

## A reply to Byers & Bekoff

ALAN GRAFEN

*Department of Plant Sciences, South Parks Road, Oxford OX1 3RA, U.K.*

*(Received 19 November 1990; accepted 21 November 1990;  
MS. number: sc-611)*

The resolution of the majority of the many criticisms of Byers & Bekoff (1991) is given in my reply (Grafen 1991a) to Stuart (1991). Namely, I use kin recognition in a strict sense, as many others do, to refer to kin recognition by genetic similarity detection. Here I wish to discuss some of the residual issues.

Byers & Bekoff are concerned about my sweeping dismissal of the existence of kin recognition. As stated in my paper, the importance and interest of work that claims to be on kin recognition is not at stake here, just whether it should be called kin recognition or not. The best studied recognition system is in *Hemilepistus reaumuri*. Linsenmair's (1987) exquisite work stands entirely on its own merits, but in my view it is not a study of kin recognition, for reasons explained in my original paper and in my replies (Grafen 1991a, b) to Stuart and to Blaustein et al. (1991).

Where is the sense, though, in having a debate about words? Why does it matter if Linsenmair's study is called kin recognition? I see a number of substantial points. First, the functional properties of a recognition system are very important, and by misnaming the system we prejudge those properties. The central point of my paper was that evidence of discrimination by genetic similarity did not suffice to show that 'individuals of this species have evolved to distinguish kin from non-kin . . . that the possession of the ability has anything to do with kin selection . . . and . . . that this ability to discriminate has any evolutionary function at all' (Grafen 1989, page 42). Calling the discrimination abilities of tadpoles 'kin recognition' undeniably prejudices these issues.

Another substantial issue is why genetic cues are used. If we assume that a system is for kin recognition, then there is a natural reason to use genetic cues. But *Hemilepistus*, with their nestmate recognition system, use genetic cues. Genetic cues are stable over a lifetime, and can provide great diversity through polymorphism. These are good reasons to use genetic cues, and they may be the

only ones. The fact that genetic cues allow weak effects of direct genetic similarity detection in *Hemilepistus* may be irrelevant to the operation of the recognition system. It is possible that those weak effects are the sum total of our knowledge of recognition systems in some organisms; only when we know more about each species will we be able to tell.

In the case of nestmate recognition, it is often the case that many of the recognized individuals are kin. But we should not ignore recognition systems in which it is not kin that are recognized, particularly when they may use exactly the same mechanisms as those in nestmate recognition.

For these reasons, the use of the term kin recognition in the loose sense is misleading, presumptive and unhelpful. I now turn to one or two more specific points raised by Byers & Bekoff. They complain that I ignored the possibility that an animal may gain information about kinship in different ways for different actions it takes towards others. This may well be so. If it is, then my arguments are unaffected, they simply apply separately to each method of acquiring information about kinship.

Byers & Bekoff also complain that I put forward an 'unacceptably simplistic standard' for identifying discrimination by genetic similarity, namely that it should be shown 'that an individual behaves differently at first encounter towards differently related groups of conspecifics'. The type of experiment I was referring to, typified by the tadpole experiments, presents those differently related groups of conspecifics with no other cues. I assumed, perhaps wrongly, that the reader would understand from her background in the subject that in experiments of this kind routine precautions are taken. In any event, I was not putting forward a standard at all, as the words 'We may accept' in the quotation given by Byers & Bekoff make clear. I was describing certain kinds of experiments, of the tadpole type, and accepting for the purpose of argument the inference drawn by the experimenters

that genetic differences were involved. This was a preliminary to the main point of my paper, which was rejecting logically subsequent inferences about the function of this discrimination. It was not my intention to state, and nor did I state, criteria by which genetic discrimination could be recognized.

Byers & Bekoff claim I neglect the fact that mothers (who they say are animals) recognize their offspring (who they point out are kin). The distinction between strict and loose kin recognition (Grafen 1991a) can be made quite nicely by describing this as loose kin recognition. Strict kin recognition would be a father recognizing which of his mate's offspring were not fathered by him.

To end by answering Byers & Bekoff's summarizing points: (1) the important dichotomy is how information about relatedness is obtained. If it is obtained by genetic similarity detection, and it is used in nature to distinguish kin from non-kin, then it is strict kin recognition. (2) I put forward no standard for identifying innate kin-aligned behaviour. (3) I did not mention offspring recognition, but it is in any event not an obvious example of strict kin recognition. (4) Whether individuals

are re-recognized for different kinds of behaviour doesn't matter: for each separate instance of recognition we can and should ask the important question of how information about relatedness was acquired.

## REFERENCES

- Byers, J. A. & Bekoff, M. 1991. Development, the conveniently forgotten variable in 'true kin recognition'. *Anim. Behav.*, **41**, 1088–1090.
- Blaustein, A. R., Bekoff, M., Byers, J. A. & Daniels, T. J. 1991. Kin recognition in vertebrates: what do we really know about adaptive values? *Anim. Behav.*, **41**, 1079–1083.
- Grafen, A. 1990. Do animals really recognize kin? *Anim. Behav.*, **39**, 42–54.
- Grafen, A. 1991a. Kin vision?: a reply to Stuart. *Anim. Behav.*, **41**, 1095–1097.
- Grafen, A. 1991b. A reply to Blaustein et al. *Anim. Behav.*, **41**, 1085–1087.
- arthropods, in particular the desert isopod *Hemilepistus reaumuri*. In: *Kin Recognition in Animals* (Ed. by D. J. C. Fletcher & C. D. Michener), pp. 121–208. New York: John Wiley.
- Stuart, R. J. 1991. Kin recognition as a functional concept. *Anim. Behav.*, **41**, 1093–1094.