

## Use of walking trails by bees

SIR — Trail use has evolved twice among the ground-dwelling social insects (ants and termites), a striking example of evolutionary convergence in behaviour. The other groups of social insects, bees and wasps, are principally flying organisms, not known to use extended walking trails for locating colony resources, although some species of stingless bees follow scent marks or aerial odour trails during flight<sup>1</sup>. Our field investigation of the Amazonian bumble bee, *Bombus transversalis*, reveals that it clears and maintains trails on the forest floor, similar in appearance to the recruitment trails of ants<sup>2</sup>.

Most bumble bees inhabit the temperate areas of the world, occurring as far north as



*Bombus transversalis* workers following one another in tandem along a trail. The field study was carried out in the Tambopata Nature Reserve<sup>3</sup>, located along the Rio Tambopata (12° 50' S; 69° 17' W), Department of Madre de Dios, Peru, approximately 280 m above sea level, during the dry season May–June 1995. Colony located by T. Rulston and P. Debes.

the Arctic Circle and at elevations up to 5,000 m. Only *B. transversalis* is known to inhabit the tropical forests of the Amazon Basin<sup>3</sup>. Our field observations focused on a colony in its relatively early growth phase, containing around 350 workers and a single queen. Specialized workers foraged for nectar and pollen throughout the daylight hours. Another subset (behavioural caste) of workers devoted much time to building and maintaining an elaborate nest canopy<sup>4</sup> composed of a stiff mass of leaves, rootlets and fibres woven into an aerated cone 10–15 cm thick. The use of marked bees indicated that this subset of workers (8–10% of colony adults) was involved in canopy building for several days at least.

Examination of how the materials for the nest canopy were gathered revealed that 'thatch-makers' walked off the nest cone periodically and followed one another in tandem along one of two cleared paths on the forest floor (see figure). Extending from opposite sides of the nest, the paths were 9–10 cm wide and 1.5 m and 2 m long, respectively. Both paths were cleared of vegetation, and terminated beneath a dense mat of fallen leaves, where bees

often remained hidden for more than 5 minutes. Bees walking outbound along the paths interrupted their movement periodically to jab at the soil surface with their mandibles, and to cut and remove or investigate plant fragments they encountered. Bees emerging from the terminal leaf litter flew directly back to the nest cone, or walked back along the cleared path and proceeded to work on the canopy.

The trails seem to be actively maintained, for when we dropped fragments of leaf litter and twigs along selected portions of the front and rear paths, outbound thatch-makers pushed them sideways off the path or backwards towards the nest cone. Items were removed within 5–10 s by the first bees encountering them, and most items were detected within 5 minutes. Observations of tagged individuals indicated that 23 out of 25 bees remained on their respective trails (92% trail specificity).

Six weeks after our initial observations, the original two trails had been extended by a further 0.5 m and three more had been newly cleared (1.5–2 m long; M. Cohen and N. Thorp, unpublished observations). The bees appeared to minimize the overlap in collection of leaf litter on the forest floor by building the

first two trails on opposite sides of the nest (180°), adding subsequent trails at maximally distant positions relative to the first (90° and 45°, respectively). The canopy increased in height and width by 10 cm during the same 6-week period. Estimated collection rate of thatching material is about 12 cm<sup>2</sup> per day.

The paradoxical use of terrestrial trails by a bee that collects its food resources by flying may, in fact, be an efficient response to the challenges this species faces in nest insulation and defence. The use of trails enables the colony to encompass a wider and more rapidly defended home range, and facilitates the efficient collection of nest-building materials.

S. A. Cameron\*, J. B. Whitfield†  
Departments of \*Biological Sciences  
and †Entomology,  
University of Arkansas,  
Fayetteville, Arkansas 72701, USA

1. Wille, A. A. *Rev. Ent.* **28**, 41–64 (1983).
2. Hölldobler, B. & Wilson, E. O. *The Ants* (Harvard Univ. Press, Cambridge, MA, 1990).
3. Milliron, H. E. *Mem. ent. Soc. Can.* **89**, 81–237 (1973).
4. Olesen, J. M. *J. trop. Ecol.* **5**, 243–246 (1989).
5. Pearson, D. L. & Dressler, R. L. *J. trop. Ecol.* **1**, 37–54 (1985).

## Robustness of cooperation

SIR — The 'Prisoner's Dilemma' is used extensively to study the conflict between individual and collective rationality<sup>1,2</sup>. Two players can either cooperate, *C*, or defect, *D*. There are four possible pay-offs: *R* each, when both players cooperate; *P* each, when both players defect; or *T* to the defector and *S* to the cooperator in the remaining cases (usually  $T > R > P > S$  and  $2R > T + S$ ). Nowak and May extended the game to a population of players arranged in a closed two-dimensional  $n \times n$  lattice. In each period, each player plays the Prisoner's Dilemma with its eight immediate neighbours and itself, adopting the strategy used by its opponent with the highest score from the previous period. Computer simulations using the pay-offs  $2 > T > 1.8$ ,  $R = 1$  and  $S = P = 0$  show that the asymptotic fraction of *C* players,  $f_C$ , fluctuates around 0.318. Recent articles have used this spatial version of the Prisoner's Dilemma to explain how "cooperation rather than exploitation can dominate in the darwinian struggle for survival"<sup>3–5</sup>.

We have analysed three independent natural variations of the spatial Prisoner's Dilemma. We find that cooperation is eliminated in all three, suggesting that the spatial Prisoner's Dilemma cannot fully account for the emergence and persistence of cooperation in natural and social systems. First (Fig. 1a), we considered the effect of players making independent and identically distributed errors. With a small probability  $\epsilon$ , each player errs and chooses evenly between strategies *C* and *D*; with probability  $1 - \epsilon$ , the player follows the Nowak and May update rule. Second (Fig. 1b), we considered the effects of different levels of synchronization as opposed to the condition of complete asynchrony<sup>6</sup>. During each period, players fail to update their previous strategy with a small probability,  $\theta$ . Third (Fig. 1c), we considered the effect of a small percentage of the cooperators resorting to cheating in order to exploit their neighbours. After following the Nowak and May update rule, each cooperator has a small independent probability,  $\phi$ , of cheating by switching to defection.

In all three variations, cooperation did not persist. Previous reports<sup>7,8</sup> on probabilistic perturbations are based on probabilistic ratios of the pay-offs, and can only affect the boundary between clusters of cooperators and defectors. Our variations allow all players to commit errors with a low probability and are not restricted to such boundaries. A lone defector can grow into a cluster of

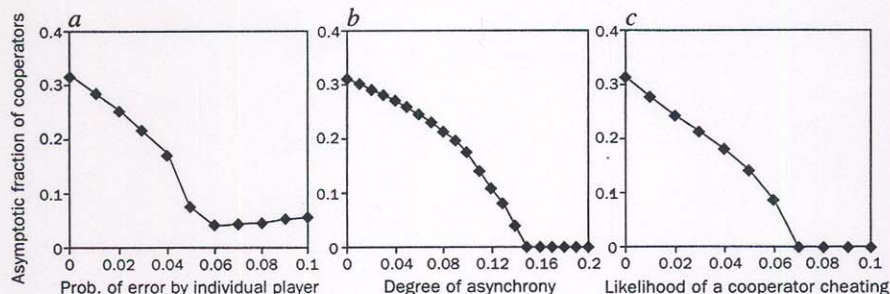


FIG. 1 Simulations were performed on a  $100 \times 100$  lattice, for 500 periods starting with a random initial configuration with 10% defectors (and 90% cooperators) and pay-offs  $T = 1.85$ ,  $R = 1$ ,  $P = S = 0$ . *a*, The asymptotic fraction of cooperators,  $f_C$ , decreases rapidly with small increases in the error factor  $\epsilon$  (the probability with which each player errs and chooses evenly between  $C$  and  $D$ ). As  $\epsilon$  approaches 0.06, some isolated cooperators remain, but they are too few and too dispersed to form clusters of cooperation. With further increases in  $\epsilon$ , the number of cooperators increases, because  $\epsilon/2$  of the population will randomly choose to cooperate. However, no clusters of cooperation were observed. *b*, A high degree of synchronization is required to maintain cooperation. Each player was allowed to skip updating its strategy during a period with a small independent probability,  $\theta$ . With  $\theta = 0$  (100% synchronization),  $f_C \approx 0.318$ . When  $\theta$  was increased to 0.1,  $f_C$  dropped by half. Cooperation is eliminated when  $\theta$  reaches 0.15. Thus, a relatively small percentage (~15%) of the population not being synchronized, as opposed to the condition of complete asynchrony<sup>6</sup>, is sufficient to eliminate cooperation. *c*, Cooperation is rapidly reduced if each cooperator has a small independent probability,  $\phi$ , of cheating after following the Nowak and May update rule. The fraction of cooperators,  $f_C$ , quickly decreases as  $\phi$  increases. Clusters of cooperation are wiped out when about 7% of the cooperators cheat.

defectors. Clusters of cooperators and defectors grow and diminish, producing a variety of spatial patterns. The asymptotic behaviour shows small, tightly knit clusters of cooperators gliding around in a world of defectors. However, even one member of a cluster of cooperators changing to defection can eliminate or shrink the cluster. For cooperation to persist in the spatial Prisoner's Dilemma, a high degree of synchronization with no errors is required, a condition that is unlikely in most natural and social systems.

**Arijit Mukherji**

Carlson School of Management,  
University of Minnesota,

**Vijay Rajan**

**James R. Slagle**

Department of Computer Science,  
University of Minnesota,  
Minneapolis, Minnesota 55455, USA

NOWAK *ET AL.* REPLY — Mukherji *et al.* investigate the question of whether cooperation can survive in the spatial Prisoner's Dilemma in the presence of noise. They perform computer simulations of three different types of stochastic perturbation: (1) a fraction of sites is occupied at random by cooperators or defectors; (2) a fraction of sites is not updated, but remains with the current strategy; and (3) a fraction of cooperators turns spontaneously into defectors (this third assumption is well chosen for attempting to eliminate cooperators). All their simulations are restricted to the particular parameter region  $2 > T > 1.8$ .

We have explored Mukherji *et al.*'s extensions of our model, but for the wider range of parameters outlined in our original papers. For the particular region considered by Mukherji *et al.*, we of course

confirm their results, but the spatial Prisoner's Dilemma has nine different parameter regions for  $2 > T > 1$  (see ref 3, 4, 7–9). For the other parameter regions we find in all three cases that cooperators can persist despite significant amounts of noise (see Fig. 2). In model (1) the baseline level of cooperators is  $\epsilon/2$  (because of the random assignment of a fraction  $\epsilon$  of sites). We find that in parameter regions 1–5 cooperators exist at abundances well above baseline for noise levels up to 25%, and in parameter regions 1–3, for noise levels up to 50% and more. In model (2) the degree of asynchrony has essentially no effect on the asymptotic abundance of cooperators in parameter regions 1–8. In model (3), survival of cooperators is possible in parameter regions 1–6 for noise levels of about 13% and in regions 1–3 for noise levels of about 26%.

The main conclusion in our original papers<sup>3,7–9</sup> was that spatial structures can facilitate the survival of cooperators. It is clear that any kind of noise that tends to destroy spatial structures will work against the survival of cooperators. But, even in the region  $2 > T > 1.8$ , our original results for the deterministic case remain valid at low noise levels and are lost only when the noise exceeds a threshold magnitude. Our present simulations (and previous work<sup>7,8,10</sup>) also show that the spatial Prisoner's Dilemma — if seen in the whole range of parameter regions — is, in fact, robust against significant amounts of stochastic perturbations, as well as several other complications<sup>8</sup>.

In contrast with Mukherji *et al.*'s final conclusion, we contend that cooperation persists in the spatial Prisoner's Dilemma even in the face of reasonably high levels of noise.

**Martin A. Nowak**

**Sebastian Bonhoeffer**

**Robert M. May**

Department of Zoology,  
University of Oxford,  
South Parks Road,  
Oxford OX1 3PS, UK

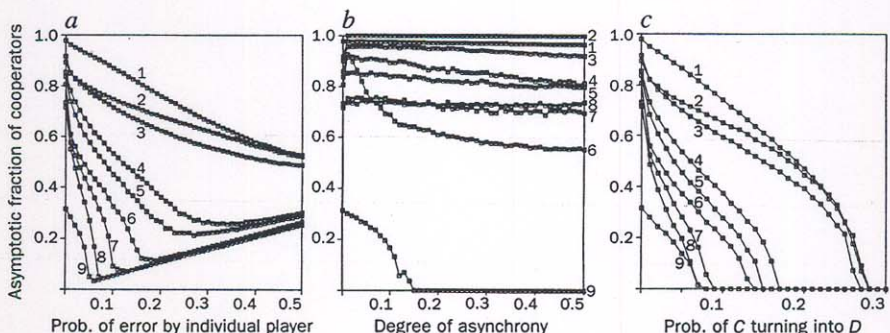


FIG. 2 Computer simulations for the spatial Prisoner's Dilemma with three different types of stochastic perturbations as proposed by Mukherji *et al.*, but for all 9 relevant parameter regions of the game<sup>7,8</sup> represented by the  $T$  values 1.05, 1.13, 1.16, 1.35, 1.42, 1.55, 1.71, 1.77 and 1.9 (corresponding to labels 1–9 in the figure). Mukherji *et al.* show results for the ninth parameter region  $2 > T > 1.8$ . The x-axis denotes: *a*, the fraction of sites given randomly to cooperators or defectors in each generation; *b*, the fraction of sites that are not updated in every generation; *c*, the fraction of cooperators that are changed into defectors in every generation. The y-axis is the asymptotic fraction of cooperators in a  $100 \times 100$  array after 500 generations with an initial condition of 90% cooperators.

1. Axelrod, R. *The Evolution of Cooperation* (Basic Books, New York, 1984).
2. Rapoport, A. in *The New Palgrave: A Dictionary of Economics* Vol. 3, 973–976 (Macmillan, London, 1987).
3. Nowak, M. A. & May, R. M. *Nature* **359**, 826–829 (1992).
4. Nowak, M. A., May, R. M. & Sigmund, K. *Scient. Am.* **272** (6), 76–81 (1995).
5. Sigmund, K. *Nature* **359**, 774 (1992).
6. Huberman, B. A. & Glance, N. S. *Proc. natn. Acad. Sci. U.S.A.* **90**, 7716–7718 (1993).
7. Nowak, M. A., Bonhoeffer, S. & May, R. M. *Proc. natn. Acad. Sci. U.S.A.* **91**, 4877–4881 (1994).
8. Nowak, M. A., Bonhoeffer, S. & May, R. M. *Int. J. Bifurcation Chaos* **4**, 33–56 (1994).
9. Nowak, M. A. & May, R. M. *Int. J. Bifurcation Chaos* **3**, 3578 (1993).
10. Herz, A. V. M. *J. theor. Biol.* **169**, 65–87 (1994).

Scientific Correspondence

Scientific Correspondence is intended to provide a forum in which readers may raise points of a scientific character. Priority will be given to letters of fewer than 500 words.