

## Kin recognition in vertebrates: what do we really know about adaptive value?

ANDREW R. BLAUSTEIN\*, MARC BEKOFF†, JOHN A. BYERS‡ &  
THOMAS J. DANIELS§

\*Department of Zoology, Oregon State University, Corvallis, Oregon 97331-2914, U.S.A.

†Department of Environmental, Population, and Organismic Biology, University of Colorado, Boulder, Colorado 80309-0334, U.S.A.

‡Department of Biological Sciences, University of Idaho, Moscow, Idaho 83843, U.S.A.

§Department of Community and Preventive Medicine, Medical Entomology Laboratory, New York Medical College, Armonk, New York 10504, U.S.A.

(Received January 1990; initial acceptance 27 February 1990;  
final acceptance 18 May 1990; MS. number: 3557)

**Abstract.** The ability of an animal to discriminate between kin and non-kin (kin recognition) has been the subject of numerous recent investigations. Grafen (*Anim. Behav.*, 1990, 39, 42–54) recently reported that the evidence in support of kin recognition is weak and the data illustrating a preference for kin to associate in the laboratory may be more consistently explained as species recognition. It is suggested here, however, that in many cases it may be impossible to distinguish between species recognition and kin recognition, but in some cases, kin recognition seems apparent. It is also emphasized that very little is known about the adaptive value of kin recognition.

The ability of an animal to discriminate between kin and non-kin (often called kin recognition) is an important phenomenon associated with kin selection theory (Hamilton 1964a, b). It is therefore a great concern to those interested in the evolution of social behaviour. Recently, Grafen (1990), in a stimulating and provocative paper, concluded that the empirical evidence in support of kin recognition is weak and that data illustrating a preference for kin to associate in the laboratory may be more consistently explained as species recognition. By narrowly defining kin recognition, Grafen is forced to conclude that kin do not recognize one another except rarely. Here, we (1) add some additional pertinent information to Grafen's point concerning species recognition and (2) make a point of which many biologists seem to be unaware; namely that, there is at best, a very poor understanding of the adaptive value of kin recognition in most species that have been investigated.

### KIN RECOGNITION OR SPECIES RECOGNITION?

Grafen uses data obtained from studies of tadpoles to illustrate how species recognition, in general, may be achieved. He suggests that a species recognition mechanism would work well if, for example,

all members of the species had essentially the same smell and some genetic variation in the smell. Then, individuals will 'acquire a standard (the smell of themselves) which is slightly more like relatives than it is like conspecifics in general' (page 44). Thus, when an individual uses its species recognition capability to join a tadpole aggregation, it will be biased to join a more related group because such a group is perceived as being closer to the 'acquired standard' (i.e. the individual itself).

Grafen's point concerning species recognition is well taken. Unfortunately, in many cases, it may be impossible to tell whether kin recognition per se or species recognition is the prime mechanism of kin association. However, with regard to tadpoles there is both empirical and inferential support for Grafen's suggestion. For example, O'Hara & Blaustein (1982) suggested that species recognition may be a parsimonious explanation for kin association in laboratory tests of toad tadpoles. They suggested that toad tadpoles may use the familiar cues emanating from conspecifics to seek optimal habitats or to aggregate with conspecifics to obtain potential benefits from group living (O'Hara & Blaustein 1982; also see discussion in Blaustein et al. 1990). Experimental results recently obtained by Pfennig (1989) suggest that kin association in spadefoot, *Scaphiopus multiplicatus*, toad tadpoles

may result from habitat selection due to diet-based environmental cues rather than from social preferences. Tadpoles with similar diets aggregate in the laboratory. In nature, owing to the spatial and temporal proximity of kin within a pond, individuals eating similar foods are likely to be related and therefore may form aggregations. Obviously, if associating the kin has selective advantages, it makes little difference whether kin associate because of similar habitat preferences or because of kin recognition per se.

Although we believe that Grafen's species recognition argument for kin association is as plausible as a kin recognition explanation in many species, it cannot explain all cases of kin preferences. For example, how can Grafen's arguments explain the experimental results showing preferences of Japanese quail, *Coturnix coturnix* (Bateson 1982) for first cousins over full siblings or other cases of potential optimal outbreeding (e.g. Barnard & Fitzsimons 1988; review by Blaustein et al. 1987)? Optimal outbreeding is more likely to result from kin recognition than from species recognition.

One way to resolve the species versus kin recognition problem is to focus on the adaptive value of the recognition phenomenon. Unfortunately, there are significant problems with kin recognition studies in general and with the literature on tadpole kin recognition in particular, because of the lack of supporting data concerning key hypotheses addressing the adaptive value of kin recognition and kin association, and the failure to test hypotheses that are not related to kin selection (see discussion in Blaustein & Porter 1990). For example, the most widely cited hypothesis concerning the evolution of kin recognition and kin association in tadpoles suggests that because toad tadpoles are conspicuously black, form large noticeable aggregations and are apparently noxious to their predators, the conspicuousness is aposematic (Wassersug 1973; Waldman & Adler 1979). Therefore, predators eating a noxious tadpole would avoid other similar individuals nearby. This scenario invokes kin selection because the tadpole that is killed by a predator receives some inclusive fitness benefits if relatives have a reduced risk of predation as a result of its death.

This is not a satisfactory explanation for the evolution of kin association in frog tadpoles and it does not seem to be parsimonious even for toad tadpoles. For example, all of the frog tadpoles studied by Blaustein and his colleagues (see Blaustein 1988) in

the context of kin recognition are palatable to their natural predators, cryptic, and hide under debris when approached. Toad tadpoles generally exist in such massive schools, composed of hundreds of kin groups, that the likelihood that kin are associating within the large school is not high. Unless discrete sibling cohorts exist within the massive toad schools, a kin selection mechanism for the maintenance of unpalatability and conspicuousness in toad tadpoles may not be parsimonious (see O'Hara & Blaustein 1982; Waldman, 1982). Many non-kin would also benefit from a predator sampling a distasteful individual and avoiding other members of the group. Even though kin association may be recorded in laboratory experiments, some species lose their preferences after they come in contact with non-siblings during development (e.g. O'Hara & Blaustein 1982). Thus, in nature, maintenance of kin association in tadpole species that lose their affiliation for kin after contact with non-kin would be difficult. One alternative hypothesis (among others and with experimental support) that is just as plausible as the aposematic/kin selection hypothesis for the evolution of sociality and dark coloration in toad tadpoles is that masses of dark tadpoles form for purposes of thermoregulation (Guilford 1988).

#### WHAT DO WE REALLY KNOW ABOUT ADAPTIVE VALUE?

The paucity of information on the adaptive value of kin recognition does not apply only to tadpole studies. Unfortunately, this point has been missed in some recent papers. For example, West-Eberhard (1989) stated (page 704) that 'kin associations are expected in cooperating social insects, birds, and mammals, but why in tadpoles?' West-Eberhard had a 'keen anticipation of being told, at last, why it is that tadpoles recognize and preferentially associate with their sibs'. But nobody really knows.

Table I illustrates that we do not know specifically why most vertebrates associate with kin. Except for social insects and perhaps some sub-social arthropods we do not have many clues as to the adaptive value of kin recognition in most of the species that have been the subject of intensive experimental investigations (see Blaustein & Porter 1990). This stems from a lack of knowledge of the natural history of the species and an almost total

**Table I.** Some commonly cited references of collateral (non-parent/offspring) kin recognition in vertebrates (excluding primates) and knowledge of adaptive value based on field evidence

Organism	Field experiments conducted	Adaptive value based on field evidence	References
<b>Mammals</b>			
Ground squirrels			
Arctic <i>Spermophilus parryii</i>	No	?	Holmes & Sherman (1982)
Belding's <i>S. beldingii</i>	Yes	Alarm calling to warn kin; nepotism	Holmes & Sherman (1982)
Thirteen-lined <i>S. tridecemlineatus</i>	Yes	Alarm calling; parental care	Schwagmeyer (1980); Holmes (1984)
Richardson's <i>S. richardsonii</i>	No	?	Davis (1982)
<b>Mice, rats and voles</b>			
Spiny mouse <i>Acomys cahirinus</i>	No	?	Porter et al. (1978)
House mouse <i>Mus domesticus</i>	No	?	Yamazaki et al. (1976); Kareem & Barnard (1982)
White-footed mouse <i>Peromyscus leucopus</i>	No	?	Grau (1982); Halpin & Hoffman (1987)
Deer mouse <i>P. maniculatus</i>	No	?	Dewsbury (1982)
Cactus mouse <i>P. eremicus</i>	No	?	Dewsbury (1982)
Prairie vole <i>Microtus ochrogaster</i>	No	?	Wilson (1982)
Gray-tailed vole <i>M. canicaudus</i>	No	?	Boyd & Blaustein (1985)
Norway rat <i>Rattus norvegicus</i>	No	?	Hepper (1983)
Muskrat <i>Ondatra zibethicus</i>	No	?	Caley & Boutin (1987)
<b>Birds</b>			
Japanese quail <i>Coturnix coturnix</i>	No	?	Bateson (1982)
Bank swallows <i>Riparia riparia</i>	Yes/no*	?	Beecher & Beecher (1983)
Canada geese <i>Branta canadensis</i>	No	?	Radesäter (1976)
<b>Amphibians</b>			
Tadpoles			
Cascades frog <i>Rana cascadae</i>	Yes	?	O'Hara & Blaustein (1981, 1985)
Red-legged frog <i>R. aurora</i>	No	?	Blaustein & O'Hara (1986)
Wood frog <i>R. sylvatica</i>	No	?	Waldman 1984; Cornell et al. (1989)
American toad <i>Bufo americanus</i>	Yes	?	Waldman (1982)
Western toad <i>B. boreas</i>	No	?	O'Hara & Blaustein (1982)
<b>Fish</b>			
Guppies <i>Poecilia reticulata</i>	No	?	Loekle et al. (1982)
Coho salmon <i>Oncorhynchus kisutch</i>	No	?	Quinn & Busack (1985)

\*Chicks were removed from nests but experiments were performed in the field.

reliance on laboratory experiments. Spiny mice, *Acomys cahirinus*, house mice, *Mus domesticus* and Japanese quail are but three examples of species in which kin recognition has been intensively studied in the laboratory but for which there is very little known about the functional significance of kin recognition in nature.

Although there are good observational data on kin relationships in the field for many vertebrates that suggest that kin associations are based on recognition abilities, and are then explained in an adaptive framework, tadpoles and ground squirrels have been the only vertebrate subjects that have been studied experimentally in the field (Table I). In fact, field experiments of Cascades frog, *Rana cascadae*, tadpoles (O'Hara & Blaustein 1985) reveal much stronger preferences for kin than do laboratory experiments, a phenomenon not addressed by Grafen. Therefore, laboratory experiments may be less sensitive assays than field experiments for assessing kin preferences.

Unfortunately, when Grafen (1990) attributes a 'febleness of the ability' (page 45) of tadpoles to recognize kin in laboratory tests, he conveys the mistaken impression that tadpoles are particularly weak in their associations with kin. In fact, the level of sensitivity in laboratory experiments with tadpoles is of comparable magnitude to that for other vertebrates that have been studied (see discussion in Waldman & Bateson 1989). However, as indicated in Table I, for the majority of vertebrates, we cannot compare the magnitude of results obtained from laboratory tests with those obtained in field tests simply because field tests have not been conducted for the majority of species.

#### ACKNOWLEDGMENTS

We thank Mike Beecher, Art Boucot, Mark Hixon, Bruce Menge, Charles Michener and Steve Rothstein for reading various drafts of the manuscript and Dan Formanowicz, Mike Beecher and Steve Rothstein for valuable discussion. We especially thank Alan Grafen and David Pfennig for allowing us access to their unpublished work. ARB thanks Karen Chang, Morty Tashman and Julius Kelp for their help. Preparation of this manuscript and research on tadpole kin recognition was supported by NSF grant BNS 8718536 to ARB.

#### REFERENCES

- Barnard, C. J. & Fitzsimons, J. 1988. Kin recognition and mate choice in mice: the effects of kinship, familiarity and social interference on intersexual interaction. *Anim. Behav.*, **36**, 1078–1090.
- Bateson, P. 1982. Preferences for cousins in Japanese quail. *Nature, Lond.*, **295**, 236–237.
- Beecher, I. M. & Beecher, M. D. 1983. Sibling recognition in bank swallows (*Riparia riparia*). *Z. Tierpsychol.*, **62**, 145–150.
- Blaustein, A. R. 1988. Ecological correlates and potential functions of kin recognition and kin association in anuran larvae. *Behav. Genet.*, **18**, 449–464.
- Blaustein, A. R., Bekoff, M. & Daniels, T. J. 1987. Kin recognition in vertebrates (excluding primates): empirical evidence. In: *Kin Recognition in Animals* (Ed. by D. J. C. Fletcher & C. D. Michener), pp. 287–331. London: John Wiley.
- Blaustein, A. R., Chang, K. S., Lefcort, H. G. & O'Hara, R. K. 1990. Toad tadpole kin recognition: recognition of half siblings and the role of maternal cues. *Ethol. Ecol. Evol.*, **2**, 215–226.
- Blaustein, A. R. & O'Hara, R. K. 1986. An investigation of kin recognition in red-legged frog (*Rana aurora*) tadpoles. *J. Zool., Lond.*, **209**, 347–353.
- Blaustein, A. R. & Porter, R. H. 1990. The ubiquitous concept of recognition with special reference to kin. In: *Methods, Inference, Interpretation, and Explanation in the Study of Behavior* (Ed. by M. Bekoff & D. Jamieson), pp. 123–148. Boulder: Westview Press.
- Boyd, S. K. & Blaustein, A. R. 1985. Familiarity and inbreeding avoidance in the gray-tailed vole (*Microtus canicaudus*). *J. Mammal.*, **66**, 348–352.
- Caley, M. J. & Boutin, S. A. 1987. Sibling and neighbour recognition in wild juvenile muskrats. *Anim. Behav.*, **35**, 60–66.
- Cornell, T. J., Berven K. A. & Gamboa, G. J. 1989. Kin recognition by tadpoles and froglets of the wood frog *Rana sylvatica*. *Oecologia (Berl.)*, **78**, 312–316.
- Davis, L. S. 1982. Sibling recognition in Richardson's ground squirrels (*Spermophilus richardsonii*). *Behav. Ecol. Sociobiol.*, **11**, 65–70.
- Dewsbury, D. A. 1982. Avoidance of incestuous breeding between siblings in two species of *Peromyscus* mice. *Biol. Behav.*, **7**, 157–169.
- Grafen, A. 1990. Do animals really recognize kin? *Anim. Behav.*, **39**, 42–54.
- Grau, J. H. 1982. Kin recognition in white-footed deer mice (*Peromyscus leucopus*). *Anim. Behav.*, **30**, 497–505.
- Guilford, T. 1988. The evolution of conspicuous coloration. *Am. Nat.*, **131**, S7–S21.
- Halpin, Z. T. & Hoffman, M. D. 1987. Sibling recognition in the white-footed mouse, *Peromyscus leucopus*: association or phenotype matching? *Anim. Behav.*, **35**, 563–570.
- Hamilton, W. D. 1964a. The genetical evolution of social behaviour. I. *J. theor. Biol.*, **7**, 1–16.
- Hamilton, W. D. 1964b. The genetical evolution of social behaviour. II. *J. theor. Biol.*, **7**, 17–52.
- Hepper, P. G. 1983. Sibling recognition in the rat. *Anim. Behav.*, **31**, 1177–1191.

- Holmes, W. G. & Sherman, P. W. 1982. The ontogeny of kin recognition in two species of ground squirrels. *Am. Zool.*, **22**, 491-517.
- Holmes, W. G. 1984. Sibling recognition in 13-lined ground squirrels: effects of genetic relatedness, rearing association and olfaction. *Behav. Ecol. Sociobiol.*, **14**, 225-233.
- Kareem, A. M. & Barnard, C. J. 1982. The importance of kinship and familiarity in social interactions between mice. *Anim. Behav.*, **30**, 594-601.
- Loekle, D. M., Madison, D. M. & Christian, J. J. 1982. Time dependency and kin recognition of cannibalistic behavior among poeciliid fishes. *Behav. neural Biol.*, **35**, 315-318.
- O'Hara, R. K. & Blaustein, A. R. 1981. An investigation of sibling recognition in *Rana cascadae* tadpoles. *Anim. Behav.*, **29**, 1121-1126.
- O'Hara, R. K. & Blaustein, A. R. 1982. Kin preference behavior in *Bufo boreas* tadpoles. *Behav. Ecol. Sociobiol.*, **11**, 43-49.
- O'Hara, R. K. & Blaustein, A. R. 1985. *Rana cascadae* tadpoles aggregate with siblings: an experimental field study. *Oecologia (Berl.)*, **67**, 44-51.
- Pfennig, D. W. 1989. Evolution, development, and behavior of alternative amphibian morphologies. Ph.D. thesis, University of Texas.
- Porter, R. H., Wyrick, M. & Pankey, J. 1978. Sibling recognition in spiny mice (*Acomys cahirinus*). *Behav. Ecol. Sociobiol.*, **3**, 61-68.
- Quinn, T. P. & Busack, C. A. 1985. Chemosensory recognition of siblings in juvenile coho salmon (*Oncorhynchus kisutch*). *Anim. Behav.*, **33**, 51-56.
- Radesäter, T. 1976. Individual sibling recognition in juvenile Canada geese (*Branta canadensis*). *Can. J. Zool.*, **54**, 1069-1072.
- Schwagmeyer, P. L. 1980. Alarm calling behavior of the 13-lined ground squirrel. *Behav. Ecol. Sociobiol.*, **7**, 195-200.
- Waldman, B. 1982. Sibling association among schooling toad tadpoles: field evidence and implications. *Anim. Behav.*, **30**, 700-713.
- Waldman, B. 1984. Kin recognition and sibling association among wood frog (*Rana sylvatica*) tadpoles. *Behav. Ecol. Sociobiol.*, **14**, 171-180.
- Waldman, B. & Adler, K. 1979. Toad tadpoles associate preferentially with siblings. *Nature, Lond.*, **282**, 611-613.
- Waldman, B. & Bateson, P. 1989. Kin association in Japanese Quail chicks. *Ethology*, **80**, 283-291.
- Wassersug, R. J. 1973. Aspects of social behavior in anuran larvae. In: *Evolutionary Biology of the Anurans* (Ed. by J. L. Vial), pp. 273-297. Columbia: University of Missouri Press.
- West-Eberhard, M. J. 1989. Kin recognition in animals. *Evolution*, **43**, 703-705.
- Wilson, S. C. 1982. The development of social behaviour between siblings and nonsiblings of the voles *Microtus ochrogaster* and *Microtus pennsylvanicus*. *Anim. Behav.*, **30**, 426-437.
- Yamazaki, K. E., Boyse, E. A., Mike, V., Thaler, H. T., Mathieson, B. J., Abbott, J., Boyse, J., Zayas, Z. A. & Thomas, L. 1976. Control of mating preferences in mice by genes of the major histocompatibility complex. *J. exp. Med.*, **144**, 1324-1335.