Kin Selection in Cooperative Alliances of Carrion Crows

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In most cooperative vertebrates, delayed natal dispersal is the mechanism that leads to the formation of kin societies. Under this condition, the possibility that kin-based cooperative breeding is an unselected consequence of dispersal patterns can never be ruled out because helpers can only help their relatives. Here we show that a population of carrion crows (Corvus corone corone) fully fits the central prediction of kin selection theory that cooperative breeding should arise among relatives. On their territory, resident breeders are aided not only by nonbreeding retained offspring but also by immigrants (mainly males), with whom they share matings. Philopatry cannot account, however, for the high degree of genetic relatedness found between breeders and immigrants of the same sex that cooperate at a nest, indicating that crows actively choose to breed cooperatively with their relatives.

Kin selection operates whenever relatives interact (1), but its role in the evolution of social behavior has recently been questioned. Despite the fact that the majority of vertebrate cooperative species live in kin groups, high relatedness among group members represents only weak evidence of the importance of kin selection in shaping the social system (2–5). In fact, kin-based cooperative breeding might be an unselected consequence of dispersal patterns. Helpers in vertebrates are typically offspring that remain with their parents on their natal territory (6) and thus do not have the option of choosing between helping relatives or helping unrelated individuals (2). In some societies, individuals disperse from the natal territory in related coalitions (such as the acorn woodpecker Melanerpes formicivorus (7)), leading again to kin-directed cooperation. On the other hand, cooperative polyandry (8) among nonrelatives is widespread among vertebrates (9) and proves that cooperative breeding can arise in the absence of indirect fitness benefits.

In a cooperatively breeding population of carrion crows (Corvus corone corone) in northern Spain, helpers are either nondispersing offspring that assist their parents on the natal territory or immigrants (mostly males) that associate with a territorial pair, forming stable groups that live year-round in all-purpose territories (10–12). Breeding units are therefore either unassisted pairs, pairs with nondispersing 1- or 2-year-old offspring, pairs with immigrants, or pairs with both immigrants and nondispersing offspring. Male immigrants often share matings with the resident breeders (67% of groups containing sexually mature immigrants) (11).

We have been banding all crow nestlings reared in a 45-km2 study area at La Sobarriba (in northern Spain, 42°N, 5°W) since 1995. Because juveniles delay natal dispersal for up to 2 years but never inherit the natal territory (10), we have been able to determine for every individual since 1997 whether it was currently living on its natal territory or not. In 1999 and 2000, we captured 61 free-flying crows (10), collecting information on 21 social groups, 13 of which contained one or two immigrants. The aim of this study was to investigate pairwise relatedness among same-sex immigrants and resident breeders (17 dyads) that associated on a territory (13). Relatedness estimates were based on allele frequencies at six polymorphic microsatellite loci (14). Relatedness between immigrants and residents was compared to the average degree of relatedness among individuals in the population, calculated on the entire sample of genotyped crows (137 individuals captured in the study area, 9316 pairwise estimates of relatedness (r) (13)).

Same-sex immigrant and resident crows showed a high degree of relatedness (mean

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Fig. 1. Distribution of pairwise r estimates in the population (solid bars) and in the sample of same-sex immigrant and resident crows cooperating on a territory (open bars).
r ± SE = 0.24 ± 0.066, n = 17, P = 0.002; Fig. 1). Because in crows cooperative immigrant/resident associations arise mostly among males (11), we calculated mean r also after removing the two dyads of females from the sample, obtaining a similar mean value (mean r = 0.23 ± 0.072, n = 15, P = 0.003) (supporting online text). Conversely, within the groups, immigrants and residents were on average not significantly more related to the breeders of the opposite sex than were individuals chosen at random in the population (mean r = 0.06 ± 0.06, n = 17, P = 0.34).

Philozy (defined here as the tendency of dispersers to settle close to the natal territory) increases the chances of an individual ending up in a territory where a relative had previously settled, and it might hence explain the immigrant/resident high degree of relatedness. However, philozy did not account for the observed pattern of relatedness among breeding associations of crows, but crows appear to actively select relatives to breed cooperatively. One consequence of philozy would be that the population would show a genetic structure in which the degree of relatedness between two individuals was negatively correlated to the distance between their territories (15–17). When we plotted pairwise estimates of r for males against the distance between the territories where they were settled, no correlation was found (Fig. 2). The same result was obtained for females. There was also no indication of a negative correlation when we plotted the relatedness between immigrant and resident against the natal dispersal distance of the immigrants, where that distance was known. In fact, the relationship was positive, although not statistically significant (Spearman’s R = 0.72, n = 7, P = 0.07). This refutation of viscosity as an explanation for the pattern of relatedness among residents and immigrants strongly suggests that crows actively choose to associate with their relatives. Field observations confirmed this scenario. Young can remain on the natal territory for up to 2 years, but when they eventually disperse, they show no tendency to settle on neighboring territories. Only 4 young out of 334 that we have banded in 6 years did so. Furthermore, we have observed how immigrants, before settling, prospect several territories, where they socially interact with the resident crows. In our best-documented case, we observed how a banded immigrant yearling prospecting 2 territories (twice each) occupied by groups that had already been banded, and eventually settled on the one held by an older sibling that had dispersed in the previous year.

Spanish carrion crows are territorial year-round and evict intruders from their territories (10). The fact that, despite territorial behavior, polyandrous associations of relatives arise on the territories implies that resident crows are selectively tolerant toward their relatives. It is as yet unclear whether immigrants also deliberately discriminate between kin and non-kin while prospecting or merely settle on territories where they are tolerated. However, our findings show that an active choice of relatives has a role in determining the formation of cooperative alliances in crows.

KIN selection theory is unirrivalled when applied to the evolution of sterile casts in eusocial insects, and it long seemed to be the most plausible explanation of helping behavior in vertebrates as well (3). Indeed, cooperation mostly arises among kin. However, cooperative breeding in vertebrates offers a variety of direct fitness benefits (such as current or future reproduction sharing within the group, increased survival, improved parental skill, and territory inheritance) that alone can explain the evolution of sociality (4, 5). Furthermore, kin societies can arise merely as a consequence of short-coverage dispersal strategies (3), and therefore a high degree of relatedness among group members can no longer be regarded as evidence of the role of kin selection in shaping social systems.

Stronger evidence may be found in the few species where individuals have a choice of whom to help. In the white-fronted bee-eater Merops bullockoides (18), the European bee-eater Merops apiaster (19), and the long-tailed tit Aegithalos caudatus (2), helpers help only their relatives even when other potential receivers are available. However, it might still be argued that helpers in those species do not choose who to help, but breeders cooperate only relatives as helpers. In the Siberian jay Perisoreus infaustus, for example, breeders are more tolerant toward their relatives in groups that comprise both related and unrelated individuals (20). In polyandrous cooperative associations, all males that share in reproduction help to rear some young that are not their own. Therefore, by showing kin preference in at least one counterpart of the polyandrous cooperative association of crows, our data support the importance of kin selection in the expression of cooperative behavior at the nest.

References and Notes
8. Cooperative polyandry is a social system in which two or more males mate with a single female and cooperate in rearing the young.
13. Materials and methods are available as supporting material on Science Online.
14. DNA was extracted from blood samples (50 to 200 l of blood from each individual). We unambiguously genotyped 137 individuals at six polymorphic microsatellite loci (five alleles on average). No loci deviated from Hardy-Weinberg expectations. For details on DNA extraction, primers, and genotyping procedure, see (17). Briefly, alleles were amplified by means of the polymerase chain reaction (PCR), separated by polyacrylamide electrophoresis, and visualized with silver staining. Estimates of relatedness (r) were calculated using the software Relatedness (21). We obtained precise average estimates for categories of individuals of known relatedness (parent-offspring, n = 96, [expected mean r]/[estimated mean r] = 0.5/0.48 ± 0.02; full siblings, n = 67, [expected mean r]/[estimated mean r] = 0.5/0.48 ± 0.04), indicating the reliability of relatedness assessment. Crows were sexed with the P2/P8 molecular sexing method (22).
Morphs, Dispersal Behavior, Genetic Similarity, and the Evolution of Cooperation

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Genetic similarity owing to kin relationship is often invoked to explain the evolution of social cooperation. In this study, male color morphs of side-blotched lizards settle nonrandomly with respect to genetic similarity. Blue morphs tend to settle in close proximity to other blue morphs with high genetic similarity. Blue neighbors have the average fitness of blue males lacking such neighbors. Conversely, genetically similar blue males depress fitness of the orange morph. Moreover, orange males are hyperdispersed with respect to genetic similarity. Pedigree and dispersal data show that genetically similar blue neighbors are not kin. Instead, conditions for the evolution of dispersal and cooperation are promoted by an emergent property of the morph locus that increases genetic similarity within morphs: genome-wide correlational selection links many traits to the morph locus, including settlement behavior.

Evolution of altruism, cooperation, or any reciprocal behavior that decreases conflicts between neighbors has generated considerable theoretical interest, given that it is at the root of sociality (1–5). Evolution of cooperative behavior is a balance between long-term benefits to donors from receivers (reciprocity) but enhanced risk of misdirected donation to cheaters. Theory suggests that negative impacts of cheaters are diminished in small neighborhoods (4). A simple solution is to evolve philopatric settlement that enhances kin cooperation (4), but this has attendant fitness costs of inbreeding and kin competition. Thus, dispersal and settlement are of prime importance for cooperation to evolve. Early theory suggested that dispersal is incompatible with evolution of altruism (5), unless individuals recognize genetically similar individuals. Recent theory suggests that altruism and dispersal may not necessarily be incompatible behaviors, particularly if dispersal polymorphisms evolve (5).

To test these ideas, we examined dispersal behavior as a function of genetic similarity in a polymorphic vertebrate, the annual side-blotched lizard, Uta stansburiana. This lizard exhibits six color genotypes (7, 8) (oo, bo, yo, bb, by, yy) that serve as genetic markers for three male strategies (6–11). Color is controlled by the OBY locus, which has three alleles (o, b, y) (6–11). Orange males (oo, bo, yo) usurp territory (O). Blue males (bb) are mate-guarders (B). Yellow males (by, yy) are sneakers (Y). Male competition drives cycles analogous to a rock-paper-scissors game: sneakers beat aggressive usurpers, mate-guarders beat

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Fig. 1. Observed and expected frequency (n) of a high degree of genetic similarity between neighbors as a function of throat-color dyads. The chi-square was significant across all male dyads (x^2 = 23.41, df = 1), for bb x bb genotypes (x^2 = 14.00, df = 1), and for orange genotypes (O genotypes pooled; i.e., oo, bo, yo) (x^2 = 6.36, df = 1). Thus, bb male genotypes are attracted by genetically similar bb male genotypes, whereas orange genotypes (oo, bo, yo) repel genetically similar males.
CORRECTIONS AND CLARIFICATIONS

ERRATUM
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REPORTS: "Kin selection in cooperative alliances of carrion crows" by V. Bagglione et al. (20 June 2003, p. 1947). In Fig. 2, the y axis should read "Relatedness" instead of "Proportion of cases."