

SHORT COMMUNICATIONS

A reply to Blaustein et al.

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I am pleased that Blaustein et al. (1991) agree with the main thrust of my paper, and aim in part to provide extra evidence in favour of some of it. I also accept a couple of minor corrections they suggest: tadpoles and other vertebrates have genetic similarity detection abilities of comparable magnitude (without prejudice as to whether the abilities are comparably strong or comparably weak!), and O'Hara & Blaustein (1982) suggested before I did that tadpoles may aggregate not to join kin but to join conspecifics. In this paper I shall use the term 'kin recognition' in the strict sense of Grafen (1991), to mean 'kin recognition by genetic similarity detection'.

Blaustein et al. are concerned that I may have drawn the net too tightly in accepting only one example of kin recognition as convincingly demonstrated, namely Grosberg & Quinn's (1986) study of *Botryllus schlosseri*. I will now discuss three rather different candidates, and explain why they do not convince me. The first is the example raised by Blaustein et al. of the optimal outbreeding example of Bateson (1982). I have some sympathy with this example. Certainly showing inbreeding avoidance looks like a comparatively easy way to demonstrate the functional properties required of a kin recognition system. It would not surprise me if Linsenmair's (1987) desert isopods used their recognition system additionally to avoid inbreeding, and this would qualify his recognition system as a kin recognition system in my sense. I agree that the Bateson study is a *prima facie* case of kin recognition. An individual recognition system is used to identify kin, and this works only because the cues are genetic and so reveal information about kinship. I have, though, reservations about the example.

First, are these discriminations used in nature? Second and more seriously, I have methodological misgivings about Bateson's (1982) experiment,

which can here be only briefly outlined. The 35 test birds were from only four sibships, and these four sibships also provided the target birds. Each sibship was therefore first cousins to another sibship, third cousins to yet another, and unrelated to the remaining sibship. One worry is that if variation in attractiveness or preferred characters occurs at the sibship level, then the sample size is more properly four than 35, and having used the same sibships as test birds and targets would complicate the analysis greatly. Such variation might arise if different strains of quail, *Coturnix coturnix*, have strain-specific preferences, and the experimental sibships comprised different mixtures of strains. Bateson (1982) provided no relevant details. In principle, and if used in nature, the kind of ability suggested by Bateson would constitute kin recognition.

The second candidate is Holmes & Sherman's (1982) ground squirrels. Holmes & Sherman showed that in two species of ground squirrels (*Spermophilus parryi* and *S. beldingi*) young females treated littermate females differently from non-littermate females. This effect was overwhelming. There were also much weaker effects, in both the laboratory and the field, apparently requiring detection of direct genetic similarity. In the laboratory study, female siblings reared apart were less agonistic towards each other than female non-siblings reared apart. Holmes & Sherman suggested a possible explanation for this, which is that although a female had not encountered the target individual before, she had encountered other siblings who were her littermates. They showed that the amount of agonism shown decreased as there was an increase in the number of siblings with whom the focal individual had been reared. This suggests a situation rather like Linsenmair's (1987) *Hemilepistus reaumuri*. The major effect the ground squirrels show is based on littermates. If the badge is partly genetic, then individuals more closely

related to the litter will be treated differently, if only because it takes longer for the focus individual to classify them as littermates or not. One question of interest is whether a ground squirrel treated her own siblings in the same way as she would have treated a sibling of her non-sibling littermates. Another is whether the difference in treatment of siblings reared apart has consequences in nature, or merely represents a delay in classification. So although some effect is observed in the laboratory, it is not convincing evidence of kin recognition. It could easily be a side-effect of a littermate recognition system.

The apparent direct genetic similarity detection in nature was not a discrimination between siblings reared apart and non-siblings reared apart, and so cannot help to answer one of the previous paragraph's questions. It was observed that females treated littermates differently according to whether they were full or half-siblings, which Holmes & Sherman themselves found out only through electrophoresis. This is a much stronger case a priori of genetic similarity detection. Holmes & Sherman described these data as preliminary, and I know of no later work on the subject. The difference was again small compared to the difference in behaviour between littermates and non-littermates. There may also be confounding factors. It is possible, for example, that multiple paternity is commoner in parts of the colony in which aggression is commoner, perhaps in more densely populated parts. This could in principle have led to the observed effect artefactually. In data that the authors describe as preliminary these kinds of things should not be ruled out. If it turns out to be true that ground squirrels treat full sibling littermates less aggressively than half-sibling littermates, then this would be an example of kin recognition in the strict sense. At the moment, the evidence is not convincing.

The third candidate is sweat bees. The data were reviewed by Michener & Smith (1987), and the experiments crucial to us here were performed by Greenberg (1979) and Buckle & Greenberg (1981). There is no doubt that genetic cues are used, and that the relatedness of a novel intruder to nestmates of the guard has an overwhelming effect on the probability of admittance. The reason it is not kin recognition is that it fails the second of my criteria (Grafen 1990): the system would perform the same function in nature if each individual were different for purely environmental reasons. As in

Linsenmair's *H. reaumuri*, the recognition system as applied to admittance to the nest is a group member recognition system. Artificially created groups of unrelated females recognize group members. And most important, the occasions when relatives of nestmates are admitted are almost certainly mistakes. If a nestmate's half sister belongs to a neighbouring nest, it is likely to be undesirable to admit her. She may rob the colony, or the whole neighbouring nest may try to take it over. The important discrimination to make is not relative/non-relative, but nestmate/non-nestmate. It happens to be genetic cues that are used to make the discrimination, and this determines the nature of the inevitable mistakes that occur in a recognition system. But there seem to be no advantages in terms of nest admittance arising from the genetic nature of the cues.

More intriguing from the kin recognition point of view are the observations of Smith (1987) on artificially created colonies of sweat bees with variable relatednesses. Some ('kin colonies') comprised sisters, others were mostly unrelated ('non-kin' colonies). In non-kin colonies, workers had more highly developed ovaries, queens responded more aggressively to workers, and there was higher worker mortality. If this flexibility of response is actually adaptive for the individual bees, and is important in the range of intra-nest relatednesses found in nature, then this would count as strict kin recognition.

In conclusion, it seems very likely that a variety of animals do show strict kin recognition. But it imposes no unnatural burden of proof to say that the only convincing demonstration to date is Grosberg & Quinn's (1986) study of *Botrylus schlosseri*, a sessile colonial ascidian. In this system both the mechanism and the adaptive significance are well understood.

REFERENCES

- Bateson, P. 1982. Preferences for cousins in Japanese quail. *Nature, Lond.*, **295**, 236–237.
- 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.
- Buckle G. R. & Greenberg L. 1981. Nestmate recognition in sweat bees (*Lasioglossum zephyrum*): does an individual recognize its own odour or only odours of its nestmates? *Anim. Behav.*, **29**, 802–809.

- Grafen, A. 1990. Do animals really recognize kin? *Anim. Behav.*, **39**, 42–54.
- Grafen, A. 1991. Kin vision?: a reply to Stuart. *Anim. Behav.*, **41**, 1095–1096.
- Greenberg, L. 1979. Genetic component of bee odor in kin recognition. *Science*, **206**, 1095–1097.
- Grosberg, R. K. & Quinn, J. F. 1986. The genetic control and consequences of kin recognition by the larvae of a colonial marine invertebrate. *Nature, Lond.*, **322**, 457–459.
- Holmes, W. G. & Sherman, P. W. 1982. The ontogeny of kin recognition in two species of ground squirrels. *Am. Zool.*, **22**, 491–517.
- Linsenmair, K. E. 1987. Kin recognition in subsocial 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.
- Michener, C. D. & Smith, B. H. 1987. Kin recognition in primitively eusocial insects. In: *Kin Recognition in Animals* (Ed. by D. J. C. Fletcher & C. D. Michener), pp. 209–242. New York: John Wiley.
- O'Hara, R. K. & Blaustein, A. R. 1982. Kin preference behaviour in *Bufo boreas* tadpoles. *Behav. Ecol. Sociobiol.*, **11**, 43–49.
- Smith, B. H. 1987. Effects of genealogical relationship and colony age on the dominance hierarchy in the primitively eusocial bee *Lasioglossum zephyrum*. *Anim. Behav.*, **35**, 211–217.