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Mechanisms and ecological correlates of kin recognition

Richard H. Porter and Andrew R. Blaustein

Kin recognition, which can be inferred from differential interactions amongst close relatives as compared to unrelated conspecifics, has been documented in a wide range of vertebrates and invertebrates. Kin may be discriminated by phenotypic traits (signatures) that are genetically mediated, acquired from the environment, or arise from an interaction between these two sources. The developmental mechanisms underlying recognition of relatives (or their signatures) include direct contact and familiarization, indirect familiarity (whereby previously unencountered individuals are recognized by their resemblance to familiar kin) and hypothetical recognition alleles. The biological significance and mediating mechanisms of kin recognition vary across species according to their ecology and natural history. To illustrate this point, the results of laboratory and field studies of larvae of several species of toads and frogs are reviewed.

Introduction

As is evident to even casual observers of animal social behaviour, members of the same species do not interact in an indiscriminate or random manner. Rather, interactions between particular animals, or members of a class or sub-group, may differ noticeably from encounters involving other conspecifics. Numerous accounts of discriminative social behaviour amongst close kin have been reported in recent years. In organisms ranging from colonial marine invertebrates and social insects through various species of rodents and primates, the frequency and characteristics of social interactions vary according to the individuals' degree of genetic relatedness. For example, honey bee guards at the hive entrance will allow their nest-mate sisters to enter but exclude intruders from other hives. Ground squirrel female kin (i.e. mothers and daughters, sisters) tend to live in closer proximity to one another and engage in more amicable interactions than do unrelated (or distantly

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related) animals. Similarly, in several primate species, preferential grooming occurs among mothers and their offspring and maternal siblings. Such differential treatment of kin versus non-kin implies that the former animals can be discriminated, either as individuals or as members of a distinct class. Kin recognition, according to this conceptualization, is inferred from observable discriminative interactions amongst relatives.

Because of the ultimate genetic advantages that it affords, kin recognition is of considerable theoretical interest. Animals that are capable of discriminating between kin and non-kin can effectively behave to the exclusive advantage of their close relatives. Thus, the primary recipients of ground squirrel alarm calls are kin of the calling animal.\(^{13}\) To the extent that such warnings increase the likelihood of survival of the responding kin, the caller may have a positive effect on the propagation of copies of its own genes shared with the latter individuals and thereby enhance its own inclusive fitness (a joint function of the animal's success due to its own reproductive effort plus its impact on the reproductive success of its kin). In line with this, obvious genetic advantages accrue to desert isopods that care for their own progeny but attack and cannibalize foreign young.\(^{15}\) Additional examples of discriminative nepotism include sharing of limited food resources by spiny mouse siblings,\(^{20}\) alliances by ground squirrel sisters to chase off territorial intruders,\(^{13}\) and brown hyenas providing nonparental care for their young cousins.\(^{18}\)

An ability to recognize one's close relatives could be of further value when choosing a mate. Animals that distinguish between kin (e.g. siblings, parents) and non-kin could accordingly avoid incestuous matings and thus the negative genetic consequences of inbreeding. Moreover, individuals who prefer mates that somewhat (but not too closely) resemble kin might thereby achieve an optimal balance between incestuous inbreeding and extreme outbreeding.\(^{1}\)

How is kin recognition accomplished?

The question of how kin recognition is accomplished can be interpreted in two different ways. First, the concern may be with the phenotypic traits or signatures by which kin are identified or discriminated. Alternatively, what are the ontogenetic processes that mediate recognition of the salient signatures (i.e. how does recognition \textit{per se} develop)? These separable, but necessary, components of kin recognition have guided much of the research on this topic.

Signatures

Across taxa, the sensory modalities involved in kin recognition tend to be those that are otherwise salient for communication. Social insects rely on chemical signatures for discriminating kin; in birds, auditory cues are pre-eminent, while olfactory signatures appear to be ubiquitous among terrestrial mammals. Recognizable phenotypic traits may have a genetic basis (as with facial appearance and the chemical make-up of
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glandular secretions). However, this is not a necessary prerequisite for kin discrimination. Cues acquired from environmental sources could also serve as signatures mediating kin recognition. Thus, if all animals in a rodent group composed of a mated pair and their offspring (littermate siblings) eat the same unique diet, they might develop discernibly similar odours differing from those of conspecifics who eat other foods. Reliance on diet-based odours for social recognition would result in discrimination between family members versus non-kin.

In a given species, olfactory signatures may incorporate both genotypically influenced and individually acquired chemical cues. Data from a series of experiments with Egyptian spiny mice will serve to illustrate this point.19,21

When weanlings from two litters are removed from their respective home cages and placed together into an observation terrarium, littermate siblings huddle together and avoid interacting with unfamiliar agemates. These results are consistently obtained even if all animals had been maintained on the same commercially-produced diet. When animals with an impaired sense of smell are tested in this same manner, discriminative littermate interactions are no longer observed. This is taken as evidence of the role of olfactory cues in spiny mouse sibling recognition.

Weanlings that become familiar with a particular individual subsequently respond preferentially to previously unencountered siblings of that same animal. The signatures of full siblings, therefore, appear to be discernibly similar, presumably because of their overlapping genotypes. Additional experiments indicate that the odours of full siblings are not functionally identical, however. Interactions among littermates raised together differ from those of members of that same litter that had been reared apart, but only if all test animals have intact olfactory capabilities (in a replication of this experiment with animals suffering temporary olfactory deficits, familiar and unfamiliar siblings sharing the same test cage interacted indiscriminately). Since all animals had been born and raised under the same laboratory conditions, perceptible differences between the signatures of full siblings are most likely to be the result of underlying genotypic variability within this kin class.

To assess the influence of diet on olfactory signatures, subgroups of spiny mice were maintained on different distinctively flavoured foods. Neonates born in these colonies oriented preferentially towards chemical cues produced by lactating females fed the same diet as the pups’ own mother when paired with the odour of females fed a different diet. Moreover, recently parturient females more readily retrieved young born of same-diet females as compared to opposite-diet mothers. In related experiments, groups comprising two unfamiliar, unrelated weanlings from each of two dietary conditions were observed after being switched to a neutral diet. Over a 5-day period, mice that had been maintained on the same diet huddled together more frequently than did agemates fed opposite diets (who were rarely in physical contact with one another). It can be concluded that the dietary manipulations altered the animals’ phenotype in a manner detectable to others.

Additional experiments have established that odour signatures are complex mosaics
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of genotypically-mediated and environmentally-acquired components. Siblings that had been raised together until weaning, then separated but fed the same distinctive diet, subsequently displayed more positive social interactions than did littermates placed into opposite diet conditions or unrelated unfamiliar agemates fed the same diet. Nevertheless, animals in the latter two conditions were discriminated from those that had no prior contact with one another and also ate opposite diets. Genotype and diet appear to have additive effects on individuals' recognizable signatures.

Although phenotypic signatures of some organisms may be restricted to a single sensory modality, other animals may be able to identify kin through redundant cues carried by various sensory channels. Humans are obviously quite adept at recognizing one another by voice or visual appearance alone. Perhaps somewhat surprisingly, mutual mother-infant recognition by olfactory cues has also been reported by several investigators. Within the first several days postpartum, breast-feeding neonates orient preferentially to breast or axillary odours from their own lactating mother. Mothers, in turn, reliably identify the soiled garment of their own infant when included amongst comparable garments worn by other neonates of the same age. Human full-siblings, like their spiny mouse counterparts discussed above, can be differentiated by their body odours, and the odours of close genetic relatives (mothers and their children) are perceived as similar by adult raters. Olfactory discrimination between kin (identical and fraternal twins; non-twin full siblings) is more difficult than that for non-kin, especially if the relatives have been eating the same diet. Olfaction is certainly not the most salient modality for social recognition in our own species, but individual odour signatures may facilitate kin discrimination beginning shortly after birth.

Mechanisms underlying signature recognition

Elucidation of the properties of phenotypic signatures provides little insight into how the ability to recognize or decode those signatures develops. What are the proximal mechanisms underlying discrimination between the odours of siblings and non-kin by honey bees and spiny mice, or bank swallows distinguishing between calls of their own young and other fledglings? Signature recognition mechanisms that have either been identified through empirical research or proposed from a theoretical basis fall into two categories: experience-based and experience-independent recognition. Additional processes that may result in heightened interactions amongst kin versus non-kin, but do not allow for discrimination between simultaneously present individuals (such as attraction of relatives to the same physical location rather than to one another), are not considered further in this discussion.

Recognition based on experience. Animals become familiar with conspecifics to whom they are exposed and may recognize those same individuals (or their signatures) during subsequent encounters. This relatively simple process of direct familiarization (or exposure learning) is quite likely to be the most widespread proximal mechanism resulting in kin discrimination. Young of litter- and brood-rearing species (e.g. many
mammals and birds) often grow up in a restricted social environment, having contact only with their siblings and one, or both, parents prior to weaning or fledging. Individual recognition based upon early social experience would be equivalent to kin recognition in this context. Direct familiarization might also account for the preferential orientation by breast-feeding human infants to body odours produced by their own mother. While sucking at the breast, infants have prolonged periods of exposure to their mother’s bare flesh and associated odours. Bottle-feeding neonates, in contrast, show no evidence of discriminating the odour of their mother within the first 2 weeks after birth. Since infants who bottle-feed do not necessarily have the same degree of routine exposure to maternal odours as do breast-feeders, they may require a longer time to become acquainted with those cues.

Because animals that engage in direct social contact in natural free-living populations often tend to be kin, it is difficult to determine the role of familiarity *per se* in kin recognition. That is, animals might interact discriminatively as a result of their relatedness or because they grew up together. Fostering of neonates into different families is an experimental manipulation by which one can assess the relative importance of direct exposure versus genetic relatedness for the development of discriminative social behaviour.

Regardless of whether they are full siblings or unrelated, spiny mouse pups that have been raised together as littermates display evidence of mutual recognition. On the other hand, siblings reared apart respond to one another in the same manner as unfamiliar non-kin—with avoidance rather than amicable behaviour. Recognition of spiny mouse littermate siblings is, therefore, primarily a function of familiarization rather than genotypic similarity. Comparable fostering experiments with other animals (vertebrates and invertebrates) have consistently found that association and direct familiarity play a significant role in the development of social discrimination.

Physical contact is not necessary for the development of recognition through direct familiarization providing that there is sufficient exposure to salient phenotypic signatures. Mice that were individually housed on opposite sides of a double-layered wire-mesh partition that prevented direct bodily investigation and touching became familiar with one another all the same. Even mice that were housed in a dark room during the exposure period, so that they had no visual contact, afterwards huddled together more frequently than did animals with no such (presumably olfactory) exposure.

Preferential interactions amongst foster littermates point out the possibility of recognition errors when kin discrimination is based upon direct familiarization. One would, therefore, expect that association-mediated kin recognition would be most likely to evolve in species whose natural history typically precludes physical overlap of kin and non-kin during the requisite exposure period. Direct association would be an effective proximate mechanism for ensuring discriminative sibling or mother-infant interactions when the mother establishes an isolated nest or den that is then defended against trespassers. Brood parasitism by European cuckoos and brown-headed
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cowbirds provides an example of kin recognition errors (on the part of the unwitting hosts) with striking negative consequences.

As previously discussed, familiarization with particular conspecifics could also facilitate recognition of close kin of those same individuals. If recognizable phenotypes are correlated with genotype (e.g. either genetically mediated traits or distinctive environmentally-acquired cues shared among family members), signatures of familiar individuals should be at least somewhat similar to those of their relatives. Animals who associate with their parents, siblings, or other classes of kin, could in theory use those family members' signatures as standards against which to assess others. Bearers of signatures that approximate or match the familiar standards could thereby be discriminated. This recognition mechanism (often referred to as phenotype-matching) is based upon indirect rather than direct familiarization since it does not require prior association with the kin to be identified. Even kin with whom one has had no prior contact could be discriminated given sufficient correspondence between their signatures and the standard.

Indirect familiarization has been evoked to explain such observations as nepotistic interactions among ground squirrel sisters that had been reared apart but with each other's siblings, and discrimination between unfamiliar kin and non-kin by rats and mice. Interestingly, human mothers who correctly identified their own neonates in tests of early visual and olfactory recognition often asserted that the infant bore a noticeable resemblance to other family members (e.g. its father or older siblings).

In a variation of this same process, an animal's own familiar phenotype could also serve as a template for comparing the signatures of others. Such self-matching appears to be the means by which mother goats recognize their newborn kids. During their initial interactions, the neonate is anointed with maternal chemical secretions. Young that bear her familiar label are accepted by the mother, but those that acquire labels from other females are rejected.

Both direct and indirect familiarization have been implicated in the development of littermate recognition in spiny mice. Mention was already made above to cross-fostering experiments indicating that pups become directly familiarized with olfactory signatures of their littermates. Once learned, these familiar traits additionally provide an indirect basis for discerning similar odours in other (unfamiliar) siblings. Sharing a common label acquired from their mother may also contribute to littermate recognition. Siblings that were housed in individual cages shortly after birth but continued to suckle one at a time from the same female interacted differently from separated siblings feeding from two different females. Sharing the same mother is sufficient for mutual recognition by unrelated pups who had never directly associated before being placed together in a testing enclosure. The normal litter situation would provide the opportunity for the simultaneous manifestation of all of these types of familiarization.

Recognition without prior experience. In theory, at least, kin recognition could develop in the absence of specific experience or familiarization; both the phenotypic
cues as well as the ability to recognize the signatures these provide could be genetically determined (i.e. pleiotropic effects of Recognition Alleles). Since animals would be responding to traits controlled by a single gene (or gene complex), this mechanism would result in discrimination of anyone carrying that genetic marker, whether they were kin or non-kin.

To date, there are no data for any species that provide unambiguous support for recognition alleles over other recognition mechanisms. While reports of kin recognition by animals raised apart from all relatives are consistent with the recognition-allele hypothesis, these same results could also be accounted for by indirect familiarization (self-matching). Animals with no kin contact will still be exposed to their own signatures (e.g. odours or vocalizations), and might use those self-produced cues to discern relatedness in others. Clear evidence in favour of recognition alleles would entail discriminative responsiveness to kin by animals having neither prenatal or postnatal kin contact, and who have also been deprived of any access to their own salient signatures. Since adequately controlled experiments have not been conducted (and indeed may not be possible in most instances), one cannot dismiss the recognition allele hypothesis, even though indirect familiarization may be a more parsimonious solution to the demand for kin recognition.

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**Fig. 1.** Kin recognition mechanisms based on experience.

**DIRECT FAMILIARIZATION**

A associates with B

**INDIRECT FAMILIARIZATION**

I. Matching Familiar and Unfamiliar Kin

A associates with B

A recognizes B−1 (close relative of B)

II. Self Matching

A becomes familiar with own signature

A recognizes A−1 (A and A−1 are kin)

**EXPERIENCE**

**SUBSEQUENT RECOGNITION**

A and B recognize each other
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Ecological implications of kin recognition

Mechanisms

As suggested above, ecological and social variables may favour some kin recognition mechanisms over others. For example, if individuals disperse from their birth sites before they have sufficient exposure to littermates or other relatives, or if they live in large groups, direct familiarity may be an inefficient mechanism of kin recognition. When multiple fertilization of females occurs, clutches or litters may be composed of full and maternal half siblings. If males mate with more than one female, paternal half siblings may be produced. In these situations, a more precise mechanism, such as indirect familiarization, or the use of recognition alleles, may be employed. These mechanisms would also be efficient if young develop in close proximity to, or are grouped with, non-kin.

Ecological processes

It is becoming clear that kin recognition may significantly influence ecological processes that play a role in community structure, such as competition and predation (including cannibalism and infanticide). Furthermore, kin recognition may influence behaviours that could potentially affect the structure of populations. By elucidating the importance of kin recognition to these ecological processes we may substantially alter ways in which we view and understand community structure and the dynamics of populations.

Changes in reproductive and aggressive behaviours may cause significant changes in the population structure of animals. The phenomenon of cycling small mammal (voles and lemming) populations has been the subject of intense research and debate for many years. It has recently been hypothesized that when vole populations are low, close relatives probably interact most frequently, and aggressive encounters are diminished because of the high degrees of relatedness in members of the population. It is also likely that reduced aggression in small (low dispersal) populations of voles is a function of heightened individual familiarity (regardless of relatedness). Furthermore, increased familiarity might also result in decreased reproduction which is consistent with experimental studies of voles showing that familiar mates produce fewer litters than unfamiliar mates. High rates of reproductive behaviour and subsequent population growth may occur only after sufficient emigration takes place. Thus, population fluctuations could be influenced by changes in behaviour as manifested in reproduction and aggression and kin recognition may play a significant role in the dynamics of these behaviours.

Competition and predation are two significant ecological processes that may play important roles in community structure by influencing the distribution and abundance of animals. Kin recognition may be especially salient in intraspecific competition for limited resources because members of the same species at the same life stage are more likely to be ecologically similar than are members of different species. Therefore, if
intraspacific competition is important, individuals would benefit if they competed most intensely with unrelated members of their species. The direction of intraspecific competition toward unrelated conspecifics could be maintained by kin selection and kin recognition could lead to the skew in competition.

Similarly, studies of cannibalism and infanticide may ultimately reveal skewed patterns. Both of these processes are important in nature.\textsuperscript{11} An argument similar to the one expressed above for competition could be made with regard to cannibalism and infanticide. Kin recognition could channel these behaviours away from relatives and toward unrelated individuals. Indeed, experiments using guppies show that females preferentially cannibalize unrelated young.\textsuperscript{16}

Habitat selection is another ecological process that seems to be influenced by kin recognition. Several studies indicate that animals including bryozoan and toad larvae, rodents and birds, settle where conspecifics are already located. In some of these studies it is likely that animals were responding to the presence of 'familiar' individuals.

In certain animals, the composition of a social group is known to influence the growth and development of individuals within the group. For example, in some insects, larval growth and development can actually be enhanced in groups composed of optimal proportions and combinations of given genotypes. In small mammals, siblings may suppress one another's growth.\textsuperscript{2}

\textit{Ecological correlates of kin recognition}

Perhaps the best way to understand the functions and ecological significance of kin recognition behaviour is to utilize extensive comparative studies of similar species that differ in key life history parameters. Larval frogs and toads have been used extensively in kin recognition studies because they are easy to manipulate for developmental studies and their kin association is easy to quantify. Laboratory and field experiments on the larvae of seven species of frogs and toads have been conducted after they were reared in a variety of regimes including individuals reared (1) with kin only, (2) with kin and non-kin (mixed rearing regime), (3) in isolation from an early embryonic stage, and (4) with non-kin only.\textsuperscript{7,24} Animals were either tested in experiments where individuals were allowed to choose to swim nearest stimulus groups of varying numbers and composition (i.e. proportion of siblings and non-siblings) or in open field tests where distances from a related or unrelated neighbour were noted using dyed individuals.

The most critical parameters associated with kin recognition in frog and toad larvae appear to be: (1) the dispersal characteristics of the larvae, and (2) their aggregation behaviour. Those species whose larvae randomly disperse from sites of hatching will have a relatively low probability of encountering and interacting with siblings. Therefore, one would not predict that such species would exhibit kin-selected behaviours. Likewise, in species whose larvae do not form aggregations with conspecifics, kin-selected behaviours would have little opportunity to evolve. If there
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is a net benefit of associating with kin, and related individuals have an opportunity to interact with one another, there would be selection pressure to maintain kin groups and an ability to discriminate between kin and non-kin would facilitate the maintenance of such groups.

Tadpoles of the Cascades frog have been tested in great detail and have shown a remarkably sensitive kin recognition system. Regardless of the rearing regime, they associated most often with kin in laboratory tests. Results of testing mixed-reared tadpoles show that individuals preferred to associate with unfamiliar siblings over unfamiliar non-siblings. They also preferred to associate nearest an unfamiliar stimulus group composed of siblings over a familiar group containing 50% siblings and 50% non-siblings. Tadpoles reared in isolation subsequently associated preferentially nearest unfamiliar siblings over unfamiliar non-siblings. These results suggest that kin recognition can occur among individuals who have had no prior opportunity for direct familiarization.

Because anuran eggs are laid within a jelly matrix produced by the female, it is possible that developing embryos learn cues that emanate from the jelly. However, tests of Cascades frog tadpoles that were reared after their jelly matrix had been removed or after the jelly had been replaced with that from a non-kin egg mass, indicate that they were unaffected by these manipulations. Moreover, Cascades frog tadpoles preferred to associate with full siblings over either maternal or paternal half siblings, and with half siblings (either maternal or paternal) over non-siblings. Because full siblings were chosen over maternal half siblings and paternal half siblings were chosen over non-siblings, it is clear that maternal cues are not necessary for kin recognition. Nevertheless, maternal cues do exert a stronger influence than paternal cues; maternal half siblings are chosen over paternal half siblings. Tests of recently metamorphosed Cascades frogs reveal that they too associate preferentially with siblings over non-siblings. Significantly, in field experiments, Cascades frog tadpoles that are dyed and released in the natural lakes and ponds they inhabit, sort into groups composed primarily of kin.

Very different results were obtained for red-legged, spotted, and Pacific tree frog tadpoles. Only those red-legged frog tadpoles reared with siblings and tested in early developmental stages associated with kin. This tendency disappeared as the tadpoles developed. Neither spotted nor Pacific tree frog tadpoles display kin recognition.

Contrary to results obtained for Cascades frog tadpoles, the ontogeny of kin recognition in western toad tadpoles is significantly influenced by the rearing regime. Those reared with kin preferentially associated with kin over non-kin in laboratory experiments. However, individuals reared in mixed rearing regimes and with non-kin only, displayed random association with respect to siblings and non-siblings. Even when preferences for siblings were fully established following prolonged rearing with siblings, short-term exposure to non-siblings nullified these preferences.

In open field laboratory tests, American toad tadpoles reared with siblings only, or in isolation, were found significantly nearer their siblings than non-siblings. Tadpoles
reared with siblings in early development and then exposed to siblings and non-siblings in later development, retained their proximal affiliation with siblings. However, tadpoles that were reared with both siblings and non-siblings in early development and exposed to siblings only in later development did not preferentially associate with familiar siblings over familiar non-siblings. This suggests the possibility of a sensitive period in early development during which they familiarize themselves with other individuals. Field experiments corroborate these laboratory results.25

**Relationship of larval behaviour and ecology to kin recognition**

Of the species tested, only spotted and Pacific tree frog tadpoles failed to discriminate between kin and non-kin. This is consistent with their larval ecology since these species form aggregations only intermittently and there is little opportunity for siblings to interact. Unfortunately, too little is known concerning the larval ecology of red-legged frogs to speculate whether there is opportunity for kin to interact. Cascades frog tadpoles appear to have sufficient opportunity to interact with siblings and they display a kin recognition system that would be efficient in their natural habitats. Dispersal is low from sites of oviposition, tadpoles aggregate in small cohesive groups and populations are generally small and patchily distributed. Therefore, it is likely that Cascades frog tadpole aggregations are composed primarily of kin. However, there is potential for mixing with non-siblings especially because egg masses may be laid communally. Thus, if there are benefits to aggregating with kin, Cascades frog tadpoles must be able to discriminate between siblings and non-siblings and this ability must be resistant to modification following exposure to non-siblings. Indeed, laboratory and field experiments indicate that the kin recognition system of Cascades frog tadpoles is established early in development and is generally not altered by exposure to non-kin.

Wood frog tadpoles aggregate in some ponds and not in others. In ponds where the tadpoles aggregate there is some opportunity for the formation of kin groups as large schools break up into smaller, feeding units. Wood frog tadpoles display a kin recognition system that is not influenced by exposure to non-siblings. As in Cascades frog tadpoles, a system that is resistant to modification following exposure to non-siblings would be required because of communal egg laying and exposure to non-kin during larval stages.

American toad tadpoles often form large aggregations that subdivide into smaller schools that could represent sibling cohorts. The kin recognition system of American toads is generally consistent with its larval ecology and behaviour. Mixing with non-siblings is frequent, and sibling preferences, once established, are resistant to modification.

In contrast, in western toad tadpoles, the formation of extremely large aggregations resulting from numerous clutches and large clutch size, may make kin associations impractical even if such behaviour conferred fitness benefits. Furthermore, the feeding behaviour of the individuals in large schools entails frequent moving, intermingling,
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and splitting off. Maintaining cohesive sibling groups would be difficult even if tadpoles retained a capability to recognize siblings following encounters with non-siblings. Most likely, western toad tadpoles seek familiar conspecifics (whether kin or non-kin) when selecting a habitat in which to feed.

Benefits of associating with kin in tadpoles

There are numerous benefits to group living, from finding food more easily to avoiding predation more efficiently. While it is not necessary for a tadpole to aggregate with kin to benefit from group living, those individuals that preferentially associate with kin may accrue additional advantages through an increase in their inclusive fitness.

Tadpoles associating in groups composed primarily of kin could warn relatives if they release an alarm substance when they are preyed upon. This seems to be one of the more likely explanations for kin association in Cascades frog tadpoles which, when injured, release a chemical cue that causes others to display an escape-like response. In this situation, kin would be warned because individuals in aggregations are, presumably, mostly close relatives, and kin recognition may be maintained by kin selection.

The adaptive significance of kin groups could also be related to the distastefulness of toad tadpoles to certain predators. If members of a single brood (kin group) aggregate with each other and a predator that samples one or more unpalatable siblings learns to avoid the group, then a gene for distastefulness could increase in frequency through kin selection. This scenario has been invoked to explain the advantage of associating with kin in American toad tadpoles.

Kin association may be critical for growth and development in anuran larvae. Tadpoles, such as those of the Cascades frog, that undergo development at high elevations where the growing season is short or where habitats are ephemeral, may be under intense selection pressure for rapid growth. Indeed, there is some evidence suggesting that tadpole development is influenced by their social regime; growth is prolonged when larvae are reared with siblings as opposed to being reared with both siblings and non-siblings.

Finally, in light of the evidence that newly metamorphosed Cascades frog tadpoles discriminate between kin and non-kin, an additional potential function of kin recognition may be to enhance optimal outbreeding in adults. The studies of adult frogs and toads that would be necessary to test this hypothesis have not been conducted.

It is now clear that there are basic differences among kin recognition systems of many species tested. In some cases, these differences may reflect selection pressures in the evolutionary history of the species. Perhaps, kin recognition was advantageous in the past but is no longer discernible because of altered social and environmental conditions. For example, predatory pressure could have been quite different in the past, resulting in an increased tendency to form groups. Many of these groups could
have been composed primarily of kin. In other species there might have been no opportunity for kin recognition to evolve. Sociality may be a necessary prerequisite for the evolution of kin recognition and pressures leading to sociality may not have existed. Assuming that kin recognition is at least partially genetically mediated, this capability would rapidly spread through evolutionary time as long as fitness benefits continue to accrue to nepotistic individuals or those whose choice of mates is correlated with relatedness.

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