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Do animals really recognize kin?

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Abstract. Species recognition and group member recognition systems produce an ability to discriminate conspecifics by genetic similarity on first encounter when kin recognition is absent. Experimental evidence of such discrimination is therefore insufficient evidence for kin recognition. The evolution of a true kin recognition system depends on three kinds of loci: matching, detection and using. Matching loci, which affect the traits used to detect kin, will have a higher genetic similarity between interactants than their common ancestry alone suggests. Selection has been erroneously thought to cause individuals to behave according to the higher relatedness implied by this extra similarity. The detection loci and using loci are not expected to be closely linked to the matching loci, implying that individuals will behave according to the relatedness based on their common ancestry. Polymorphism at the matching loci is essential for effective discrimination of kin, and is sustained by the evolution of the kin recognition system in those cases where it is advantageous to interact with kin.

Recent studies have shown that individuals of many species of animal have remarkable abilities to behave differently at first encounter towards groups of conspecifics who differ in their relatedness to the individual. These findings have been reviewed by Hepper (1986) and in several chapters of the book edited by Fletcher & Michener (1987). In this paper I discuss two conceptual matters arising from this large and impressive body of empirical work.

The first concerns what can be concluded when it is shown that an individual behaves differently at first encounter towards differently related groups of conspecifics. We may accept that the difference between the conspecifics must be genetic, and that the individual must be able to sense some feature of the conspecifics which is correlated with their genotype. I shall refer to this neutrally as an ability to discriminate by genetic similarity. The first main point I shall make is that we cannot then conclude that individuals of this species have evolved to distinguish kin from non-kin, we cannot conclude that possession of the ability has anything to do with kin selection, and we should not presume that this ability to discriminate has an evolutionary function at all. I shall argue that an ability to discriminate by genetic similarity can easily arise as an incidental by-product of either species recognition, or individual or group member recognition. It follows that the literature on 'kin recognition' is really about all kinds of recognition system and would less confusingly be called 'animal recognition systems'. Indeed only one study cited in a recent book entitled *Kin Recognition* (Fletcher & Michener 1987) can in my view reasonably be called kin recognition, and this study will be discussed later.

The second conceptual point is an elaboration of how a kin recognition system might evolve genetically. This is like unlinking the three parts of a green beard gene (Hamilton 1964; Dawkins 1976), and asking how the system will evolve. Two questions are tackled. When an individual detects relatives by matching at a particular locus, it is likely that the individual will be genetically more similar at the matched locus than in the genome as a whole. Should we expect individuals to behave according to the extent of genetic similarity at the matched locus, as some authors have assumed, or should we expect them to behave according to the extent of genetic similarity through the genome as a whole? To distinguish kin from non-kin there must be considerable genetic variability. The second question is does the operation of kin recognition and kin selection tend to increase the supply of genetic variability at the loci used for detection, or does it, as Crozier (1986) suggested, tend to decrease this supply? If it decreases the amount of variation, the system tends to remove a necessary condition of its own operation.

Hamilton (1964) gave two conclusions about how a system of kin recognition and kin selection would evolve. They are: 'The social behaviour of a

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species evolves in such a way that in each distinct behaviour-evoking situation the individual will seem to value his neighbours' fitness against his own according to the coefficients of relationship appropriate to that situation' and 'The situations which a species discriminates in its social behaviour tend to evolve and multiply in such a way that the coefficients of relationship involved in each situation become more nearly determinate' (Hamilton 1964, pp. 19 and 24). Both of these conclusions are supported by the analysis.

MATCHING

I shall use the term matching to refer to a type of mechanism of discrimination, and one that I believe logically must be involved in kin recognition. It may also be used in species recognition mechanisms. An ability to recognize is an ability to assign a stimulus reliably to one of a number of classes. A set of classes may be defined in absolute terms, such as the frequency of monochromatic light, and these classes will be the same for all discriminators. Alternatively a set of classes may be defined relative to the discriminator. Here the discriminator must logically use information about itself in the process of discrimination. This individuating information about discriminators may be called a standard, and the process of using this standard to classify stimuli can be called matching. The actual mechanism may not look like matching, but logically it is equivalent to it. This matching is the same as the 'phenotype matching' of Lacy & Sherman (1983) except that I claim that kin recognition must occur by matching in its generalized form. Further, the standard must be genetic if it is kin that are recognized, as kin are defined by genetic similarity.

It follows that any kin recognition system must work by matching alleles, in the extended sense of matching. As recognition alleles are often contrasted with phenotype matching, let us consider in an example how phenotype matching implies the existence of matched alleles. Consider a species in which individuals favour conspecifics who do not smell very much. As each individual is habituated to its own smell, this rule leads it to favour among its objectively equally smelly conspecifics those who smell similar to it. If enough of the variation in the quality of the smell is genetic, this will lead to the individual favouring its relatives. This is certainly phenotype matching. It is also allele matching, at those loci that influence the smell. Hence we can say that this system matches (perhaps imperfectly) at the loci that influence the smell. This is a statement about the effect of the process of discrimination, not about its mechanism. Any kin recognition system must do this: no mysterious ability to inspect DNA is required to match alleles in the extended sense of matching.

It is easy to imagine acquiring the standard by inspecting self or selected conspecifics in the same way in which the individuals to be discriminated will later be inspected. This just involves comparing two stimuli of the same sort. It is harder to imagine working out from one's genotype which stimuli show genetic similarity and which do not. These different mechanisms may nevertheless have similar evolutionary consequences.

'KIN RECOGNITION' AS ARTEFACT

In the previous section we saw that kin recognition must involve matching. Now we shall see that matching is useful for species recognition, and that matching almost inevitably confers an ability to discriminate by genetic similarity. I shall argue that this ability is easy to mistake for kin recognition. Then I shall show that other kinds of recognition system can also lead to an artefactual detection of 'kin recognition'.

Species recognition is used in mating and in selfish herding (Hamilton 1971). Matching is a likely mechanism for species recognition. As a species changes in evolution, a matching mechanism will automatically track the changes. It will even continue to work unchanged in an effective way in both daughter species of a speciation event, so that the same unchanged mechanism can allow individuals in those daughter species to discriminate between each other.

The acquisition of the standard in each individual, from contemporary exemplars, prevents any 'fossilization' of the species recognition mechanism. But which will those exemplars be? To acquire a standard that is reliably of a conspecific, the obvious possibility is the individual itself. A bird that learnt the properties of those who fed it would gain a standard that was reliably of a conspecific. So would tadpoles that learnt the smell surrounding them in the early days of their lives. Note that it is likely in each case, though irrelevant

to the purpose of species recognition, that the standard is acquired from relatives.

Various authors, reviewed by Blaustein et al. (1987a), have shown that tadpoles of a number of species have remarkable abilities to discriminate between classes of conspecifics differing in their relatedness to the discriminator. I want to explain how the species recognition mechanism just discussed is quite compatible with most of the evidence reviewed. The species recognition mechanism would work perfectly well if all members of the species had the same smell, but it is likely that there is some genetic variation in the smell. This genetic variation, combined with the matching mechanism of species recognition, will incidentally produce discrimination by genetic similarity. Individuals will acquire a standard which is slightly more like their relatives than it is like conspecifics in general. So when an individual uses its species recognition ability to join an aggregation of tadpoles, it will have a slight tendency to join a more related aggregation because it is perceived as closer to the acquired standard. Aggregations of tadpoles in nature might therefore be expected to have a slight tendency to consist of relatives.

This incidental ability to discriminate is truly genetic, so that paternal half-siblings will be recognized in the laboratory. It is likely to be a weak effect because it is an unlooked for by-product of a species recognition system. These consequences are fully in accord with many of the experimental findings. The effects are often highly statistically significant, so there is no doubt they exist. But this is because sample sizes are large, not because the effect detected is large. Blaustein et al. (1987b) reported that there is much variation in this ability between species and between populations of the same species, which is to be expected of a by-product. Perhaps the degree of genetic variation at matched loci varies between species and populations. The tadpoles' abilities are highly ineffective as a kin recognition system, and are much more consistent with the view that they are a highly effective species recognition system with the incidental side-effect of a faint ability to distinguish kin from non-kin.

As well as species recognition, other kinds of recognition system can produce an ability to discriminate by genetic similarity as a side-effect. Consider a system of group member recognition, such as that described by Linsenmair (1987) for the desert isopod *Hemilepistus reaumuri*. Experiments show that individuals can distinguish with exceptional reliability between members of their own group and non-members, even when the groups are formed artificially of unrelated individuals. The recognition system has nothing to do with kinship, and everything to do with group membership. This is to be expected, as natural groups consist of a mated pair and their offspring. An adult must admit its mate as a group member, but not admit its adult sibling that is a member of a neighbouring group. Its sibling is as related to it as its offspring, so relatedness is a poor guide to group membership.

The system is used for kin selection purposes, namely preserving a burrow as a necessary resource for rearing offspring. But just as we do not call vision 'kin vision' when we use our sight for kin selection purposes, it does not make sense to call *Hemilepistus'* group member recognition system a 'kin recognition' system. Of course this does not detract from the interest of Linsenmair's exquisite study; it just suggests changing the name of the subject it belongs to.

Does *Hemilepistus* have 'kin recognition' abilities? Its remarkably precise group member recognition system has in fact produced a much weaker ability to distinguish kin from non-kin, which has been revealed in the laboratory but is not known to be important in nature. The chemical cues used to distinguish individuals happen to be genetic. The group member recognition system would work just as well if they were environmental, provided they were fixed for life. But because they are genetic, there is an incidental ability to discriminate by genetic similarity. Linsenmair (1987, pp. 155–156, his Fig. 12) showed that foster parents can discriminate between siblings of adoptive offspring and other offspring unrelated to parent and offspring. This fact is analogous to the total sum of our knowledge for many species, but is only a small part of what is known about *Hemilepistus*. I draw the moral that finding an ability to discriminate by genetic similarity in a species does not imply that the species uses its ability to distinguish between different degrees of kin.

The cues used by *Hemilepistus* are known to be genetic. This is probably because genetics can provide lifetime consistency, and a great deal of variability. The fact that the use of genetic cues allows kinship to be assessed seems to be irrelevant to *Hemilepistus*.

As well as species recognition and group member

recognition, an incidental ability to detect kinship may arise through a system of individual recognition. To be able to discriminate between individuals, it might be possible to measure a sufficient number of cues that each other individual is distinct. Assigning one dimension to each cue, an individual can be represented by a point in a multidimensional space. Measurement error can be conceived as smearing each point into a sphere. One condition for reliable individual recognition is that these spheres should not overlap. But this kind of system also allows distances between points to be measured, and if the cues are genetic, then the distance will be a measure of relatedness. This can be used to assess the relatedness between two strangers as well as the relatedness to self.

Any individual recognition system using genetic cues therefore allows some degree of kinship assessment. But this may not be very reliable, and it may not be used in nature. Information about relatedness may be gained instead by social and spatial cues at first meeting, and then remembered as belonging to the individual. In this way, assessment of relatedness is never made on the basis of the recognition system itself. Of course, there is a grey area where varying degrees of information about relatedness come from spatial and social cues. But as with the previous systems considered, evidence of an ability to discriminate by genetic similarity is not by itself evidence that a species assesses kinship in that way, or that it has evolved the ability in order to assess kinship. Waldman (1987) has discussed the incidental ability to discriminate kin that can arise from group member recognition, with special reference to sweat bees, *Lasioglossum zephyrum*, and from individual recognition.

I now propose two conceptual tests for deciding that a recognition system should not be considered a kin recognition system, that is, a system whose use and function is to assess the kinship of conspecifics. A recognition system is a species recognition system to the extent that it would perform the same function if all individuals in the species had the same cues. A recognition system is an individual or group member system to the extent that it would work in the same way if all individuals in the species were different, but solely for environmental reasons.

The conclusion of this section is that evidence of an ability to discriminate by genetic similarity does not show a kin recognition ability, but is consistent with other interpretations. The species recognition interpretation of the tadpole data explains its most puzzling features: its inconstancy and the feebleness of the ability. To show kin recognition it is necessary to show that the ability is used to assess kinship.

EVOLUTIONARY RELATIONSHIPS

It would be very exciting to discover that tadpoles had only a species recognition mechanism, because it would imply that if kin recognition becomes important in the evolutionary lifetime of a species, there are mechanisms available which can be adapted for that purpose. Presumably the initially crude kin recognition mechanism would be improved until tadpoles were rather better at it than they are now.

Individual recognition might have evolved from a system of kin recognition, and may for many purposes make kin recognition itself unnecessary, as a number of authors have pointed out (for example in Fletcher & Michener 1987). Only once in each relationship is it necessary to establish kinship, and the social and spatial context often provides good information. Using this information may well be the evolutionarily advanced method of kin recognition, a method in which direct recognition of genetic differences is no longer needed. A major force against employing social cues is uncertainty of paternity, so perhaps species with paternal care are more likely to retain the direct mechanism.

THE EVOLUTION OF KINSHIP RECOGNITION SYSTEMS

The substance of the second principle quoted from Hamilton (1964) in the introduction was that kinship recognition systems should evolve in such a way that organisms treat each other according to their ancestral relatedness. Hamilton himself gave no special justification for asserting that ancestral relatedness would be the important quantity, but treated it as a corollary of his general theory of inclusive fitness. I believe this position to be wholly sound, and so some justification must be given for providing a longer and more explicit argument here. The difficulty arises when kin recognition occurs by a process of matching, as defined above.

The difficulty is that the process of matching creates genetic similarity between an individual and those it 'recognizes' as kin, over and above any genetic similarity that arises from common ancestry. The question is then whether Hamilton's rule should apply with the ancestral relatedness as Hamilton claimed originally, or whether it should apply with an inflated relatedness which takes into account this extra genetic similarity brought about by the process of matching.

The idea that individuals may be related differently at different loci can easily be made acceptable with an example. The inheritance of the X chromosome in humans has the same pattern as that of the entire genome of haplodiploids. Supposing the Y to be inactive for present purposes, it follows that humans have haplodiploid patterns of relatedness, including asymmetries, on the sex chromosomes. The autosomes have the usual diploid inheritance. For an explanation of how different loci among the autosomes may have different relatednesses, see Grafen (1985).

Two examples may help to explain the problem. First, suppose that an individual can recognize the genotype of other individuals at a particular locus, and that it lives in an area with its own siblings and with some unrelated individuals. Assume that at that locus alleles are rare and so effectively only relatives share alleles. If it meets an individual with the identical genotype at the matching locus to its own, should it behave according to Hamilton's rule using a relatedness of one-half on the grounds that this individual must be a sibling rather than unrelated, or should it use a relatedness of one on the grounds that genetic identity implies a relatedness at that locus of one? The second example assumes that the individual lives in a place where there are only unrelated individuals, say because it has dispersed a long distance. By chance it meets an individual which happens to share one allele at the matching locus. Should it treat this individual as a sibling, because the relatedness at this locus is one-half, or should it treat it as unrelated because it shares no recent common ancestry?

It is sometimes assumed that it is the inflated relatedness that applies, and one purpose of this section is to argue that this assumption is erroneous. Another purpose is to indicate the kind of selection that will operate as a kin recognition system evolves, as it has some interesting properties. In the rest of this section the problem will be set out more precisely, the conceptual apparatus needed to analyse the evolution of a kin recognition system will be developed, and a firm conclusion will be drawn in favour of Hamilton's original statement. The analysis will also be used to argue that at least one case of genuine kin recognition is known.

It is important to begin the analysis of the evolution of a system of kin recognition by stating explicitly what I shall take to be the meanings of and connections between the terms relatedness, genetic similarity and common ancestry. These ideas are discussed more fully elsewhere (Grafen 1985), and only a brief summary can be given here. 'Genetic similarity' has no special meaning, and refers in a general way to any similarity between the genomes of individuals. This could be identity at one locus, but no similarity elsewhere, or identity at all loci, or a tendency towards sharing one allele at each locus. 'Common ancestry' is one possible cause of genetic similarity: having a recent common ancestor causes a very special kind of genetic similarity to arise between genomes. It is special because, when measured in a certain way, it causes the same amount of genetic similarity at each locus in the genome. That special measure of genetic similarity is 'relatedness', which is therefore a particularly appropriate way to measure genetic similarity caused by common ancestry. I use the term 'ancestral relatedness' to refer to a level of relatedness brought about by common ancestry, which is therefore constant throughout the genome. (Strictly, it brings about one constant level of relatedness at the autosomes, and another at each other type of chromosome with a distinct pattern of inheritance.)

Relatedness plays another role. Hamilton's rule is true no matter how genetic similarity arises, and so even when it arises other than by common ancestry, genetic similarity should be measured by relatedness to analyse the action of natural selection. Notice that Hamilton's rule can be applied separately to each locus affecting a trait, and that if genetic similarity does not arise through common ancestry different relatednesses will need to be used in the applications of Hamilton's rule to the different loci.

Three Types of Loci

There are three different types of loci affecting a system of kin recognition by matching. If matching by some phenotypic character helps to detect kin, matching for the character must tend to cause

matching at the locus or loci that determine that character. I argued earlier that any kin recognition system must match at some loci. For the sake of simplicity let us assume that only one locus is involved and call it the 'matching locus'. The second type of locus controls whether the similarity at the matching locus is detected or not, which we may call the 'detection loci'. The third type of locus controls how the information about matching is used, and these may be termed the 'using loci'. The distinction between these three types matters because genetic similarity is caused not only by common ancestry, but also by the process of matching. It is important to see how the process of matching creates genetic similarity at these three types of loci, and how Hamilton's rule applies to each of them. In combination, this will show how the kin recognition system evolves.

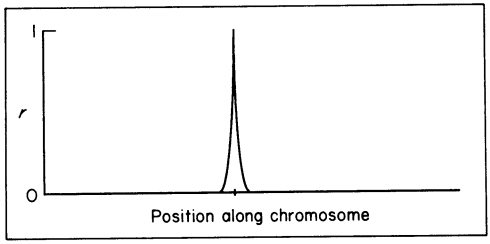

Figure 1. The figure shows how relatedness (r) varies along the chromosome when an exact match is guaranteed at one locus, but the selected individual is unrelated. The matched locus is marked with a tick. Relatedness at neighbouring loci arises through linkage disequilibrium only, and so decays very quickly to zero. Relatedness on other chromosomes is also zero.

How Matching Creates Genetic Similarity

It is convenient to assume a simple situation in which kin recognition by matching takes place. One individual selects one other from a group, by ensuring that the selected individual matches it exactly at one locus. Two elements will be relevant. The first is how the group is composed, and in particular how many relatives it contains, and of what degree. The second element is how rare the alleles at the matching locus are.

Take first the case where the group consists of non-relatives, and the alleles at the matching locus are fairly rare. It is unlikely that the selecting individual will find a match, but supposing one is found, what can we say abot genetic similarity between the selector and the selected? There will be complete similarity at the matching locus, but what about the rest of the genome? As the group consists of unrelated individuals, there will be genetic similarity at another locus in the genome only if there is a correlation in the population as a whole between the contents of that locus and the contents of the matching locus. Such a correlation is called linkage disequilibrium.

Two factors can cause linkage disequilibrium in a large population: selection acting on the combination of genotypes at two loci, and very tight linkage. For the moment I shall ignore the first possibility, as there seems no reason to expect it in general, and concentrate on the second. There will then be no genetic similarity between selector and selected except on the same chromosome as the matching locus, on which the similarity is high only very close to the matching locus, decaying very rapidly on either side as illustrated in Fig. 1.

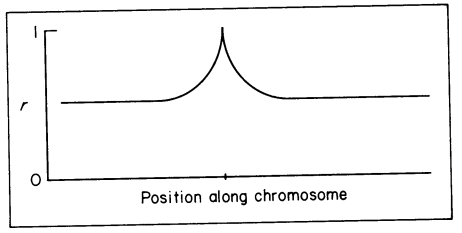

Figure 2. The figure shows how relatedness (r) varies along the chromosome when an exact match is guaranteed at one locus, and this ensures that the selected individual is a sibling. The matched locus is marked with a tick. Relatedness at neighbouring loci arises through linkage, and so decays slowly. The relatedness decays to a half, the value for a sibling. Relatedness on other chromosomes is also a half.

Now consider the case where the group consists of nine-tenths unrelated and one-tenth siblings, and again the alleles at the matching locus are fairly rare. Here, by matching, the selector ensures that a sibling is selected, because matches will be much more common among siblings than among unrelated individuals. It follows that relatedness at all the other chromosomes is one-half. On the chromosome with the matching locus, there is a relatedness of one at the matching locus, decaying to a half at distant loci. This is illustrated in Fig. 2.

Notice that the rate of decay is not nearly as fast in Fig. 2 as in Fig. 1. This is because the chance that

a locus near to the matching locus is identical is enhanced if crossing-over between it and the matching locus in the gamete formation of the parents is unlikely. Linkage between two loci is much stronger than the linkage disequilibrium it creates between them. This is because linkage is a local effect. Suppose there is an A-locus with alleles A_1 and A_2, close to a B-locus with alleles B_1 and B_2. Then in the descendants of an individual with haplotype A_1B_1, there will be a tendency for individuals to possess both or neither of A_1 and B_1; similarly the descendants of an A_1B_2 will tend to possess both or neither of A_1 and B_2; and so on for A_2B_1 and A_2B_2. When averaged over the whole population, however, there need be no systematic correlation between the contents of the A-locus and the contents of the B-locus, because the correlations induced by linkage go in all possible directions in the different lineages, and so tend to cancel each other out when averaged in the population as a whole. Only if there is a correlation in the population as a whole between possession of A_1 and possession of B_1 does linkage disequilibrium exist.

The last point to be made concerns the rarity of the alleles at the matching locus. The arguments so far show that if there are non-relatives and siblings present in the group, then matching with rare alleles succeeds in picking out siblings. What happens in such a group if the alleles are common? The important quantities are the frequency of the genotype in the population as a whole, and the frequency of the genotype among siblings. With rare alleles, the genotype is much commoner among siblings. With common alleles, the genotype is reasonably common among non-relatives and somewhat commoner among siblings. It follows that to the extent that the alleles are common, the selected individual is more likely to be unrelated. When they are very common, then the selected individual is effectively a randomly selected member of the group. Rarity of alleles is essential to effective discrimination of relatives.

The conclusions of this section are that the major effect of matching on the rest of the genome arises when it allows the discrimination of different degrees of kin. The genetic similarity induced by matching over most of the genome is only as great as expected from the extent of common ancestry. The importance of this conclusion is that it is reasonable to suppose that the detection loci and using loci are not very closely linked to the matching locus. It follows that while the matching

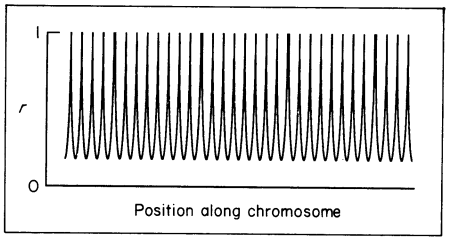

Figure 3. The figure shows how relatedness (r) would have to be maintained by matching at very many loci if an average relatedness of a half is required along the length of a chromosome of a non-relative. Relatedness arises through linkage disequilibrium only, and so decays very quickly to zero from each matched locus.

locus is under selection according to Hamilton's rule with an enhanced relatedness as a result of matching, the detection loci and using loci are under selection according to the relatedness arising from common ancestry. This contrasts with the implication of the assumption that the three kinds of loci are very tightly linked, in the so-called green beard gene (Hamilton 1964; Dawkins 1976).

This conclusion may seem to depend strongly on the supposition that there is only one matching locus. If there were matching loci at frequent intervals along all the chromosomes, might not relatedness be kept up throughout the genome, as in the telegraph poles of Fig. 3? The general answer is that an implausible ability to detect the genome with precision at many loci would be required. The particular case of picking out genetically similar individuals from an unrelated group is discussed further in the section on 'quasi-relatives' below.

Selection on Three Types of Loci

Selection at the detection loci and the using loci proceeds in an ordinary way. Selection at the using loci will favour actions according to Hamilton's first principle quoted in the introduction, so that 'in each distinct behaviour-evoking situation the individual will seem to value his neighbours' fitness against his own according to the coefficients of relationship appropriate to that situation'. The situation in this case includes how efficient the matching mechanism is at finding relatives for interacting with. If there are advantages to the current level of ability to distinguish kin from non-kin (this could be measured by summing rb-c for each kind of action that depends on the

recognition, where r is the coefficient of relatedness between donor and recipient, b is the gain of fitness of the recipient and c is the loss of fitness of the donor), selection at the detection loci will maintain detection.

The more interesting problem is how selection acts at the matching locus itself. By hypothesis, there is no direct selection acting, so we must examine how selection at other loci affects the alleles at the matching locus. The crucial question is how the success of an allele depends on its frequency. If common alleles tend to become commoner, and rare alleles tend to go extinct, then the possibility for recognition ceases to exist. Once the matching locus has only one allele, it is not possible to discriminate on the basis of its contents. If, on the other hand, common alleles become rare, and rare alleles become common, this will have the consequences that existing alleles tend to become equally frequent and that new mutants will be retained so increasing the number of segregating alleles. The resulting rarity of alleles at the matching locus would then make the recognition system highly efficient at picking out relatives from a mixed group, as explained above.

The relevant question, then, is how indirect selection acts on the matching locus. I shall assume that the detection loci are fixed so that each individual makes the discrimination, but that there is variability at the using loci. A particularly important kind of variant is the cheat, which takes advantage of its partner. Whether cheating is advantageous depends on the relatedness between interactants.

The following argument leads to the conclusion that at the matching locus, common alleles become rarer and rare alleles become commoner. Suppose that there is a range of altruistic acts that can be performed, then each will have its own 'critical relatedness' at which it becomes advantageous for a potential donor to perform it to a potential recipient. If an action is performed on average to individuals who are more related than the critical value, the tendency to perform the act will spread through the population (because $rb\text{-}c > 0$); while if it is performed to individuals who are on average below the critical relatedness the tendency to perform the act will tend to be eliminated from the population (because $rb\text{-}c < 0$).

Suppose also that there is a number of alleles at the matching locus, and these alleles have different frequencies. Individuals with a rare allele will pick out close relatives to interact with, because non-relatives with the allele are very rare. Those with a common allele will pick out a mixture of close relatives and those non-relatives who happen to share the allele. It follows that the tendency to be altruistic will increase more in the progeny of those with rare alleles (because the altruistic acts have been performed to close relatives) than in the progeny of those with common alleles (because the acts have been performed more indiscriminately). Individuals will therefore tend to have either a rare allele at the matching locus and genes for more altruism than average, or a common allele at the matching locus and genes for less altruism than average.

This association between the matching locus and loci affecting the degree of altruism means that there will be indirect selection at the matching locus. In the present case, we need to know whether the genes for altruism are advantageous or not from the point of view of the matching locus. If they are, they tend to increase the frequency of rare alleles at the matching locus and decrease the frequency of common alleles.

The genes of altruism do indeed seem to be advantageous. First notice that, so far as the matching locus is concerned, every interaction takes place at a relatedness of one, because identity at the matching locus is guaranteed by the matching mechanism. Every altruistic act retained in the population satisfies the Hamilton's rule condition $rb\text{-}c > 0$, and therefore satisfies by a greater margin the condition for it to be advantageous to the matching locus, which is $b\text{-}c > 0$. The linkage disequilibrium that selection creates between the matching locus and the using loci will therefore cause the matching locus to become highly polymorphic.

The above arguments show that selection on the whole system of kin recognition by matching will evolve close to the way suggested by Hamilton's principles. The using loci will evolve so that other individuals are treated according to their ancestral relatedness, and the matching locus will evolve towards a high degree of polymorphism so that the picking out of relatives from a mixed group of relatives and non-relatives will become very reliable.

Previous Theory on Kin Recognition

Much previous work on kin recognition has a

different aim from the preceding section, and it is reviewed by Crozier (1987). The main theme is how effective discrimination can be, depending on how many loci are matched, how many alleles there are, and what their frequencies are. Crozier (1986), however, has considered the question of interest in the preceding section, and come to an opposite conclusion, namely that matching loci should lose variability. Crozier's models are diploid and have one locus with two alleles. The fitness of a genotype is proportional to the frequency of the population with which it can peaceably interact. In one model, only genetically identical individuals can do so, while in the other, individuals sharing at least one allele can do so. Crozier showed that in both models polymorphism is transitory, and the system fixates on one allele or the other.

The difference between Crozier's models and that of the present paper is that Crozier has no cheating. Cooperating with another individual is reliably beneficial: there is no disadvantage of any sort to cooperating. As we have seen, the occurrence of cheating maintains polymorphism at the matching locus because common alleles are hit harder when cheating arises, because they are too 'trusting'. It is natural to find kin recognition failing to evolve, or the necessary genetic variability disappearing, in a circumstance in which universal cooperation is more advantageous than cooperation restricted to kin. With uncheatable cooperation there is no reason to restrict cooperation to kin. Selection at the using loci would cause individuals to be willing to fuse with any other, independent of their genetic similarity, because there is no penalty for it. Crozier's conclusions do not hold for cheatable cooperation, of primary interest here, which can sustain polymorphism at the matching locus, and maintain detection of and use of genetic differences.

Consequences

Quasi-relatives do not work

The first consequence to be drawn is that even when kin recognition occurs by matching, the resulting behaviour will be in accord with Hamilton's rule using ancestral relatedness. The enhanced relatedness at the matching locus does not affect the behaviour unless the using loci are very tightly linked to the matching locus (a green beard gene). There is no reason to expect this to occur in general.

The likely evolutionary importance of unrelated individuals who are genetically similar at one locus or throughout the genome will be considered in a discussion of two papers on 'genetic similarity theory' and 'genetic similarity detection' by Rushton et al. (1984) and Russell et all. (1985). I propose the term 'quasi-relative' to describe an individual who is as genetically similar as a relative throughout the genome, but is not a relative.

The central idea of Genetic Similarity Theory is that a quasi-relative should, from the point of view of inclusive fitness, be treated in exactly the same way as a genuine relative of the same degree. This point, as it was made by Hamilton (1964), and discussed at some length by Hamilton (1975), may be readily admitted. (Notice again the important restriction that the genetic similarity must extend throughout the genome, and not be limited to one or a few small regions.) The area for disagreement arises in the likely evolutionary significance of this fact.

Take, for example, the study of assortative mating by humans by Russell et al. (1985). They argue that by mating assortatively humans gain the advantage that their mate is genetically similar to them, and so offspring are more genetically similar to their parents than the usual relatedness of one-half would suggest. The consequent gain in inclusive fitness is offered as an explanation of the existence of assortative mating. The idea, translated into the terms of the discussion above, is that by matching phenotypically on a large number of traits, albeit weakly on each, a human succeeds in raising the general level of genetic similarity, across the genome as a whole, in its mate.

Now the obvious explanation of assortative mating is heterogeneity of the population in race, age, class or geography. Any kind of subdivision that is correlated with a character, and within the units of which mating tends to take place, will lead to similarity of mated pairs. No sensory assessment of potential mates is required, and so it would be unnecessary to postulate any selective advantage for such assessment. Heterogeneity is exactly the kind of cause that would lead to a long list of curious characters with low but significantly positive correlations between mates. Many forms of heterogeneity would also lead to correlations between parents and offspring, resulting in possibly spurious heritabilities. Heterogeneity may therefore explain the main result of Russell et al., which

was that characters that assorted more strongly in mates also had higher reported heritabilities, without implying their main conclusion that humans actively seek out genetically similar mates for reasons of inclusive fitness. However, the general question this example raises may be discussed without regard to the facts of the case in the populations reviewed by Russell et al. When would choice of a mate by phenotypic similarity lead to an advantage in inclusive fitness?

The general answer provided by the analysis given above (see How Matching Creates Genetic Similarity) is: any effect it does have, it must have by succeeding in finding a relative as a mate, and not merely by matching at a few loci. So we may ask first whether that is what it does, and second whether mating with a relative is advantageous from the point of view of inclusive fitness. It should be possible to find out if mates are related, and if so by how much, to a reasonable degree of accuracy; and the extent of the advantage would be proportional to the actual relatedness between mates. The fact that there are easier ways of finding relatives to mate with than phenotypic assessment suggests that this cannot really be the purpose of assortative mating. Whether mating with relatives is advantageous is a complicated issue, as inbreeding depression counts against it. Whether any advantage can be gained depends on a complex of phenomena: would both individuals have mated anyway? Help from relatives is relevant. Mating with a relative reduces the number of relatives, but increases the relatedness of some of them to the offspring of the mating. How this balance works out is a matter of conjecture, and may well vary from case to case. Assortative mating in humans therefore seems unlikely to be explained by genetic similarity theory because it probably does not succeed in creating substantial relatedness between mates, it would be an unnecessarily costly way of mating with a relative, and it is dubious whether it is advantageous to mate with a relative anyway.

There is one respect in which the assortative mating argument falls outside the scope of our analysis so far. There is the possibility, and this is I suspect the burden of Russell et al.'s idea of 'genetic similarity detection', that matching takes place at so many loci that the telegraph line of Fig. 3 may really be held above ground for most of its distance; in other words, that genetic similarity may be positive throughout the genome even though the two individuals are unrelated. It may be judged how likely this is by considering an individual in search of a mate in an unrelated group. What fraction of the group are as genetically similar as siblings, as cousins, as second cousins, etc? I have previously presented an argument (Grafen 1985) that, in humans, unrelated individuals who are as genetically similar as second cousins ($r = 1/32$) have a frequency of less than one in a million. The costs of screening so many potential mates, along with the rigorous phenotypic assessment needed to establish genetic similarity at the necessarily many loci in the genome, would have to be weighed against any advantages there might be; and be compared with the costs of mating with a real second cousin, who must in most cases be much easier to find. Notice that the 'quasi-cousin' is no less likely to share deleterious recessives than the real cousin, for the genetic similarity is established throughout the genome.

This section may be concluded by considering the potential factors that can create genetic similarity, and their likely evolutionary effect. Recent common ancestry has a direct effect on genetic similarity, which imposes the same kind of selection with respect to social traits on all loci in the genome. This selection does not depend to a biologically significant extent on the frequency of alleles or on dominance relations between alleles. Other causes, such as matching on phenotype and population structure, cause a much more inconstant sort of genetic similarity. As measured by relatedness, this similarity will be different at different loci in the genome, will be different for the different alleles at one locus, and will change as allele frequencies change. It has not been demonstrated either in theory or practice that any of these causes of inconstant genetic similarity can continue to influence selection in a population in such a way that we should expect it to evolve to behave according to Hamilton's rule with a relatedness above the ancestral relatedness. This is discussed at more length in Grafen (1985).

True kin recognition

Grosberg & Quinn (1986) reported a genetic matching rule in the planktonic larval stage of *Botryllus schlosseri*, a sessile colonial ascidian. I shall briefly recap their observations and conclusions, because they show how true kin recognition may be demonstrated convincingly. This counteracts the rather disappointing conclusion of the first half of the present paper, in which I argued that

many cases that are called kin recognition may not deserve the name. Also, at one important step in their argument Grosberg & Quinn make use of Hamilton's principle that ancestral relatedness will determine the interactions of individuals even when they identify each other as kin by genetic matching. By elaborating on that part of their argument, the general principle established in the preceding sections of this paper may be made clear by reference to a particularly apposite example.

Grosberg & Quinn studied the settlement patterns of the planktonic larvae of *B. schlosseri*. The first result of their series of ingenious experiments was that groups of siblings settled non-randomly, tending to clump together, while groups of unrelated larvae did not clump and settled at random on a homogeneous surface. Adjacent colonies which grow into each other can fuse, which means sharing a blood vascular system as well as growing in intimate contact, and it was already known that whether two colonies do fuse depends on their genotypes at one locus, a histocompatibility locus. If they share at least one allele, they fuse; if they share no allele at that locus they do not. The second conclusion of Grosberg & Quinn was that the non-random settlement occurred according to the genotype at that locus (or at a locus very tightly linked to it). Siblings that happened not to share an allele at that locus did not aggregate, while unrelated or distantly related individuals that did share an allele at the histocompatibility locus aggregated as strongly as siblings that shared one allele. Grosberg & Quinn's analysis of the evolutionary significance of their results includes the following passage 'The promotion of co-settlement of histocompatible colonies, coupled with the restriction of fusion to closely related genotypes, indicate that colony fusion may be beneficial, but only among kin. First, colony fusion immediately increases colony size. . . . Second . . . fusion may lower the age at first reproduction. . . . Third, a chimaera may have different physiological attributes from either component colony, potentially increasing the range of environmental tolerance. . . . Finally, fused botryllid ascidians . . . freely exchange cells that can differentiate into gametes. . . . Under these conditions, somatic cell parasitism, in which one member of a chimaera increases its reproductive output at the expense of another, can occur. However, because the polymorphism and genetics of the *Botryllus* histocompatibility system limit fusion almost entirely to closely related individuals, the parasitic losses, in evolutionary terms, would be considerably less than if the fused colonies were unrelated' (Grosberg & Quinn 1986, page 458, superscripts for references omitted).

The situation described by Grosberg & Quinn is, as they state, exactly what is required for kin recognition to be successful. The rarity of alleles at the matching locus, in this case the histocompatibility locus, ensures that matched individuals nearly always are close kin. There are gains from cooperation, but it is possible to cheat instead of cooperating. By cooperating with kin, a colony makes it less likely it will be cheated.

What I wish to consider is how the recognition system would evolve if for some reason cheating became impossible, so that it was advantageous to cooperate with any other individual. This hypothetical possibility will illustrate, in reverse, how polymorphism is maintained at a matching locus where it is important that interactions are with kin.

Consider first how our theory suggests the polymorphism is maintained at the histocompatibility locus when cheating is possible, and the histocompatibility locus has no function except the control of fusion. As cooperation is advantageous, there will be a tendency for commoner alleles at the histocompatibility locus to be favoured, because they have a higher chance of growing next to a histocompatible colony. However, cooperation is cheatable, and the tendency to cheat will be greater in individuals with common alleles than with rare ones. This is because cheating is more successful when attempted by an individual with a common allele, which in turn is because more of its neighbours will be prepared to cooperate with it. The general tendency for common alleles to be more successful is counteracted in a dynamic balance with cheating. Selection maintains a correlation between commonness of histocompatible allele and tendency to cheat, which implies linkage disequilibrium at the controlling loci.

Now if cheating becomes impossible for some reason, there will be no force to counteract the intrinsic advantage of being able to cooperate with a higher proportion of potential neighbours. The commoner alleles are then favoured at the histocompatibility locus, which inevitably leads to there being only one allele at that locus. The result is that all individuals in the population now cooperate. When cheating is impossible, this is the outcome to be expected from the point of view of individual fitness.

This example has provided a well demonstrated case of genuine kin recognition. The genetics of matching are known, and this allowed an application in somewhat more concrete terms of the general theory about the evolution of matching loci developed earlier in the section.

CONCLUSIONS

An ability to discriminate genetic similarity is to be expected as a side-effect from any type of recognition mechanism that makes use of cues that are genetic, for example from species recognition systems and group member recognition systems. It is to be expected that these systems have not evolved to assess kinship, that they are not used to assess kinship in nature, and that the ability to assess kinship in nature, and that the ability to assess kinship is too weak to be useful. Therefore an experiment showing that a species has an ability to discriminate by genetic similarity does not show that the species has a kin recognition system. In a true kin recognition system, individuals use sensory information to make decisions about social behaviour in which the role of the sensory information is to ensure an accurate assessment of relatedness. Grosberg & Quinn (1986) described such a system.

A second set of conclusions concern how kin recognition systems could be expected to evolve. The analysis in the second half of the paper justifies the claim of Hamilton (1964) that such systems should lead to individuals behaving towards each other according to ancestral relatedness. The possibility for confusion arises because at matching loci a genetic similarity can arise which mimics an increased relatedness, which, however, is restricted to those loci and closely linked loci. Common ancestry is the major source of genetic similarity of the right kind for selecting for altruism. No other cause of genetic similarity has been demonstrated in theory or practice to be capable of providing genetic similarity of a sort to select consistently for altruism. The most important application of Hamilton's rule, that a trait spreads through the population when $rb\text{-}c > 0$, is in the case when $r = 0$. The rule then states that no altruism is to be expected between non-relatives. The requirements for genetic similarity to select consistently for altruism are first, continuing similarity in time as gene frequencies change and the altruistic trait spreads through the population; and second, the similarity must hold through a large enough fraction of the genome, as it must be expected that modifiers will arise at distant loci. These conditions are not met by the local and transient additional similarity imposed by the process of matching at the matching locus itself.

Finally, the literature on 'kin recognition' really contains work on all kinds of recognition system. One major type of experiment, showing an ability to discriminate by genetic similarity on first encounter, simply shows that genetic cues are used. Work focused on kin recognition proper needs to show that the recognition system is used to assess kinship in nature, and that this proven ability does not arise artefactually. Work focused on recognition systems in general would be needlessly restricted if genetic cues were given too much emphasis, or if it was assumed that the only reason for using genetic cues was the assessment of kinship.

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