Mass aggregations in tropical harvestmen (Opiliones, Gagrellidae: *Prionostemma* sp.)

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Résumé

Des expériences de marquage et recapture, ainsi que des expériences en laboratoire, sur deux espèces d'opilions (Opiliones, Gagrellidae: *Prionostemma* sp.), indiquent que ces animaux se regroupent rapidement après un dérangement. Contrairement à ce que l'on pourrait imaginer, les petites colonies sont plus densément regroupées et se stabilisent plus rapidement pendant le processus de regroupement que les plus grandes colonies. Ces animaux préfèrent des endroits verticaux et protégé, tels que les coins.

Summary

Mark-recapture experiments and time-course experiments on two opilionid species (Opiliones, Gagrellidae: *Prionostemma* sp.) show that animals do aggregate, and that, contrary to expectation, smaller colonies are more tightly clumped and reach stability sooner during the aggregation process than do larger colonies, and that animals prefer aggregation sites with vertical surfaces and protected spaces, such as corners.

Introduction

Impressively large aggregations of harvestmen (Opiliones: Phalangiidae s. lat.) are familiar to many naturalists and although the aggregations have been described and illustrated (HOLMBERG et al., 1984 (fig. 1-3); MARTENS, 1978; MCALISTER, 1962; WAGNER, 1954), it has been little studied. These animals are common, nocturnal, vagile, and generally solitary omnivores, but during the day they are often encountered in stationary aggregations of hundreds to thousands of individuals. Why

do harvestmen aggregate? Initial reasonable hypotheses include avoiding light or aridity, and/or defense. Research on North American gagrellids confirm a preference for dark, humid conditions in some species (EDGAR, 1968; 1971). Phalangiid harvestmen have repugnatorial glands which are effective in repelling predators (MARTENS, 1978). If individuals aggregate, their pooled response to a threat may be more effective than their response as solitary individuals (ALLEE, 1931). If so, one might expect individuals to prefer to join larger groups, and to be more likely to leave smaller groups during the aggregation process. As such, larger groups should be more stable over time than smaller groups.

CODDINGTON (1979) gathered preliminary data showing that under a variety of caged conditions, individuals of a *Prionostemma* species always assume a clumped distribution (unfortunately, the most recent revision [ROEWER, 1953] is not detailed enough to permit identification to species; J. COKENDOLPHER, pers.comm.). Those preliminary data suggested that aggregation behavior was not correlated with light, humidity, sex ratio, or olfactory cues. However, the individuals used in those experiments never failed to aggregate within a half-hour or so. The process seemed random, with the probability of an individual moving being inversely proportional to group size. Small groups therefore would lose members more quickly than large groups during the aggregation process, and eventually all individuals should end up in one large group.

We report here a series of experiments on free-ranging and caged animals addressing the following basic questions: 1. Do animals always form clumped distributions? 2. Do individuals return to the same aggregation sites? 3. Are smaller groups less stable over time than larger groups? 4. Is the degree of clumping correlated with group size? 5. Do groups prefer edges, corners or horizontal surfaces?

Materials and methods

The experiments were conducted on February 3-13, 1986, on opilionid aggregations observed at two sites: the Monteverde Cloud Forest Reserve, Puntarenas, Costa Rica, and the OTS Palo Verde Field Station, Guanacaste, Costa Rica. The Monteverde species (= *Prionostemma* "A") used the crowns of ca. 2 m high understory spiny palms (*Bactris* and/or *Geonoma* sp.) as aggregation sites. The Palo Verde species (= *Prionostemma* "B") species aggregated in crannies on cliffs, in hollow tree trunks, and on less natural surfaces such as the stone wall of a cattle watering trough. In both cases the aggregations consisted of immatures, mature males, and mature females; no one category seemed unusually numerous. Vouchers are deposited in the Dept. Entomology, National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A.

To learn whether animals return to the same aggregation site and from what distances, on one morning we captured and then marked all individuals in an aggregation of 207 *Prionostemma* "A" individuals and released 107 animals at the original aggregation site, 10 at 1 m distance, 20 at 2 m, 30 at 5 m, and 40 animals 10 m away. Members of each group were marked on a different tibia with opaque correcting fluid. The next morning we searched the area for marked animals.

To test site preference and the effects of group size and time on aggregation behavior, we captured about 300 *Prionostemma* "B" individuals from one aggregation at Palo Verde, and placed them in a holding cage provided with water, fruit, and table scraps for food. Four identical arenas used for experiments were 40 cm wide × 50 cm long × 25 cm tall. The floor of each arena was lined with clean paper and divided into 10 cm² grids, yielding 10 edge grids, 6 center grids, and 4 corner grids. We did not test overhead horizontal surfaces (such as ceilings) as aggregation sites. Most of the trials were conducted between 1200 and 1400 hours. We conducted four trials simultaneously, with groups of 5, 10, 20, and 40 individuals. At the beginning of each trial, we rotated and shuffled arenas and randomized the test animals throughout the arena. For 20 minutes at 2 minute intervals, we mapped the number of individuals per grid. All animals were then returned to the holding cage and new individuals were selected for each trial. We conducted five trials over three days; all tests were performed in a shaded area during daylight hours.

The Poisson dispersion coefficient (s^2/x), was used to estimate degree of clumping. To compare trial runs using different densities of individuals, the coefficients within each density were scaled to the maximum possible coefficient (e.g. all animals in one grid) for that size group and a one-way analysis of variance performed on these transformed data. Because this transformation minimizes between and within-group differences, our results are conservative.

To examine the effect of group size on recruitment of new individuals to the group, we established groups of 3, 5, 7, and 14 individuals in the four corners of an arena, and released single, randomly chosen individuals in the center of the arena. We scored an individual as having joined a group if it remained in that group for 2 minutes. We recorded the length of time it took an individual to join a group, and examined the correlation between time to join and group size.

To examine site preference we tabulated the number of corner, edge and center grids still occupied after 20 minutes, and tested these counts against the null hypothesis that grids would be occupied in proportion to their relative frequency (edge : center : corner = 10 : 6 : 4). We performed an additional experiment to see if animals preferred corners by constructing a partition with 4 additional inside corners in the center of an arena, and allowed a group of 79 individuals to select aggregation sites in the arena.

Results

Mark-recapture experiment.

Fifteen *Prionostemma* "A" individuals were found at the original site, of which 5 were marked; 1 had been released on the aggregation site, 1 at 1 m, and 3 at 10 m away; the remaining 10 individuals were unmarked, "new" members of that group. No individuals or aggregation were found within a 25 m radius of the original site, but an aggregation of about 300 individuals found 50 m away from the original site contained 5 individuals that had been released at the original site. A third aggregation 85 m away contained 17 animals released at the original site, and 4 released at varying distances from the original site.
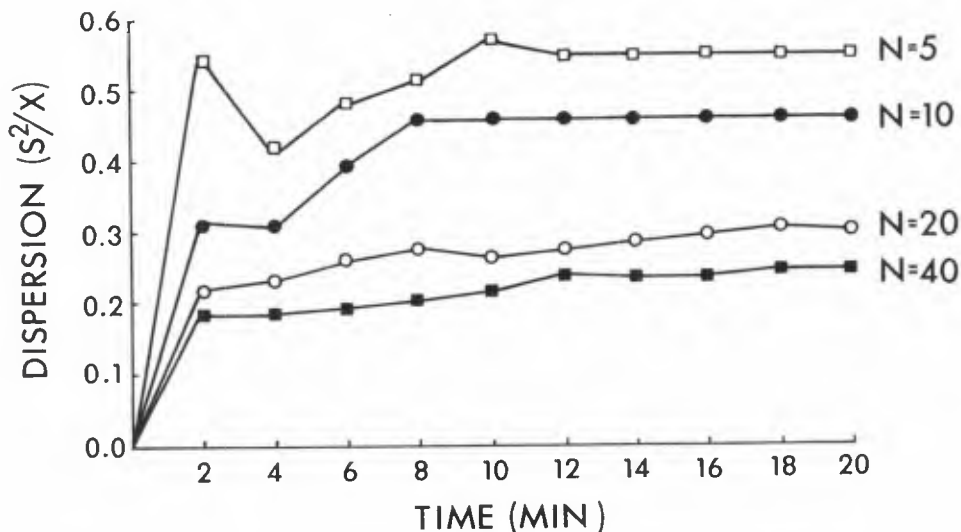
Figure 1. — Graph of dispersion coefficients (normalized to unit scale) versus time for 4 densities of *Prionostemma* individuals (5, 10, 20, and 40 individuals).

Tendency to aggregate.

These and the subsequent results refer to *Prionostemma* "B". During the five days that individuals were observed in the holding cage or in arenas, they never failed to aggregate. The time trials to study aggregation behavior of individuals showed that in almost all cases (N = 199) the dispersion coefficients were > 1 (range 1.22-13.64), hence *Prionemma* "B" formed clumped distribution under all conditions examined.

Effect of density on aggregation.

One-way Anova shows a significant effect of density on clumping (F = 36.71, p < 0.001). Lower densities showed more clumped distributions than higher densities (fig. 1).

Effect of time on aggregation.

One-way Anova shows no significant effect of time on clumping within groups. In effect, all trials at all densities showed clumping within the first 2 minutes observation period, and no significant increase thereafter, in most cases. However, the mean time for animals to cease moving between grids (e.g. time for groups to stabilize) is affected by density (F = 7.94, p < 0.002). Lower densities formed stable groups sooner than at higher densities.

Effect of group size on individual recruitment.

For N = 14 trials, in every case the test individual moved about until it encountered a group, and then remained with that group, regardless of size.

Substrate preference.

Individuals strongly prefer to aggregate on sites including vertical surface $(G = 49.02, p < 0.001)$, and never formed groups on horizontal grids. Groups significantly preferred corners over edges, and edges over center grids $(G = 898, p < 0.0001)$.

Discussion

The mark-recapture experiment provided the most surprising results. Few (5 out of 207) of the marked individuals returned to the original aggregation site, but 10 new individuals appeared. On the other hand, the discovery of 17 marked individuals at a distance of 85 m from the release site implies that individuals wander widely. The small number of recaptures at the original site compared to the large number of recaptures at a great distance implies that they can locate aggregations from great distances, but that they probably don't use a "homing" ability to do so. Between-group mixing of *Prionostemma* "A" individuals does occur. The low numbers of recaptured animals at the original site may have been due to the disturbance caused by capture and marking the day before, but 10 new individuals nevertheless used that site. We did not study night-to-night variation in use of a particular site; large natural variation would also explain the failure of most of the marked individuals to return to the original site. To our eyes, the vicinity provided many adequate aggregation sites, so we judge that *Prionostemma* "A" aggregations are probably not limited by the availability of sites. Because the two new aggregation sites included 5 and 21 marked individuals, respectively, it would seem that individuals do select particular aggregation sites. MCALISTER (1962), studying local movement of *Leiobunum townsendi* (also Gagrellidae) in Texas, found similar results. He found that some animals were relatively faithful to aggregation sites, but that many shifted, that the dispersion of the total population was clumped, and that most animals had a home range with a radius of about 20 m, but some ranged more widely.

The cage studies are more difficult to interpret, and are interesting chiefly as documentation of the striking tendency of *Prionostemma* "B" individuals to aggregate. Contrary to our predictions, at low densities *Prionostemma* "B" individuals clump more and stabilize earlier than at higher densities. This result may be partly artifactual because more grids were occupied in the arenas with 20 or 40 individuals than in arenas with 5 or 10 individuals, and more occupied grids will depress the dispersion coefficient. However, we often observed densities of several hundred individuals per grid in the holding cage (compare HOLMBERG, 1984; fig. 2). Viewed from the perspective of animal behavior in general, these results are not surprising; larger groups should show more activity and occupy more space than smaller groups. Thus the tendency of *Prionostemma* "B" to form clumped distributions does vary in a way typical of animal groups in general, but contrary to our prediction of the factors influencing the aggregation behavior of *Prionostemma* "B" individuals. Furthermore, the evidence from the individual choice experiment suggests that individuals are relatively indifferent to group size, and will stay with the first group they encounter.

Because these results were obtained in caged situations during the day, they must be interpreted with caution. They suggest that individuals don't choose groups they join on the basis of group size, and that individuals are not more likely to remain in larger groups, once chosen. One would like to know the typical behavior of a single individual in an arena; are they more or less active than in arenas containing other individuals? Given the strong preference for aggregation sites including vertical surfaces (e.g. corners) our arena design may have biased some of those results. Animal in cages often come to rest in the corners (HEDIGER, 1950), and if they tolerate conspecifics, one would expect aggregations to form in corners. However, our observations of feral aggregations also suggest that animals prefer protected situations that include vertical surfaces. Also, the animals kept in the holding cage formed extremely tight aggregations, with bodies and legs so entangled that an aggregation took 10 to 15 seconds to disentangle when disturbed. These extremely tight and consistently formed aggregations are not likely to be "cage artifacts". Finally, although the factors influencing the behavior of individuals which are arriving at a site after night-time foraging probably differ from those influencing aggregation behavior during the day, natural situations certainly occur in which individuals form (or re-form) groups during the day, and our results relate best to such situations. Harvestmen stick together!

Acknowledgments

Literature cited

ALLEE, W.C., 1931. — Animal Aggregations: A Study in General Sociology. *Univ. Chicago Press, Chicago, Il.*

CODDINGTON, J.A., 1979. — Opilionid aggregations at Palo Verde. OTS Course Book 79-1 : 122-125. Available from the Organization for Tropical Studies, P.O. Box DM, Durham, NC, 27706.

EDGAR, A.L., 1968. — Daily locomotory activity in Phalangium opilio and seven species of Leiobunum (Arthropoda: Phalangiida). — *Bios, 39* : 167-176.

EDGAR, A.L., 1971. — Studies on the biology and ecology of Michigan Phalangida (Opiliones). — *Misc. Publ. Mus. Zool. Michigan,* **144** : 1-64.

HEDIGER, H., 1950. — Wild Animals in Captivity. *Butterworth, London.*

HOLMBERG, R.G., ANGERILLI, N.P.D. & LACASSE, L.J., 1984. — Overwintering aggregations of Leiobunum passleri in caves and mines (Arachnida: Opiliones). — *J. Arachnol.,* **12** : 195-204.

MCALISTER, W.H., 1962. — Local movements of the Harvestman Leiobunum townsendi (Arachnida: Phalangida). — *Texas J. Sci.,* **14** : 167-173.

MARTENS, J., 1978. — Weberknechte, Opiliones (Spinnentiere, Arachnida). *In* : Tierwelt Deutschland, **64** : 1-464.

ROEWER, C.F., 1953. — Neotropische Gagrellinae (Opiliones, Arachnida). (Weitere Weberknechte XVII). — *Mitt. Zool. Mus. Berlin,* **29** (1) : 180-265.

WAGNER, H., 1954. — Massenanssammlungen von Weberknechten in Mexico. — *Z. Tierpsychol.,* **11** : 348-352.