COMMENT – The size-grain hypothesis in ants: conflicting evidence or confounded perspective?

ALEJANDRO G. FARJI-BRENER Laboratorio Ecotono, Departamento de Ecología, CRUB, Universidad Nacional del Comahue, Bariloche, Argentina.

Longer legs decrease the cost of running and permit animals to walk over environmental interstices instead of through them. However, long legs can complicate the ability of an organism to penetrate interstices that contain food sources and refugia. Because the perception of environmental interstices (i.e. rugosity) increases as body size decrease (Size-Grain Hypothesis; SGH), Kaspari and Weiser (1999) propose that the benefits of long legs are outweighed by the cost of leg construction in small ants, and thus natural selection should favour proportionally smaller legs with decreasing body size. Two studies have demonstrated that leg length decreases disproportionally to body size in 142 ant species belonging to five subfamilies mainly from the New World (Kaspari & Weiser, 1999; Espadaler & Gómez, 2001). However, Parr *et al.* (2003) recently obtained apparently contradictory results. Using data from Southern African ants, they analysed the scaling of leg length and body length of 86 ant species using phylogenetic independent contrasts, and also compared the body sizes of ant species from areas of contrasting habitat complexity (unburned and experimentally burned plots). The allometric approach using the phylogenetic independent contrast method provided strong support for the SGH; but the smaller body size classes were no more speciose on the control (rugose) plots than on the annually burnt (planar) plots. Parr *et al.* (2003) interpreted this field evidence contrary to the predictions of the SGH.

I believe that this field evidence does not contradict the SGH because the manipulative nature of the experiment of Parr *et al.* (2003) represents an ecological rather than an evolutionary test. The SGH proposes that natural selection should favour proportionally smaller legs with decreasing body size, and thus that the degree of rugosity of an environment will favour or disfavour different body sizes in different lineages of ants. Because natural selection depends on sustained interactions between the biological actors implicated (in this case, ant species and the rugosity level of the environment) over evolutionary time, different body size distributions of ant species between burned and unburned plots are not necessarily predicted by the SGH. Although for the ants burned plots are more planar than unburned plots, the experimental situation of the Parr *et al.* (2003) experiments is probably not the natural environment where the morphology of the ants evolved. Moreover, because foundress queens of many ant species can fly great distances and disperse widely from their nest to establish new colonies (Hölldobler & Wilson, 1990), the spatial association between ants and the rugosity condition of the plots may be temporally inconsistent even for a given ant species, making the allometric relationships less consistent than predicted by the SGH.

I agree with Parr *et al.* (2003) that this hypothesis needs more field tests to reinforce its validity, including measurements of the functional relationship between the allometric pattern proposed by the SGH and habitat perception (e.g. Farji-Brener *et al.*, 2004). Because the SGH concerns evolutionary patterns, natural habitats with different levels of rugosity (e.g. Yanoviak & Kaspari, 2000), rather than experimental plots, should offer more useful tests of predictions of SGH concerning body sizes classes of ant assemblages.

Correspondence: Alejandro G. Farji-Brener, Laboratorio Ecotono, CRUB-UNC, Quintral 1250 (8400) Bariloche, Argentina. E-mail: alefarji@crub.uncoma.edu.ar

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References

Espadaler, X. & Gómez, C. (2001) Formicinae ants comply with the size-grain hypothesis. *Functional Ecology*, **15**, 136–139.

Farji-Brener, A.G., Barrantes, G. & Ruggiero, A. (2004) Environmental rugosity, body size, and access to food: a test of the size-grain hypothesis in tropical litter ants. *Oikos*, **104**, 165–171.

Hölldobler, B. & Wilson, E.O. (1990) *The Ants*. Belknap Press, Cambridge, Massachusetts.

Kaspari, M. & Weiser, D. (1999) The size-grain hypothesis and interspecific scaling in ants. *Functional Ecology*, **13**, 530–538.

Parr, Z.J., Parr, C.L. & Chown, S.L. (2003) The size-grain hypothesis: a phylogenetic and field test. *Ecological Entomology*, **28**, 475–481.

Yanoviak, S. & Kaspari, M. (2000) Community structure and the habitat templet: ants in the tropical forest canopy and litter. *Oikos*, **89**, 259–266.

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