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Kin recognition in social insects and other animals—A review of recent findings and a consideration of their relevance for the theory of kin selection

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Abstract. Kin selection is a widely invoked mechanism to explain the origin and evolution of social behaviour in animals. Proponents of the theory of kin selection place great emphasis on the correlation between asymmetries in genetic relatedness created by haplodiploidy and the multiple origins of eusociality in the order Hymenoptera. The fact that a female is more closely related genetically to her full sister than to her daughters makes it more profitable for a Hymenopteran female, in terms of inclusive fitness, to raise full sisters rather than daughters or full siblings with a female biased sex ratio rather than offspring. This is sometimes referred to as the haplodiploidy hypothesis. In reality however, genetic relatedness between workers in social insect colonies and the reproductive brood they rear is far below 0·75, the value expected for full sisters, often below 0·5 the value expected between mother and daughter and, not uncommonly, approaching zero. Such values are on account of queen turnover, multiple mating by queens or polygyny. This situation raises doubts regarding the haplodiploidy hypothesis unless workers can discriminate between full and half sisters and preferentially direct their altruism towards their full sisters only. This would still mean an effective coefficient of genetic relatedness of 0·75 between altruist and recipient. For this to be possible however, workers should be able to recognise their full sisters inspite of growing up with and being habituated to an assortment of full sisters, half sisters and perhaps other even less related individuals. Even outside the Hymenoptera, social animals may find themselves growing up together in the company of individuals of varying degrees of relatedness. An ability to tell apart the more and less related individuals under such circumstances should favour kin selection.

Much effort is now going into assessing the abilities of animals to discriminate between kin and non kin. In every case studied carefully so far, animals appear to be capable of recognising their kin. Ants, wasps, sweat bees, honey bees, frogs, toads, mice, rats, voles, squirrels, monkeys and even humans appear to be able to recognise their kin in one circumstance or another. An ability to recognize true genetic relatedness requires genetically specified recognition labels and these must therefore be present. Recent findings of the role of the histocompatibility system provides some clues to the possible nature of recognition labels. An ability to recognise full sisters for example, inspite of being habituated to full and half sisters requires not merely genetically specified labels but also recognition templates which are based on the characteristics of the individual animals making the recognition and not templates based on all animals one grows up with. Some animals such as honey bees, tadpoles and ground squirrels appear to have such templates but others such as sweat bees and some mice appear not to. It is entirely possible that our inability to devise natural enough assays for recognition prevents us from understanding the full potential of the kin recognition abilities of many animal species. In any case, genetically specified labels and self based templates should greatly facilitate the evolution of social behaviour by kin selection.

Keywords. Genetic relatedness; kin recognition; kin selection; hymenoptera; haplodiploidy; evolution of social behaviour.

1. Introduction

There are two main grounds for expecting that animals must be capable of distinguishing between close genetic relatives and non or distant relatives. The first has to do with inbreeding avoidance (or for achieving an optimum balance between inbreeding and outbreeding; see Bateson 1980). On theoretical grounds it can be shown that inbreeding leads to homozygosity of recessive lethal genes resulting in inviable offspring. In conformity with this expectation inbreeding avoidance is widely observed in most animal groups. The second has to do with models for the spread of 'altruistic' alleles by natural selection. The basic idea of current models is that animals must behave altruistically towards close genetic relatives and selfishly towards non relatives. Such 'nepotistic' behaviour has again been observed in a wide variety of animals. In spite of such strong theoretical and empirical grounds, efforts to unravel animals' abilities to recognise kin (other than parent-offspring recognition) began just over 5 years ago. In this paper I will review experimental evidence of kin recognition from different animal groups, both among insects and vertebrates. Given an ability to recognise kin, any animal can potentially use it both for mate selection and for structuring altruistic and selfish interactions. I will not specifically allude to the function of kin recognition in each case.

Whether animals can discriminate between close and distant relatives inspite of being habituated to both classes of relatives is of great theoretical interest. Such an ability is essential for the tenability of a widely discussed form of kin selection theory (the haplodiploidy hypothesis) that purports to explain the evolution of insect sociality. Even outside the Hymenoptera, an ability to discriminate between close and not so close relatives within a mixed cohort or family group will greatly facilitate the operation of kin selection. This is because such an ability can raise the effective coefficients of relatedness between donor and recipient in altruistic interactions. My intention here is not so much to exhaustively review the literature on kin selection or kin recognition but to examine the consequences of our present understanding of kin recognition and its possible mechanisms to the theory of kin selection.

2. The theory of kin selection

The concept of 'inclusive fitness' first put forward by Hamilton (1964a, b) has promised to provide a plausible mechanism for the evolution by natural selection of altruistic behaviour in general and sterile castes and 'worker behaviour' in Hymenoptera in particular. The basic idea is a very simple one and has now come to be known as the theory of kin selection. Since organisms are ephemeral combinations of genes it is the individual alleles that form the connecting link from one generation to the next. This being the case one must be concerned with the changes in frequency of alleles *per se* in a population and not merely with the numbers of offspring produced by the bearers of the alleles in question. An allele can increase in frequency not only by programming its bearers to produce more offspring (who are likely to carry the same alleles) but also by programming them to aid genetic relatives (who too are likely to carry the same alleles) and the latter could well be at the cost of offspring production. If an individual aids n_i relatives (other than offspring) who are related to it by r_i at the cost of producing n_o offspring who are related to it by r_o then, as long as

$$n_i r_i > n_o r_o, \tag{1}$$

even sterility could evolve by natural selection (this form of eq. is from Craig 1979). (Notice that this argument rests on the assumption that the offspring given up and relatives reared are of equal reproductive value). Eq. (1) can be rewritten as

$$\frac{n_i}{n_o} > \frac{r_o}{r_i}. \tag{2}$$

This inequality is possible either if $n_i > n_o$ (i.e., the individual is able to rear more relatives than it is capable of rearing offspring) or if $r_i > r_o$ (i.e., if the individual is more closely related to the relatives in question than to its own offspring). The possibility of rearing more relatives in a social group compared to offspring in a solitary mode of living is conceivable for any group of animals under certain severe ecological conditions. One cannot say the same thing for the other alternative, namely, closer genetic ties with relatives compared to offspring because, no other genetic relatives can be more closely related to oneself than one's own offspring who bear a coefficient of relatedness of 0·5 with their parents in any diplo-diploid system. The insect order Hymenoptera is unusual in this regard because it is not diplo-diploid.

Two facts make Hamilton's arguments particularly attractive. First, haplodiploidy, which is nearly universal in Hymenoptera but rare outside that order makes a female more closely related (coefficient of genetic relatedness, $r = 0{\cdot}75$) to her fullsister than to her daughter ($r = 0{\cdot}5$) (table 1) so that r_i can potentially be greater than r_o. Second, eusociality, a condition characterised by overlap of generations, cooperative brood care and reproductive division of labour, has arisen at least eleven times independently in the order Hymenoptera (Wilson 1971). On the other hand eusociality has only arisen twice in the rest of the animal kingdom [namely termites and the naked mole-rat; see Jarvis (1981) for evidence of eusociality in the naked mole-rat]. In other words, haplodiploidy, which makes possible for r_i to be greater than r_o has been an important factor in the multiple origins of eusociality in Hymenoptera. We shall henceforth refer to this as the "haplodiploidy hypothesis". It is true of course that if Hymenopteran workers rear sisters and brothers in equal numbers in place of sons and daughters, they gain nothing as the low relatedness to brothers ($r = 0{\cdot}25$) exactly cancels out the advantage due to high relatedness to sisters. In other words average relatedness to fill-sibs $\left(r \text{ siblings} = \dfrac{0{\cdot}75 + 0{\cdot}25}{2} = 0{\cdot}5\right)$ is the same as relatedness to offspring ($r = 0{\cdot}5$). It has now been pointed out however that if Hymenopteran workers (who are always females) skew their investment in favour of sisters, then they would capitalise on the asymmetries in genetic relatedness created by haplodiploidy. In fact at equilibrium workers would be expected to invest in their full sisters and brothers in the ratio 3 : 1 (being the ratio of their genetic relatedness to full sisters and brothers) (Trivers and Hare 1976; for a recent review see

Table 1. Co-efficients of relatedness under haplodiploidy assuming complete outbreeding.

	Daughter	Son	Sister	Brother	Mother	Father
Female	0·5	0·5	0·75	0·25	0·5	0·5
			Av = 0·5			
Male	1·0	0·0	0·5	0·5	1·0	0·0
	Av = 0·5				Av = 0·5	

Joshi and Gadagkar 1985). If workers who give up the production of a certain number of offspring in fact invest in an equivalent number of siblings skewing investment in favour of sisters, average r_i would be greater than r_o, satisfying the condition for the evolution of sterile or other altruistic behaviour by the haplodiploidy hypothesis. The current status of theory and data on evolution of social behaviour has been extensively reviewed (Hamilton 1972; West-Eberhard 1975; Wilson 1975; Starr 1979; Gadagkar 1985).

3. Lower than expected levels of relatedness—the evidence

The legitimacy of the haplodiploidy hypothesis outlined above is crucially linked to the demonstration that values of r_i greater than r_o in fact occur. Isozyme patterns revealed by electrophoresis are now routinely used to determine genotypes of individual organisms (see Lewontin 1974 for a comprehensive as well as historical introduction to this subject). In recent years a number of methods with increasing levels of sophistication have been developed to estimate levels of genetic relatedness within subgroups of a population, using electrophoretic data (Metcalf and Whitt 1977a; Lester and Selander 1981; Craig and Crozier 1979; Pamilo and Varvio-Aho 1979; Pamilo and Crozier 1982; Pamilo 1984). Many social insect species have now been subjected to such an analysis and a sample of the results (not an exhaustive list) available in the literature are presented in table 2. With few exceptions most estimates of genetic relatedness among workers or between workers and the female reproductive brood they rear are very low; almost always less than 0·75, the value expected for full sisters, often below 0·5, the value for mother and daughter and, not uncommonly the values are not significantly different from zero. Most species listed in table 2, however, are ants which are all highly eusocial. In the context of the evolution of social behaviour by kin selection our focus should naturally be on the primitively eusocial species but there have been surprisingly few attempts to estimate genetic relatedness in such species. And the few attempts that have been made are not very encouraging (table 2).

Determining the frequencies of alleles in 5 polymorphic esterase loci Metcalf and Whitt (1977a) showed that in the primitively eusocial wasp *Polistes metricus*:

(i) foundresses mate at least twice using sperm from the two males in the ratio 9 : 1;
(ii) α foundresses share reproduction with their subordinate β foundresses, the former contributing 78 percent of the females and 87 percent of the males;
(iii) workers lay male eggs if foundresses die and even here one worker produces 19 times as many eggs as another. Intra-nest genetic relatedness can vary drastically depending on the fate of the foundresses.

On these criteria six different types of nests were defined and intra-nest relatedness was calculated for each nest type: (a) solitary foundress alive, (b) solitary foundress dead, (c) α and β foundresses alive, (d) α foundress alive, β dead, (e) α foundress dead, β alive and (f) α and β foundresses both dead. Using the data provided by Metcalf and Whitt (1977a, b), Lester and Selander (1981) have calculated an average relatedness of 0·63 between a worker and her female reproductive siblings. Of the three studies pertaining to primitively eusocial wasps listed in table 2, this is in fact the only case where r_i is greater than r_o. In *P. exclamans* and *P. apachus-bellicosus*, respectively, similar electrophoretic techniques revealed an average genetic relatedness of 0·390 and 0·429 between workers and their reproductive sisters. This value is not only far below

Table 2. Genetic relatedness in colonies of social insects.

Species	Average genetic relatedness between workers and the reproductive female brood they rear or among workers	Reference
Wasps		
Polistes metricus	0·63[a]	Metcalf and Whitt 1977a, b; Lester and Selander 1981
Polistes exclamans	0·390[a]	Lester and Selander 1981
Polistes apachus-bellicosus	0·429[a]	Lester and Selander 1981
Bees		
Apis mellifera	Approaching 0·25[b]	Page and Metcalf 1982
Ants		
Aphaenogaster rudis	0·75[c]	Crozier 1973
Myrmecia pilosula	0·172 ± 0·053[b]	Craig and Crozier 1979
Formica sanguinea	0·378 ± 0·173[a]	Pamilo and Varvio-Aho 1979
Formica sanguinea	0·19[b]	Pamilo 1981
Formica transkaucasica	0·33 ± 0·07[b]	Pamilo 1982
Formica aquilonia (Espoo[d])	0·09 ± 0·09[b]	Pamilo 1982
Formica aquilonia (Vantaa[d])	– 0·02 ± 0·14[b, e]	Pamilo 1982
Formica polyctena (Siuntio[d])	0·19 ± 0·34[b]	Pamilo 1982
Formica polyctena (Kauniainen[d])	0·30 ± 0·23[b]	Pamilo 1982
Myrmica rubra Site A-1975	0·1056[b, e]	Pearson 1983
Myrmica rubra Site A 1977	0·0218[b, e]	Pearson 1983
Myrmica rubra Site A 1978	0.0828[b, e]	Pearson 1983
Myrmica rubra Site B 1977	0·5428[b]	Pearson 1983
Formica exsecta (Espoo[d])	0·04 ± 0·07[b, e]	Pamilo and Rosengren 1984
Formica exsecta (Tuusula[d])	0·09 ± 0·08[b, e]	Pamilo and Rosengren 1984
Formica exsecta (Joskar[d])	0·62 ± 0·13[b]	Pamilo and Rosengren 1984
Formica exsecta (Kalvholm[d])	0·78 ± 0·13[b]	Pamilo and Rosengren 1984
Formica pressilabris (Espoo[d])	0·29 ± 0·13[b]	Pamilo and Rosengren 1984
Formica pressilabris (Tuusula[d])	0·07 ± 0·08[b, e]	Pamilo and Rosengren 1984
Rhytidoponera mayri	0·158 ± 0·037[b]	Crozier *et al* 1984

[a] Genetic relatedness between workers and the female reproductive brood they rear.
[b] Genetic relatedness among workers.
[c] Inferred because monogyny and monoandry were demonstrated.
[d] Localities from where the populations were sampled.
[e] Not significantly different from zero.

0·75, the value expected for full sisters in a haplodiploid system, but even lower than 0·5, the value expected between a female and her offspring.

In the honey bee *Apis mellifera*, which of course is highly eusocial, Page and Metcalf (1982) again used isozyme polymorphism and set out explicitly to study multiple mating and patterns of sperm usage by queens. Their results showed that honey bee queens used sperm from at least 3 males at any given time and mixing of sperm in the spermatheca resulted in the average relatedness amongst her daughters approaching 0·25.

4. The causes and consequences of low levels of relatedness

The main reasons attributed to such low levels of relatedness are polygyny, queen turnover and multiple mating followed by sperm mixing. Queen turnover can reduce the average relatedness between workers and the reproductives they rear in the kinds of *Polistes* nests studied by Metcalf and Whitt (1977a, b) and Lester and Selander (1981). If the α foundress lays worker eggs and dies paving the way for the β foundress to lay the reproductive eggs, then workers are not rearing their full sisters (r = 0·75) as future reproductives, but their cousins (α and β are assumed to have been full sisters) [r = 0·1875; relatedness of workers to their mother α (0·5) × relatedness of α to β (0·75) × relatedness of β to her daughters who are the future reproductives (0·5) = 0·1875]. In tropical wasps the queen's daughters often replace the queens (see for eg. Jeanne 1972). Here the workers who are sisters of the new queens now raise nieces (r = 0·375) rather than full sisters (r = 0·75). Notice that this value would be even lower if the original foundresses α and β were not full but half sisters in the temperate species and if the workers in the tropical species were not full but half sisters of their new queens. Polygyny or the simultaneous presence of more than one egg layer (a condition known among many social insects) would also similarly lower the levels of relatedness between workers and the reproductive brood they rear. For a discussion of the role of polygyny see West-Eberhard (1978). Yet another factor contributing to low levels of relatedness between workers and the reproductive brood would be usurpation of nests by unrelated conspecifics (Gamboa 1978).

When the queen mates with more than one unrelated male, her daughters would not all be full sisters of each other if she used sperm from more than one male at any given time. Any two randomly picked daughters would be full sisters with a certain probability p and half sister with a probability $1-p$. Suppose a female mated with n males who are respectively responsible for proportions $f_1, f_2, f_3, \ldots, f_n$ of her female progeny where, $\sum_{i=1}^{n} f_i = 1$. The average coefficient of relatedness ($\bar{r}$) between daughters is then

$$\frac{1}{2}\left(\frac{1}{2}+\sum_{i=1}^{n} f_i^2\right),$$

and if all males contribute equally, we have

$$\bar{r} = \frac{1}{2}\left(\frac{1}{2}+\frac{1}{n}\right) \text{ (Hamilton 1964b).}$$

The larger the number of males she has mated with the closer the relatedness between two average daughters approaches 0·25, the relatedness between two half sisters. This perhaps partly accounts for the low relatedness in the wasp studies referred to above and is in fact the reason behind the results in *Apis mellifera* (Page and Metcalf 1982). Although Page and Metcalf (1982) first conclusively demonstrated multiple mating and sperm mixing, these ideas have a long history. Indeed social insects have long been known to be notoriously polyandrous (Wilson 1971; Page and Metcalf 1982; Cole 1983). In fact this was well known at the time Hamilton first proposed the ideas of kin selection and the role of haplodiploidy. Hamilton's reaction to this was first (1964b) that 'multiple insemination will greatly weaken the tendency to evolve worker-like altruism and $n > 2$ . . . should prevent its incipience altogether' and later (1972) that 'the occurrence of this special relatedness to sisters must not be over emphasized. Male haploidy is certainly not the only prerequisite for evolving a sterile caste'.

Queen turnover might be of unpredictable accidental occurrence. But polygyny and multiple mating by the queens, widespread as they are, are clearly evolved traits that might have some adaptive significance. From the point of view of social evolution one might wonder why polyandry has evolved at all in social hymenopterans. By mating with only one male a queen ensures the highest possible relatedness amongst her daughters and thereby might be expected to maximise the chances of their cooperating and helping each other. It is possible that in ancestral hymenopterans natural selection placed a higher premium on other factors correlated with multiple mating such as greater brood viability (Page 1980; Page and Metcalf 1982; Woyke 1963) and larger colony size (Cole 1983) rather than the evolution of sociality. In the few cases where it has been studied, sex determination in Hymenoptera appears to be determined by one or a few polymorphic loci. Diploid heterozygotes (heterozygous in at least one locus in multi-locus systems) are females; haploids (hemizygotes) are males while diploid homozygotes (homozygous at all loci in multi-locus systems) are inviable or sterile males (see Wilson 1971 for a lucid treatment of sex determination in Hymenoptera). In such a system (let us consider the single locus system for simplicity) a queen who mates with a male carrying one of her own sex determining alleles is destined to produce 50 % inviable offspring. It thus pays for the queen to mate with several males and thereby reduce the proportion of inviable offspring (Page 1980; Page and Metcalf 1982). On the other hand Cole (1983) has shown that multiple mating is strongly correlated with large colony sizes in ants, and argues that multiple mating ensures sufficient sperm in the queen to make possible the maintenance of larger colonies (see Starr 1984 for a more comprehensive account of the consequences of multiple mating). Similarly polygyny has been considered as an adaptation against extinction in small or rare populations (Wilson 1963).

5. Rendering the low levels of relatedness consistent with the haplodiploidy hypothesis

There are several ways in which attempts have been made in the literature to explain away the difficulties rendered to the haplodiploidy hypothesis by the low levels of genetic relatedness especially when they result from multiple mating.

(i) If the two or more males that mate with a queen are very closely related to each other then their sperm will be nearly identical thus negating the effects of multiple mating (Wilson 1971).

(ii) If multiple insemination is restricted to the more highly advanced social groups and absent in the primitive ones, it can be thought of as secondarily evolved after sterile castes had already evolved by kin selection and had gone so far as to be now irreversible. Such irreversibility could arise because workers may no longer have any immediate reproductive options in response to low levels of relatedness to the brood on their parental nests. Neither of the above ideas is however supported by any strong empirical observations (Wilson 1971; Starr 1984).

(iii) Low levels of relatedness in general and multiple insemination in particular can be thought of as posing no special problems for the haplodiploidy hypothesis as long

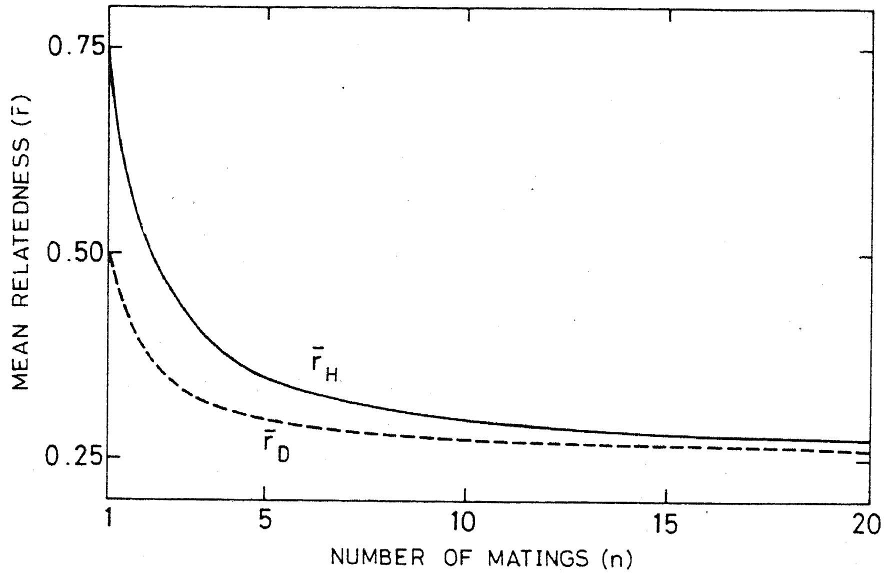

Figure 1. Mean relatedness among daughters as a function of the number of matings by the mother in haplodiploid ($\bar{r}_H$) and diploid ($\bar{r}_D$) genetic systems. This graph is drawn using the following equations provided by Page and Metcalf (1982): Assuming that each mate contributes equal amount of sperm $\bar{r}_H = 1/2(1/2 + 1/n)$ and $\bar{r}_D = 1/4(1 + 1/n)$.

as one does not find these phenomena more often in haplodiploid than in diploid groups. At any level of multiple mating haplodiploid groups are always at least slightly more predisposed towards sociality than their diploid counterparts (Page and Metcalf 1982). Note from figure 1 that if the queen mates with two males, then any two of her daughters on the average are related to each other by 1/2, which is the same as that between mother and daughter. The asymmetry in genetic relatedness caused by haplodiploidy is thus completely lost. This is probably why Hamilton (1964b) believed that more than 2 matings should prevent altruism altogether. It is true however that at any given number of matings two sisters in a haplodiploid populations are more closely related than two sisters in a diploid population. Ecological factors being identical haplodiploid populations are therefore more likely to develop female altruism than diploid populations (Page and Metcalf 1982).

(iv) A very popular way of getting out of the difficulty created by multiple mating has been to assume that although queens mate with more than one male the sperms from different males do not mix appreciably in the spermatheca. The queen is therefore effectively monoandrous using sperm from only one male for long stretches of time (Trivers and Hare 1976; Orlove 1975; Charnov 1978; Cole 1983). Taber (1955) conducted perhaps the first detailed investigation of sperm usage patterns using naturally and artificially inseminated queens. His results indicated a non-random usage of sperm but clearly sperm from different males was at least partially mixing in his experiments (Page and Metcalf 1982; Crozier and Brückner 1981). Other studies on honey bees (Alber *et al* 1955; Kerr *et al* 1962) strongly suggest sperm mixing. Comparable experiments have also been performed with solitary wasps (Wilkes 1966; Holmes 1974) and the conclusion here is that while sperm from different mates is not used in a perfectly random fashion there is no evidence of perfect sperm precedence either. Evidence for multiple mating and patterns of sperm usage had until recently to depend entirely upon dissections or the use of genetic markers. In modern times however the use of isozyme markers has begun to yield far more reliable data. Some 9 species of Hymenopterans have been investigated using this technique (review in Page and Metcalf 1982; Starr 1984) of which 3 are polyandrous with a certain degree of sperm precedence in two species. The varying degrees of sperm precedence or biased sperm usage demonstrated in various species reduce the effective number of matings but the resultant relatedness between daughters would nevertheless be less than 0·75, the value expected for full sisters.

(v) Finally an ingenious way of getting out of the difficulty caused by lower levels of relatedness between the workers and the reproductive brood is to argue that workers are capable of discriminating their full sisters apart from half sisters and that workers selectively rear their full sisters. This would still make worker behaviour advantageous by virtue of closer genetic ties between workers and their full sisters compared to that with daughters (Getz *et al* 1982; Page and Metcalf 1982).

6. Kin recognition—the evidence

6.1 *Sweat bees*

Lasioglossum zephyrum is a primitively social sweat bee that lives in a system of burrows under the soil. One of the bees usually assumes the role of a guard and, sitting at the entrance to the burrow, prevents both parasites as well as non-nest mate conspecifics from entering the burrow. Breeding these bees in artificial nests in the laboratory, Greenberg (1979) presented guard bees with intruders who are of known genetic relatedness to the guards (known to Greenberg!). Testing bees of 14 different geneological relationships against one another in this fashion a highly significant positive correlation between probability of acceptance into the nest and the genetic relatedness between intruder and guard bee was demonstrated (figure 2). This clearly implies a capacity to recognize different levels of genetic relatedness and there are reasons to believe that such recognition is based on odours (Barrows *et al* 1975). Using artificial laboratory colonies constituted by unrelated bees Buckle and Greenberg (1981) concluded that the bees do not recognise genetic relatedness to themselves. The guard bees appear to learn the odours of their nestmates and then, using these learnt odours as a guide, they accept or reject intruders depending on the similarity of the intruders' odour to those of the guard's nest mates (table 3). (see Getz 1982 for a refutation of this conclusion). Previous work had suggested that both genetic homogeneity as well as adult learning opportunities enhance nestmate recognition abilities (Kukuk *et al* 1977). Since environmentally acquired difference in odours are eliminated in these experiments it is presumed that similarity in odours reflect genetic relatedness. In this species males are also capable of assessing the genetic relatedness between successive female partners through a process of learning or becoming habituated to female pheromones (Smith 1983). Notice that such a system of recognition involving a template based on learning from individuals other than oneself is unlikely to permit workers to distinguish between full and half sisters in the same colony. This type of kin recognition will therefore not help get us out of the difficulties

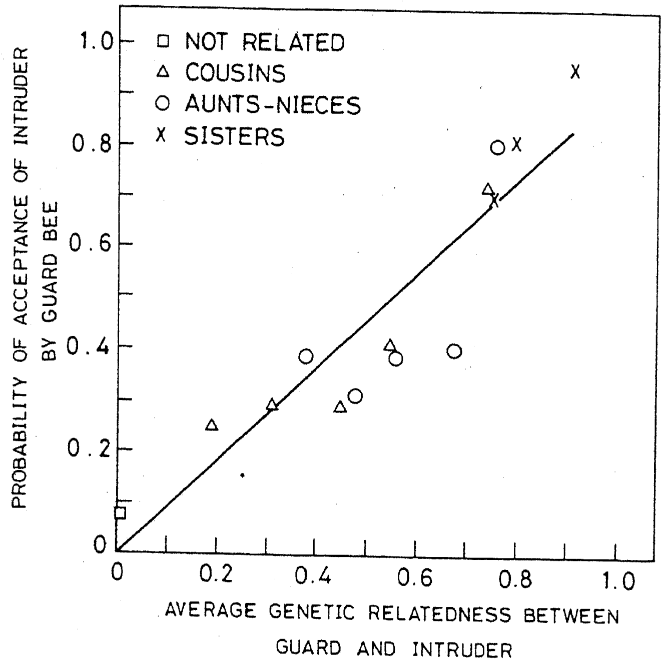

Figure 2. Individuals of the primitively eusocial bee *Lasioglossum zephyrum* were raised in the laboratory. In artificially constituted laboratory colonies guard bees were presented with intruder bees whom they had never encountered before. But these intruders were infact related to the guard bees as sisters, aunts, nieces, cousins or were unrelated to them. The probability of acceptance into the nest of the intruder bee by the guard bee was significantly positively correlated with the average genetic relatedness between guard and intruder bees. After Greenberg (1979). Copyright AAAS.

for the haplodiploidy hypothesis created by the low levels of genetic relatedness between workers and their reproductive siblings.

6.2 *Honey bees*

While colony odours and the recognition of hive mates is well known in honey bees, Breed (1981) first demonstrated a genetic basis in recognition of queens by workers. Replacing existing queens by new queens and observing the response of workers, Breed showed that the acceptance of new queens by the workers depends on genetic relatedness of the replacement queens to former queens (table 4). Thirty five per cent of the new queens were accepted if they were inbred sisters ($r \simeq 1$) of the previous queen, 12 % if they were outbred sisters ($r \simeq 0{\cdot}75$) and 0 % if unrelated. As in the case of sweat bees recognition by the workers is a learned phenomenon. Carbon dioxide narcosis abolished the memory of the recognition cue so that strange queens were now accepted. With time, of course, the identity of the new queen was learned as shown by rejection of subsequently introduced queens unrelated to that whose identity has been learned. Similar results were obtained when workers were transferred from one hive to another in the field or from a box containing one group of workers to one containing a different group of workers (Breed 1983). Although environmentally acquirable cues were held constant including the entire duration of larval development, genetically unrelated workers were attacked more often than genetically closely related ones. There

Table 3. Sweat bees don't smell themselves[a].

Colony	Guard	Intruder	Accepted/ rejected
3X 3Y[b]	X	Sister of X	Accepted
3X 3Y	X	Sister of Y	Accepted
3X 3Y	Y	Sister of X	Accepted
3X 3Y	Y	Sister of Y	Accepted
3X 1Y	X	Sister of X	Accepted
3X 1Y	X	Sister of Y	Accepted
3X 1Y	Y	Sister of X	Accepted
3X 1Y	Y	Sister of Y	Rejected

[a] Data from Buckle and Greenberg (1981).
[b] This means a colony consisting of 3 sisters from one inbred genetic line X and 3 bees from another inbred genetic line Y.

Table 4. Acceptance of foreign queens by honey bee workers[a].

Queen type transferred	Sample size	Percentage transfers accepted
Inbred sister of old queen	23	35
Outbred sister of old queen	26	10
Non sister of old queen from same genetic line	20	10
Non sister of old queen from unrelated genetic line	39	0
Disturbance control	10	90
Non sister of old queen from unrelated genetic line transferred after CO_2 narcosis of workers	20	90

[a] Modified from Breed (1981). Reprinted with permission.

is a strong suggestion of genetically determined odours and these appear to be already present at 5 days after post emergence. Getz and Smith (1983) performed similar experiments but with genetic relatedness more precisely defined. They set up experimental hives using queens of known genotypes which were artificially inseminated with sperms from males of known genotypes. In such hives full and half sisters among workers were obvious to the experimenter because the genetic markers used led to different colour morphs. Groups of worker bees were then removed from their parental hives little before their expected emergence and maintained as small groups of full sisters for 5–6 days. Now, when bees were transferred from one group to another, they were found to be significantly more likely to bite half sisters than full sisters. This result clearly indicates a genetic basis for the cue which is recognised because both full and half sisters were raised in the same hive and must therefore be almost identical in any environmentally acquired odours. The ability to recognize cues could however be based on learning the odours of one's nestmates because each test bee had been allowed to habituate to its full sister for 5–6 days prior to testing. It is therefore possible that the test bee had learned the odour of its full sisters during this period.

In an earlier paper on the other hand, Getz *et al* (1982) suggest that distinction between half and full sisters could be occurring even when both are present in the same hive and therefore habituated to each other. The basis for this conclusion is the result that in hives with two different genetic lines of workers, the patrilineal worker groups segregate non-randomly during swarming. One colony had 36,700 bees with 74 % of the cordovan mutant and 26 % wild type. After swarming the bees remaining in the hives were 64 % cordovan and 36 % wild type while those in the swarm were 79 % cordovan and 21 % wild type. Another colony had 30,000 bees with 54.5 % cordovan and 45·5 % wild type. The swarm contained 58 % cordovan and 42 % wild type while those staying back in the parent hive were 43 % cordovan and 57 % wild type. The conclusion (Getz *et al* 1982) that, of the two patrilineal lines of workers, one line of full sisters leave while another line stay home is obviously very weak because of the very slight differences in composition. The high statistical significance of the data appear to be due to the inordinately large sample sizes (> 30,000 bees). Besides, as the authors themselves suggest, their data could simply 'reflect a propensity for cordovans to swarm more readily than normal workers'. Significantly, the same author states in a subsequent paper (Getz and Smith 1983) that 'at this stage there is no evidence that bees discriminate between full and half sisters in the hive once they are habituated to both sets of workers'. Unless this is shown we are still left with the difficulties posed by multiple mating for the haplodiploidy hypothesis.

In more recent experiments (Breed *et al* 1985) honey bee workers were allowed to mature (in cardboard boxes!) from day 1–5 after emergence either with other bees from the same hive (i.e. with full or half sisters) or with unrelated bees. When such bees were introduced into boxes holding other bees, an introduced bee is attacked depending only on its genetic relationship to the recipient bees. There is no effect of mixed rearing (from day 1–5) so that no odours appear to be transferred from one bee to another. Bees, however, appear to learn the odours of their nestmates (or boxmates!). If recipient bees are housed together in mixtures of two different genetic lines, bees of both genetic lines are equally likely to attack on introduced bee of either genetic line. This suggests that discrimination of heterogeneity within a hive is not possible. On the other hand, there is a tantalizing suggestion that bees learn the odour of their own genetic line as well as any other genetic line in their association and store these two memories separately. When feeding behaviour was studied, bees kept in mixed groups nevertheless interacted more often with unfamiliar kin than with the other genotype, some individuals of which they were also habituated to. In other words, as far as feeding behaviour goes, different genetic lines appear to be distinguished. As a matter of fact, if kin recognition is to counteract the effects of multiple mating and thereby rescue the haplodiploidy hypothesis, differential feeding of different genetic lines is probably more important than differential aggression. In any case, one cannot overemphasize the need for caution in interpreting results based on assays of kin recognition which, almost always bear unknown relationships to behaviour under natural conditions. Be that as it may, here is the first indication of what we have been looking for—ability of workers in a social insect colony to potentially discriminate between full and half sisters.

A conserted attack on the honey bee as a model system to unravel the possibility of discrimination of different genetic lines within a hive appears to have been conspired. Since the preparation of the first draft of this essay, I have received 4 unpublished manuscripts, each taking us a step closer to a decisive answer to this question. Briefly, Getz W M, Bruckner D and Smith K B (unpublished results) asked if there is sufficient variability in the odours of full and half sisters to permit their differential recognition in the first place. The answer seems to be in the affirmative because they succeeded in conditioning bees to extend their probosides to only one of the two choice odours derived from their full and half sisters respectively. Getz W M and Smith K B (unpublished results) have now eliminated a lacuna in their previous experiments by showing that bees reared in complete isolation can still discriminate between their full and half sisters. Their results also corraborate those of Breed *et al* (1985) that, while odours from more than one genetic line can be learned, the respective templates used in recognition are not confounded. There is however a suggestion of possible transfer of labels from one bee to another unlike in the case of the experiments of Breed *et al* (1985). Noonan K C (unpublished results) has now demonstrated that worker honey bees in colonies of mixed patrilines show preferential care to queen and worker brood of their own patrilines. It thus appears that at least in the honey bee effective genetic relatedness between workers and the female reproductive brood they rear can be as high as 0·75. One hopes that further experimentation will reveal similar phenomena in primitively eusocial insects which is the critical focus for the haplodiploidy hypothesis.

6.3 *Ants*

Ants are a group where colony odours that help discrimination of nestmates from non-nestmates have been suggested almost a 100 years ago. There has been much discussion in the literature regarding the genetic versus environmental origins of such odour. It was not until a series of simple experiments by Jutsum *et al* (1979) however that it became clear that both exogenous (from diet) and endogenous (probably but not necessarily genetic) components exist and act synergistically. These experiments also indicated that even in the complete absence of any exogenous differences there exist sufficient differences in the endogenous component to permit distinction between nestmates and non-nestmates (table 5). The experiments just described used colonies of the leaf cutter ant *Acromyrmex octospinosus* maintained in the laboratory and where the endogenous and exogenous source of odour difference could be carefully controlled. Field experiments on aggression between workers drawn from local versus widely separated

Table 5. Endogenous and exogenous components of colony odour in ants[a].

Colony (endogenous factor)	Forage (exogenous factor)	Mean time spent in investigating (minutes)[b]	Sample size
Different	Different	12·4	60
Same	Different	7·0	15
Different	Same	4·4	55
Same	Same	2·6	23

[a] All means are significantly different from each other ($P < 0.05$)
[b] Modified from Jutsum (1979). Copyright Baillière Tindall.

colonies confirmed these laboratory findings. More recently, experiments have been performed with interspecific mixed laboratory colonies using 5 species of monogynous carpenter ants belonging to the genus *Camponotus* (Carlin and Hölldobler 1983). When worker larvae from an alien species were introduced into a queen-right colony of a different species the larvae were accepted, groomed and fed to grow into adults. In several such colonies studied no pattern of preference for kin or rejection of heterospecific nestmates was observed. Moreover when interaction between an adoptee from a mixed colony was tested with its non nestmate genetic sisters taken from a stock laboratory colony, there was always intense aggression showing lack of recognition of genetic relatedness (figure 3). In other words the alien adoptee workers had acquired as

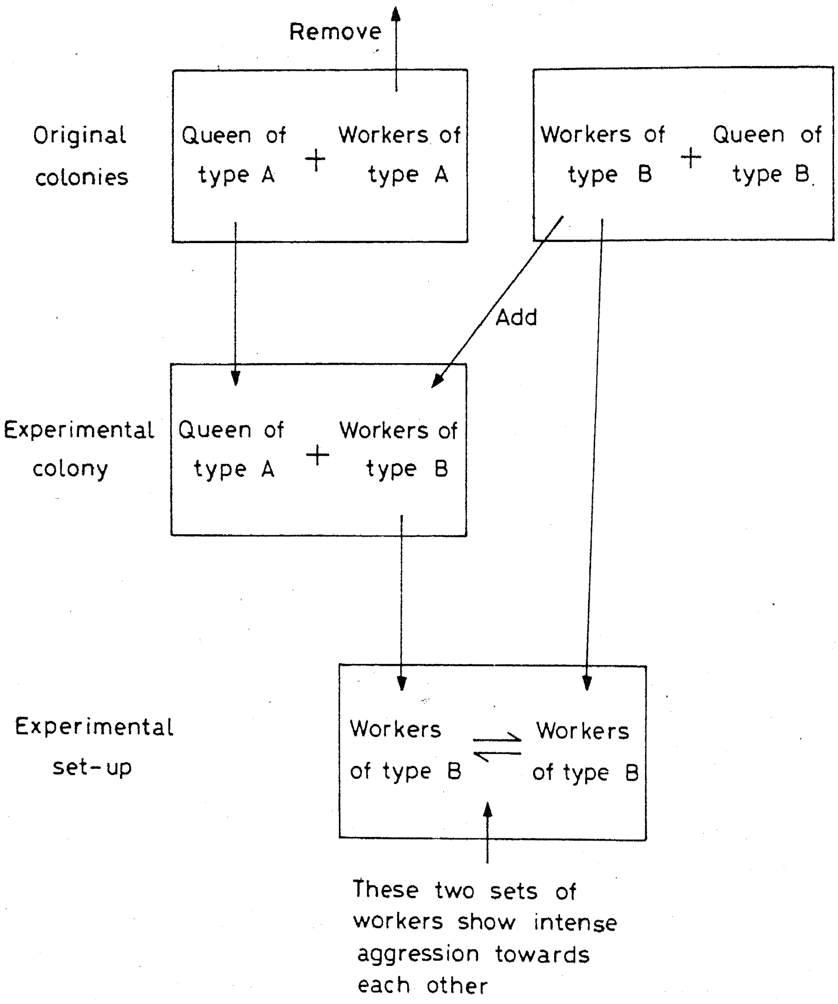

Figure 3. In laboratory colonies of the carpenter ants belonging to the genus *Camponotus* one colony (species A) was deprived of its workers and alien workers from a different laboratory colony of another species (species B) were introduced. The experimental colony thus consisted of a queen of one species (species A) while the workers were of a different genetic line (species B). These workers of species B in association with the queen of species A showed evidence of having learned as well as acquired the properties (odours) of their foster Queen. This is inferred from the observation of intense aggression between these workers of species B and other workers of species B drawn from the original species B colony. Data from Carlin and Hölldobler (1983). More recent experiments suggest that colony-specific odours and not species-specific odours are involved in these phenomena (Carlin and Hölldobler unpublished results).

well as learned an odour from the queen in its new nest. The adoptee workers must have acquired the queen's odour because they are discriminated against by their non nestmates genetic sisters and they must have learned the queen's odour because they now discriminate against their non nestmate genetic sisters. It is also clear that it is the queen that is the source of the discriminator odour because the same results were obtained with all-adoptee colonies where all the queen's brood had been removed. These results suggest that the queen's odour is learned by all workers in a colony and later used for discrimination of different individuals. Although interspecific colonies were used in these experiments, more recent studies have confirmed that indeed, colony-specific and not species-specific cues are being transferred from the queens to the workers. It also appears that in the absence of the queen, worker-derived as well as food-derived cues begin to exert their influence on recognition (Carlin N F and Hölldobler B, unpublished results). In any case, since the queen-derived cues are dominant there is little scope for different genetic lines of workers in the colonies of multiply mated queens to preferentially aid full sisters and discriminate against half sisters. On the contrary, nestmate recognition in the Acacia-ant *Pseudomyrmex ferruginea* appears to be of a rather different kind. The queen is not the source of recognition pheromone in this system because groups of worker brood separated from a stock colony and reared separately by different foster reproductives failed to show antagonistic interactions; although workers from different colonies are normally incompatible. Recognition must therefore be based on genetically specified cues although, whether the ability to discriminate nestmates is learned or not is unclear (Mintzer 1982). A follow-up study using colonies initiated by inbred lines suggests a multiple locus model for the production of recognition pheromones (Mintzer and Vinson 1985).

6.4 *Social wasps*

Comparable experiments have been performed using the primitively eusocial wasp genus *Polistes*. These wasps have not been bred in the laboratory and it has therefore not been possible to control genetic relatedness between experimental animals as precisely as in the case of sweat bees or honey bees. The discussion of the wasp data will therefore be in terms of nestmate discrimination. When nests are drawn from reasonably well separated localities, nestmates (wasps emerging in the same nest) must be significantly more closely related to each other than to non nest mates (animals emerging in different nests). The exact degree of genetic relatedness may however vary in an undefined fashion between different experiments. Wasps from the same nest will certainly be related and the values of relatedness may even fall within narrow limits. Wasps from nests drawn from distant localities will certainly bear low relatedness to each other. But pairs of wasps drawn from different pairs of distant nests may have very different values of relatedness. This can contribute to increase in variation in the results from experiment to experiment. Nestmate discrimination has been studied in *Polistes* in 4 situations: association of overwintered foundresses in spring, artificial associations of nest mates and non nestmates under experimental conditions, recognition of brood and mate preferences. For a review of the wasp work, see Gamboa *et al* (1985).

6.4.1 *Foundress associations:* *Polistes* wasps in the temperate regions terminate their nest cycle during the fall season and newly emerged females overwinter by hibernating in places away from the nest sites. At the beginning of the following spring season the overwintered females return preferentially to the natal nesting sites and initiate new colonies, often by several females cooperating in what are termed multiple foundress colonies. Because females preferentially return to their natal nesting sites it has been possible to mark emerging females in the fall and observe association patterns in the following spring. This has been done repeatedly in several species of *Polistes* and two species of *Mischocyttarus* (another genus belonging to the sub-family Polistinae). The general result has been that cofoundresses are usually females emerging from the same nest (see West-Eberhard 1969; Noonan 1981 and references therein). Klahn (1979) working with *Polistes fuscatus* and Pratte (1982) working with *P. gallicus* have argued that preferential association of nest mates as cofoundresses is not based on recognition of nest mates *per se* but because of *philopatry*—the phenomenon of returning to the site of emergence. Because nests can be located very close to each other, however, philopatry is unlikely to be sufficient to ensure relatedness of cofoundresses. Besides, other workers have since provided strong evidence of recognition of nest mates *per se*. Ross and Gamboa (1981) collected nests from different localities and allowed the gynes (females emerging in fall which are potential foundresses for the next spring) from each nest to overwinter in the laboratory along with their nests and nest mates but separated from other gynes and other nests. After thus overwintering in the laboratory for 6·5 months the wasps were exposed to spring conditions. At this stage nest mates and non nest mates were introduced into enclosures where nest mates preferentially associated with each other to initiate nests. Behavioural interactions among such overwintered females who were isolated from all other conspecifics for 74–99 days showed that they still retained the ability to recognise the nestmates with whom they had hibernated. Similar results have been obtained with *P. fuscatus* where sample sizes were larger and observations blind (Bornais *et al* 1983). Using *P. fuscatus*, Post and Jeanne (1982) went a step further and showed that females overwintered in the laboratory preferentially associated with former nest mates even if they had not hibernated along with them and that they do not associate with non nest mates even if they had been forced to hibernate with them. The characteristics of nest mates must thus have either been learnt during the fall season soon after emergence and remembered or animals must be able to recognise nest mates without the need to have to learn anything from them. In other words, they must be selfsufficient in producing a template in their brain with which to compare other animals and assess relatedness to themselves. That the ability to distinguish nest mates from non nest mates does not depend on having to arrive at the same nesting sites is further strengthened by the observation of clumping patterns during overwintering in the laboratory by *P. exclamans* females. Artificial hibernating boxes containing only nestmates show few and large clumps during hibernation while those containing a mixture of nestmates and non nestmates contain many small clumps throughout the period of hibernation (Allen *et al* 1982).

6.4.2 *Associations of females emerging in the laboratory:* Shellman and Gamboa (1982) collected natural nests of *P. fuscatus* and kept them in the laboratory to allow emergence of adults from the puparia. Upon emergence females were either (i) isolated from the nest and nestmates within minutes of emergence, (ii) isolated from the nest but kept along with other newly emerged nestmates or (iii) exposed both to their natal nest and nestmates. After such treatment for 15–120 days each female was isolated into individual boxes for 14–20 days. Now two nest mates and one unrelated female were introduced into a test box and the 3 females were observed for discrimination of nest mates from non nest mates. Using time spent in close proximity (less than 5 cm apart) as an assay of discrimination, Shellman and Gamboa (1982) showed that only females exposed to their natal nests and nest mates are capable of discriminating between nest mates and non nest mates. From more recent studies using newly emerged workers exposed to unrelated nest fragments and to unrelated conspecifics (Pfennig *et al* 1983a, b) it is quite clear that nest mate discrimination depends on learning of chemical cues from the natal nest or its brood by newly emerged adult wasps. Similar experiments have recently been performed with the bald-faced Hornet, *Dolichovespula maculata* (Hymenoptera: Vespidae) (Ryan *et al* 1985). These results are somewhat difficult to interpret because there appear to be discrepancies between different measures of recognition. Wasps isolated from their nests and nestmates also probably are capable of nestmate discrimination (unlike *Polistes*, see above). However, the authors conclude that the nest is somehow involved in the ontogeny of nestmate recognition ability because there is much more variability in the responses of the isolated wasps compared to those allowed to learn the characteristics of their nests and nestmates.

6.4.3 *Recognition of brood: Polistes fuscatus* wasps destroy brood or desert a nest significantly more often if their own nest is replaced by the nest of an unrelated female than if their nest is replaced by those of their sisters (former nest mates). Sisters normally nest in close proximity of each other and may therefore share common food, nesting material and other environmental odours. But the involvement of such environmentally originated odour is ruled out because brood destruction is based only on genetic relatedness even when sisters nesting far apart and non sisters nesting in close proximity were tested. A nest and its brood appear to be recognised as a unit and there is no evidence of discrimination of differently related brood within the same nest (Klahn and Gamboa 1983).

6.4.4 *Mate preferences:* In contrast to the female's demonstrable ability to discriminate nestmates from non nestmates, males of *P. fuscatus* appear to lack the ability of discriminating between nestmate and non nestmate females but, appear to recognize nestmate males at least under certain experimental conditions. When paired with nestmate and non nestmate females, males seem to choose their mates without regard to relatedness. This has been shown both by visual observation of mating behaviour (Larch and Gamboa 1981) as well as by actual assessment of insemination (Post and Jeanne 1982). The males also do not discriminate between nestmate and non nestmate males, as shown by Ryan *et al* (1984) in experiments where, spatial associations were observed in artificial associations of males in the lab. The techniques used were similar to those used for female-female recognition (e.g. Shellman and Gamboa 1982). Using slightly modified procedures, however, Shellman-Reeve and Gamboa (1985) conclude that mates can recognize their male nestmates. Here we must perhaps distinguish between ability to discriminate and actual discrimination. As suggested by Post and Jeanne (1982) these species are probably not selected to inbreed and therefore males, while still being able to distinguish between sisters and non sisters perhaps indiscriminately inseminate them. Similarly if the best strategy for males in natural situations is to ignore all other males, they are not likely to pair more (or less) often with nestmates in the laboratory.

In summary, studies on social wasps have shown that discrimination of nestmates from non nestmates depends on learning of recognition cues from their natal nests. Discriminations of different levels of genetic relatedness among nestmates has not so far been investigated. What we do know of kin recognition therefore does not help overcome the problems of low levels of relatedness caused by multiple mating for the haplodiploidy hypothesis.

6.5 *Vertebrates*

In recent years recognition of kin, other than offspring, in the absence of locational and other indirect cues has been demonstrated in several species of vertebrates. These studies also appear to have begun approximately around the year 1979 when the kin recognition abilities of ants and bees were first demonstrated (Greenberg 1979; Jutsum *et al* 1979). In many species of vertebrates there is evidence that totally naive individuals reared in isolation from all conspecifics also appear to recognize siblings. Although we are no longer concerned with the haplodiploidy hypothesis, our interest in kin recognition in vertebrates stems from a very similar logic. Given similar ecological conditions, altruistic behaviour can evolve more easily by kin selection if there is a high degree of genetic relatedness between the interacting individuals. Animals may however grow up with atleast some individuals who are not their full siblings (due to multiple mating for example). If kin recognition depends on learning the characteristics of all the individuals one grows up with coupled with an inability to distinguish different levels of genetic relatedness among them, the average coefficients of genetic relatedness between participants in social interactions will be relatively low. On the other hand, if kin recognition depends on matching encountered animals with oneself (either through an innate or learned knowledge about oneself) different levels of genetic relatedness can be recognised. Thus altruism can be so distributed that the effective coefficients of genetic relatedness between donor and recipient is relatively high. We will therefore once again be concerned with the possibility of discrimination between levels of genetic relatedness within a family unit.

6.5.1 *Toads and frogs:* Tadpoles of the toad *Bufo americanus* associate preferentially with siblings in the laboratory. Waldman and Adler (1979) released marked tadpoles of two different genetic lines in an indoor test pool and measured the positions of all tadpoles in repeated trials. The experiment was repeated 6 times with different sets of tadpoles and in each experiment the mean nearest neighbour distance between siblings was significantly less than that between non siblings, indicating a preferential association of siblings. In 37 % of the trials the mean coordinates of the two groups were different indicating that the sibling groups separated out into different regions of the pool. But it was not as if the two groups of tadpoles preferred different regions of the pool due to any possible environmental gradients. They simply preferred to stay away from non siblings and closer to siblings. This is inferred because the position of the tadpoles kept changing from time to time. These experiments were subsequently repeated by releasing the tadpoles in outdoor ponds which are the natural habitats of the tadpoles. Here the sibship composition of 64 % of all schools sampled were significantly biased in favour of one siblings or the other, once again demonstrating the ability of tadpoles to preferentially associate with siblings. There was again no evidence of preferences for any specific habitats and the preference was clearly for siblings *per se* (Waldman 1982). Some light has been thrown on the mechanism of sibling recognition by rearing groups of tadpoles either in isolation or along with non siblings. Tadpoles reared together with siblings and non siblings together throughout their development failed to distinguish between familiar siblings and familiar non siblings in laboratory tests (Waldman 1981) although they appeared to be capable of doing so in field trials (Waldman 1982). It is now clear that the failure to distinguish siblings from non-siblings upon being reared together is not because of any convergence in recognition characteristics (labels) but because of learning of the characteristics of the non siblings by the experimental animals (Waldman 1985). On the other hand, tadpoles reared only with siblings for the first 18 days of their development and later exposed to non siblings successfully discriminated between familiar siblings and familiar non siblings in laboratory tests. Besides, tadpoles reared in total isolation from all conspecifics beginning prior to neural plate formation distinguished between unfamiliar siblings and unfamiliar non siblings. They also distinguished full siblings from paternal half siblings but not from maternal half siblings (Waldman 1981). It can be concluded from these experiments that tadpoles are capable of sibling recognition even without the aid of post-embryonic experience with conspecifics. However learning of the cues from conspecifics during early development not only reinforces recognition but also probably over-rides any ability innately present, acquired environmentally but pre-embryonically or acquired by learning from self (we must say 'probably' because here there is a discrepancy between laboratory and field experiments).

A number of very similar experiments have been conducted with tadpoles of the frog *Rana cascadae*. Here the testing procedure involved recording the time spent by test tadpoles in two different halves of a tank each holding different kinds of stimulus individuals. The basic result is similar to that with the toad study; tadpoles prefer to associate with siblings over non siblings (O'Hara and Blaustein 1981). With many controls and different kinds of rearing regimes it has been shown that tadpoles (a) reared with siblings, (b) reared with siblings and non siblings, (c) reared in isolation with their egg jelly mass, (d) reared in isolation without their egg jelly mass and (e) reared in isolation with egg jelly mass of non siblings all prefer full sibling over maternal half siblings, maternal half siblings over paternal half siblings and the latter are preferred over non siblings (Blaustein and O'Hara 1981; 1982; O'Hara and Blaustein 1981). These results reinforce our conclusion that there may be more than one mechanism of sibling recognition but the *Rana cascadae* study argues very strongly in favour of either an innate ability to recognise siblings or an ability dependent only on learning characteristics of oneself. More recent studies have shown that even adult *Rana cascadae* frogs prefer to associate with siblings over non siblings (Blaustein *et al* 1984).

6.5.2 *Bank swallows:* Bank swallows (*Riparia riparia*) breed in large dense colonies where errors in recognition of one's own burrow by young birds is not uncommon. Under such situations parent swallows recognise and evict their neighbour's chicks by means of what has been termed a 'signature' call given by the chick (Beecher *et al* 1981a, b). Siblings also appear to recognize each other by means of a similar call. Beecher and Beecher (1983) have recently shown that chicks recognise siblings by giving more calls in response to the recorded calls of their own sibling groups than they did to the calls of unrelated groups. Chicks hand reared in isolated from all their conspecifics but who had heard calls of unrelated chicks responded however to the familiar calls of the unrelated groups rather than to the unfamiliar calls of their own siblings. Here again is an example of a learned recognition system but the critical data do not exist which might tell us if a residual innate recognition capacity persists in the absence of learning stimuli.

6.5.3 *Mammals:* Among mammals most work on kin recognition has involved rodents: mice, rats, squirrels and voles. Kin recognition can clearly take place in the absence of prior contact in white-footed deermice (*Peromyscus leucopus*) (Grau 1982). These mice were tested in pairs for frequency and duration of behavioural interactions. The mice investigated related but completely unfamiliar individuals (non litter mate siblings who were non cage mates) significantly more often than they did unrelated strangers (non siblings, non cage mates) showing evidence of kin recognition without prior contact with the very individuals tested with. All mice however had considerable social experience with their siblings both before and after weaning which must have provided them sufficient opportunity to learn the odours of at least some of their siblings. It is possible that they could later have used this information to discriminate between related and unrelated individuals as in the case of sweat bees (Buckle and Greenberg 1981). Similar results have been presented by Hayashi and Kimura (1983). In contrast Hepper (1983) ensured that at least some of his rats had no post natal experience with any related individuals. Preferences of the pups were tested in a *T* maze. When presented with an unrelated cage mate and an unrelated non cage mate, the pups preferred to associate with the unrelated cage mate suggesting that the characteristics of the cage mate had been learnt postnatally. On the other hand when pups were given a choice between genetically related but unfamiliar individuals and unrelated unfamiliar individuals, they now preferred genetically related strangers over unrelated strangers. In this case the discrimination had obviously been made without an opportunity for postnatal learning of sibling odours. Since the pups were not given a choice between familiar but unrelated individuals and unfamiliar relatives it is not clear whether any one mode of acquisition of information regarding the characteristics of relatives (self based or non self based) can be dominant over the other mode.

Gavish *et al* (1984) investigated sibling recognition in Prairie voles in the context of incest avoidance. They showed that individuals, whether related or not, but reared together, did not mate with each other while those not reared together mated whether or not they were genetically related. In nature this species has been shown to exhibit incest avoidance and the capability to do so is obviously due to postnatal learning abilities.

In two studies the importance of innate (or self based learning) and non self based learning were specifically investigated. In laboratory mice full sibs, half sibs and non sibs differed significantly from each other in aggressive interactions, but all such differences disappeared completely when the tested partners were familiar to each other (Kareem and Bernard 1982). The authors conclude that the mice use familiarity as a 'rule of thumb' during interactions. Porter *et al* (1983) applied artificial odours like musk oil, oil of clove, lemon lime and cherry to spiny mice pups. Pups who had a particular odour applied to themselves alone or to themselves and their littermates housed with them later reacted preferentially to unfamiliar animals treated with the identical artificial odour, indicating both the importance of postnatal learning in the recognition process as well as the possibility of using one's own odour as a standard of comparison. These results, however, are in contrast to earlier results where untreated littermates isolated for a comparable period of time displayed no evidence of recognition (Porter and Wyrick 1979). It is somewhat difficult however to compare these results with the other mammalian studies because according to Porter and Wyrick (1979) spiny mice appear to be incapable of recognising unfamiliar siblings, quite in contrast to all the other studies described above.

Ground squirrels have been subjected to an impressive array of laboratory and field experimentation by Holmes and Sherman (1982). Each baby squirrel was marked for identification within about 3 hr of birth and from then was raised by either its biological mother or its foster mother along with some siblings and some non siblings. When later tested for aggressive interactions, animals reared together are much less aggressive than those reared apart. Among animals reared apart, biological sisters were more tolerant of each other than non kin. These results suggest that both genetic relatedness as well as rearing conditions affect recognition. In field studies there was clear evidence that animals were more tolerant to and cooperative with their full sisters than with their half sisters. Here full and half-sisters were reared together and genetic relatedness was assessed electrophoretically. As the authors have noted, there is an apparent contradiction between lab and field studies in whether different levels of genetic relatedness can be distinguished within a group being reared together, and this is the crucial question we have been interested in throughout this survey of the literature. Holmes and Sherman (1982) believe that their field tests are more sensitive and therefore that full and half sisters can be distinguished inspite of being reared together.

The study most cited as an illustration of kin recognition, not only in the absence of an opportunity to learn the characteristics of siblings or other relatives, but one which persists even if the experimental animal grows up entirely with unrelated conspecifics is that of Wu *et al* (1980). Sixteen infant pig tail monkeys (*Macaca nemestrina*) were separated from their dams within 5 min of birth and reared separately while allowing for social interaction with unrelated conspecifics for several hours a day. When tested subsequently these monkeys preferred to associate with their paternal half siblings over unrelated individuals. These results suggest that the monkeys were capable of distinguishing between related and unrelated animals without any prior experience with relatives and indeed inspite of prior experience with unrelated individuals. Fredrickson and Sackett (1984), however, appear not to have been able to reproduce these findings. Notice that the results of Wu *et al* (1980) in contrast to Buckle and Greenbergs' (1981) sweat bees, Breed's (1981) honey bees, *Polistes* wasps (Gamboa and colleagues, referenced above), Beecher and Beecher's (1983) bank swallows or Kareem and Bernard's mice squirrels where subjects preferred relatives of those individuals whose characteristics they had learned or those individuals emerging from nests whose characteristics they had learnt.

MacKenzie *et al* (1985) have studied the effects of companionship, kinship and rearing in social preferences of stump-tailed macaques (*Macaca arctoides*) using a qualitatively different set of techniques. A whole range of social interactions were observed as they occurred naturally in a heterogeneous group of 26 monkeys occupying a large enclosure. The monkeys varied widely in age, kinship and rearing conditions. Data on social interactions were subjected to partial correlational analysis. The results suggest that familiarity was the most important variable affecting social preferences. This was followed by correlation with kinship and very interestingly, kinship through the father was important but not through the mother. These results are in broad agreement with studies of other vertebrates suggesting an ability to recognise kinship *per se*, but a strong masking influence of familiarity. As the authors note familiarity is probably sufficient to recognise matrilineal kinship (as the offspring of a female will grow up together) but natural selection appears to have favoured a special mechanism (not based on familiarity) to recognise patrilineal kinship. This is reminiscent of the ground squirrel study (Holmes and Shermann 1982; Holmes 1984) where, recognition abilities appear only at about the time that offspring are old enough to emerge from their natal burrows, move about and get mixed up. This is true both for the mother's ability to recognise her offspring as well as sibling recognition by the offspring itself.

There is some evidence that humans too are capable of assessing degrees of genetic relatedness amongst themselves. Dizygotic or fraternal twins are genetically no different from any pair of siblings but are likely to have shared a very similar environment during embryonic development. While the average genetic relatedness between co-twins would be 0.5, any pair of same sex twins could share from 1 to 46 chromosomes in common. The exact degree of genetic relatedness between a given pair of twins can be determined by the analysis of a large number of blood group factors. In a couple of rather fascinating studies it was found that the degree of genetic similarity as revealed by blood group analysis was significantly positively correlated with similarity in physical appearance as rated by the twins themselves, their mothers or other observers (Pakstis *et al* 1972; Carter-Saltzman and Scarr-Salapatek 1975). In retrospect this result is not so surprising after all. Some human siblings appear so similar to the casual observer that it is impossible not to guess their relationship. On the other hand, we all have remarked at one time or another that it would have been impossible to guess that certain pairs of individuals were siblings unless we were told of the fact. That same sex siblings can vary in their genetic relatedness by as much as from 1 to 46 shared chromosomes appears to be manifested in the widely varying degrees of similarity in physical appearance apparent even to the casual observer. We do not however know if this relationship between genetic relatedness and physical similarity is actually used by humans in recognition of unfamiliar relatives. Besides, our logic would be of course be in some trouble if all the genes controlling physical appearance (especially of facial features) were clustered on a single or a very small number of chromosomes but there is no evidence for or against this.

While sight may be more important than smell in the lives of humans we may be using smell in subtle ways not obvious without carefully controlled experiments. Such an idea is reinforced by a recent study showing that human mothers are capable of telling their infants apart from other infants by means of smell alone if they have been allowed to interact with their infants only for half an hour immediately after birth. Clearly here is an imprinting like phenomenon. Interestingly enough, fathers were unable to show any such capacity (Russell *et al* 1983).

7. The mechanism of recognition

There has been an explosion of studies on kin recognition in the last 5 years. Different studies use different methods to assess animals' abilities to discriminate kin from non kin and use a variety of different conditions for rearing experimental animals. Wilson (1986) provides a glossary that helps to face up to a concomitant explosion of terminology used by researchers in this field. There is also much discussion of

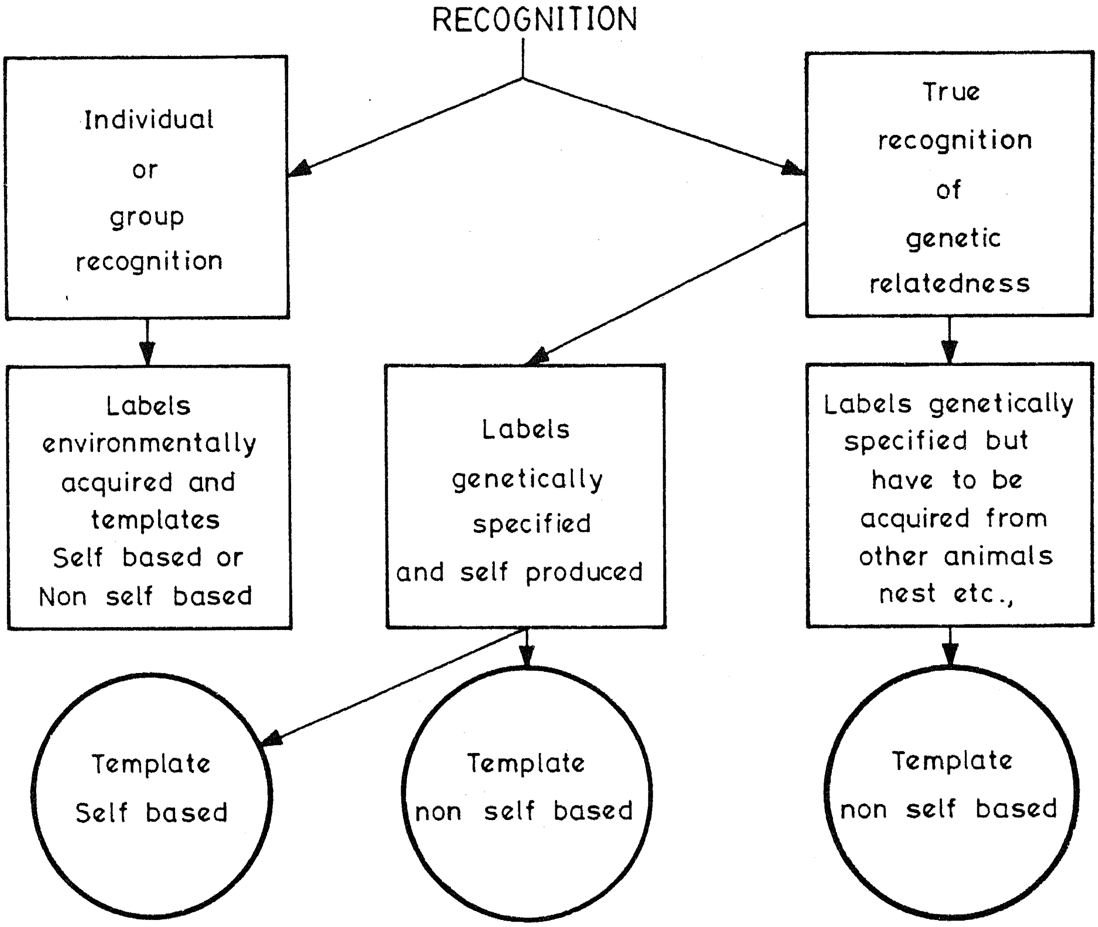

Figure 4. Facets of kin recognition.

In order for kin recognition to take place every animal must carry a label on its body and a template in its brain. Animals must examine the labels of any individual encountered and compare them with the template in their brains to determine the extent of relatedness between themselves and the individual encountered. The labels may be genetically specified or environmentally acquired. Genetically specified labels may be produced by each animal or some animals may acquire them from other animals (eg. from queens in social insect colonies), nests etc. Templates may be self based (either innate or dependent on learning from oneself) or non self based (dependent on learning from individuals other than oneself).

genetically determined versus learned or acquired abilities to recognise kin. For a discussion of quantitative genetic models for kin recognition see Crozier (1986). To facilitate comparison between different studies I suggest that we view the phenomenon of kin recognition in the following general frame work (figure 4).

7.1 *Group or individual recognition versus recognition of genetic relatedness per se*

This is an important distinction which is not always made. Group recognition by means of colony specific odour has long been well known in social insects such as ants and bees (Wilson 1971; Michener 1974). It is only in recent times however that the capabilities of ants and bees to assess actual genetic relatedness have become evident (Greenberg 1979; Jutsum *et al* 1979; Breed 1981).

7.2 *Distinction between labels and templates*

All that we know about kin recognition abilities of animals is consistent with the following scheme. In order to make kin recognition possible every animal should carry a label (or set of labels) on its body and a template in its brain. It should then compare any animal encountered to the template in order to decide if the label is similar to the template and therefore if the encountered animal is related to it. Although this scheme and terminology are used by some (Lacy and Sherman 1983; Holmes and Sherman 1982; Sherman and Holmes 1985; Waldman 1985; Getz 1982; Breed and Bennett 1986) the distinction between labels and templates has not always been made in discussing kin recognition abilities of animals.

7.3 *Labels*

Since most experimental results suggest olfaction as the sensory modality involved in recognition we shall refer to the labels as odours although a label could just as well be a visual label as it probably is in the human twin studies (Pakstis *et al* 1972; Carter-Saltzman and Scarr-Salapatek 1975) or an auditory label as in the case of bank swallows (Beecher and Beecher 1983). Unless labels used in recognition are genetically specified true recognition of genetic relatedness cannot occur. Entirely environmentally acquired labels can only be used in group or individual recognition. It is conceivable however that insects living in large colonies may use environmentally acquired labels for group recognition and thereby maintain colony integrity without having the ability to assess genetic relatedness. This is why much effort should go into discerning between group recognition and recognition of genetic relatedness (eg. Kalmus and Ribbands 1952; Boch and Morse 1979). Labels can be produced directly by the metabolic machinery of an animal or it can be acquired either from other animals (who have produced it by their metabolic machinery) or from the products of other animals (fecal matter, nests built by other animals etc.). These two possibilities were explicitly contrasted by Crozier and Dix (1979) who considered two kinds of models. In the 'individualistic' model each colony member is expected to 'retain its pheromonal integrity with no significant transfer of colony odour pheromones between colony members'. This clearly appears to be the case in the acasia ant studied by Mintzer (1982), Mintzer and Vinson (1985) as well as in Waldman's (1985) tadpoles. In contrast the 'gestalt' model supposes transfer of colony odour pheromones between different members of a colony by grooming and trophallaxis so that each individual responds to a common gestalt odour. A case intermediate between the gestalt and individualistic models is that where the queen is the source of the label which the workers acquire. This certainly seems to be the case in some ants (Carlin and Hölldobler 1983; Carlin N F and Hölldobler B, unpublished results). In most studies one cannot really distinguish between each animal producing its own label and labels being acquired from others because of the lack of distinction between labels and templates. Taking the case of the *Polistes* wasps, for example, in the experiments described so far, we do not know whether the wasps that were not exposed to their natal nests lacked the labels or templates or both. If they lacked labels then we may conclude that the labels must be acquired from the nest.

Getz (1981, 1982) has considered genetic models for the production of a sufficient diversity in labels to provide for recognition of genetic relatedness. Applying these models to existing data on *Lasioglossum zephyrum* they suggest a genetic labelling system of 4 or 5 loci with 2 to 3 alleles at each locus. Only if labels are individualistic (self produced, figure 4) and not 'gestalt' or acquired from a common source such as the queen or nest (figure 4) will it be possible for animals to recognise different levels of relatedness within a hive or family unit. From the point of view of the haplodiploidy hypothesis or kin selection this distinction is thus essential.

7.4 *Templates*

Are templates the products of learning or are they somehow innately specified? This seems to be a question of great interest (Holmes and Sherman 1982, 1983; Sherman and Holmes 1985). The idea of innately specified templates by means of recognition alleles was first suggested by Hamilton (1964b). Dubbed as the 'green beard' effect by Dawkins (1976) in his inimitable style, the idea simply is that we need to postulate a gene that makes its bearer not only have a 'green beard' but also program it to aid all individuals in the population possessing 'green beards'. Such genes have been repeatedly considered highly improbable (Hamilton 1964b; Alexander and Borgia 1978; Dawkins 1976; Holmes and Sherman 1982). In contrast Alexander and Borgia (1978) and Lacy and Sherman (1983) have suggested 'phenotype comparison or matching' mechanisms with a learned component. Lacy and Sherman (1983) have modelled situations where an 'observer' assesses its genetic relationship to the 'observee' by means of 'templates' determined by 'referants' where the referants could be known relatives such as a parent or the observer itself. Given this definition of phenotype matching it cannot really be disproved (Blaustein 1983). The results of even the most carefully controlled experiments where learning of cues from relatives is ruled out (e.g. Blaustein and O'Hara 1981, 1982) can be construed as phenotype matching where individuals use themselves as 'referants' (see Holmes and Sherman 1982).

Holmes and Sherman (1982, 1983) and Sherman and Holmes (1985) distinguish 4 mechanisms of kin recognition namely, spatial distribution, association, phenotype matching and recognition alleles. Kin recognition based on predictable spatial distribution or predictable patterns of association are widespread and well-known (the relevant literature is reviewed in the just mentioned three papers). It is only in recent years that kin recognition in the absence of spatial and associational cues has become apparent. All known cases of such recognition are lumped under phenotype matching by these authors because recognition alleles have hitherto been defined in a way that precludes their search and possibly their very existence! I will argue here that it is useful to distinguish between two types of templates: (i) Self based templates where the templates do not have to be learned or they can be learned from oneself without the intervention of any other individual and (ii) non self based templates where the templates are learned from individuals other than oneself or even from some structure such as the nest as in some social insects. Once an individual produces a chemical label by means of its own metabolic machinery then, whether it releases this substance to the surface of its body, smells itself and then produces a template or whether a template is produced without it having to smell the surface of its body postnatally is perhaps not a terribly important distinction at the moment. Whether an animal acquires a template by smelling other individuals in the population (non self based) or whether the template is produced without the intervention of any other individuals (self based) is perhaps the more important distinction. These two different mechanisms could drastically affect the abilities of animals to recognise levels of genetic relatedness. Consider for example the different lines of daughters in a honey bee hive with a multiply mated queen. The workers could get habituated to both their full and half sisters and acquire a template that prevents them from discriminating between full and half sisters as seems to happen in the case of sweat bees (Buckle and Greenberg 1981). If on the other hand each worker acquires a template by the action of its own alleles then even within a hive with a multiply mated queen, workers can selectively aid their full sisters. The effective genetic relatedness between a worker and the beneficiary of her altruism could thus be as high as 0·75, thereby drastically altering the conditions for the evolution of sociality by kin selection.

In this framework of the two kinds of templates there is evidence of self-based templates in honey bees (Breed *et al* 1985; Getz and Smith unpublished results; Noonan K C unpublished results) tadpoles of frogs and toads (Waldman 1981; Blaustein and O'Hara 1981, 1982; O'Hara and Blaustein 1981), rats (Hepper 1983), pig tailed monkeys (Wu *et al* 1980) as well as ground squirrels (Holmes and Sherman 1982). An example of the absence of self based templates and the need for non self based templates is the study of sweat bees by Buckle and Greenberg (1981). Several studies suggest a combination of self based and non self based templates. Indeed, most studies cited above as examples of self based templates are in fact instances of a combination of both kinds of templates. Notice that familiar individuals are almost always treated as kin. Given this fact what we need to be concerned about is how the self based and non self based templates are weighted. If self based templates are dominant over non self based ones then recognition of different genetic lines is possible within a mixed hive or family. This is what appears to be happening in the cases of ground squirrels (Holmes and Sherman 1982) and *Rana cascadae* tadpoles (Blaustein and O'Hara 1981, 1982; O'Hara and Blaustein 1981). On the contrary non self based templates appear to override any self based templates in sweat bees (Buckle and Greenberg 1981), *Bufo americanus* tadpoles (Waldman 1981), and laboratory mice (Kareem and Bernard 1982). In summary, what future experimental work should focus on is whether templates are self-based or non self based and if a mixture of the two kinds, whether the two templates are stored separately (as appears to be the case in honey bees, Breed 1985; Getz W M and Smith K B, unpublished results; Noonan K C unpublished results) and also whether the two templates can be differentially weighted during interaction. I suggest that we need not concern ourselves with whether true recognition allels exist and whether true genotypic comparison occurs simply because, these questions are not experimentally tractable. It has been hard enough to understand whether animals come with fully specified, hard wired knowledge of some features of the external world or they need some experience for complete specification, without getting lost in an irresolvable nature-nurture controversy. Understanding whether features of the animal itself can be hard wired can only be much worse.

7.5 *An experimental approach to distinguish between labels and templates*

Let us now consider a specific example to illustrate an experimental approach to discriminate between labels and templates. For the purposes of illustration let us use the experiments of Shellman and Gamboa (1982) with *Polistes* as our paradigm [although

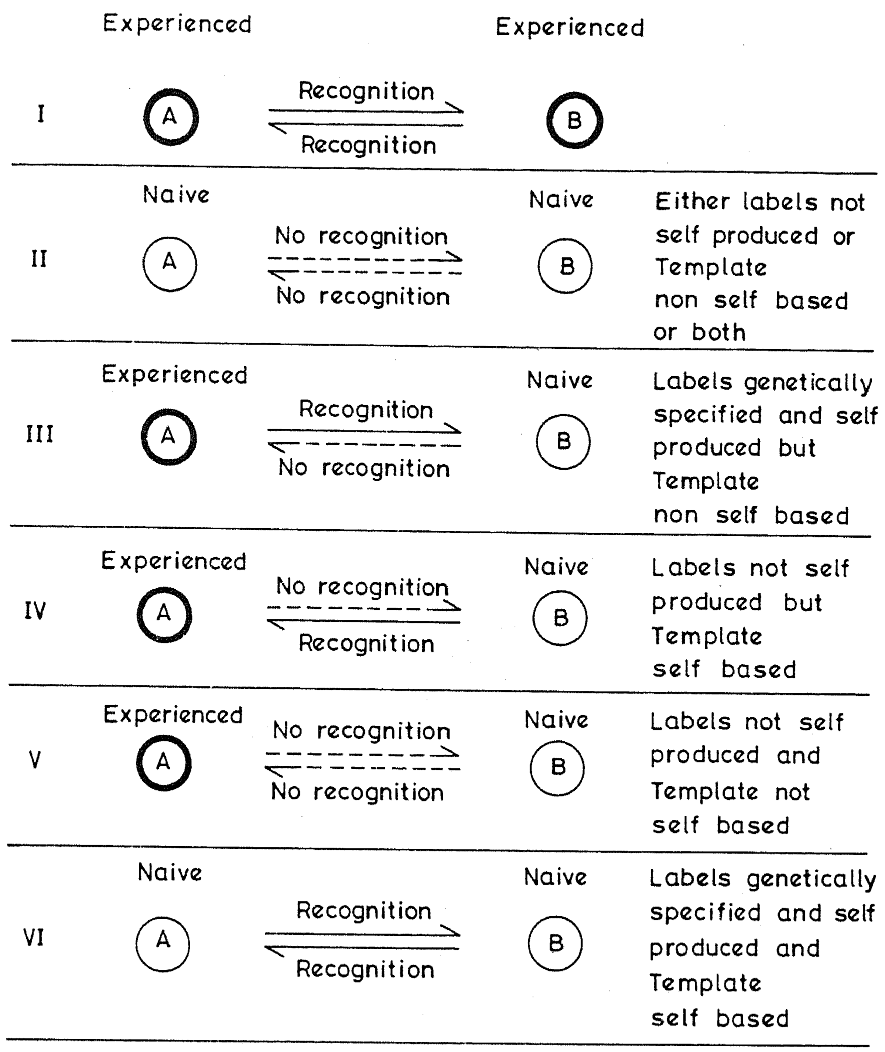

Figure 5. An experimental approach to distinguish between the roles of labels and templates in kin recognition.

A and B are two animals (say, wasps) who may or may not recognise each other as close genetic relatives depending on their rearing conditions. Based on this one can infer the ontogeny of the labels and the templates. See text for details.

Gamboa *et al* (1985) have recently used a different approach to address these questions and provided some additional information—see below]. Consider two wasp nestmates A and B (figure 5). We shall refer to the animals exposed to their natal nests during early life as 'experienced' and those animals isolated immediately after emergence from their natal nests as 'naive'. Let both animals A and B be able to recognise each other when both are experienced (figure 5, panel I). Let neither animal however be able to recognise the other when both are naive (panel II). This suggests that either the label is acquired after eclosion from the nest or the template is not self based or both. But notice that only one of these may be true. Consider now an extension of the experiment where animal A alone is experienced while animal B is naive. Now if animal A recognises B but B does not recognise A (panel III) we can conclude that A must have a normal template and B must have had a normal label. Since B did not recognise A this must mean that B did not have a normal template because A, being an experienced animal, must necessarily have had a normal label. In other words it is the template that must be non self based while the label must have been innately specified and produced by B itself. This is because B is a naive animal. On the contrary consider a situation where A, the experienced animal, fails to recognise B but B, the naive animal, recognises A (panel IV). In this case we must conclude that A, being an experienced animal, must have had a normal template and therefore B lacked a normal label. B however must have had a normal template since it recognised A. In other words it is the label that must be acquired from the nest while the template is self based. If neither A nor B can recognise each other although one of them is experienced (panel V) then we must conclude that the label has to be acquired from the nest and that the template is not self-based. Finally, it is possible that even when both A and B are naive they may be able to recognise each other (panel VI) in which case labels must be self produced and templates must be self based. It should be possible to devise such experiments and understand the distinction between the possible ontogenies of labels and templates. Lack of distinction between labels and templates can potentially lead to erroneous conclusions. For instance Shellman and Gamboa (1982) showed that wasps exposed to their nestmates alone did not acquire the capacity to recognise nestmates. They therefore concluded that exposure to nestmates is neither a sufficient nor a necessary condition for the development of kin recognition abilities (Pfennig *et al* 1983a). But this conclusion will depend on the history of the animals that were used for exposure. Consider a situation where labels have to be acquired after emergence, which is certainly possible in the *Polistes* studied by them. Now if the animals used for exposure were themselves naive ones then they would not have acquired the required labels. On the other hand, if experienced animals were used for the exposure, then exposure to such experienced animals may be sufficient for other animals to acquire recognition abilities.

Recently Gamboa *et al* (1985) have used a different approach to address the same questions. Assuming that the templates are non self based (which is suggested by their earlier experiments) they set out to ask if the labels are self-produced or acquired from the nest. Taking wasps from two unrelated nests they exposed the animals not to their own nests but to each others nests. Now if labels are acquired from the nest (and templates are any way assumed to be learnt from nests) the animals should have labels and templates that match with each other (although corresponding to the unrelated nests). Two animals coming from a nest when exposed to the same alien nest should treat each other tolerantly. On the other hand, if labels are genetically specified and self produced then each animal should have mismatched labels and templates and be intolerant of each other. Since the results happen to be intermediate between these two possibilities the authors assumed that both endogenous odours as well as odours acquired from the nest are involved.

7.6 *A possible genetic basis for recognition labels*

True recognition of genetic relatedness must involve genetically specified labels that vary in a quantitative fashion between animals of different levels of genetic relatedness. This suggests a highly polymorphic multi locus system. A search for such a genetic system no longer appears like looking for a needle in a haystack with the recent demonstration of the role of the histocompatibility system in kin recognition. All multicellular animals, especially vertebrates, have a well developed immunological system to prevent the invasion of their bodies by foreign cells. It is this histocompatibility system that frustrates transplantation of organs from one individual to another. The body's immune system unfailingly distinguishes between self and non self tissue by means of a set of antigenic molecules commonly referred to as transplantation antigens which are present on the surface of all cells. As this implies, the exact nature of the transplantation antigens present on the cells of any two individuals are different from each other unless of course the individuals are identical twins. There is considerable information on the genetic basis and Mendelian inheritance of the genes coding for the transplantation antigens. A large number of transplantation antigens coded for by an equally large number of genetic loci have been identified. Of the many gene complexes, the one known as the major histocompatibility complex (MHC) (designated as the H-2 in the mouse and the HLA in man) dominates the body's reaction to a graft. The MHC is a rather complex and highly polymorphic set of loci (see Roitt 1980 for an overview).

Recent work has unravelled another profound and rather surprising function for the MHC. The H-2 locus in the mouse appears to produce genotypically variable odour components on the basis of which mice can potentially assess their genotypic similarity with other conspecifics (see Jones and Partridge 1983 for an interesting commentary and Beauchamp *et al* 1985 for a non technical account). We know this from two kinds of experiments. Firstly, by various tricks strains of mice have been bred which differ from each other almost exclusively in the H-2 locus. Using such strains it has been demonstrated that mice can be trained to distinguish specific H-2 types by scenting the arms of a Y maze with the urine of an appropriate mouse (Yamazaki *et al* 1982). The idea that the H-2 loci produce distinctive odours which enable mice to distinguish one another is also supported by the observation that males of a certain H-2 type largely prefer to mate with females of alternative H-2 types (Yamazaki *et al* 1976). The second kind of experiment involves the use of the well known Bruce effect or 'pregnancy block'. If pregnant mice are exposed to 'strange' (males different from the one they have mated with) or even the urine or bedding of 'strange' males within the first 6 days of pregnancy, a neuroendocrine imbalance results leading to abortion of the embryo. This experimental situation has been utilized to show that the frequency of pregnancy block is higher if the 'strange' male is of a different H-2 type compared to the stud male (the original male with which the female was mated). Similar results were obtained with 'strange' females differing in H-2 type from the stud male although to a lesser extent (Yamazaki *et al* 1983). This once again suggests a role for the MHC in chemosensory recognition.

Another rather spectacular result that we should mention here is the recently discovered role of the *t* locus in determining mating preference in mice. The *t* locus is a highly polymorphic locus closely linked to the H-2. Most of the alleles at this locus are recessive lethals in spite of which a considerable amount of polymorphism is maintained in natural populations. It has been established that due to segregation distortion heterozygous males produce about 95% *t*-bearing sperm. There has been considerable interest in the *t* locus because the frequency of *t* alleles in natural populations is higher than would be expected on the basis of their lethality but less than would be expected after taking segregation distortion into account. It is now known that female mice given a choice between wild type males and males heterozygous for the *t* locus preferred to mate with the wild type males. (Levine *et al* 1980; Lenington 1983). The adaptive significance of this behaviour is easy to see because a wild type female mating with a heterozygous male would produce 50% heterozygous offspring and could therefore potentially have some inviable grandchildren. On this argument a female who is herself heterozygous would be much worse off mating with a heterozygous male because she would then have 50% heterozygous offspring and 25% inviable offspring (homozygous for the lethal allele).

Females who are themselves heterozygous show a much stronger avoidance of heterozygous males when given a choice of mating with wild type and heterozygous males (Lenington 1983). Similarly males also prefer to mate with wild type rather than heterozygous females (Lenington 1983). These results suggest that the mice are capable of assessing their own as well as their potential mate's genotype at a single locus. There is evidence that this assessment is also on the basis of chemosensory perception of odours in the urine (Lenington 1983). It is unlikely that animals would be able to make such assessment at every genetic locus and these results were obtained probably because of the close linkage of the *t* locus to the H-2 locus. The H-2 is a highly polymorphic locus which is well known to produce sufficient genetic diversity in cell surface glycoproteins (the histocompatibility antigens) to permit recognition of self versus non self at the cellular level. Perhaps the H-2 locus also produces a similar diversity of odourous molecules that permits recognition of self versus non self at the behavioural level.

8. The physical basis of recognition

Today we understand rather little regarding the physical basis of kin recognition. That olfaction must be involved in most cases had however been suggested quite early. Most recent studies have confirmed this (except possibly in the case of birds where recognition could be acoustic and humans where recognition may be visual). Olfaction also appears to be the most suitable sensory modality to combine metabolically produced and environmentally derived cues in recognition, as many insects appear to do. The most precise statements regarding the basis of kin recognition have been made by Hölldobler and Michener (1980) who have coined the terms 'discriminators' or 'recognition pheromones' for 'the odour signals that differ among individuals in a population' but 'not of extrinsic origin'. It has also been hypothesised as discussed by Hölldobler and Michener (1980) that the recognition pheromones consist of several active components. What is believed to make a particular pheromone unique is not only its qualitative composition but also the concentrations of its different constituents (Barrows *et al* 1975). The resultant economy in producing and detecting pheromones under such a scheme is obvious. The properties of several known pheromones are clearly consistent with this idea (see for instance Cammaerts *et al* 1981).

There is one more aspect of the recognition system that we already know and that is that an imprinting like phenomenon is involved. Notice that while this strongly suggests a role for learning in kin recognition it does not rule out 'recognition alleles'. Animals might have to smell themselves and get imprinted on their own odour before acquiring the capacity to recognise kin. A recent neurophysiological study with Norway rat pups reinforces the idea of odour imprinting. Experimental Norway rat pups were exposed to peppermint odour during early postnatal development while control pups were exposed to clean air. The experimental pups showed an enhanced olfactory bulb response to peppermint odour as measured by radioactive glucose uptake, compared to the control pups (Coopersmith and Leon 1984). It seems likely that a similar phenomenon may be involved in kin recognition. The idea that a developing animal forms olfactory representations in the nervous system which serve as templates to which incoming odours are later matched has already been suggested in the context of olfactory preferences in animals (Freeman 1981).

Apart from the involvement of olfaction and an imprinting like phenomenon we know scarcely little else. It should however be possible to begin to identify the recognition pheromones. Given that several complex pheromone systems have been identified it is well within the present technological capabilities to chemically identify recognition pheromones. One expects this to be a particularly exciting area of research in the coming years. Our knowledge of the basis of kin recognition thus seems to be poised for a quantum leap.

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