

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 flight¹. 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 ants².

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 Reserve³, 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 Basin³. 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 canopy⁴ 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 cm² 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.

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Robustness of cooperation

SIR — The 'Prisoner's Dilemma' is used extensively to study the conflict between individual and collective rationality^{1,2}. 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"^{3–5}.

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 ϵ , 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 asynchrony⁶. During each period, players fail to update their previous strategy with a small probability, θ . 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, ϕ , of cheating by switching to defection.

In all three variations, cooperation did not persist. Previous reports^{7,8} 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