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Mechanisms of Kin-Correlated Behavior Group Report

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INTRODUCTION

Behavioral interactions between individuals within a population are often non-random with reference to the identities of the participants. Frequently, kin relationships are the source of such asymmetries. This paper discusses the mechanisms of kin-correlated behavior. We first define kinship for operational purposes and ask whether it can be measured in natural populations. We then discuss the relevance of various models that either describe or invoke kin relationships when considering population structure. Our discussion continues with a consideration of the reasons for expecting kin-correlated behavior to evolve in natural population, followed by a brief overview of the data base. Proximate mechanisms for effecting kin-correlated behavior and the ecological conditions under which it is likely to evolve comprise our closing sections. Overall, we attempt to identify areas of ignorance, particularly those that have a strong bearing on attempts to distinguish between various theories proposed for the evolution of kin-correlated behavior.

DEFINITION OF KINSHIP

Kinship can be either social (see below) or genetical. The latter can be measured over many hundreds of generations or over few. For present purposes, a suitable operational definition of kinship is provided by the regression measure b_{IJ} of genetic relatedness between recipient J and donor I. This represents the probability that J contains a gene identical by descent with a random gene at the same locus sampled from I. As far as our discussion pertains to pedigree analysis for measuring relatedness, b_{IJ} is appropriate. We stress that this is not a correlational measure (r) so that under certain genetic systems (e.g., haplodiploid inheritance) b_{IJ} need not always have the same value as b_{JI}.

RELIABILITY OF KINSHIP MEASURES

Many genetic models for the spread of behavioral traits demand accurate estimation of b_{IJ}, especially those involving altruistic behavior (behavior causing a reduction in fitness of the donor that results in an increase in fitness of the recipient). An important general question for the behavioral ecologist must be: Can we draw reliable conclusions about actual kinship from apparent kinship? A knowledge of certainty of paternity is extremely important. The Hymenoptera have been the subject of most speculation and provide a good case study. Among species producing monogynous colonies, repeated matings are often reported for a single queen and we do not yet have a good idea about the sequence in which the sperm of the different males are released. If random release occurs, then the supposed 3/4 relationship between worker females may be a gross overestimate. Among truly polygynous species (those containing many, sometimes hundreds, of queens that do not compete for egg laying), circumstantial evidence indicates a lower frequency of multiple matings and higher inbreeding. However, certainty of maternity now becomes a key variable.

There is very little evidence for a marked effect of sperm clumping. This question, together with the frequency of multiple matings, is best studied using polymorphic enzyme loci (in the absence of suitable genetically controlled morphological variation). For instance, at the moment we depend on inference to describe the mating structure in termite colonies; genetic marker studies will soon provide data that will allow us to produce a more accurate assessment of the true picture. Recent Polistes studies indicate a b_{IJ} between workers of about 1/2, but in other populations or other species frequent inbreeding and single inseminations could raise the value above 3/4. R. H. Crozier (this volume) reports recent evidence that interspecific differences in average degree of relatedness among workers in some genera may be considerable. Similarly, among congeneric species (e.g., Lasioglossum spp.) the readiness of queens to accept multiple matings may be quite different (C. D. Michener, personal communication), varying from those willing to mate again within 30 minutes to others that refuse to remate after several days.

Genetic marker studies allow us to examine both intracolony and intercolony genetic differences among the social insects. At present, very little is known about the latter.

Behavioral ecologists studying vertebrates have only recently recognized that certainty of paternity is an important problem. However, recent evidence using both vasectomized males (see M. C. Baker and P. Marler, this volume, for a discussion of the technique which may underestimate the extent of certainty of paternity) and genetic markers is beginning to reveal the extent of extra-pair-bond copulations and sperm competition in monogamous bird species. Forced copulations have been recorded in about 40 species of Anatidae and a genetic marker experiment with captive mallards showed that they can be effective in fertilizing eggs. In one polygynous bird species, vasectomy studies indicated that harems may be infiltrated to the extent that the harem holder may only father about 1/2 the offspring produced during his tenure (see M. C. Baker and P. Marler, this volume). The problem is not confined to studies of birds: the Cayo Santiago work on rhesus monkeys used both observational and genetic marker data to suggest that perhaps 5% of offspring are fathered by males from outside the group. And among bats, McCracken and Bradbury's recent work (39) indicates a certainty of paternity of between 60 and 90% in one harem species. Sneaking copulations by extragroup males (kleptogamy) is reported from a variety of vertebrate taxa although the genetic consequences (the likelihood that the kleptogamist actually fathers offspring) are virtually unknown. The need for further genetic marker work in long-term field studies is evident.

MODELS OF POPULATION STRUCTURE

Several long-term field studies are beginning to produce detailed descriptions of population structure, including patterns of mating success, demography, dispersion, and dispersal. There is a tendency to attempt to relate these descriptions to the population drift models of Sewall Wright and others, and then to draw conclusions about effective population size (N_e), the spread of genes that might influence behavior, and the accumulation of genetic variation among demes. Several problems should be considered. First, it is particularly difficult to apply these models to real data. For instance, we should not take it for granted that there will be a correspondence between population subsets in the models and those in real populations. Second, it is important to know who moves: stepping-stone models show that genetic differentiation between sub-populations is rapidly reduced if very few individuals move long distances. It is not the modal distance moved that should concern us here, but the tail of the dispersal curve; the 2% of animals that move the longest distances are very important in destroying or slowing down sub-population differentiation. Third, the importance of measuring the inbreeding coefficient in relation to a particular population is relevant (see R. A. Metcalf, this volume). And fourth, such models are usually based on neutral alleles; selective pressures which may vary between sub-populations can result in considerable genetic differentiation.

Before leaving the topic of models of population structure, it is important to note that the inclusive fitness model, due to Hamilton (30), postulates a gene with a particular effect. A "rule of thumb" is used to determine the individuals to which a particular animal should dispense altruistic acts (see below). As the gene spreads through the population, that same rule of thumb is used. If a gene programs an animal to help sibs under certain circumstances, even when it has reached fixation within the population, sibs are still the only animals helped (see Dawkins (20) for an extended discussion of these and other fallacies). Similarly, although overall homozygosity within the population (or effective population size) may correlate with the conditions under which such a gene might spread, it does not determine those conditions. There is no current theory that helps us to make any predictions about the effect of population subdivision on the dynamics of kin selection.

WHY SHOULD WE EXPECT KIN-CORRELATED BEHAVIOR?

Kin are more likely to share genes that are identical by descent than are individuals selected at random from the population. Increasing the fitness of kin increases the inclusive fitness of an individual so long as costs are not incurred; if there are costs involved, then, depending on the degree of relatedness of the kin and the cost:benefit ratio, inclusive fitness may still be increased. This is the nub of Hamilton's argument for the evolution of altruistic behavior by kin selection (30).

Cooperation between kin will generally be favored over cooperation between non-kin, whether this involves mutualism, reciprocal altruism (48) or passive interactions, since additional benefits will accrue through kin selection. In addition, kin are likely to be associated spatially and will, therefore, interact more frequently than will individuals taken from the population at random. Vehrencamp (50) has argued that there may be exceptions to this generalization when strong skew in reproductive success among group members is possible and when the costs of dispersing between groups are low. The conditions under which kin might be preferentially excluded from groups have not yet received formal attention.

There are, however, limits to cooperation between kin. These have been discussed elsewhere - in particular the development of parent-offspring conflict (49) and the evolution of parental manipulation (1, 19). It may be that consideration of the effect of genes among offspring for resisting manipulation by the parents (or even for "psychologically manipulating" the parents: Trivers (49)) will be a profitable area of research; that is not to say that such genes will inevitably spread, just that they might under certain circumstances.

Nevertheless, close kin are often expected to avoid each other as mates. The degree of inbreeding depression expected may, to a large extent, depend on the history of inbreeding in the population (e.g., see (44)). Although inbreeding depression has been widely demonstrated in laboratory populations, there are, as yet, very few field data. It is generally true that populations appear to be structured so that close kin rarely interbreed. However, the extent of inbreeding and its effects in the wild (which are likely to be more striking than under less harsh laboratory conditions) are clearly identified as important areas of research (28).

DATA ON KIN-CORRELATED BEHAVIOR

The data base on kin-correlated behavior is large and reviews have generally focused on apparent cases of altruism, particularly where these appear to have evolved independently among several closely related taxa. Eusociality in the Hymenoptera and termites (31) and cooperative breeding in birds (21) are cases in point. In both instances, the functional significance of the described behavior or social system is still a matter for debate. Data that will allow us to distinguish between various hypotheses that postulate the spread of genes which determine changes from purely selfish to apparently altruistic behavior are not available. For example, among the social Hymenoptera, workers are female offspring of the queen who remain in the nest and help to rear reproductive siblings (full or half); kin selection and parental manipulation are competing (and to some extent complementary) hypotheses (19). Among the termites, ecological factors leading to high levels of inbreeding may be relevant to the evolution of eusociality (5).

It is often costly, in terms of survival or fitness, to initiate a breeding group or to enter one. In Polistes, sisters may cooperate to found a new colony. Even if one sister subsequently leaves the nest or acts as a subordinate (producing few or no eggs), she may gain indirectly through kin selection (reproduction by a sister) compared with the possible direct benefits resulting from attempting to set up a colony alone. Assortment of sisters is marked (N. M. Ross and G. J. Gamboa, personal communication): keeping 50 females isolated over winter and then placing them into groups of ten, consisting of five sisters from one source and five from another resulted in 44 resting associations of two or more wasps; 41 of these involved sisters only. Among mammals, it may be common for brothers (or half brothers) to help each other to gain reproductive access to groups of females. Hrdy (34) reports this among langurs (Presbytis entellus) where a group of related males may cooperate to oust the harem male, and subsequently all but one of the invading males are ejected. In lions (8, 10), brothers cooperate both to oust previous reproductive males from prides and, subsequently, to prevent takeovers. Similarly, brothers (or half brothers) may help each other to enter breeding groups of rhesus monkeys on Cayo Santiago (D. S. Sade, personal communication); sometimes an older brother who is already a member of the troop helps a younger sib to join and on other occasions brothers migrate together. And among chimpanzees, uterine kin often form coalitions against others in the same group.

Group fission may also be kin-correlated in that groups may divide along kin lines. Group fission has now been observed in free-ranging populations of three species where individuals were known: Japanese monkeys (24, 25, 26, 36), rhesus monkeys (13, 16, 35, 40), and olive baboons (41). The pattern has been similar in each: groups have split along matrilines so that certain females and their offspring leave together. This has the consequence that the average degree of relatedness within new groups is higher than that between individuals in the original troop (14, 15).

Clutton-Brock and Harvey (17) have produced simple models that attempt to describe such group splits in functional terms. They assume that the rate at which dominant animals direct aggression towards subordinates depends on the degree of relatedness between the animals involved. The number of threats received by an animal is, therefore, a consequence of the extent to which it is unrelated to dominant group members. As group size increases, the lowest animal will, for example, suffer such feeding interference that she will wish to leave the group. Since daughters rank below mothers, the mother (acting in the interests of her own inclusive fitness) might also leave in order to protect her offspring. Groups would therefore split along matrilines, and it would also be predicted that the lowest ranking matrilines should be those to split away first. This was indeed the case in each of the three species mentioned above. Models such as these are clearly over-simplified. For example, males are not considered, yet in Nash's (41), Furuya's (25) and Koyama's (36) studies, group fission followed a period of instability in the male dominance hierarchy. However, Chepko-Sade and Olivier (15) found that matrilineages involved in group fission subdivided when the average degree of relatedness between members fell below that of first cousins.

Whole social groups fissioned when the average degree of relatedness between members fell below the level of second cousins. In these cases, degrees of relatedness were calculated only through the maternal line, and therefore the types of model outlined above may be relevant.

Group fission has also been observed and well-documented in the Yanamamö Indians of the Amazon Basin (11). Although the Yanamamö did not split along matrilines, the average degree of relatedness within the new groups was markedly higher than in the old group. One important aspect of the Yanamamö split was that although kinship terminology is sometimes applied to individuals who are social but not biological kin (e.g., calling a non-relative "uncle" or "brother"), when group fission occurred the new subgroup tended to contain biological kin. Chepko-Sade (14) also reports that, in Chagnon's study, internal solidarity is higher in equal sized groups of more highly related individuals than in groups with lower average degrees of relatedness.

Alarm calling among a variety of vertebrate taxa is also often kin-correlated and a review of the hypotheses and tests can be found in Harvey and Greenwood (32).

The evidence for incest avoidance is largely (though not wholly: (9, 43, 46)) circumstantial. For instance, sex differences in dispersal rates and distances occur among most vertebrates (42) that have been studied: in birds, females generally move longer distances than males from their natal area to the site of first breeding, while in mammals it is the males who more commonly move from their natal group and the females who tend to remain (see Greenwood (27) for a review). However, among most species of vertebrates, the distances moved are small (generally less than 10 home ranges or territory widths), and it may be that there exists some optimal level of outbreeding. Bateson (6) reports that Japanese quail appear to select potential mates so that neither close inbreeding nor maximal outbreeding would result. More data are clearly required, but Bateson's experiments provide an important start.

MECHANISMS OF KIN-CORRELATED BEHAVIOR

If animals are to interact assortatively with kin, how do they recognize kin? Animals do not need to be able to recognize kin for kin-selected behavior to evolve; they may simply interact preferentially with animals who are more likely to be kin. There are several likely mechanisms.

It has already been pointed out that vertebrates tend to be philopatric (although one sex more than the other). It may be that the sex that does not disperse treats other conspecifics of the same sex in the group as though they were kin of a particular degree of relatedness (B. Hölldobler and C. D. Michener, this volume).

Familiarity provides a more fine-grained mechanism for kin recognition than does simple philopatry. A well-known example is filial imprinting. Shortly after hatching, birds such as ducklings and chicks narrow their filial preferences to their mother (or, in experimental conditions, some substitute for her). Simultaneously the mother learns the characteristics of her young and becomes so selective in her parental behavior that she may attack and even kill young of other broods. Meanwhile, the young birds also learn the characteristics of their siblings. This process of familiarization together with filial imprinting can leave a long-term effect on the choice of a mate since the birds prefer not to mate with their immediate kin. They do, however, prefer a mate looking rather like the individuals to which they were exposed when young - as can be strikingly demonstrated when birds are reared with members of a different species. Sexual imprinting, as it is called, is found to occur after siblings have moulted into their adult plumage but before they have dispersed (7).

Bateson's optimal discrepancy theory (6, 7) proposes that a single learning process sets a standard of what immediate kin look like, and the birds subsequently prefer to mate with an individual who looks slightly different. Bischof (9) proposes an alternative idea, namely, that sexual imprinting involves learning the general characteristics of the species and that, at maturity, previous attachment to mother and sibs is replaced by active detachment and exploration. The result is that, while under natural conditions the birds prefer to mate with their own species, they also prefer not to mate with close kin. Differential predictions arising from Bateson's and Bischof's theories have not yet been tested.

Familiarization required to detect kin could involve something as simple as sensory adaptation to own odor; subsequently individuals that smelled the same as self could be distinguished from those that smelled differently. However, the available evidence from invertebrates, which might be expected to employ such simple devices, suggests that they employ processes resembling, at least superficially, classical imprinting in birds. Greenberg's data (reviewed by B. Hölldobler and C. D. Michener, this volume) are of this type. Here Lasioglossum zephyrum guards are more likely to allow individuals with familiar odors into the natal burrow, but the guard does not use its own odor as a cue. There is clearly a genetical component to variation in odor production in this case (so that sibs have similar odors), though there does not appear to be innate knowledge on the receptor side.

Another example comes from Linsenmair's study of the isopod Hemilepistus ((38), and in preparation). Up to 100 offspring from a single monogamous pair live together for their first year of life in a burrow up to 1 meter deep and between 2 and 3 meters long. There is severe competition for access to burrows and associated cannibalism of conspecifics (though not of close kin). Strangers are attacked when they approach the entrance to the burrow, but members of the sibship are allowed to enter.

Since the young leave the burrow on occasion (to forage), a clear kin recognition signal is essential. Linsenmair has conclusively demonstrated that there is an important genetic component to the odor or taste (so that sibs smell or taste very much the same as each other), but that sibs do not use their own odor as a signal for kin recognition; this must be learned through previous association with sibs.

There are, as yet, no reported instances of innate sib-recognition systems among arthropods or vertebrates.* It will be interesting to follow the development of the work by Waldman and Adler (51) who reported sib-association among tadpoles. This may be determined by mechanisms similar to those described by Greenberg and Linsenmair (learning).

Kin recognition by demographic characteristics (e.g., maternity which must be certain in viviparous animals) together with other mechanisms listed by J. L. Brown (this volume) are, of course, also relevant.

The absence of innate kin recognition systems on the hard-wired receptor side may be a consequence of one or more factors. Perhaps plasticity has been selected for because particular sensory cues may vary through an individual's lifetime (e.g., among the social insects where colony odor changes through time because of differences in dietary mix (B. Hölldobler and C. D. Michener, this volume) or replacement of the queen). There may also be selection, under certain circumstances, against genes for the reception of kin recognition because they may be "cheated against." This highlights the need for a whole class of formal genetic models that examine the conditions under which genes for kin recognition as opposed to genes for the absence of kin recognition would be selectively favored; already, several papers (2, 23, 45, 47) have considered the possibility that such genes might exist in one form or another.

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*Footnote added in proof: but see Wu, H.M.H.; Holmes, W.G.; Medina, S.R.; and Sackett, G.P. 1980. Kin preference in infant Macaca nemestrina. Nature 285: 225-227.

Various animal groups use different sensory modalities to recognize conspecifics (and presumably, kin), as well as combinations of different modalities during the course of a lifetime. We assume that individuals adapt to use an optimal combination given the species sensory capabilities and the environmental constraints operating at a particular time.

ENVIRONMENTAL CONSTRAINTS RELEVANT TO KIN-CORRELATED BEHAVIOR

Kin-correlated behavior will evolve when kin associate (or disperse). This section focuses on some of the environmental conditions that are likely to favor kin association.

Among the social insects, defense against predators is likely to have been a potent force favoring cooperative behavior. For instance, among the wasps and bees, ground nesting species are likely to be subject to attacks by predators, parasites, and even conspecifics. Solitary individuals are less able to defend themselves against such attacks than groups. Note that viral, bacterial, protozoan, and other internal parasites are more easily maintained as population density increases, so that this factor works against group formation; some of these effects can be differentially disadvantageous for groups of kin compared with groups of unrelated individuals - see, e.g., the reviews of Anderson and May (3, 4). However, as group size increases in the absence of predators, so productivity per individual decreases; the rate of decline of productivity with increase in group size varies enormously between species. Colony size presumably represents a balance between defense against natural enemies and loss of productivity with increased colony size. The evolution of sociality is, therefore, a reversible process. A possible example of such a transition back from sociality to asociality is provided by the halictids or sweat bees (C. D. Michener, personal communication). Augochlora contains two taxa, one of which is ground nesting and social while the other lives in rotten logs (where natural enemies are few) and is asocial. The close relative, Augochlorella, is ground nesting and social. The most parsimonious interpretation of the phylogeny of the group would interpret asociality as having evolved once, rather than sociality having evolved twice.

Also among the wasps, if sisters were to clump nests around that of the mother and the mother had only been inseminated once, then it would not matter to them if the mother placed her eggs in their nests; each would have the same degree of relatedness to the offspring (assuming a 50:50 sex ratio). The mother would gain a great deal if she were able to manipulate the daughters to accept the eggs. Clearly, such a system is fragile and open to potential exploitation but could represent an early stage in the evolution of worker castes. It is interesting to note that the system does not depend on haplodiploidy and would work equally well for diploid species: it is the life history pattern of the wasp involved (presumably responding to environmental conditions and clumping the nests) that would favor the evolution of the system (12).

Why then, among the Hymenoptera, might polygyny evolve from a monogynous system? Based on a simple classification reproduced in Figure 1, Hölldobler and Wilson (33) offer several plausible explanations. When considering the adaptive significance of secondary polygyny in the ants, they argue that two sets of ecological conditions may be relevant. "(1) The first set is specialized on exceptionally short-lived nest sites. Such species are opportunistic in the sense employed by ecologists--they occupy local sites that are too small or unstable to support entire large colonies with life cycles and behavioral patterns dependent on monogyny. (2) The second adaptation is specialization on habitats--entire habitats, as opposed merely to nest sites--that are long lived, patchily distributed, and large enough to support large populations. The two forms of specialization are not mutually exclusive; some ant species, for example Iridomyrmex humilis

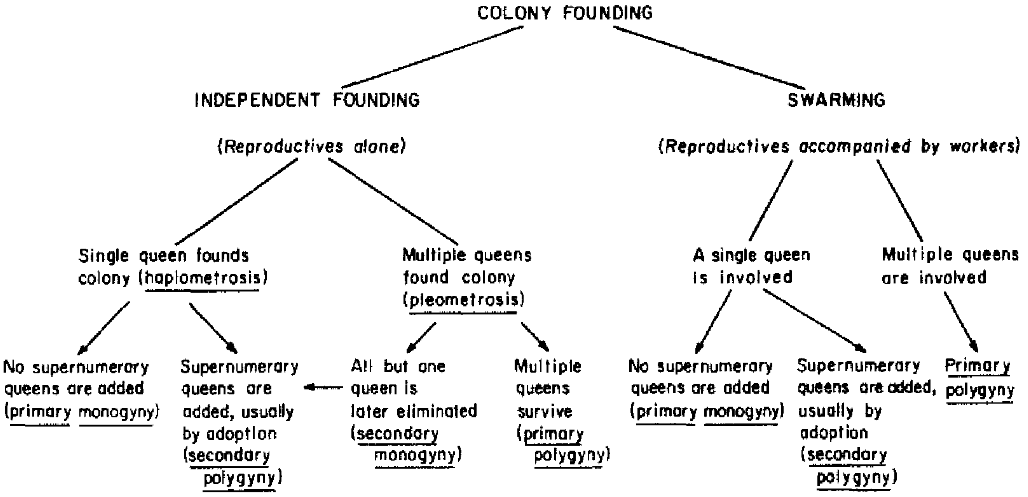

FIG. 1 - An elementary classification of colony founding and later colony composition, with reference to the number of queens.

and Pheidole megacephala, possess both." The reader is referred to Hölldobler and Wilson (33) for further elucidation of the relevant ecological parameters. Under certain circumstances (see above, as in Polistes) individuals may be unable to found colonies alone; several animals may need to cooperate and primary polygyny will evolve. An additional hymenopteran example to Polistes is provided by the honey-pot ant, Myrmecocystus mimicus, where three or four queens are necessary to produce honey storage castes within the short period of the rainy season. The queens (who are unlikely to be relatives) cooperate in this venture, each producing a supply of workers who subsequently and cooperatively eject all but one of the queens (B. Hölldobler, personal communication). An adaptive explanation for this behavior is obscure, though the rejected queens can remain near the colony and might reenter if the old queen dies.

Recently, several papers and reviews have considered the environmental conditions (and the taxonomic constraints) under which group living is favored and, as a consequence, how any one of a variety of breeding systems can evolve among vertebrates (17, 22, 52). Particularly relevant to the present discussion is Emlen and Oring's (22) distinction between resource defense and mate defense breeding systems; it has recently been argued (27) that the dispersing sex (and therefore the one that is least likely to benefit from kin associations) is likely to be the male when the breeding system is one of female defense and the female when the system is based on resource defense by the male. This fits the gross picture of female-biased movement in birds and male dispersal in mammals. Whether the exceptions are also explained is a matter for speculation at present.

We finish on a note of speculation. When considering the conditions likely to favor kin association and kin cooperation, it is important to examine the reasons for grouping in the first place. We might profitably distinguish between conditions under which mutualism does not involve costs to other conspecifics and those where it does involve such costs (R. Wrangham, personal communication and in preparation). In the latter case, kin associations will be more strongly favored. This will be especially true when the costs of migration and exclusion from group membership are high. Other relevant factors are likely to include the costs involved within particular interactive situations; for a given benefit conferred on a recipient, a donor is more likely to help when the costs are high if the recipient is related (a straightforward application of kin selection theory).

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