Kin recognition: function and mechanism in avian societies

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Cooperative behaviour resulting from kin selection is widespread among animals and the ability to recognize and discriminate between kin and non-kin is a critical element in kin selection theory. Current evidence suggests that associative learning is the most likely mechanism of kin discrimination. However, surprisingly, there have been no studies on the role of associative learning in kin discrimination. The likely recognition mechanisms enabling fine discrimination between close and distant kin of similar familiarity, whether generic or individual cues are employed in kin recognition, and the role of kin recognition in different stages of a species' life history are central to the evolution of social behaviour and to identify key factors in the evolution of cooperation.

In many cooperatively breeding birds and mammals, individuals help conspecifics to produce offspring rather than have young themselves. An individual can increase its genetic representation in future generations by helping close relatives who share copies of its genes identically by descent. The role of kin selection (the selection process that enhances the fitness of close relatives through increased survival and/or increased reproductive success) is regarded as highly important in the fitness consequences of kin recognition. However, surprisingly, there have been no studies on the role of associative learning in kin discrimination. The likely recognition mechanisms enabling fine discrimination between close and distant kin of similar familiarity, whether generic or individual cues are employed in kin recognition, and the role of kin recognition in different stages of a species' life history are central to the evolution of social behaviour and to identify key factors in the evolution of cooperation.

Cooperative breeding systems are used by many birds, particularly in species with low individual reproductive fitness. Cooperatively breeding species have evolved various strategies to increase reproductive output, including caring for offspring of closely related individuals. Kin recognition is a critical component of cooperative breeding, as it enables individuals to distinguish between kin and non-kin and to provide appropriate care only to kin. Studies on kin recognition in cooperative breeding species have revealed that the ability of parents to recognize their own young, or the ability of young to recognize their siblings, is an important factor in the evolution of cooperation.

Experimental evidence for kin-directed care

Most experimental studies of kin-directed care among birds have dealt with parent-offspring recognition in monogamous birds, examining either the ability of parents to recognize their own young, or the ability of young to recognize their parents. In general, three types of discrimination tests have been used to test offspring-parent recognition: (1) choice tests between two loud-speakers simultaneously playing begging calls of one or the other type; (2) sequential discrimination tests (swap tests) between two loud-speakers simultaneously playing recorded begging calls of different begging calls; and (3) auditory tests to examine the parents' ability to recognize and locate their young when moved from the nest site. In most species, it seems that parents and offspring do not discriminate conspecific from heterospecific chicks both depend on the ecological circumstances and type of cross-fostering used (e.g. swapping entire broods or parts of the brood).

Finally, we have to be careful about drawing general conclusions about kin recognition in a particular species if the species' ability to recognize kin varies with different life history stages - recognition at one stage (e.g. eggs or chicks) does not imply recognition at another. There are few experimental studies on parent-offspring and sibling recognition for cooperatively breeding birds. Given that many cooperative-breeding systems involve the acquisition of indirect fitness benefits through kinship, there might be some mechanism of cooperation between kin and non-kin. Kin recognition studies offer exciting opportunities to advance our understanding of cooperative systems. First, they will provide insight into the their offspring. If the parents are simultaneously played recorded begging calls (auditory cues) of their own offspring with those of offspring of the closely related rough-winged swallow (Stelgidopteryx serripennis), bank-swallower parents fail to recognize the calls of their own offspring.

However, cross-fostering experiments showed that bank-swallower parents fail to recognize visually between their own offspring and those of rough-winged swallow (Box 1). A second shortcoming of discrimination tests is that the outcome is often inconclusive. For instance, an experiment on adelie penguin (Pygoscelis adeliae) showed that parents attempt to foster unrelated young (Box 1). A second shortcoming of discrimination tests is that the outcome is often inconclusive. For instance, an experiment on adelie penguin (Pygoscelis adeliae) showed that parents attempt to foster unrelated young.

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potential complexity of the rules used by individuals to recognize kin and, second, they will reveal how these rules might make sense given particular ecological circumstances.

**Kin recognition mechanisms**

The occurrence of facultative adjustment of provisioning effort according to relatedness and (cooperatively) breeding animals implies that some sort of mechanism for kin discrimination. Four categories of mechanisms have been proposed: recognition alleles, phenotype matching, recognition through association or familiarity and spatially based recognition (Box 2).

Although an attractive idea, the existence of recognition alleles among birds, or other taxa, is unlikely. First, there is no empirical evidence for recognition alleles. Second, recognized individuals might simply share recognition traits and need not be kin, so this mechanism would be vulnerable to the evolution of alleles producing the phenotypic trait but not the associated altruistic behaviour. Third, metabolic shuffling of genes (when dealing with more than one allele or gene) might also make genetic templates unreliable. Finally, there could be competition among individuals over whether phenotypic traits that give unambiguous information on kinship are expressed.

In practice, it is probably extremely difficult to distinguish between recognition through phenotype matching and recognition alleles. Among birds, phenotype matching has been invoked to explain the mating preference of Japanese quail (Coturnix coturnix japonica) for first cousins. A simple spatially based recognition rule, such as ‘feed anything in my nest or territory’, is widespread and successfully exploited by bird species that are Spring in my natal territory’ could serve as a reliable discriminator between kin and non-kin. However, the longer the helpers remain on their natal territory the higher the probability that there will be some turnover of breeders with a subsequent diminution of relatedness to the helper. In theory, recognition through association avoids this problem, provided that breeder turnover occurs outside a putative ‘associative-learning period’.

There have been no published experimental studies of kin recognition among cooperatively breeding species, and little attention has been paid to the actual cues used by helpers when making helping decisions. Just two studies have explicitly addressed the question of how kin discrimination is achieved by helpers. Helping behaviour by Galapagos mockingbirds (Nesomimus parvulus) sometimes occurs among non-kin, and the care of helpers is better predicted by prior association than by kinship per se. Similarly, in the Seychelles warbler (Acrocephalus sechellensis), which helps raise all birds which are not related to its parent (Rahel, in press), kinship is probably the main factor determining the presence or absence of helping. However, another study showed that Mexican jays (Aphelocoma caudacuta) and Seychelles warblers (Acrocephalus sechellensis) exhibit the predicted adjustment in helping behaviour. Each study found that the proportion of nonbreeders that helped decreased when unrelated step-parents became breeders.

Experimental evidence

- An intraspecific cross-fostering experiment in the rough-winged swallow (Stelgidopteryx serripennis) and bank swallow (Riparia riparia), both breeding in the same colony, showed similar results. When bank swallow and rough-winged swallow broods were exchanged from adjacent burrows, both sets of parents were attracted to the calls of their own young and soon began to feed their chicks at the new location, implying brood recognition. In addition, when a single rough-winged swallow chick was added to a bank-swallow brood, foster chicks were typically rejected, implying individual recognition. However, when a single barn swallow chick was added to a rough-winged swallow brood, the foster chick was invariably accepted.

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**Box 1. Observational and experimental evidence for kin-directed care**

**Observational evidence**

- When faced with a choice of potential recipient nests, helpers preferentially help the breeding pair to which they are more closely related. This has been documented for the white-fronted bee-eater (Merops bullockoides), Galapagos mockingbird (Nesomimus parvulus), and Mexican jay (Matinga mexicana). Among birds, phenotype matching involves the learning and assessment of kin and non-kin. However, the longer the helpers remain on their natal territory the higher the probability that there will be some turnover of breeders with a subsequent diminution of relatedness to the helper. In theory, recognition through association avoids this problem, provided that breeder turnover occurs outside a putative ‘associative-learning period’.

**Box 2. Kin recognition mechanisms**

**Recognition alleles:** This mechanism requires that a gene (complex) confers an identifiable phenotype on its carrier, which also enables the carrier to perceive that phenotype trait and discriminate accordingly. An allele with these characteristics would be expected to spread more rapidly by natural selection with more than one allele or gene) might make genetic templates unreliable. Among birds, phenotype matching involves the learning and assessment of kin and non-kin. However, the longer the helpers remain on their natal territory the higher the probability that there will be some turnover of breeders with a subsequent diminution of relatedness to the helper. In theory, recognition through association avoids this problem, provided that breeder turnover occurs outside a putative ‘associative-learning period’.

**Kin recognition in avian societies**

What evidence is there for the various mechanisms of kin recognition among cooperative breeders? Typical cooperative breeding systems, with helpers at the nest, are characterized by natal philopatry and an extended period of association with kin on a family territory. In most cases, kin-directed helping precedes dispersal and independent breeding. In this situation, a decision rule ‘care for any offspring in my nest’ is widespread and success-
feed the broods of their parents, but not of their siblings, even when the relatedness of nestlings to helpers is identical. Given that benefits of helping other kin are available, one might not expect such a restrictive discrimination rule. However, the presence of more than one brood with identical relatedness of nestlings to potential helpers is extremely rare and, under these circumstances, it might be impossible for more powerful discrimination rules to evolve. However, even if such a rule cannot be universal because in other cooperative species, such as in long-tailed tits (Aegithalos caudatus)28, care for the offspring of siblings from the same brood is the typical pattern. Therefore, although current evidence suggests that recognition through association and/or familiarity is the most likely mechanism for kin discrimination among cooperatively breeding birds, it appears that the precise rule of thumb will vary from species to species.

Among cooperative breeders, there is no evidence that kin-directed helping behaviour ever occurs when there are no opportunities to learn the phenotypic characters of kin. It seems likely that helpers use visual or auditory cues to discriminate between familiar and unfamiliar individuals. However, this does not mean that associative learning is the only possible mechanism; indeed, all four mechanisms are not mutually exclusive. In small families of cooperating birds, recognition of specific individuals can be relatively straightforward, but it might be a greater cognitive challenge for larger families of cooperating birds, such as the acorn woodpecker (Melanerpes formicivorus)29, even if non-kin are also family members, such as superb fairy-wrens (Malurus cyaneus)30, recognition through association can offer only approximate information on kinship.

The third limitation is that if familiarity arises through provisioning of nestlings or fledglings by helpers, there is a risk that the mechanism of associative learning can be exploited by cheats, a phenomenon dubbed ‘kinship deceit’28. For example, in the white-winged chough, an obligate cooperative breeder in which reproductive success is positively related to group size, groups kidnap unrelated fledglings. Kidnapped young who survive subsequently become unrelated helpers in their adoptive groups28. However, even when helpers usually gain indirect fitness benefits through helping, the resulting selection against care for non-kin could weaken if significant direct fitness benefits are gained by helping.

Potential helpers will be selected to employ recognition mechanisms that result in an optimal balance between two kinds of error: helping non-kin recipients and rejecting kin as recipients31. A cautious strategy with a high recognition threshold might avoid giving care to all non-kin, but might also result in care not being given to kin. A generous strategy with a low recognition threshold might ensure that all kin are recognized and helped, but might also result in frequent care for non-kin. The frequency and cost of errors in a recognition system will depend on the fitness benefit of discrimination, which in turn is likely to be a function of the ecology and life history of the species. In those species where indirect fitness gains are the major fitness benefit of helping, the fitness cost will be small if occasional care for non-kin by helpers resulting from recognition errors occurs at low frequency. An alternative explanation, and one that is likely to apply widely, is that there are also direct fitness benefits of helping, so apparent errors might not be maladaptive. Indeed, in most species for which sufficient data are available, it appears that direct fitness benefits play an important role in the evolution and/or maintenance of cooperation in both two species, white-fronted bee-eaters and the primary helpers of pied kingfishers (Coryphaena rupestris), are direct fitness benefits thought to be absent19,21. Selection for error-free kin recognition will be weaker in the presence of direct fitness benefits through cooperation.

The role of kin recognition in the evolution of cooperative breeding

The crucial question is which of the four kin discrimination mechanisms (Box 2) is sufficiently reliable to permit the evolution of cooperative breeding in those species where kin selection is an important factor. It is perhaps surprising that so little attention has been paid to the question of how kin discrimination is achieved among cooperative breeders. Historically, the emphasis of research in this field has focused on the ecological basis for natal philopatry (why delay dispersal?) and the fitness benefits of helping among offspring that have ‘stayed at home’ (why help?) (Box 3). A better understanding of the mechanism of kin recognition and discrimination will contribute to our understanding of both issues. Generally, cooperative systems tend to be characterized by a long period of close association before helping, relative to non-cooperative systems, enabling helpers to
direct care towards kin with a high degree of confidence (Box 3). Recognition through associative learning is the usual mecha-
nism of kin discrimination, comparative studies that focus on the timing of natal dispersal and the opportunity for family-
arity to develop could reveal important but hitherto elusive differences between cooperative species. This does not imply that cooperation is an inevitable consequence of long associ-
ative relationships. For example, in Siberian jays (Perisoreus infaustus), grown offspring stay at home on the natal terri-
try with their parents for a year or more as nonbreeders but do not assist their parents in caring for offspring.12,13 The frequency with which such errors occur depends on the level of relatedness between parents and offspring. Recognition mechanisms that are widespread among birds suggest that a long-term association (i.e. more than a few weeks of dependence) might not be necessary to learn individ-
ual identities. However, little (if anything) is known of the persistence of parent–offspring recognition beyond the point of independence. There is also an important distinction to be drawn between parent and offspring recognition. In noncooperative species, offspring might gain little selective advantage by discriminat-
ing parents from nonparents, whereas in cooperative species this ability could be critical to the development of families. Finally, as already mentioned, any recognition system is unlikely to be error-
free. The frequent with which such errors occur depends on the roles of indirect and direct fitness benefits in the mainte-
nance of helping behaviour. But, as in other fields of evolutionary biology, it is clear that it is essential to study underlying mechanisms if we are to fully understand the limits of adaptive behaviour.

Conclusions and future work
Current evidence suggests that asso-
ciative learning is the most likely mecha-
nism of kin recognition enabling helpers to discriminate kin from non-kin in avian societies. However, despite the signifi-
cance of such mechanisms for the evolu-
tion and maintenance of cooperative breeding systems, there is a distinct lack of empirical studies in this area. In particu-
lar, we highlight three potentially very interesting avenues of investigation: First, experimental studies of: (1) the putative ‘associative-learning period’; (2) how good recognition mechanisms are at enabling fine discrimination between close and dis-
tant kin of similar familiarity; (3) whether generic or individual cues are employed in kin recognition; and (4) how recognition ability varies at different stages of a species’ life history.

Second, studies of kin recognition that include both simultaneous and sequential discrimination tests should reveal more about the cues used to dis-
criminate kin from non-kin. In particular, investigation of whether such cues and the ability to discriminate accordingly are fixed in space and time. For example, the recognition threshold might vary according to the selection pressure to recognize kin.

Finally, we suggest that comparative studies of kin recognition and discrimi-
nation in cooperative and noncoopera-
tive species would be worthwhile.

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References
There is no doubt about the growing magnitude of human impact on the oceans. More than half of the world’s population lives within 60 km of the coast, and the figure could reach 75% by the year 2020 (Ref. 1). Collapsed fisheries have become commonplace and we are beginning to appreciate that the impacts of fishing extend far beyond the species we target. Approximately 95% of marine fish catches come from continental shelf regions, where fisheries now consume an estimated 24-35% of primary production. Coastal waters are becoming increasingly polluted, and there is a large-scale loss of coastal wetland habitat. It is in these same coastal waters that most known marine biodiversity resides.

Despite this evidence of human influence, most marine scientists probably still share the views of Lamarck and Huxley, that although we might be able to deplete populations of marine species, we cannot cause their extinction. Lamarck put it succinctly in the early 19th century: “Animals living in the waters, especially the sea waters are protected from the destruction of their species by Man. Their multiplication is so rapid and their means of evading pursuit or traps are so great that there is no likelihood of his being able to destroy the entire species of any of these animals” (Philosophie Zoologique, 1809). Huxley, in his 1863 address to the International Fisheries Exhibition in London, reinforced the point in relation to the rapidly industrializing fisheries of the time, stating “Any tendency to over-fishing will meet with its natural check in the diminution of the supply, …this check will always come into operation long before anything like permanent exhaustion has occurred.”

We surveyed 253 scientists from among those most likely to appreciate the possibility of extinction in the sea. Fourteen of the 45 who replied did not think that marine species were at serious risk of extinction. We think that this faith in the resilience of marine species is misplaced, that there might already have been numerous extinctions in recent times that we have simply failed to notice, and that the coming decades are likely to see many more.

Evidence for contemporary marine extinctions

Shells, such as those of the cow (Hydrodamalis gigas), the Caribbean monk seal (Monachus tropicalis) and the great auk (Pinguinus impennis) are long gone, victims of relentless exploitation. But these were air-breathing animals that spent time on land, an exceptional lifestyle compared with most marine species. Until recently, there has been only one well documented