Social Learning and Kin Recognition
An Addendum and Reply to Sherman

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As Sherman (this issue) notes, I tried (Alexander 1990) to determine "the extent to which social learning, especially without self-reference, can account for the kin recognition findings of different investigators with different organisms . . . (p. 273). I had two motivations. First, I have had difficulty modeling the evolution of kin recognition via mechanisms that can function in the absence of social learning (Alexander and Borgia 1978; Alexander 1979, 1990). Second, it seemed to me that virtually all investigators of kin recognition were searching for unusual or cryptic mechanisms like use of self (without additional referents. Alexander 1979, 1990) or so-called "recognition alleles" or "genetic models," and partly for that reason were in danger of biasing themselves away from thorough searches for opportunities for social learning. I think I provided evidence that the second argument is sometimes appropriate, by showing that several results previously regarded as unexplainable except as a result of self-referencing may indeed be outcomes of social learning opportunities that had been overlooked. Examples are Holmes' (1986b) results with paternal half siblings in ground squirrels and Sherman and Holmes' (1985) results with full and (maternal) half sister discrimination in ground squirrels. In Holmes' experiment, juvenile ground squirrels were in fact exposed to the traits of fathers they shared with unfamiliar (nonlittermate) paternal half siblings through littermates that also shared that father. For the more complicated case of full and (maternal) half sisters in ground squirrels, I provided non-intuitive predictions (Alexander 1990, p. 277) that can be used to test my hypothesis based on imperfect social learning.

I also tried to explain two effects that might be mistaken for either self-referencing or "recognition alleles." The first is that imperfections in social learning can give the impression of unusual mechanisms by causing organisms to behave as though they recognize relatives with which they have not associated when in fact they are simply mistaking them for associates. I

showed that such a hypothesis seems to account for the various results of kin recognition experiments in sweat bees. The second is that effects evolved as an aspect of mate choice, or in other contexts different from kin recognition, can give the impression of evolved kin recognition (see also Grafen 1990) but do not present the theoretical problems that I think self-recognition or recognition alleles do for kin recognition. I suggested examples in which this might be the case (see also below).

Social learning, as I am discussing it, implies that the animal evolves to learn who its actual associates are and to remember them, and that the learning evolves because associates in a particular stage and circumstance have during evolution represented kin of the kind appropriate to whatever is learned or done as a result of the learning. In this kind of kin recognition the only comparing or matching of phenotypes is consecutive matching of the associate's phenotype against what was originally learned about it. In experiments, whether or not the particular traits possessed by an associate are like those of relatives is irrelevant. This mechanism is thus implied whenever non-relatives can be caused to treat one another as if they were relatives or individuals can be caused to imprint to bizarre objects. The questions whether or not in particular cases learning of associates is cumulative, continues for long periods, involves recognizing individual kin as opposed to classes of kin, or evolves to enable "recognition" of strangers appear still to be unanswered (but see below).

Sherman's efforts to support self-referencing from existing evidence on honey bees and ground squirrels have enabled me to see that the results of the authors he cites—Visscher (1986), Getz and Smith (1983), Breed et al. (1985), Frumhoff and Schneider (1987), Evers and Seeley (1986), Noonan (1986), and Holmes (1986a, b)—may also turn out to be explainable either as imperfect social learning or as effects evolved outside the context of kin recognition.

As Sherman relates, Visscher caused honey bee larvae to be nursed by unrelated workers. When these larvae pupated, he returned the pupae to combs populated by sister workers. There the pupae eventually emerged as callow adults and presumably were groomed and fed by their sisters during the precise period that, for example, sweat bee callows learn who their nestmates are (Greenberg 1979; Buckle and Greenberg, 1981); on this account, it is not reasonable to argue that these honey bees must have been using themselves as references because they had no opportunity to learn from their sisters' phenotypes. To counter this argument, Sherman cites the experiments of Getz and Smith (1986), who found that female honey bees who spent their callow period with a maternal half sister later behaved approximately the same toward full sisters and toward half sisters who had the same father as the sister with which they had spent the callow period. Getz and Smith believed that this result indicated use of self as well as associates. To make this interpretation, however, it is necessary to demonstrate that the bees (1) did not learn about their patrilines' attributes while

larvae and (2) could not have been treating their full and half sisters alike solely as a result of their common maternal inheritance (i.e., because of *imperfect* social learning). Neither question has been answered. It is unsatisfying to depend upon a failure to distinguish different kinds of relatives as the sole evidence against imperfect social learning; when social learning is imperfect enough, in particular ways, it gives precisely this result.

To counter this argument, Sherman cites Visscher's finding that workers reared "significantly more" larvae from queen-destined eggs related to the workers' associates while they were callows than from those related to the workers' nurses (which were not related to the workers they nursed). Sherman seems to believe that this demonstrates that social learning does not occur in honeybee larvae. This experiment, however, was obviously not designed to show any such thing, and it does not. All we really know from all these various experiments is that imperfect social learning apparently occurs in callow adult honeybees, and the possibility of it occurring in larvae has not been excluded. Whether or not imperfect social learning explains all special reactions of honeybees to their nestmates, as it apparently does in sweat bees, remains unknown because appropriate experiments have not yet been conducted.

The work of Breed et al. (1985), cited by Sherman as comparable to Getz and Smith's work and supporting it, is vulnerable to criticisms similar to those given above if it is argued to demonstrate self-referencing. Breed et al. (and Getz and Smith) found that honeybee workers caged as adults with both sisters and nonsisters (the latter sisters of one another) respond with approximately equal levels of aggression to introduced unrelated females like those with which they are caged and to introduced (strange) own sisters. In Breed et al.'s experiments, because in 20% of tests as well as 20% of controls there was biting and stinging, one is not inclined to argue for a refined recognition system based on genetically varying attributes; similarly, sisters of the introduced bee were as likely as nonsisters to initiate attacks (both findings suggesting an environmental aspect to "recognition" of nestmates). But Breed et al. did find in this experimental situation that "bees interacted significantly more often with sisters than with nonsisters," and there was "a [nonsignificant] trend for bees to be involved in more feeding interactions with sisters" [than with nonsisters] (p. 3058). Because all of these females were fed by their sisters when they were larvae, Breed et al.'s findings are consistent with an imperfect social learning model that allows learning by either larval or adult stages of honeybees (or both). This interpretation, moreover, might be regarded as reasonable because feeding is at least the principal social interaction in which larvae are involved, and aggression is restricted to adult bees.

Three experiments cited by Sherman, but not emphasized or discussed in detail (Frumhoff and Schneider 1987; Noonan 1986; and Evers and Seeley 1986; see also Noonan and Kolmes 1989, and below), may involve explanations other than kin recognition. In each case the authors used male honey

bees from two different strains of bees to produce full and (maternal) half sisters within nests and then showed that full and half sisters produced in this fashion treated each other differently, either attacking half sisters more frequently (Evers and Seeley), grooming and feeding full sisters more frequently (Frumhoff and Schneider; Noonan and Kolmes), or differentially rearing full sisters as queens (Noonan). All of these authors emphasized a single locus difference between the two kinds of sires which affects color of offspring, thus allowing them to be separated by human observers. In fact, the bees almost certainly differed in numerous loci and represented different strains or "races" of bees. Accordingly, there is a distinct possibility—discussed by Noonan (1986), Noonan and Kolmes (1989), Carlin (1989), Carlin and Frumhoff (1990), and Visscher and Seeley (unpublished)—that the response being given in both cases may reflect not evolved reactions to full and half siblings but something else, such as ability to react to either conspecific or heterospecific intruders in the hive.

There is another problem with the first two of these studies—and in fact nearly all studies that have reported distinguishing of full and half siblings in the absence of social learning. To the extent that the biases of the investigators involved in these studies favor the detection of unusual (that is, not socially learned) mechanisms of kin recognition, we are justified in requiring that the behavioral observations be carried out by investigators who are blind to the reasons for the test and the significance of the results. We are actually justified in this requirement whether or not there is evidence of directional bias among investigators, especially when the observations require subjectivity and interpretation. This may often be the case when aggression or other behaviors cannot be identified unequivocally, and when it is important to identify the initiator of an interaction and this fact cannot be determined unequivocally. Most investigators have not even mentioned the topic or discussed the degree of subjectivity or objectivity of their observations. The study of Noonan (1986) was blind with respect to the genetic relatedness of workers and the larvae they were tending because the genetic markers useful in adults are not apparent in larvae. Noonan's results are, however (as already noted), subject to the criticism that the genetic markers used may not be behaviorally "neutral" (see especially Carlin 1989; Visscher and Seeley, unpublished).

The challenge I am making here obviously does not imply that any investigator is dishonest. Everyone is aware that even inadvertent biases can influence results of experiments, and that is the reason for the universal requirement in scientific work for the stipulation I am discussing, which, curiously, has been ignored by investigators, referees, editors, and readers in experiments on both honey bees and ground squirrels. Waldmann et al. (1988) and Visscher and Seeley (unpublished) have made the same point; Visscher and Seeley (personal communication) have noted further that when "the magnitude of kinship-related differences . . . is small, the possibility of small bias effects [is] especially worrisome."

My arguments on all of the above points (which I have made for years to several of the involved investigators) seem strengthened by a series of papers published after the manuscript of Alexander (1990) was submitted (Carlin 1989; Carlin and Frumhoff 1990; Oldroyd et al. 1990; Page and Robinson 1990; Grafen 1990). Carlin (1989) argues that ''in at least some experiments'' with honey bees ''degree of genetic heterogeneity within artificially constituted colonies, and hence the differentiability of matrilines and patrilines, is unrealistically high,'' and that ''kin biases [in experiments ''conducted under approximately normal conditions''] ''have proven to be surprisingly slight'' within honey bee colonies (p. 93) (see also Carlin and Frumhoff 1990). Carlin (1989) and Carlin and Frumhoff (1990) argue that workers should rear *only* full sisters to be queens if they can recognize them compared to half sisters. Page and Robinson (1990, p. 1708) acknowledge that the result of Page et al. (1989) with differential rearing of full and (maternal) half sisters from queen eggs was in fact ''the result of a sampling bias in the Monte Carlo simulation we used'' and state that ''. . . a conclusive demonstration of nepotistic queen rearing remains elusive.'' Noonan and Kolmes (1989) seem to leave room for social learning in preferential care of genetically different lines by saying that ''. . . the patriline of worker brood given preferential treatment was not always the same as the patriline of the workers providing the brood care,'' and ''The more common patrilines of brood might sometimes provide a stronger stimulus for the tending workers and result in preferential care for brood of that patriline.'' Carlin (1989) and Visscher and Seeley (unpublished) both imply that distinction of full and half sisters has yet to be demonstrated among honey bees in a fashion suggesting evolved kin recognition. Contrary to Sherman's implications, then, arguments for self-referencing as an evolved kin recognition mechanism among social insects seem to have grown more doubtful within the past two years.

Sherman next turns to ground squirrels, eventually citing Holmes' (1986b) study as the rebuttal to my suggestion that self-referencing may not be needed to explain his and Holmes' various results (see also, Holmes 1988). Holmes switched ground squirrels between litters as soon as possible after birth (1–3 days) to yield different proportions of related and unrelated nestmates (both sexes included). In later dyadic tests with sisters and nonsisters reared apart from each other he found that proportions of nestmates of different genotypes (related:unrelated) made no difference in agonism between matched unfamiliar pairs of sisters and nonsisters. As he noted, however (pp. 41, 43), he did not control for the possibility of juveniles learning from the mother's phenotype. This means that no female was actually reared so as to be exposed, with respect to kin, to only her own phenotype. This fact is crucial, for it means that appropriate social learning was possible for at least one member of each tested pair in every test involving a female and her sister or a female and the sister of her nestmates. As he also noted, Holmes did not distinguish between the sexes in tabulating numbers of related and unrelated nestmates for each female. Males of Belding's ground

squirrels are not nepotistic, and females are evidently not nepotistic toward males (because males disperse). Thus, we have no reason to suspect, under a social learning model in which females are evolved to learn the actual identities of their female littermates, that the presence of male nestmates carried any significance at all for females, with regard to degrees of agonism shown later toward other female ground squirrels. It seems to me that from this omission alone the significance of the reported proportions of related and unrelated nestmates can be challenged.

Suppose we temporarily ignore the problem of sex ratios. When unfamiliar sisters were tested against one another (Holmes' first kind of test), one of the two had been reared with the genetic mother of both and either an unrelated male or female (kin:nonkin = 1:1) or both siblings and nonsiblings (kin:nonkin = 1:3, 2:3, 3:3, 3:2, 3:1). Depending on the extent of the mother's influence, the test pair could have been asymmetrical in their responses to one another because one member of a pair had been reared by her genetic mother and may have learned from her mother's phenotype. Holmes (personal communication) indicates that during dyadic tests a female tends to return the response initially given to her by her test partner; even if this effect is small it is important: different test pairs may be judged differently because either one or both individuals within a pair have changed responses to the other (see also, Holmes 1986a, p. 43).

Thus, in this first kind of test one or two unfamiliar sisters tested against one another encounters an individual half (on average) like the mother by which she herself was raised and either half (when with at least one kin of her own, or when kin:nonkin > 1:n) or not at all (when k:nk = 1:n) like other individuals with which she was raised (i.e., depending on whether any of her littermates were her sisters or brothers—see below); the other sister encounters an individual either half like or unlike the nestmates with which she was raised and unlike the mother that raised her. In contrast, in the second test when unfamiliar nonsisters were tested against one another each would encounter a nonrelative unlike the mother that reared her but which was a sister of (some or all of) her nestmates. From a model of imperfect social learning this second situation would be expected to lead to greater agonism, and it did. The third case, and most agonistic, were unfamiliar females not reared with any relatives (mothers, sisters, or brothers) of the females against which they were tested; this result is also consistent with a social learning model.

As noted, because of the mother's possible influence, the first situation described above (unfamiliar sisters tested against one another) could engender an asymmetry in the two females' responses to one another, lowering their degree of agonism if the lowered aggressive tendency of one of the two females affected the overall interaction between the two, as Holmes has suggested (1986, p. 43; personal communication). This possibility, based on an imperfect social learning model, must be eliminated before social learning not involving self-matching can be excluded as an explanation in this case.

For this interpretation it is not necessary, as Sherman claims, that pups in any of Holmes' tests "learned only their dam's phenotype and ignored the phenotypes of nestmates . . ." The familiar aspects of the mother's phenotype could affect a female's interaction with her strange sister and her interaction with a nestmate could affect her response to an unfamiliar individual related to that nestmate, and yield the results Holmes obtained.

The result from Holmes' tests that to me at first seemed puzzling from a social learning hypothesis are that previously non-associating sisters tested against one another after associating with different proportions of relatives and nonrelatives to not show significantly different degrees of agonism (Holmes 1988, Fig. 5). I find it difficult to predict the results of this test, however, not only because numbers of individuals of the two sexes are not taken into account (see above), but also because (1) there are not merely differing *proportions* of related and unrelated young in each litter (1:1; 1:3; 2:3, 3:3, 3:2, 3:1), but also different *numbers* (2–6 per rearing cage, or, including mothers, 3–7), (2) the mothers' phenotypes could cause an unknown (and possibly varying) degree of asymmetry in the sisters, responses to one another, and (3) the differing proportions of relatives and nonrelatives also cause different degrees of *asymmetry* between the rearing conditions of sisters matched against one another. Whether or not there are effects from any or all of these conditions is not known, but it seems to me reasonable to expect such effects. Thus, smaller litters might cause differences between individuals to be more stark and also increase the mother's influence, particularly in instances in which females' only littermates are males. Greater asymmetry between the rearing conditions of females tested against one another might cause a greater or lesser amount of the agonism to depend on one of the two individuals' initial responses to the other. Even with these reservations, looking at Holmes' results (1988, Fig. 5), one sees that larger litters (2:3, 3:3, 3:2) appear to show more agonism; the litter expected from social learning to yield the fewest agonistic encounters between unfamiliar sisters (3:1) does and the litter expected to yield the most agonistic encounters among the smaller litters (1:3) does. Although none of these trends is statistically significant, they are in the right direction.

The answers to the above questions could be derived by cross-fostering such that all juvenile ground squirrels are with an unrelated mother (and the female against which each is to be tested is not with the mother of the other individual to be tested), and such that litter size variations are minimized and asymmetries among numbers of relatives is maximized. It also seems necessary to me to analyze the data on the basis of associations between females only, excluding implications of equal effects from male juveniles. These modifications of the experiments would reduce asymmetries that might confound the results, eliminate effects from the possibility that the mother's influence becomes more important as litter size is diminished, and test for social learning explicitly between females.

The alternative to a social learning interpretation in comparing sister

and nonsister pairings is the unlikely one that only in the first set of tests (pairing female against unfamiliar sister), or at least in the particular instances when kin:nonkin = 1:n, did the squirrels use only their own phenotypes. The phenotype of littermates could give no information that would reduce agonism, so to *exclude* social learning (assuming no biases from effects of male nestmates) we would have to assume that exposure to their mothers' phenotypes did not influence their responses. In the second kind of pairs (female against a nonsister that was a sister of the first female's littermates) it is obvious that the squirrels *did* use the phenotypes of littermates. This interpretation derives from comparing the degree of agonism in the second set of tests with that in the third set of cases. It would therefore seem that no *single* hypothesis other than social learning (of both mothers' and littermates' phenotypes) can explain the relationship to one another of the results from these three kinds of pairs. I did not realize this in my earlier analysis because I did not fully understand the nature of Holmes' results.

As indicated earlier, there is another problem here. It is not clear that any species living in small social groups (such as sweat bees and ground squirrels) actually evolves to use either itself or its associates *as references for the appropriate treatment of previously unencountered individuals*. If, instead, individuals are simply learning the attributes of their associates as a part of treating those particular associates appropriately, and only learning enough to do this—hence, my hypothesis of "imperfect social learning" to explain results with strange individuals—then there also is no reason necessarily to expect particular responses to different proportions of one or another general kind of genotype (see below).

Relying on an imperfect social learning hypothesis (and also showing greater prescience than we perhaps have a right to expect) one might have predicted (or not been surprised at) the results obtained by Sherman and Holmes (1985) with full and (maternal) half sisters (Alexander, 1990, p. 277). I doubt, however, that anyone would have expected to obtain the results of Holmes (1986a) with differing proportions of associates. Holmes' (1986a,b) results seem to require that "amounts of time spent in the presence of siblings' traits, number of times exposed to such traits, numbers of individuals associated with that carry the traits, or likelihood of encountering a specific trait . . . are all irrelevant to learning and remembering how to respond to relatives." (Alexander 1990, p. 279). The interesting implication is that the necessary learning is accomplished very quickly, in one or a few learning experiences. To the extent this is true the question is raised whether, in Holmes' experiments, the experiences may already have occurred before the juveniles were transferred to other litters 1–3 days following birth.

Without my realizing it, my initial thoughts were biased away from the idea of single-trial learning in the recognition of kin, I think because humans seem to learn continually and cumulatively about the phenotypes of their relatives, perhaps across their entire lives. On reflection, I can see that the (selective) reasons for this kind of cumulative or continual learning in humans

probably have to do with changes in phenotypes across lifetimes and the significance of such changes in dispensing nepotism and engaging in reciprocity in changing circumstances all through life. In any nepotistic organism, however, including humans, the learning that actually establishes "recognition" (or relationship) may be brief and specific, as with imprinting between parents and offspring in birds and mammals. In humans such brief learning events may be less likely to be thought important because they may never be conscious to either party, as evidently is the case with those that erase sexual interest between relatives (or nonrelatives) who associate closely while one or both of the two interactants is very young.

Even in one-trial learning, there are difficulties in predicting the results of a test like that of Holmes (1986b). Suppose the animals are simply learning the particular individuals with which they are associating, and they use one or another trait do to this. Will they tend to use different traits for each individual, thereby distinguishing them better in later encounters? Or, if they are being favored simply for somehow learning the category of "sister," and not for distinguishing individual sisters, then if they encounter the same trait repeatedly when learning about different individuals how likely is there to be a cumulative or reinforcing effect? Such questions about social learning can only be answered by further careful experimentation of the sort that Holmes, in particular, has attempted with ground squirrels.

Honey bees and other large-colony eusocial forms are different from sweat bees and ground squirrels: they must respond appropriately not to one, two, or three siblings but to thousands, often including both full and half siblings, and in honeybees, 15 or 20 patrilines as well. One does not expect that such forms will evolve to respond to the attributes of individual nestmates. It appears that cues originating from the environment (and passed among individuals) are much more important to such "large-colony" social forms (e.g., Mintzer 1982). This suggests that permanent "gestalts" are not acquired by repeated encounters of the same (unchanging) traits shared by individuals through common genetic heritage, or that if this particular kind of gestalt is possible it is not useful within large-colony nests.

Aside from possibilities that may still remain with respect to the above studies, in the context of evolved kin recognition only the results of Wu et al. (1980) with pig-tailed macaque paternal half siblings now seem not readily explainable by imperfect social learning. The macaque case may be in doubt not only because it has not been repeated but also because if evolved self-referencing occurs here it may reflect mate selection rather than kin recognition; this is unlikely to be the case in Belding's ground squirrels, in which only females have been shown to give special response to former associates (and assuming that males do indeed disperse irrevocably, as has been suggested). Indeed, it now seems to me appropriate to be skeptical that kin recognition has evolved to be accomplished by self-referencing in any species. This possibility does not necessarily support my argument (Alexander 1979, 1990) that self-referential phenotype matching in kin recognition

is theoretically unlikely; my bias in this respect, however, has been re-
sponsible for the skepticism that caused me to pursue this topic.

It is perhaps disappointing to some that exotic organisms appearing at
first to accomplish amazing feats of kin recognition may actually be exhib-
iting incidental effects of using a mechanism at least similar to those used
by humans. This is particularly true because humans appear to use social
learning (sometimes) at a considerably higher level of refinement, recogniz-
ing large numbers of individuals and rarely mistaking one relative for another
(Alexander 1990). There is little doubt that had ability to distinguish full and
half sisters in ground squirrels been seen from the start as potentially ex-
plainable as an incidental effect of imperfection in social learning, it would
not have attracted as much attention. Once self-referencing had been hinted,
moreover, the tendency to invoke it uncritically seems to have increased,
with a concomitant tendency to underestimate the explanatory power of
social learning models and overlook possibilities of social learning in ex-
perimental situations. This effect may have contributed to assertions by
prominent biologists, some quoted by Sherman, that particular kinds of kin
recognition mechanisms are reasonable possibilities or that social learning
cannot explain particular kinds of results. It has not helped that incidental
effects of imperfect social learning—as, apparently, in both bees and ground
squirrels—often give a superficial impression of uncanny recognition ca-
pacities of a sort unknown in humans. (We do make the same kinds of
mistakes, failing to distinguish strangers from associates they resemble, es-
pecially when using the sometimes strikingly different attributes of persons
from different geographic regions to distinguish them as individuals; because
we do not often make this kind of mistake as an aspect of kin recognition,
however, in that context it seems strange.)

It seems possible, as well, that investigators convinced of the evolu-
tionary importance of the concept of inclusive fitness have somehow be-
lieved that the finding of a wide variety of mechanisms of kin recognition—
and perhaps, especially, cryptic or unexpected ones—was either a support
for their view of things or a requirement of it. Likewise, there has long been
a tendency to believe, erroneously, that social learning is not a suitable
adaptive mechanism, partly because learning has always seemed to many
an alternative to specific underlying mechanisms for particular kinds of
evolved behaviors or even a way of bypassing or superseding such mech-
anisms. Thus, a prominent biologist in this field once became extremely
angry with me for continuing to argue for a prevalence of social learning in
kin recognition, exclaiming, "What about the distinguishing of full- and half-
siblings in ground squirrels? I suppose you believe that is *simply learned*
too!" This attitude, I believe, reflects the widespread assumption that learn-
ing is more or less a blank slate phenomenon; it is the attitude responsible
for some of the published arguments about the adaptiveness of learning that
led me to write the 1990 paper.

It is surprising that so many authors have consistently overlooked ob-

vious opportunities for social learning that could explain their results, and that reviewers are sometime reluctant to acknowledge their importance even after having had them called to their attention. This bias has been so powerful that some authors have written almost as though kin recognition by social learning is not kin recognition at all (e.g., Grafen 1990). Yet, through social learning and circumstantial evidence alone, humans evidently distinguish a far greater number of different kinds of relatives than does any other organism. They accomplish this not only by learning about associates as individuals but also by calculating the numbers of genetic linkages between themselves and other humans with whom they either associate directly or learn about indirectly (Alexander 1979: 43ff, 108ff, 144ff).

I agree with Sherman that it is appropriate to consider the possibility of self-referencing in species with consistent large differences in relatedness among nestmates and other social interactants. The challenge, however, is to legitimate evolved self-referencing in the context of kin recognition. In ground squirrels, for example, the adaptive possibilities cannot be calculated merely by variations in relatedness among associates. They depend as well on such things as likelihoods of association of particular kinds of relatives and the importance of nepotism. If, for example, littermate sisters are less likely to associate than mothers and daughters (because sisters are less likely to survive than mothers), then we might expect that it is more important for a female to remember her mother than to learn something about her varying relationships to sisters. If nepotism also is trivial, then the regular presence of full and half sisters does not necessarily indicate potent selective pressure for distinguishing the two classes of relatives. My purpose is not to question all possibilities of evolved adaptiveness in the distinguishing of any particular kinds of relatives. Rather, I am expressing skepticism about *particular kinds* of adaptiveness, such as evolved abilities to recognize strange individuals, and *particular mechanisms*, such as self-referencing. Most specifically I challenge the supposition that opportunities for social learning have been excluded in any study to date that has demonstrated an effect more reasonably interpretable as evolved kin recognition in the adaptive context of nepotism than as functional in some other context such as sexual selection, incest avoidance, or exclusion of heterospecific interlopers.

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