



## FORUM

### Reply to Kirchner & Arnold (2001)

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We thank Kirchner & Arnold for their careful re-examination of our 1991 study (Oldroyd et al. 1991) in which we suggested that honey bee, *Apis mellifera*, dance recruits preferentially follow dances performed by supersisters rather than half-sisters. We agree with their overall conclusion: there is no tendency for dance followers to recognize and preferentially follow the dances of supersisters based on genetically based subfamily recognition.

In hindsight, the title of our 1991 paper was unfortunate, as it drew attention to subfamily recognition and nepotism rather than the more important findings of genetically based within-colony variance in foraging and dancing behaviour. These latter findings stand.

We argued (1991, 1994), and as is discussed by Kirchner & Arnold (2001), that genetically based differences between subfamilies in foraging preferences and the tendency to dance were a likely cause of the apparently nepotistic interactions we observed. As we pointed out in our 1991 paper, if pollen dancers attract followers with a preference for pollen foraging, then this could lead to the appearance of a bias towards dance followers following dancing supersisters. For these kinds of bias to be manifest, subfamilies need to differ strongly in their foraging preferences and their probability of performing and following dances. We understand that during the course of their study, Kirchner & Arnold found extreme differences between subfamilies in their tendency to dance and follow dances (unpublished data). Thus it is somewhat

surprising that they did not observe the same positive subfamily associations that we did.

This may be because the appearance of nepotism can be artefactual. We discussed this phenomenon in 1994 (Oldroyd et al. 1994), and cautioned that our 1991 results could be misleading. The inherent problem with the experimental design in the 1991 paper is that bees were not individually identified. This means that in all probability we observed the same bees dancing together repeatedly. As we showed in 1994, this can lead to the appearance of nepotistic interactions and significant chi-squares. Kirchner & Arnold sampled dance participants just once, so the effect was not seen.

The way in which scouts and recruits interact continues to be of great interest. Genetically based task specialization is potentially a very important component of the task allocation system in social insects (Frank 1999). We now view biases towards subfamilies preferentially interacting with each other as an emergent property of task specialization and varying task thresholds among subfamilies. The adaptive significance, if any, of this emergent property is unresolved.

#### References

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