorded on a "map" of the chute at frequent time intervals after release. With repeated trials in which each of several population sizes was used, effects of population density on dispersal rate could be expressed quantitatively.

The experimental chute for *H. azteca*, the bottom of which was square in cross section, was carved from paraffin. The chute was 185 cm long, 1¼ cm wide, and the water depth was 1½ cm. The chute was marked at 5 cm intervals. The entry at 0 cm was guarded by a cork barrier or "gate," behind which was an area 5 cm long and as wide and deep as the rest of the chute; here the animals could acclimatize for a few minutes prior to each experiment, which began with the removal of the gate. Oxygenated lake water was used for all experiments. Water temperatures averaged 22° C, comparable to the summer temperatures of the local natural habitats of this species. Incandescent, overhead light provided approximately uniform lighting of moderate intensity over all parts of the chute. Experimental populations of *H. azteca* consisted of 10, 30 and 100 animals. Forty replicate experiments, each 20 minutes or more in duration, were performed using each population size. Twenty-five control experiments using a single animal were also performed.

A larger but similar chute of aluminum embedded in concrete was constructed for the *G. pseudolimnaeus* experiments. It was 235 cm long, 3 cm wide, and the water was 2½ cm deep. The chute was marked at 10 cm intervals. The area for acclimatization, behind an aluminum gate at 0 cm, was 8 cm long. Filtered,

aerated tap water was used. Temperature averaged 10° C, comparable to the spring brook habitat from which the animals were obtained. Overhead fluorescent units provided uniform lighting of moderate intensity. Experimental populations of *G. pseudolimnaeus* consisted of 10, 20 and 30 animals; larger populations were not used because the rapid movements of so many animals rendered impossible the accurate recording of their positions. Forty replicate experiments, each 20 minutes in duration, were performed using 10 animals and 30 animals, respectively; 25 replicates of the same duration were performed using 20 animals, and 25 replicates using single animal controls.

For each experiment, the gate at 0 cm was removed at time "zero"; positions of all animals were then recorded on the "map" at frequent time intervals (the latter indicated in Figures 2 and 3). These data yielded, altogether, more than 60,000 position recordings for the *H. azteca* populations, and over 27,000 for those of *G. pseudolimnaeus*. For each experiment, mean distances from release at each time interval were calculated. For each population size, a mean of means was then calculated from the forty replicates for each time interval. Rates of dispersal were indicated by plotting changes in the average distribution of each population size against time (see Figures 2 and 3).

Aggregation Experiments.

A measure of the tendency of amphipods to aggregate, related to population density, was desired to check the results of the dispersal experiments. Water-filled finger bowls 18 cm in diameter were the experimental environments. Light and temperature conditions and sources of water were the same as for the dispersal experiments in the respective species. Water depth was 1½ cm for the *H. azteca* experiments, and 2½ cm for the *G. pseudolimnaeus* experiments. The experimental variable was population size, groups of 30 and 100 animals being used in the *H. azteca* experiments, and 15 and 50 animals in those with *G. pseudolimnaeus*.

Each experiment began with the introduction of an experimental population into a finger bowl containing water; the animals were scattered as uniformly as possible, and mated pairs were excluded. The bowls were left undisturbed for one hour, after which the three largest aggregations in each bowl were removed and counted. The percentage of animals aggregated in these groups was then calculated, providing data for quantitative comparison of aggregation tendency in different population sizes. Twenty replicate experiments were performed using each population size of each species.

A duplicate set of experiments was performed with one varia-

tion: the addition of a sprig of vegetation from the respective natural habitats of the two species. For *H. azteca*, a terminal growth shoot of hornwort (*Ceratophyllum demersum*) 4 cm long was gently added to the bowl after the population had been allowed to acclimatize for 30 minutes. For *G. pseudolimnaeus*, a 10 cm section of water cress stem (*Nasturtium officinale*) with several leaves was utilized in a similar manner. After one hour the percentage of animals aggregated around the vegetation was determined. It was anticipated that the results of these experiments when compared with those where no vegetation was present could clarify the role of vegetation in natural aggregations of amphipods.

Some additional aggregation experiments with *G. pseudolimnaeus* made use of larger populations in a larger container, a round plastic pan 28 cm in diameter. Population sizes were 30, 100 and 200 animals. In experiments involving vegetation, two pieces of water cress totalling 25 cm in stem length were used.

<center>RESULTS</center>

Dispersal Experiments.

The rate of dispersal of *H. azteca* was strongly but inversely related to population density. (Figure 2 presents data for the first 10 minutes.) After three minutes, populations of 10 animals had moved a distance of 61 ± 7 (Standard Error) cm; of 30 animals, 38 ± 5 cm; and of 100 animals, 16 ± 3 cm. The probability that these differences in mean dispersal rates would occur by chance alone is less than 0.01; the differences were therefore significant (at the 0.05 level).

The rate of dispersal of *G. pseudolimnaeus* was little affected by population density (Figure 3). After three minutes, populations of 10 animals had moved a mean distance of 92 ± 7 (Standard Error) cm; of 20 animals, 86 ± 6 cm; and of 30 animals, 78 ± 6 cm. The probability that these differences would occur by chance alone is about 0.3. They are therefore *not* statistically significant.

After about 5 minutes the *H. azteca* populations tended to reach a distribution equilibrium because of the movements of animals in both directions, and this was maintained for the remainder of the experiment. In like manner net outward dispersal of *G. pseudolimnaeus* ceased after about 4 minutes, and a distribution equilibrium was then maintained.

Both species showed tremendous individual variability of movement within each experiment. This was especially evident when single animal controls were used. Some animals were very active, traversing the length of the chute in two minutes or less.
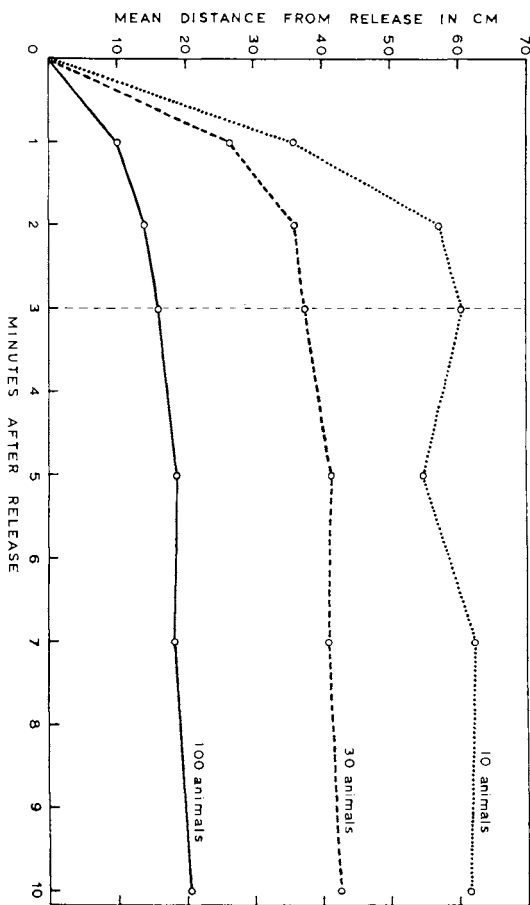
Figure 2. Rates of dispersal in *Hyalella azteca*. Mean distances moved by 10, 30 and 100 animals during a 10 minute period; based on 40 replicate experiments with each population size. Note that the greatest outward dispersal occurred during the first three minutes (to left of vertical broken line). Since these curves are means, they do not reflect the variability.

Others did not move for several minutes, and a few stayed behind the release point during the whole experiment. Also, although aggregation of *H. azteca* in the release area increased with density, some of the animals were nearly always active, "exploring" the experimental chute. The absolute number of these active animals was usually greater in the larger populations, but the percentage of the total population of this species which was active at any one time was much less in the larger populations.

Aggregation Experiments.

All populations of both *H. azteca* and *G. pseudolimnaeus* definitely tended to aggregate around vegetation. Populations
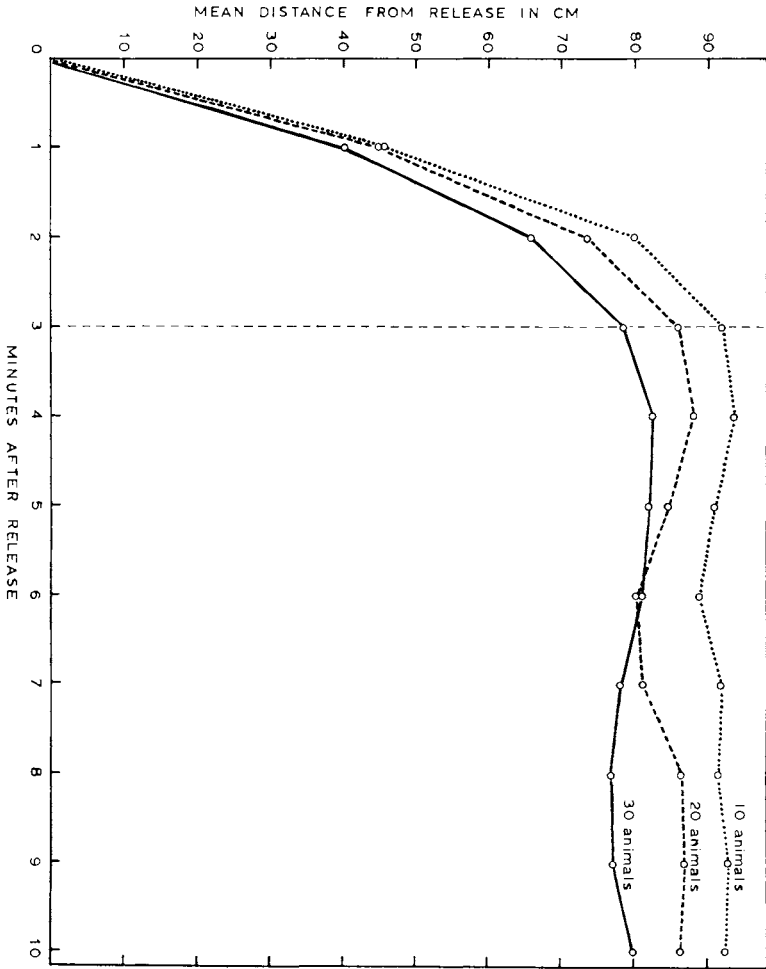
Figure 3. Rate of dispersal in *Gammarus pseudolimnaeus*. Mean distances moved by 10, 20 and 30 animals during a 10 minute period; based on 40 replicate experiments with 10 and 30 animals, 25 replicates with 20 animals. Note again that the greatest outward dispersal occurred during the first three minutes. Since the curves are means, they do not reflect the variability.

of both 30 and 100 *H. azteca* aggregated an average of 81 ± 4 (Standard Error) % around the 4 cm sprigs of hornwort (Figure 4). Aggregation of *G. pseudolimnaeus* around vegetation (25 cm of water cress) averaged 70% to 80% for populations of 30, 100, or 200 animals; aggregations were less pronounced when less water cress was present. Thus, it appeared that for both species population density had no effect on aggregation in or around vegetation.

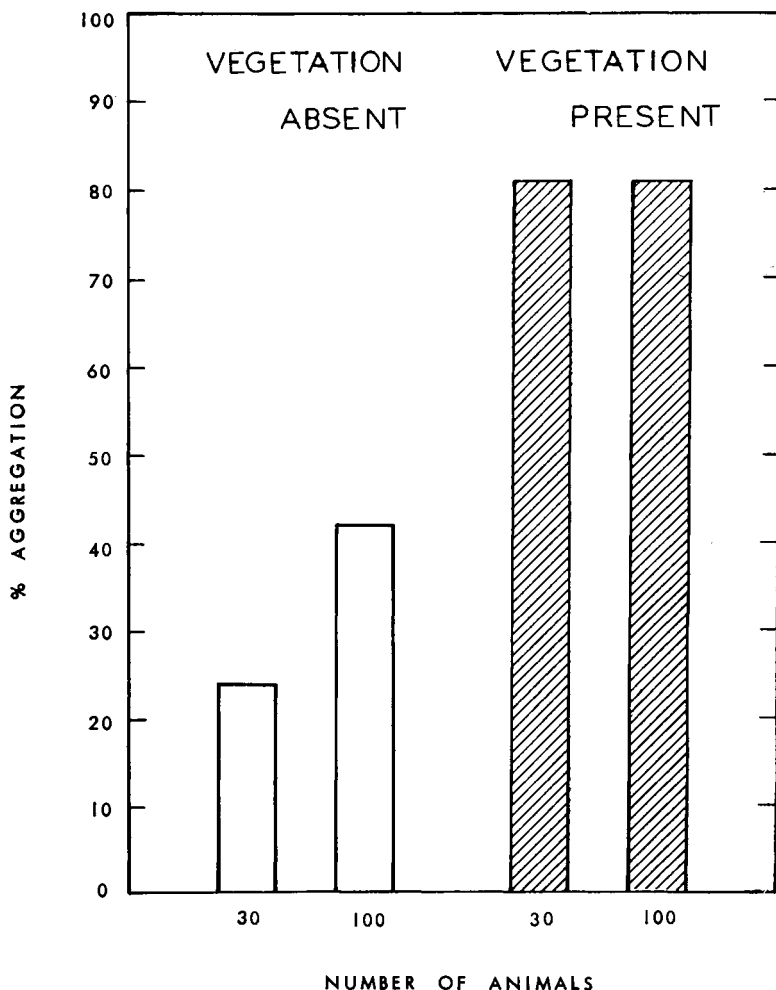The aggregation of *H. azteca* was much less pronounced in

Figure 4. Aggregation of *Hyalella azteca*. Based on 20 replicate experiments each with 30 and 100 animals without vegetation (left) and with vegetation (right). (See text for explanation).

the absence of vegetation than in its presence, but was significantly greater in populations of 100 animals than in populations of 30 animals (Figure 4). In groups of 100 animals the three largest aggregations together averaged 42 ± 4 (Standard Error) %, compared with 24 ± 4% in groups of 30 animals. The average size of the single largest aggregation of *H. azteca* in populations of 100 was 24 animals or 24%, compared with 5 animals or 17% in populations of 30 animals. The probability that these differences in degree of aggregation would occur by chance is less than 0.01.

G. pseudolimnaeus failed to aggregate even at high densities in the absence of vegetation, and no definite relationship between population density and degree of aggregation could be detected. The lack of aggregations was in marked contrast to the strong aggregation tendency of the larger populations of *H. azteca*.

Frequency of chance collisions between animals, and their subsequent clinging together, appeared to contribute toward building the aggregations of *H. azteca* in the absence of vegetation. The greater the population density and resulting number of chance encounters, the greater was the aggregation tendency. Aggregations of *H. azteca* tended to become stable, and the larger aggregations appeared to be the most stable. Frequency of contact increased with population density also in the *G. pseudolimnaeus* experiments. However, aggregations was much less pronounced an dappeared not to be density-related. A tentative explanation of this difference between species is that the thigmotactic behavior of *H. azteca* extended to contact with others of the species, whereas the thigmotactic behavior of *G pseudolimnaeus* did not.

DISCUSSION

The results of this study show a curious difference in the dispersal and aggregation behavior of the two species investigated. While in *H. azteca* the rate of dispersal is inversely proportional to initial density, in *G. pseudolimnaeus* density has little effect on dispersal rate. In *H. azteca* aggregations form spontaneously at the higher densities even apart from vegetation, while in *G. pseudolimnaeus* such aggregations fail to form. It is beyond the scope of this study to account fully for these differences or to speculate concerning their adaptive significance, but the results do serve to illustrate the dangers of overgeneralizing about the behavior of a group of animals on the basis of studies of a single species.

While differences between the two species do exist, the similarities are probably more fundamental. Neither species shows an increase in dispersal rate with increased density, and both are strongly attracted to vegetation and other materials of their respective natural habitats. In these characteristics and in their non-aggressive intraspecific behavior, both species contrast strongly, as was expected, with the crayfish, *Cambarus alleni*, and the crab, *Pachygrapsus crassipes* (Bovbjerg 1959, 1960).

Of what adaptive significance is the behavior of these amphipods as demonstrated in these experiments? The strong tendency of both species to collect around vegetation and other objects may protect them from water currents or wave action and prob-

ably also from predators, and allows the amphipods to be in the immediate presence of a source of food.

Another adaptive trait is the tolerance of both species for close association with other members of the same species. Amphipods are decidedly omnivorous (Gaylor 1921, Sexton 1928, Pennak 1953, Berner 1955), so food is rarely a problem where other environmental conditions are favorable. The relatively small size of the amphipods, especially of *H. azteca*, allows them to hide in various small crevices in and around vegetation, under stones, and in other materials of their natural habitats. The rapid growth and high reproductive potential of *H. azteca* (Embody 1911, Geisler 1944, Bovee 1950) enables this species to populate favorable microhabitats rapidly during the summer growing season. *G. pseudolimnaeus* may have a slower rate of growth, but the more stable conditions of its favored spring brook habitat compensate for this.

In both species the combination of thigmotactic behavior, mutual tolerance, omnivorous food habits, small size, and fecundity help to account for the accumulation of large populations in favorable locations.

Both species, in addition to their thigmotactic behavior, are rather active swimmers. This activity and their rather acute sensory apparatus (Berner 1955), together with agents of passive dispersal such as waves and currents, enable them to disperse widely into favorable microhabitats in a connected body of water. How either species becomes dispersed from one body of water to another is not clear.

Questions which this study leaves unanswered include the following: What is the mechanism behind the dispersal and aggregation behavior of the two species? What kinds of sensory signals are received by the amphipods, and exactly what is the nature of their response? Does the peculiar aggregation behavior of *H. azteca* have some adaptive value for the species? What are the respective roles of thigmotaxis and response to light (amphipods generally being somewhat photonegative) on the dispersal and aggregation behavior displayed in this study? Such questions await further investigation.

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Notes on Iowa Ants

R. L. KING[1] AND R. M. SALLEE[2]

Abstract. Data are presented for 19 years (1945-1963 inclusive), and include collections of *Formica rubicunda, Formica spatulata, Formica reflexa* and *Polyergus rufescens breviceps.* Included also is information on longevity records and additional slave species (*Formica ravida* and *Formica spatulata* slaves with *Formica rubicunda*).

The following brief notes refer to ants collected at the Iowa Lakeside Laboratory, Dickinson County, Iowa, during the years 1945-1963.

Formica rubicunda Emery

We now have records of 108 nests of this species with eight species of slaves: 67 with *Formica montana* Emery, 43 with *Formica fusca* Linné, 7 with *Formica fossaceps* Buren, 3 with *Formica lasoides* Emery, 2 with *Formica pallidefulva nitidiventris* Emery, and one each with *Formica obscuriventris clivia* Creighton, *Formica ravida* Wheeler, and *Formica spatulata* Buren. There are 96 colonies with one species of slaves (57 with *F. montana,* 34 with *F. fusca,* 3 with *F. lasioides,* one with *F. fossaceps* and one with *F. p. nitidiventris*); 8 colonies with two species of slaves (4 with *F. montana* and *F. fusca,* 3 with *F. montana and F. fossaceps,* and one with *F. fusca* and *F. p. nitidiventris*); 3 colonies with three species (one with *F. montana ,F. fusca* and *F. fossaceps,* one with *F. fusca, F. fossaceps* and *F. o.*

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