

## Reply from G. Bernasconi and J.E. Strassmann

It is unfortunate that small, initially closed, newly founded ant colonies are so difficult to study in the field. If this were not the case, we might have much more complete information on the advantages of multiple-founding queens. As it is, we rely principally on laboratory studies<sup>1</sup>. Advantages of group nesting in the face of intraspecific brood raiding during colony founding were first reported in *Myrmecocystus mimicus*<sup>2</sup>, where brood raiding also occurs between mature colonies after ritualized territorial fights<sup>2</sup>. In *My. mimicus*, *Messor pergandei* and *Acromyrmex versicolor*, evidence that workers of neighbouring incipient nests reciprocally steal brood comes from the laboratory<sup>1,3,4</sup>. To date, brood raiding has been investigated and observed in the field only in the red imported fire ant, *Solenopsis invicta*<sup>3</sup> (with one excellent field study of *Me. pergandei* not observing any occurrences<sup>5</sup>). From these field studies<sup>6,7</sup>, we know that the intensity of brood raiding and colony survival depend on queen density, as well as on the density and local spacing of new nests. Consistent with density-dependent benefits, queens are more likely to form groups when crowded, with local queen densities within one or a few metres probably being relevant for joining decisions<sup>8</sup>. Density also increases the frequency of usurpation attempts by raided queens<sup>6</sup>. Density-dependent advantages accruing to multiple-queen colonies are, therefore, potentially less important in the species' native range (as suggested by Brown<sup>4</sup> and previous studies<sup>6</sup>), where mound densities are lower than in the USA (Ref. 9) (but similar at selected sites<sup>9</sup>); thus, alate densities might also be lower.

Clumping and comparable densities of young nests have been reported in all four of these species<sup>2,3,5,10</sup> (Table 1), a finding that underlies the laboratory studies on differential colony success at brood raiding. It is true that density might not have the same effects in all species; for example, in *Me. pergandei* nests are clumped also in sites where most queens found solitarily<sup>11</sup> and associations can be common under low queen density<sup>12</sup>. Density-independent advantages (e.g. predation avoidance by joining already-dug nests, faster nest construction, earlier colony growth and maturation, and higher survival) might also promote joining<sup>2,5,8</sup>. However, high pre-emergence colony mortality<sup>13</sup> and attacks from mature colonies<sup>8</sup>, which are suggested by Brown<sup>4</sup> to potentially lessen the impact of brood raiding in the other species, have been documented for the imported fire ant<sup>8,13</sup>.

Addressing the importance of brood raiding in the field (relative to other sources of colony differential success<sup>4</sup>) and extending the elegant field studies carried out with fire ants<sup>3,6,7,13</sup> to other species<sup>1</sup> are valuable undertakings in their own right. However, inferences about the relationship between invasiveness and the importance of brood raiding might be premature, because colony founding has not yet been studied in the fire ant's native range in South America. Additional studies of young colonies in natural circumstances would be beneficial to our understanding of the advantages of group nesting in ants.

### Acknowledgements

We thank Mark Brown and Bert Hoelldobler for helpful discussion.

### Giorgina Bernasconi

Institut für Umweltwissenschaften,  
Universität Zürich, Winterthurerstr. 190,  
8057 Zürich, Switzerland  
(bernasco@uwinst.unizh.ch)

### Joan E. Strassmann

Dept of Ecology and Evolutionary Biology,  
Rice University, PO Box 1892, Houston,  
TX 77251, USA (strassm@rice.edu)

### References

- 1 Bernasconi, G. and Strassmann, J.E. (1999) Unrelated cooperators: the ant foundress case. *Trends Ecol. Evol.* 14, 477–482
- 2 Bartz, S.H. and Hölldobler, B. (1982) Colony founding in *Myrmecocystus mimicus* Wheeler (Hymenoptera, Formicidae) and the evolution of foundress associations. *Behav. Ecol. Sociobiol.* 10, 137–147

- 3 Tschinkel, W.R. (1992) Brood raiding in the fire ant, *Solenopsis invicta* (Hymenoptera, Formicidae): laboratory and field observations. *Ann. Entomol. Soc. Am.* 85, 638–646
- 4 Brown, M.J.F. (1999) From the laboratory to the field: the advantage of pleometrotic colony founding. *Trends Ecol. Evol.* 15, 116
- 5 Pfennig, D.W. (1995) Absence of joint nesting advantage in desert seed harvester ants, evidence from a field experiment. *Anim. Behav.* 49, 567–575
- 6 Adams, E.S. and Tschinkel, W.R. (1995) Density-dependent competition in fire ants: effects on colony survivorship and size variation. *J. Anim. Ecol.* 64, 315–324
- 7 Adams, E.S. and Tschinkel, W.R. (1995) Effects of foundress number on brood raids and queen survival in the fire ant *Solenopsis invicta*. *Behav. Ecol. Sociobiol.* 37, 233–242
- 8 Tschinkel, W.R. and Howard, D.F. (1983) Colony founding by pleometrosis in the fire ant *Solenopsis invicta*. *Behav. Ecol. Sociobiol.* 12, 103–113
- 9 Porter, S.D. et al. (1992) Fire ant mound densities in the United States and Brazil (Hymenoptera: Formicidae). *J. Econ. Entomol.* 85, 1154–1161
- 10 Rissing, S.W. et al. (1986) Natal nest distribution and pleometrosis in the desert leaf-cutter ant *Acromyrmex versicolor* (Pergande) (Hymenoptera, Formicidae). *Psyche* 93, 177–186
- 11 Cahan, S. et al. (1998) An abrupt transition in colony founding behaviour in the ant *Messor pergandei*. *Anim. Behav.* 55, 1583–1594
- 12 Pollock, G.B. and Rissing, S.W. (1985) Mating season and colony foundation of the seed-harvester ant *Veromessor pergandei*. *Psyche* 92, 125–134
- 13 Tschinkel, W.R. (1992) Brood raiding and the population dynamics of founding and incipient colonies of the fire ant, *Solenopsis invicta*. *Ecol. Entomol.* 17, 179–188

Table 1. Natural densities of newly founded nests<sup>a</sup>

Species	Density of new nests	Refs
<i>Myrmecocystus mimicus</i>	$d = 0.5$ m	2 <sup>b</sup>
<i>Messor pergandei</i>	$d = 3–4$ m	5 <sup>c</sup>
<i>Acromyrmex versicolor</i>	New nests clumped underneath trees	10
<i>Solenopsis invicta</i> *	$d = 2.2$ m	3

<sup>a</sup>Abbreviations:  $d$  = mean distance to nearest neighbouring young nest; \* = US population.

<sup>b</sup>Information found in Fig. 4.

<sup>c</sup>Information found in Fig. 3 and Table 2.