Charles Darwin *In Memoriam*

Evolutionary looks at the why of biological and cultural phenomena.

Harvestmen as a model to explain the aggregations of *Macrohaltica* beetles (Coleoptera: Chrysomelidae)

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ABSTRACT: **Neotropical beetles of the genus *Macrohaltica* form aggregations exceeding 5000 individuals, but there are no studies testing the four hypotheses available to explain why. Based on the better studied Opiliones aggregations, I propose that *Macrohaltica* aggregations were selected for three of the reasons proposed by William Eberhard and colleagues in 1993: enhanced defense against parasites and predators; keeping adequate moisture and temperature; and facilitating mating. Additionally, also based on Opiliones, I suggest that two unreported behaviors may occur: males occupying the exposed parts of groups; and females leaving the aggregation after mating.**

KEYWORDS: enhanced defense, optimal microhabitat, mating, cumulative aposematism, males, females, daddy-longlegs, harvestmen.

Beetles of the genus *Macrohaltica* occur throughout the Neotropics and can form aggregations exceeding 5000 adult individuals (Hilje & Coto, 1996; Santisteban, 2006); for example, large groups of *Macrohaltica patruelis* feed on the giant leaves of *Gunnera insignis* in Costa Rica (Eberhard, Achoy, Marín, & Ugalde, 1993).

No one knows why they form these large groups, but Eberhard et al. (1993) suggested four hypotheses: mating; overcoming the plant's chemical defenses; staying in optimal microclimate; and cumulative aposematism.

Apparently, there are no follow up studies testing any of these hypotheses, but here I suggest a model based on a better known group with a similar behavior: Opiliones, also known as daddy-longlegs or harvestmen.

In some harvestmen, large aggregations are known from tropical and temperate ecosystems, and they do serve three non-exclusive functions for which there is good evidence:

Enhanced defense: the groups concentrate chemical and active defenses against parasites and small predators like spiders, and in a group, each individual has a much higher chance of not being the one attacked (in comparison with alone encounter with a parasite or predator (Machado & Vasconcelos, 1998; Wijnhoven, 2011).

Optimal microhabitat: the close physical association, sometimes of several layers of individuals, helps conserve adequate levels of moisture and temperature (Wijnhoven et al., 2007; Wijnhoven, 2011).

Mating: even though aggregations also occur outside the reproductive season, mating takes place inside the aggregations; the males move to the periphery to protect the females and impregnated females leave the group to find secluded places to lay their eggs (Wijnhoven, Schönhofer, & Martens, 2007; Wijnhoven, 2011).

In favor of the model: several characteristics are equal in *Macrohaltica* and harvestmen aggregations. One is the grouping in layers (Figure 1), in which the lower layers are better protected from environmental conditions and enemies, particularly considering that *Macrohaltica* occurs in cold areas (Eberhard et al., 1993; Wijnhoven et al., 2007). Another is the sexual ratio close to equal proportions of females and males (Wijnhoven, 2011) and the fact that, in both groups females can prevent males from mating (Eberhard & Kariko, 1996; Wijnhoven et al., 2007; Wijnhoven, 2011).

FIGURE 1. **Aggregation of *Macrohaltica* beetles on leaves of "poor man's umbrella", a plant of the genus *Gunnera*, in Cascajal de Coronado, Costa Rica. Notice the multiple layers of insects and their conspicuous coloration (probably aposematic). Photos by J. Monge-Nájera.**

Against this model: not all group characteristics are equal between *Macrohaltica* and harvestmen, one key difference is that harvestmen must leave the group to feed (Eberhard et al., 1993; Wijnhoven et al., 2007), but this does not necessarily invalidate the model.

Final comments: Eberhard et al. (1993) explained that the group feeding hypothesis is less probable because the aggregations also occur outside food plants. Comparison with Opiliones suggests that *Macrohaltica* aggregations may have been selected for the same general advantages, and also suggests that the beetles should be studied for other similarities, like males occupying the exposed parts of groups and females leaving the aggregation after mating.

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