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The early history of Hamiltonian-based research on kin recognition

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Kin recognition, differential treatment of conspecifics based on correlates of genetic relatedness, is a central topic in the field of behavioral ecology, which became a focus of empirical investigation thanks largely to W. D. Hamilton's (1964) theory of inclusive fitness. In this review of early research on kin recognition, I (1) describe the abstract theoretical idea that catalyzed much of the original kin recognition research, (2) examine some of the conceptual issues that are part of the kin recognition literature, including various definitions of kin recognition, (3) describe some of the classic early research programs on kin recognition, (4) review the work that Paul W. Sherman and I did on the kin recognition abilities and mechanisms of ground squirrels (*Spermophilus*), and (5) offer some thoughts on valuable avenues to pursue in future kin recognition studies.

Introduction

I was invited by Philip T. Starks, the editor of this special issue on recognition systems, to provide a historical perspective on kin recognition research because I was one of the early contributors to this topic of study, often working with Paul W. Sherman (Holmes & Sherman 1982, 1983). Like many other animal behavior graduate students in the early 1970s, I was bowled over by W. D. Hamilton's (1996) evolutionary insights and his development of inclusive fitness theory (Hamilton 1964), including the functional explanation that it offered for a variety of apparently-altruistic behaviors in many organisms (e.g. Alexander & Tinkle 1981, Murie & Michener 1984). I also got hooked on the relationship between kinship and social behavior by an unexpected empirical finding that Hannah M. Wu and I made as graduate students at the University of Washington (Wu *et al.* 1980, details below). Hannah and I had access to a unique set of monkeys in the Regional Primate Center at the University of Washington where planned matings produced paternal half-siblings, after which newborns were removed from their mothers and reared socially but apart from all of their kin. Stimulated by Hamilton's landmark paper, which included a discussion of how "strangers" might be recognized (Hamilton 1964: p. 23), Hannah and I wondered whether infant pigtailed macaques (*Macaca nemistrina*) would be able to recognize their paternal half-sibling on first encounter. Hannah's Ph.D. advisor, Gene P. Sackett, had already shown that young macaques (*M. mulatta*) could recognize socially meaningful stimuli like species-typical threat faces without any prior social interactions with conspecifics (Sackett 1966). Thus, an ability to recognize unfamiliar paternal half-siblings did not seem like a pipe dream.

We did find that *M. nemistrina* could recognize their half-siblings (discussed below), but we were disappointed that we could not place our findings in a functional context because little was known about how social interactions varied with kinship in free-living pigtailed macaques and yet it was Hamilton's functional thinking that had stimulated our study in the first place. Because I wanted to study kin recognition at both the proximate and ultimate levels of analysis, I sought a study organism in which social behavior was known to covary with kinship in nature and one that was experimentally tractable in captivity. Paul W. Sherman, who had just published his seminal paper on nepotism and alarm calls in ground squirrels (Sherman 1977), was not only amenable to collaboration, but he had already begun to collect relevant data and was anxious for us to design parallel field and laboratory studies that addressed both the how and why of ground squirrel kin recognition (e.g. Holmes & Sherman 1983, details below).

I have five purposes in this paper. First, I will describe the abstract theoretical idea that catalyzed early research on kin recognition, which was "… shaped to a remarkable degree by the concept of kin selection." (Wilson 1987: p. 7). Second, I will examine the definition of "kin recognition", which has meant different things to different investigators, including the kind of evidence needed to demonstrate its occurrence. Third, I will describe some of the early research programs on kin recognition that included conceptual and empirical foundations on which later work was often based. This review will admittedly be biased toward vertebrates given the vastness of the invertebrate recognition literature (Michener & Smith 1987, Breed & Bennett 1987, Crozier & Pamilo 1996) and my own research interests, which have focused on mammals. Thus my review will be somewhat idiosyncratic and reflect the theoretical ideas and empirical evidence that were especially salient to me when they were published. Fourth, I will review the work that Paul W. Sherman and I did on ground squirrel kin recognition and the proximate recognition mechanisms we proposed based, in part, on our empirical results. Finally, I will offer some thoughts on what I think would be valuable avenues to pursue in future kin recognition studies. Throughout this paper, I will concentrate on kin recognition in the context of nepotism, although kin recognition abilities are also clearly important to mate choice (Bateson 1983, Barnard & Aldhous 1991, Sherman *et al.* 1997, Lewis *et al.* 2004). Nepotism is favoritism shown to genetic relatives that enhances their direct fitness (Alexander 1979: pp. 43–58, Sherman 1980, Fletcher 1987), which I will use interchangeably with kin favoritism.

Evolutionary theory and the origins of research on kin recognition

The seeds for an evolutionarily-informed analysis of kin recognition were sown in 1963 when a British entomologist and evolutionary theorist, William D. Hamilton, published a 3-page paper on "the altruism problem" (Hamilton 1963). Altruism occurs when a donor provides a reproductive benefit to a recipient and incurs a reproductive cost by assisting the recipient. What Hamilton did in his dissertation research was to introduce the concept of *inclusive fitness* and develop a population genetics model to explain how an "altruistic allele" could spread in a population despite the cost that it imposed on its bearer.

Hamilton's 1964 paper is widely acknowledged as one of the most important extensions of evolutionary theory ever to have been published "… because it is the only true advance since Darwin in our understanding of natural selection." (Trivers 2000: p. 828). Yet, it took several years for the importance of Hamilton's mathematically-challenging paper to become apparent to animal behaviorists and evolutionary theorists (Brown 1987). The publication of Wynne-Edward's (1962) book on group selection, *Population Regulation and Dispersion*, and G. C. William's (1966) critique of group selection, *Adaptation and Natural Selection*, were pivotal in drawing attention to the question of whether traits evolved because of group- or individual-level benefit and altruistic behavior was often at the heart of this debate. Thus, when empiricists "discovered" Hamilton's rule, $r \times b > c$*, the conditions under which altruism could evolve, a number of field studies were undertaken to determine whether, as predicted by Hamilton (1964), "The social behaviour of a species evolves in such a way that in each distinct behaviour-evoking situation the individual will seem to value his neighbours' fitness against his own according to the coefficients of relationship appropriate to that situation." (p. 19).

Hamilton knew that his general prediction about the evolution of social behavior required organisms to *act as if* they could assess the coefficients of relationships between themselves and their potential social partners. In other words, Hamilton understood that the ability to recognize relatives was crucial to his theory of inclusive fitness. For example, Hamilton (1964) wrote, "If he could learn to recognize those of his neighbours who really were close relatives and could devote his beneficial actions to them alone an advantage to inclusive fitness would at once appear." (p. 21). Kin recognition studies predated Hamilton to be sure, although they were limited largely to parent–offspring dyads (e.g. Lashley 1913, Tinbergen 1953, Cullen 1957) and usually addressed proximate rather than functional questions (e.g. Beach & Jaynes 1956). What Hamilton did when he introduced inclusive fitness theory was to broaden the concept of kin to include non-descendant or collateral relatives, like siblings, nieces and uncles, which subsequently became subjects for kin recognition research grounded in inclusive fitness theory (e.g. Fletcher & Michener 1987, Blaustein *et al.* 1988, Gamboa 1988).

Just what is *true* kin recognition?

When Hamilton's (1964) ground-breaking paper was "discovered" by animal behaviorists, a small explosion occurred in kin recognition studies, as demonstrated by the subsequent publication of edited volumes that reviewed the field (Fletcher & Michener 1987, Blaustein *et al.* 1988, Hepper 1991a). A number of methodological and conceptual issues have characterized kin recognition research since its beginnings (Gamboa *et al.* 1991) and, appropriately, one of the first conceptual issues to emerge was the very meaning of "kin recognition." For many investigators, kin recognition was the differential treatment of conspecifics based on correlates of their genetic relatedness (Holmes & Sherman 1983). Byers and Bekoff (1986), however, argued that kin recognition was actually being used in two different ways by investigators: first, to refer to observable differential treatment of kin, and second as an unobservable neural process used to evaluate kinship. An important reason for keeping these two meanings in mind is that the absence of observable differential treatment does not necessarily mean that an unobservable neural process to evaluate kinship has not occurred; in other words, "recognition" in the second sense can occur without "recognition" in the first sense having occurred, which makes the meaning of "recognition" problematic. To avoid confusion between the two possible meanings of "recognition" (Byers & Bekoff 1986), many researchers used "kin discrimination" to describe differential treatment of conspecifics based on correlates of genetic relatedness and "kin recognition" to describe the unobservable neural processes used by individuals to assess genetic relatedness (Waldman *et al.* 1988).

The meaning of "kin recognition" was raised again by Grafen (1990), who argued that the neural process which mediates differential treatment should be labeled kin recognition only if it had been specifically selected to assess relatedness *per se* based on genetic similarity and not if the neural process had evolved as an incidental by-product to facilitate individual, group or species recognition. It is certainly true that social recognition abilities have evolved for a host of functional reasons (Colgan 1983, Sherman *et al.* 1997, Pfennig *et al.* 1999). However, the proximate control and the functional

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* r is the coefficient of relationship between a donor and recipient, which indicates the average probability that the two individuals share copies of the same allele that they inherited from a recent common ancestor. b is the direct-fitness benefit that the recipient gains due to the donor's actions and c is the direct-fitness cost that the donor incurs by aiding the recipient.

significance of recognition behavior represent different levels of analysis and tying the definition of kin recognition at the proximate level to its functional significance seems unnecessarily restrictive and has no obvious heuristic value (at least to me, *see* also Komdeur & Hatchwell 1999a). Grafen's (1990) arguments have been incorporated into the kin recognition nomenclature scheme of some investigators (Barnard 1990) but his ideas have not gone unchallenged (*see* replies to Grafen (1990) in *Animal Behaviour*, vol. 41(6), Sherman *et al.* 1997) and most empiricists operationalize kin recognition as differential treatment based on correlates of genetic relatedness (examples in this issue).

Another issue concerning the meaning of kin recognition was whether spatially-mediated differential treatment represented "true" kin recognition because kin-differential behavior was based on contextual or spatial cues rather than on cues borne by conspecifics themselves (Waldman 1987, Pfennig & Sherman 1995). That is, X treats Y like a relative not because of Y's phenotype, but rather because X encounters Y near X's natal burrow or within X's territory. Recognition by spatial distribution (Holmes & Sherman 1982) was considered kin recognition by many investigators, in part, because they were posing functional questions that stemmed from Hamilton's (1964) theory of inclusive fitness, and Hamilton had written, "In fact, the individual may not need to perform any discrimination so sophisticated as we suggest here; a difference in the generosity of his behaviour according to whether the situations evoking it were encountered near to, or far from, his own home might occasion an advantage of a similar kind." (p. 22). Some investigators argue that differential treatment of kin based on spatial cues is not kin recognition. For example, Halpin (1991) claims that animals which use spatial cues to mediate differential treatment are actually unable to recognize their kin, and "The failure to distinguish between spatially-mediated nepotism and true kin recognition has resulted in semantic and theoretical confusion which has been detrimental to a clear understanding of the dynamics of kin recognition." (p. 221). I am unaware of the theoretical confusion to which Halpin alludes (*see* also Tang-Martinez (Halpin) 2001), but I do believe that the distinction between *direct* kin recognition, which is based on phenotypic cues like odors that are borne by individuals, and *indirect* recognition, which is based on contextual cues like spatial locations, has been valuable and is used by many investigators to specify what they mean by kin recognition (Waldman *et al.* 1988, Hepper 1991b, Pfennig & Sherman 1995).

Early empirical studies on kin recognition

To my knowledge, the first series of studies published on vertebrate kin recognition that was based explicitly on Hamilton's (1964) ideas was by Richard Porter and his associates, who investigated sibling recognition in spiny mice (*Acomys cahirinus*), a precocial murid rodent indigenous to the Near East. Ethologists and comparative psychologists had a long-standing interest in the recognition of descendant kin, especially the recognition of avian young by their parents (references above), but Hamilton's (1964) theory of inclusive fitness stimulated much interest in the identification of non-descendant kin. In a sibling recognition study of spiny mice, for example, recently-weaned juveniles were more often in physical contact with their familiar (reared together) sibling than with an unfamiliar (reared apart) non-sibling during laboratory tests, and huddling preferences were interpreted to mean that spiny mice could discriminate between siblings and nonsiblings (Porter *et al.* 1978). The authors also found that if after being reared with only their siblings juveniles were housed with only nonsiblings for five days and then tested they preferred to huddle with their recent, nonsibling cagemates rather than their siblings. This suggested to the authors that sibling preferences had waned and that weanlings may no longer have been able to recognize siblings after being separated from them and housed with unrelated agemates.

In subsequent studies, Porter and his coworkers manipulated the relatedness of cagemates in unweaned and weaned young and verified that the familiarity established between spiny mice housed together mediated sibling recognition and social preferences for kin (e.g. Porter *et al.* 1981, Porter *et al.* 1984). The investigators also found that kin recognition depended on olfactory signatures, which included both environmental and genetic components that were learned through direct exposure to rearingmates (Porter *et al.* 1989). Although Porter and his coworkers answered a number of important questions about the immediate cause and the development of sibling recognition in *A. cahirinus,* they could not present a functional interpretation for sibling recognition because so little was known about the socioecology of free-living spiny mice.

Recognition of unfamiliar kin on first encounter

A paper published in 1979 and another published in 1980 had an important impact on early kin recognition research, in part, because both papers reported the identification of never-before-encountered kin. In nature, sweat bees (*Lasioglossum zephrym*) construct nests in which females act as guards, admitting colony members and aggressively rejecting non-nestmate intruders, which might try to usurp the nest (Kukuk & Decelles 1986). Working with captive sweat bees, Greenberg (1979) used controlled matings to produce intruders that varied in genetic relatedness to guards (e.g. sisters, aunts, nieces, cousins, distant kin) and then conducted recognition tests by presenting to guards intruders that they had not previously met (hereafter, "unfamiliar intruders"). Guards titrated their aggression to unfamiliar intruders based on guard–intruder relatedness with striking precision (the slope of the regression line between relatedness and aggression was almost exactly one, Fig. 1), which raised the question of how guards assessed their relatedness to unfamiliar intruders. In his treatment of kin recognition mechanisms, Hamilton (1964: p. 25) raised the possibility of a "supergene" that would simultaneously affect (1) the expression of a phenotypic trait, (2) the perception and evaluation of that trait by other conspecifics and (3) the social response of an actor trying to make a discrimination. Could these "recognition alleles", which are assumed to operate independently of learning (e.g. Blaustein 1983), mediate recognition by guards of unfamiliar relatives?

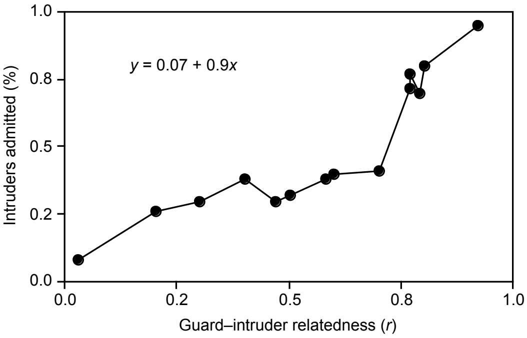

Fig. 1. The percentage of unfamiliar intruders admitted by guards to sweat bee nests in the laboratory. There is a significant positive correlation (r = 0.93) between guard–intruder relatedness and the likelihood that a guard will admit a never-before-encountered intruder to the guard's nest. Captive mating, including inbreeding, was used to create 14 different degrees of guard–intruder relatedness. After Greenberg (1979).

Hamilton (1964) was quite clear that kin recognition could be mediated by several different "correlates of relationship", including some as simple as indirect spatial cues. Alexander (1991), however, argued that "… virtually all investigators of kin recognition were searching for unusual or cryptic mechanism like … 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." (p. 387). So, how did investigators interpret sweat bee's ability to assess their relatedness to unfamiliar conspecifics? Corresponding with Les Greenberg about his 1979 paper, I learned that, indeed, some of his findings had been misinterpreted. Specifically, some investigators (e.g. May & Robertson 1980) thought that the phrase "genetic component" in the title of Greenberg's paper referred to the perception of kin labels rather than to their expression, as he intended: "The most probable mechanism is a genetically determined odor coupled with a learned component by which guard bees discriminate between odors of close kin and other bees." (Greenberg 1979: p. 1095). Thus, sweat bees discriminated a heritable odor, the "genetic" expression component, based on the learning experiences that they had during early development, which I discuss below.

Shortly after researchers discovered that sweat bees could recognize their unfamiliar kin,

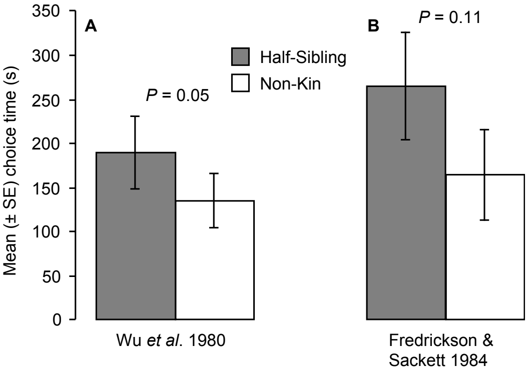

Fig. 2. Mean (± SE) time spent in proximity to an unfamiliar paternal half-sibling and an unrelated (to the subject) conspecific during 10-min kin-preference tests of captive pigtailed macaques conducted by (**A**) Wu *et al.* (1980; *n* = 16 monkeys) and (**B**) Fredrickson and Sackett (1984; *n* = 13 monkeys). In both studies, half-siblings elicited more proximity time than nonkin, but only in Wu *et al.* (1980) was half-sibling preference statistically significant. Whether juvenile pigtailed macaques can recognize their paternal half-siblings on first encounter remains an open question (*see* text). After Holmes (1988).

a similar ability was described in an Old World monkey, pigtailed macaques. Wu *et al.* (1980) "… caused a minor sensation when they reported that juvenile monkeys showed behavioral preferences for unfamiliar half-siblings over unfamiliar nonrelatives." (Silk 2002: p. 855). In the study, infants were reared apart from all kin, including their mother, and later allowed to choose between an unfamiliar half-sibling and an age- and sex-matched unfamiliar nonkin. Based on visual orientation times and spatial proximity scores, 13 of 16 monkeys preferred their half-sibling, demonstrating recognition of an unfamiliar relative on first encounter (Fig. 2A). At a time when inclusive fitness theory and sociobiology were being praised by some and excoriated by others (Segerstråle 2000), our half-sibling recognition study (Wu *et al.* 1980) was rejected twice by *Science* before it was published in *Nature*. In addition, one of the study's authors tried to replicate the original finding and claimed to fail, asserting that the statistically significant kin preference in Wu *et al.* (1980) represented a Type I error (Fredrickson & Sackett 1984). In the replication, monkeys were given 2-choice preference tests in which the relatedness and familiarity of stimulus monkeys to test animals were varied and a potent "familiarity effect" was found. That is, test monkeys preferred familiar over unfamiliar stimulus monkeys and relatedness had neither an independent nor an additive effect on social preferences. However, in only one experimental group were test animals presented with their unfamiliar paternal half siblings and an unfamiliar nonkin as stimulus monkeys, the stimulus set that matched that of Wu *et al.* (1980). In this group, half siblings elicited 58% more choice time from test animals than did nonkin, a difference that approached statistical significance (Fig. 2B), as I have discussed previously (Holmes 1988).

Since the original pigtailed macaque study (Wu *et al.* 1980), recognition of paternal half-siblings has been experimentally documented in various taxa, including, for example, rodents (e.g. Kareem & Barnard 1982, Holmes 1986a, Mateo 2002, Pillay 2002), anuran amphibians (e.g. Waldman 1981, Blaustein & O'Hara 1982, Cornell *et al.* 1989) and fishes (e.g. Arnold 2000). Indirect evidence for paternal half-sibling recognition has also been documented in free-living primates. Paternal half-sisters were more affiliative towards one another than were unrelated females in rhesus macaques (*M. mulatta*, Widdig *et al.* 2001), and adult female baboons (*Papio cynocephalus*) biased their affiliative behavior toward paternal half-sisters rather than toward nonkin (Smith *et al.* 2003, but *see* Erhart *et al.* 1997). It is unclear whether the statistically-significant preference in Wu *et al.* (1980) represented a Type I error (Fredrickson & Sackett 1984). However, given the importance of patrilineal social relationships in many primates (Strier 2004), a quote from Rendall's (2004) recent review of primate kin recognition is timely: "Although it might be tempting, then, to conclude that familiarity is the mechanism by which primates recognize their kin, full stop, this conclusion would be premature and might tend to seal the matter before it has been properly opened." (p. 311).

Anuran kin recognition

The ability to recognize unfamiliar kin like paternal half-siblings raises interesting developmental questions about how individuals acquire such an ability. Although learning-independent mechanisms were discussed in the early kin recognition literature (e.g. Blaustein 1983), most investigators have sought evidence for learning-based recognition by manipulating the early rearing environments of developing young to determine how social experience affects subsequent recognition abilities. Two research programs on anuran amphibians (toads and frogs) led the way in uncovering the role of early experience on learned kin recognition.

Bruce Waldman, working primarily with toads (*Bufo*), and Andrew R. Blaustein, working primarily with frogs (*Rana*), each conducted an independent series of laboratory experiments to examine how different rearing regimens (e.g. with kin only, with kin and nonkin, isolation rearing) affected tadpoles' ability to recognize close kin, as measured by tadpoles' preferences to associate spatially with conspecifics (reviewed in Blaustein 1988, Waldman 1991). These studies on anuran amphibians were among the first to verify recognition of collateral kin in vertebrates, including siblings, paternal half-siblings and maternal half-siblings. These investigators and their associates found that the development of recognition abilities was affected by the social makeup of early rearing environments in some species but not (or very little) in others (table 1 in Waldman 1991). For example, *R. cascadae* tadpoles recognized their siblings whether they were reared only with siblings, with siblings and nonsibling, and even when fertilized eggs were reared individually in isolation from all other tadpoles (reviewed in Blaustein & O'Hara 1986). Waldman's work on *B. americanus* tadpoles yielded some results like those in *R. cascadae*, but there were also some differences, which hinged on when during early development kin and nonkin were encountered. If *B. americanus* tadpoles were reared for two weeks with only siblings or in isolation from conspecifics, they could later recognize their siblings, as did *R. cascadae* tadpoles. However, *B. americanus* tadpoles exposed to both siblings and nonsiblings during early development appeared unable to recognize their siblings unless they were first housed with only siblings before being moved to live with both siblings and nonsiblings (Waldman 1981).

Experimental studies of kin recognition must address several methodological issues (Gamboa *et al.* 1991, Todrank & Heth 2001, Mateo & Holmes 2004) and, accordingly, most such studies have been conducted in the laboratory where experimental control can be achieved. However, many early kin recognition studies were undertaken to address functional hypotheses (Sherman & Holmes 1985) that required field data to ensure ecological validity. Thus, one of the strengths of Waldman's and of Blaustein's research programs is that they investigated kin recognition in tadpoles which occupied natural ponds. Both sets of investigators found that the kin recognition abilities of laboratory reared and tested tadpoles were also displayed in nature (e.g. Waldman 1982, O'Hara & Blaustein 1985). However, despite the field verification of recognition abilities first reported in the laboratory, the functional value of kin recognition in anuran amphibians remains unclear, despite a number of possibilities (Blaustein *et al.* 1991, Waldman 1991), and Blaustein and Waldman (1992) make the important point that, "We cannot infer, upon finding that larvae associate with their kin or otherwise show evidence of recognizing them, that these responses necessarily confer functional advantages …" (p. 216).

The expression component of kin recognition

Michael D. Beecher organized a symposium, "From Individual to Species Recognition: Theories and Mechanisms", which was presented at the annual meeting of the (then) American Society of Zoologists in 1980. Two papers from the symposium were influential in the early development of kin recognition studies. First, Beecher (1982) made the important conceptual point that the kin recognition process comprises two distinct components. The *expression component* (also labeled the production component) refers to the phenotypic attributes that make one individual or set of individuals distinguishable from another like a unique odor or vocalization (reviewed by Tsutsui 2004). Second, the *perception component* includes (1) the sensory detection of phenotypic attributes and (2) a comparison of them to an internal kin model, which is often acquired as a result of prior interactions with relatives (reviewed by Mateo 2004). (Beecher (1982) used "identification" and "recognition", respectively, for these two components (*see* Liebert & Starks 2004), which I have replaced with terms that have become more frequently used in the kin recognition literature.) Beecher suggested that investigators had over-emphasized the perception component in recognition studies, noting, for example, that most researchers would explain the (apparent) absence of kin recognition as a failure of the perception component rather than because there was insufficient phenotypic variation among kin to make them recognizable (the expression component). He introduced the concepts of "signature systems" and "kin signatures" in his mathematical treatment of the expression component (reviewed and extended by Beecher (1991)). I now turn to his research program on inter-specific differences in parent–offspring recognition in swallows, which convincingly demonstrates the importance of kin signatures in the recognition process (also called "kin labels" (Waldman *et al.* 1988)).

Parents are expected to invest preferentially in their own offspring, and parent–offspring recognition has evolved in many species to ensure that, indeed, parents direct care to their own young rather than to young produced by other conspecifics (hereafter "aliens"). In group-living species or in those that nest at high densities, parent–offspring recognition poses different challenges for both adults and young than it does in solitary species or those that rear young in isolation (examples in Holmes 1990). Beginning with this inter-specific premise, Beecher and his associates designed field and laboratory studies on acoustic adaptations for parent–offspring recognition in several closely-related species of swallows (Hirundinidae), which differ in their degree of coloniality and thus the challenges of parent–offspring recognition. The investigators pursued questions about kin recognition in both highly colonial (e.g. Stoddard & Beecher 1983) and relatively non-colonial species of swallows (Medvin & Beecher 1986), but here I concentrate on what they learned from their comparative work on the expression component of the recognition process.

Bank swallows (*Riparia riparia*) are highly colonial and parents feed their own offspring rather than aliens when young are restricted to the nest and later when young join crèches shortly after they fledge, although parents also make mistakes and sometimes feed aliens (Beecher *et al.* 1981a). Parents accept alien chicks fostered into parents' nest, but only until parents' own chicks reach 16–17 days of age, which is when chicks' begging calls are replaced by individually-distinctive signature calls. This temporal pattern is adaptive because chicks begin to fly and mingle with other chicks a day or two after signature calls appear (Beecher *et al.* 1981b). Relative to bank swallows, barn swallows (*Hirundo rustica*) are described as non-colonial or living in much smaller colonies than bank swallows and thus offer a different parent–offspring recognition scenario. Cross-fostering results provide little evidence for parent–offspring recognition at the nest, playback experiments show that parents appear unable to recognize their offspring by individually-distinctive calls and after young fledge family groups remain apart for a few days, which ensures that parents feed only their own offspring. These results (Medvin & Beecher 1986) support the hypothesis that "… adaptations permitting parent–offspring recognition in cliff and bank swallows may have evolved as a result of colonial living and the attendant extensive intermingling of young." (p. 1636).

If signature calls have evolved in swallows to facilitate parent–offspring recognition and if selection for parent–offspring recognition has been stronger in colonial than non-colonial species, then signature calls should be more individually distinct, and thus more readily discriminated, in colonial than non-colonial swallows (Medvin *et al.* 1986, *see* Thom & Hurst 2004 for a review of individual recognition). This reasoning stems from the signature-adaptation hypothesis, which predicts that "… if we compare several closely-related species, which vary with respect to selection pressure for recognition, signature information will be greater in the species requiring recognition." (Beecher 1991: p. 112). In tests of this hypothesis (Beecher 1982), investigators found that the information capacity of signature calls from colonial cliff swallows (*H. pyrrhonota*) was almost twice that of calls from non-colonial (relative to cliff swallows) barn swallows (Beecher *et al*. 1989). That is, signature calls that might vary among individuals in features like duration, peak frequency and modulation rate differ more in colonial cliff swallows, and thus have greater information capacity, than they do in non-colonial barn swallows. But, does "information capacity" matter to swallows? Yes, because when the investigators used animal psychophysics techniques, training birds to discriminate between calls for food rewards, the investigators discovered that it was easier for adults of *both* species to discriminate between the calls of individual cliff swallows than between the calls of individual bank swallows. Beecher *et al.* (1989) also tested to see whether colonial cliff swallows had evolved special *perceptual* adaptations for discriminating signature calls that non-colonial bank swallows lacked and found no evidence to support this possibility. That is, the expression component of the recognition process rather than the perception component has been the target of selection for parent–offspring recognition in swallows, as the work of Beecher and his colleagues has shown so convincingly (reviewed in Beecher 1991).

The perception component of kin recognition

The second paper from the 1980 "recognition symposium" that influenced the early development of kin recognition studies provided data on the kin recognition abilities of two species of ground squirrels and described four general mechanisms that could mediate differential treatment of kin (Holmes & Sherman 1982). Two of the proposed recognition mechanisms, prior association and phenotype matching, explain how various kinds of kin are identified in many species (*see* reviews in Fletcher & Michener 1987, Hepper 1991a, Sherman *et al.* 1997, Mateo 2003), and I will concentrate on them as I describe how ground squirrels and other organisms recognize certain classes of kin. I begin with some natural history information to place ground squirrels' recognition abilities in a socioecological context, and I concentrate on Belding's ground squirrels (*Spermophilus beldingi*), the species whose recognition abilities and social behavior have been studied most intensively in the field.

Adult female *S. beldingi* treat descendant and non-descendant kin nepotistically in two contexts: when terrestrial predators appear, females emit vocalizations that warn relatives of danger (Sherman 1977), while increasing callers' chances of mortality (Sherman 1985), and females cooperate with other female kin during territorial defense of natal burrows to thwart conspecific infanticide (Sherman 1981a). *S. beldingi* nepotism depends on direct kin recognition because females live among conspecifics of varying degrees of relatedness and kinship does not covary predictably with female spatial distribution, except for mothers whose unweaned young are confined in a natal burrow (Sherman 1980, 1981b). Mother–offspring recognition and littermate recognition were the initial targets for our laboratory and field studies on kin recognition, and I will first consider the mother–offspring dyad, including how mothers' recognition abilities reflect the early rearing ecology of *S. beldingi* litters (*see* also Mateo 2004).

The typical *S. beldingi* mother produces one litter per year, which she rears alone in an underground burrow (the natal burrow) for about 25 days when infants come aboveground for the first time as nearly-weaned juveniles (their natal emergence; Sherman 1981a, Holekamp 1984). Before natal emergence, mothers respond to an indirect cue, the location of their natal burrow, which ensures that they care for their own offspring, and mothers appear unable to distinguish between their own and alien pre-emergent young, based on infant-borne kin labels. For example, in Sherman's field cross-fostering experiment, mothers whose litter had not undergone natal emergence retrieved alien young placed next to mothers' natal-burrow entrance and reared aliens like their own genetic offspring (Holmes & Sherman 1982). Similarly, in Holmes' (1984) laboratory cross-fostering experiment, mothers caring for their *unweaned* young indiscriminately retrieved both their own offspring and age-matched aliens. If, however, a female's litter had emerged in the field or reached emergence age in the laboratory, mothers rejected aliens and thus demonstrated that they could recognize their own weaned offspring. The cross-fostering results (Mateo 2004: fig. 1) led Holmes and Sherman (1983) to suggest (1) a time-dependent ontogeny for mother–offspring recognition, which first appeared around the time of weaning and natal emergence, and (2) that mothers learned the kin labels of their offspring during a sensitive period that roughly coincided with when young underwent their natal emergence.

In retrospect, there were two possible problems with our time-dependent recognition hypothesis. First, in theory mothers could have learned their infants' kin labels anytime before their young first emerged, rather than just prior to natal emergence, but delayed using what they had learned until after natal emergence when mothers routinely encounter related and unrelated juveniles for the first time. We still do not know exactly when mothers learn their pups' kin labels, nor do we know when pups first begin to produce their own individually-distinctive kin labels (odors). Second, researchers who study kin recognition have long been aware that the absence of differential treatment does not necessarily imply an inability to recognize relatives (e.g. Gamboa *et al*. 1991). This means that, for instance, in the laboratory retrieval tests of 15-day-old *S. beldingi* young (Holmes 1984), the "failure" of mothers to differentiate between their own young and age-matched, unfamiliar aliens may have reflected mothers' high level of maternal motivation rather than an inability to recognize their own offspring. Indeed, in later work when I placed unfamiliar 15-day-old aliens in mothers' nestboxes, mothers spent more time investigating the unfamiliar aliens than investigating their own offspring, which shows that *S. beldingi* mothers could make the own–alien discrimination (Holmes 1990). That mothers proceeded to rear to weaning the 15-day-old aliens inserted into their nestbox suggests a high level of maternal motivation which may have masked mother–offspring recognition abilities in the original field (Holmes & Sherman 1982) and laboratory (Holmes 1984) studies.

Besides parent–offspring recognition, sibling recognition is likely to evolve in many species because siblings are as closely related as parents and their offspring ($r = 0.5$). Siblings are the most numerically common class of collateral kin in many species and frequently have opportunities to affect each other's reproductive efforts. Inclusive fitness theory suggests that kin recognition will evolve when siblings routinely coexist over evolutionary time and affect each other's reproduction, but the theory does not specify any particular proximate mechanism for recognizing siblings. However, Hamilton wrote about kin recognition that (1964: p. 22), "… if any correlate of relationship is very persistent, long-continued weak selection could lead to the evolution of a discrimination based on it …". In many species, including ground squirrels, there are two particular correlates of relationship that mediate kin recognition, sharing a common rearing environment and phenotypic similarity, each of which I will consider in turn.

Recognition by prior association

The early rearing environment of many species includes nests or burrows in which young associate only with rearingmates like their siblings before they start to encounter other agemates. Young that become familiar with the kin labels of their rearingmates and later distinguish between "familiar" and "unfamiliar" agemates would be acting as if they could discriminate between siblings and nonsiblings (Bekoff 1981). The *prior association* mechanism for recognizing kin (Holmes & Sherman 1982) is often studied by reciprocally cross-fostering infants between litters to test the prediction that "familiar" individuals will be treated one way and "unfamiliar" individuals another way, regardless of actual relatedness. In early research on ground squirrel kin recognition, results of cross-fostering studies on four species supported the operation of the prior association mechanism (reviewed in Sherman & Holmes 1985, Schwagmeyer 1988).

Despite the widespread occurrence of recognition by prior association, our understanding of this kin recognition mechanism remains modest. We know, for example, that in some species former rearingmates must continue to interact every so often or kin recognition based on "familiarity" disappears (e.g. Porter & Wyrick 1979, Paz y Miño & Tang-Martinez 1999) whereas in other species early association results in long-term familiarity that does not require updating (e.g. Insley 2000, Mateo & Johnston 2000a). On the other hand, we know little about (1) exactly when familiarity is established during early development (young could be cross-fostered at different ages to investigate this), (2) the nature of the learning mechanism that generates familiarity (what, if any, are the instrumental contingencies that underlie the learning of kin labels?), (3) whether familiarity is based on a relatively irreversible, imprinting-like process or one in which "future" interactions with nonkin could disrupt what was learned during early development and compromise recognition based on prior association (e.g. Hare 1996) and (4) the possible role that a "third party" like mothers might play in mediating the development of familiarity between rearingmates (e.g. Holmes & Mateo 1998, Berman 2004), among a host of other issues.

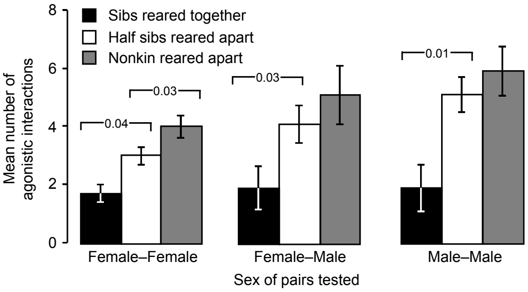

Fig. 3. Mean (± SE) number of agonistic interactions during 5-min paired-encounter tests of three groups of captive-bred ground squirrels, defined by relatedness (siblings, paternal half-siblings or nonkin) and prior rearing association (reared together or apart). Within each group, pairs are stratified by the sex of the interactants. Sibling pairs were significantly less agonistic than all other pairs for each sex-of-pair combination, but only in the case of female–female pairs were paternal half-siblings significantly less agonistic than nonkin pairs. After Holmes (1986a).

Two types of relatives cannot be recognized by prior association. First, when *unfamiliar* kin initially encounter each other, prior association cannot, by definition, mediate their interactions. One of the most common sets of unfamiliar close kin is paternal half-siblings, and in free-living *S. beldingi* such kin are numerous given the highly polygynous nature of their mating behavior (Hanken & Sherman 1981). To study recognition of this kin class, I used controlled breeding and later, during paired-encounter tests, recorded the frequency of agonistic interactions that occurred between familiar siblings, between unfamiliar paternal half-siblings and between unfamiliar nonkin (Holmes 1986a). Sibling pairs were significantly less agonistic than all other pairs, revealing a prior-association effect (Fig. 3). However, unfamiliar half-sibling pairs were also significantly less agonistic that unfamiliar nonkin pairs, which demonstrates that half-siblings were recognized and indicates the existence of a recognition mechanism besides prior association. That half-siblings were recognized was intriguing, but more intriguing was that only females displayed the recognition ability. That is, females, the nepotistic sex, recognized their unfamiliar half-sisters whereas males, which do not display nepotism (references above), appeared unable to recognize their unfamiliar half-siblings (Fig. 3). Nepotistic behavior is sex-limited in several taxa (Michener 1983, Silk 2002, Griffin & West 2003) which suggests that it would be valuable to analyze for sex differences in the kin recognition abilities of these species (e.g. Insley *et al.* 2003), but, with the exception of work on social insects (e.g. Gamboa *et al.* 1986a, Crozier & Pamilo 1996), investigators rarely test for sex differences.

Second, the prior association mechanism is also inadequate to facilitate recognition of kin that are equally familiar but unequally related to each other, and when a female mates with multiple males the full- and maternal half-siblings she produces meet these criteria. Most *S. beldingi* females produce multiply-sired litters (Hanken & Sherman 1981), which means that littermates, young born into the same litter, comprise full- and maternal half-siblings, which associate in utero and share a common natal burrow. Sherman and his field assistants observed yearling full- and maternal half-sisters (identified by electrophoretic analyses of blood proteins) at his field site near Yosemite National Park, California, and found that full-sisters were more cooperative and less agonistic with each other than were maternal half-sisters (Holmes & Sherman 1982). Differential treatment of these two classes of kin that occupied the same early rearing environment indicates that females can discriminate between them.

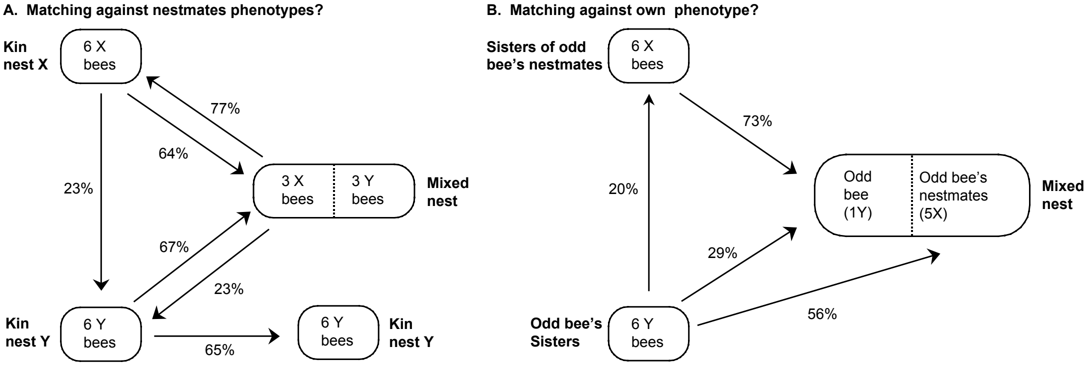

Fig. 4. The percentage of unfamiliar intruders that sweat bee guards allowed into guards' nests. Experimental nests (boxes) were created by placing six bees in each nest, which were drawn from different family groups (e.g. family X or family Y). In **A**, for example, the mixed nest comprised three X family and three Y family bees, each one of which could be tested as a guard. Arrows indicate nests from which intruders were taken and point to nests to which intruders were introduced to assess guards' ability to identify unfamiliar conspecifics. Guards admitted intruders (*see* percentages) depending on whether intruders' phenotypes matched those of the nestmates with which guards were reared (**A**), regardless of relatedness. Guards did not appear to use their own phenotype in the matching process (*see* the odd-bee result in **B**). From Buckle and Greenberg (1981).

Recognition by phenotype matching

What mechanism accounts for the identification of unfamiliar kin like paternal half-siblings and for the ability to distinguish between familiar but unequally-related kin like full- and maternal half-siblings? Recall Hamilton's (1964: p. 22) proposition that discrimination could be based on a "correlate of relationship." Thus, if phenotypic and genotypic similarity were correlated then individuals might recognize certain types of kin by "comparing phenotypes" of unknown conspecifics (Alexander 1979: p. 116) with those of known family members. Holmes and Sherman (1982, 1983) introduced the term *phenotype matching* to describe a recognition mechanism in which an individual learns something from (1) the phenotypes of its family members (by interacting directly with them or their phenotypic cues) or (2) its own phenotype and acquires a kin template, as a result of this learning. Later, the individual compares the phenotype to be identified (the "unknown" phenotype) with its kin template and uses some kind of matching rule (e.g. Getz 1981, Lacy & Sherman 1983, Gamboa *et al.* 1986a, Gamboa 2004) to assess the kinship status of the unknown phenotype. In the matching process, *referents* are the individuals whose phenotypes provide a model for the kin template, the prototypic set of features that are commonly shared among all closely-related kin (Mateo 2004). To recognize unfamiliar kin like paternal half-siblings, an individual could acquire its kin template from referents like its familiar family members or from itself, and to distinguish between familiar but unequally-related kin like full- and maternal half-siblings an individual could rely on a template acquired from itself as a referent (Holmes & Sherman 1982, 1983). Phenotype matching occurs in *S. beldingi* (Holmes 1986b, although *see* Alexander 1991), but I will describe Buckle and Greenberg's (1981) study on sweat bees which provided the first experimental demonstration of this recognition mechanism.

These investigators manipulated kin templates in female *L. zephyrum* by rearing bees in one of three kinds of nests each of which comprised six bees: (1) pure colonies included just sisters (from family X or family Y), (2) mixed colonies (three X-family females and three Y-family females) or (3) odd-bee mixed colonies (1 X-family female, the "odd bee", and 5 Y-family females or vice versa). Recognition was assessed by presenting an intruding bee from one colony to a female guard stationed at the nest entrance of her own colony (Buckle & Greenberg 1981). Thus, intruders were unfamiliar to guards, which eliminated the possibility of recognition by prior association. Guards from pure colonies allowed entry to (admitted) their sisters (Fig. 4A, *see* 65% value) and generally rejected nonkin intruders (Fig. 4A, *see* 23% value between Kin Nest X and Kin Nest Y). Guards from mixed colonies were about equally likely to admit their own sisters (Fig. 4A, *see* 64% value) and the sisters of guards' *unrelated* nestmates (Fig. 4A, *see* 67% value). And, finally, odd-bee guards from mixed colonies admitted the sisters of their unrelated nestmates (Fig. 4B, *see* 73% value) while rejecting their own sisters (Fig. 4B, *see* 29% value).

Collectively, Buckle and Greenberg's (1981) results show that guards compared the phenotypes of unfamiliar intruders with the template that guards had acquired from the nestmates with which they were reared and accepted or rejected intruders if their phenotypes matched or did not match, respectively, guards' learned templates. The mixed-colony results (Fig. 4A) showed that the phenotypes of both related *and* unrelated nestmates mates were incorporated into guards' templates because guards admitted both their own unfamiliar sisters and also the unfamiliar sisters of their unrelated nestmates. There was no evidence that guards incorporated their own phenotype into their recognition template because odd-bee guards, females reared only among nonkin, rejected their own sisters and accepted only the sisters of their unrelated nestmates (Fig. 4B, but *see* Getz (1981) for another view on the possibility of self matching by guards*). In summary, the data show that female sweat bees recognize unfamiliar intruders by comparing intruders' phenotypes to guards' kin templates, which guards acquire by learning something from the phenotypes of their rearingmates (probably an odor). Unfortunately, we do not know whether *L. zephyrm* use phenotype matching in nature because we do not know how often guards encounter unfamiliar but closely-related intruders at their nest, although females do found colonies near their natal nests, which would produce neighborhoods occupied by related females (Kukuk & Decelles 1986).

An important conceptual question about phenotype matching is whether the mechanism actually produces recognition "errors". (Here, I am considering acceptance errors in which nonkin are classified as kin or distant kin are classified as close kin rather than rejection errors in which kin are categorized as nonkin (Reeve 1989).) Phenotype matching requires a correlation between genotypic and phenotypic similarity (Porter *et al.* 1983, Sun & Müller-Schwarze 1997, 1998, Todrank & Heth 2003). However, if close kin share many phenotypic features in common, it could be more difficult to distinguish between two closely-related individuals than between two distantly-related individuals. (In this argument, I assume that kin labels arise from heritable traits, although kin labels can also potentially be acquired from the environment (Gamboa *et al.* 1986b).) In the extreme, for example, imagine that you recently met Richard at a party and a few days later encountered him again at a horse show. You re-introduce yourself to Richard and, after a moment of awkwardness, discover that you are talking to Robert, who is Richard's identical twin. Returning to sweat bees, could it be that guards committed acceptance errors because they mistakenly perceived the phenotypes of unfamiliar intruders as if the phenotypes belonged to their familiar nestmates (Waldman 1987)? Alexander (1990, 1991) has been the most forceful advocate of the "recognition errors" hypothesis to explain phenotype matching and he writes, "… 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." (Alexander 1990: p. 387). It is interesting to note that even if Alexander's "imperfect social learning" hypothesis is correct (*see* the exchange between

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* It is difficult to study self-referent phenotype matching for various reasons (Blaustein 1983, Mateo & Holmes 2004), which is especially unfortunate given the variety of socioecological conditions in which it is the most likely mechanism to facilitate recognition of kin, such as when young develop alone, among heterospecifics (e.g. brood parasites; Hauber *et al.* 2000) or in groups of mixed relatedness (e.g. due to multiple maternity or paternity). Hauber and Sherman (2001) review the self-referent phenotype matching literature and the recognition mechanism is also discussed in this issue of the journal in papers by Mateo and by Goth and Hauber.

Sherman (1991) and Alexander (1991)) phenotype matching could still generate inclusive fitness benefits if unfamiliar kin were treated as relatives that otherwise would have been treated as nonkin.

There is much work to be done to deepen our understanding of phenotype matching, including whether this mechanism generates proximate recognition errors. When unfamiliar relatives are treated like kin in accord with inclusive fitness theory, phenotype matching may be involved (e.g. Alberts 1999, Petrie *et al*. 1999, Widdig *et al*. 2001, Smith *et al*. 2003). However, I suggest that real progress in understanding this recognition mechanism at the proximate level requires manipulating kin templates by altering early social experience (e.g. by cross-fostering newborns or changing individuals' phenotypes) in ways that would result in some individuals being identified as relatives whether they were or were not actual kin (e.g. Fig. 4). Kin templates are crucial constructs in the phenotype matching process (Göth & Hauber 2004, Mateo 2004), and thus experiments that directly manipulate phenotypes to test specific predictions about recognition behavior (e.g. Hauber *et al*. 2000, Tibbetts 2002) offer the most rigorous test of a phenotype matching hypothesis (Hauber & Sherman 2001). Unfortunately, template manipulation studies can be quite challenging to design because even in planned experiments developing young experience an array of phenotypes any of which could affect template formation (Mateo & Holmes 2004).

Some thoughts on future research in kin recognition

Kin recognition research informed by Hamilton's (1964) inclusive fitness theory has been going on for about 25 years and we have learned a lot about how and why animals recognize their relatives during this period. Much remains to be learned, however, and in this final section I want to identify a few conceptual and empirical issues that I think could be profitably pursued. My list is not exhaustive and reflects my own biases rather than a representative sample drawn from the current literature on kin recognition.

Kin recognition and kin favoritism

Whenever social insects (e.g. Gamboa *et al*. 1986a, Crozier & Pamilo 1996, Gamboa 2004), rodents (e.g. Sherman 1977, Hoogland 1986), primates (e.g. Silk 2002, Chapais & Berman 2004) or members of any species display kin-biased behavior, it is correct to conclude that kin recognition has occurred even though the mechanism that mediated the kin-biased behavior remains unknown (Holmes 2001). However, there is a risk associated with inferring kin recognition from kin favoritism. Hamilton (1964) was clear that functional predictions about kin favoritism must consider the fitness benefits to recipients and the fitness costs to donors, in addition to donor-recipient relatedness. This means that when kin are recognized it does not automatically follow that they should be targets for nepotism, which, in turn, means that the absence of nepotism should not be taken as proof that kin cannot be recognized. For example, in an important paper on what the authors refer to as "kin discrimination" and helping behavior in cooperatively-breeding vertebrates, Griffin and West (2003) show that individuals often preferentially help kin rather than nonkin, and suggest that "stronger discrimination" (their words) occurs in those species in which the reproductive benefits of helping kin are the greatest. Based on a meta-analysis of 18 vertebrate species, the authors conclude, "Overall, these studies show a significant pattern of kin discrimination, with helpers preferentially aiding closer relatives." (p. 634). The implication is that the absence of kin favoritism would mean that kin could not be recognized (and thus not treated favorably) when the absence of kin favoritism could mean that the benefit/cost ratio was too low to favor preferential treatment of kin that could be recognized.

If an investigator's goal is to determine whether and how kin recognition occurs in a particular species, it will usually be best to conduct a *direct-inference study* (Holmes & Mateo [in press]). In such a study, a fitness-neutral assay like olfactory investigation (e.g. Mateo 2003: table 1), visual orientation (e.g. Wu *et al*. 1980, Cheney & Seyfarth 1985) or time in proximity (e.g. Waldman 1981, Blaustein & O'Hara 1986) is used to investigate discrimination abilities rather than an assay that imposes clear phenotypic costs on test animals as occurs, for example, when helpers feed nestlings in cooperatively-breeding species (Heinsohn & Legge 1999). In my own work on *S. beldingi* littermate recognition, for example, I recorded the frequency of agonistic interactions during paired-encounter tests and found that males appeared unable to recognize their unfamiliar (reared apart) littermates, a discrimination that females did make (Holmes & Sherman 1982: fig. 5). However, when Mateo (2002) tested *S. beldingi* males' discrimination abilities by presenting dorsal-gland and oral-gland odors as test stimuli, she found that males could distinguish between the odor of an unfamiliar littermate and an unfamiliar nonkin conspecific. In other words, the fitness-neutral assay, olfactory investigation time, that Mateo (2002) used in her direct-inference study uncovered kin recognition abilities that were not apparent in my study (Holmes & Sherman 1982), which relied on an assay, agonistic interactions, that could impose costs on test animals. In field studies designed to search for evidence of nepotism, it makes sense to use behavioral measures like feeding alien young (Curry 1988, Komdeur 1994), forming coalitions (Bernstein 1991, Chapais 1995) or emitting antipredator warning calls (Sherman 1977, Cheney & Seyfarth 1985). However, because the occurrence of behaviors like these should depend not only on actor–recipient relatedness but also on the cost incurred by the actor, such fitness-costly measures may not be the most sensitive assays to study recognition abilities (Holmes & Mateo [in press]). Whether a particular assay (e.g. time in proximity) is fitness neutral will vary across species and, admittedly, it may not be possible to know in advance whether a given assay is, indeed, fitness neutral. Nevertheless, readers of the kin recognition literature would benefit, I believe, if authors worked hard to specify whether they were studying kin recognition *per se* or drawing inferences about kin recognition abilities from the occurrence of kin favoritism.

Kin recognition and cooperative breeding

Behavioral ecologists have worked hard to provide functional explanations for cooperative breeding (Emlen 1997, Cockburn 1998, Hatchwell & Komdeur 2000), which occurs when parent-like behavior is given to young by individuals (hereafter, "helpers") other than the genetic parents of the young. (*See* discussions by Brown (1987) and Solomon and French (1997) on the various meanings of "cooperative breeding.") At the mechanistic level of analysis, cooperative breeding does not necessarily complicate kin recognition for helpers because reliable correlates of relatedness often exist that helpers can use to identify genetically-appropriate targets for assistance. In some cooperative breeders, for example, helpers are individuals that have delayed dispersal and provide assistance to young on helpers' natal territory (Emlen 1997, Cockburn 1998). This means that helpers will assist their younger siblings rather than unrelated young, as long as there has not been a turnover of breeders on the territory. Under such circumstances, helpers would care for siblings by responding to nest-site cues as a correlate of relatedness rather than to the phenotypic cues of nestlings (their siblings) on the territory (i.e. indirect recognition; Waldman *et al.* 1988).

Alternatively, *direct* kin recognition, which depends on phenotypic cues borne by conspecifics themselves (*see* above), could also mediate kin favoritism in some cooperatively-breeding species (Komdeur & Hatchwell 1999b). In Seychelles warblers (*Acrocephalus sechellensis*), for example, young cross-fostered as nestlings and reared by unrelated foster parents become helpers the following year for the foster parents that reared them rather than for their own genetic parents (Komdeur *et al.* 2004), which suggests that the prior association mechanism facilitates kin recognition by helpers (*see* also Hatchwell *et al.* (2001) on kin recognition in long-tailed tits, *Aegithalos caudatus*). However, the nestlings that were fostered in Year 1 and acted as helpers in Year 2 were not reared with the nestlings that they helped in Year 2 so in what sense, if any, did older helpers recognize their younger siblings by the prior association mechanism? Holmes and Sherman (1983) described *mediated recognition* as a type of prior association in which two unfamiliar relatives first encounter each other in the presence of a third individual (a "go between") that is related and familiar to both of the unfamiliar individuals. In Seychelles warblers, when a helper can choose to provision at either of two different nests on its natal territory, the helper feeds nestlings only at the nest occupied by the breeders that fed the helper as a nestling (Komdeur 1994). Thus, the breeders function as a "go between" and mediate recognition between older helpers and their younger siblings. And, more specifically, the "go between" seems to be the putative mother that fed the helper rather than the putative father (Richardson *et al*. 2003).

Cross-fostering studies of cooperative breeders like those by Hatchwell *et al*. (2001) and Komdeur *et al*. (2004) provide valuable insights into the proximate cues that helpers use to make their provisioning decisions. However, as I have argued above, there are compelling reasons for distinguishing between kin recognition and kin favoritism, and so I believe that we will make the most progress in understanding the proximate basis of kin recognition in cooperative breeders when fitness-neutral measures are used to evaluate differential treatment of kin (e.g. *see* the results of the first experiment in Hatchwell *et al*. (2001) on long-tailed tits in which breeders discriminate between the broadcast calls of kin and non-kin during playback trials). Fitness-neutral assays are especially important when helpers can gain direct-fitness benefits from assisting others (Cockburn 1998) because under these conditions it may pay helpers to provision young indiscriminately, giving the impression that helpers cannot recognize their relatives. (Keller (1997) discusses other instances when indiscriminate helping makes functional sense.)

Kin recognition and communal breeding

When two or more females produce and rear their young together in a single nest or burrow, communal breeding occurs (although other definitions of communal breeding have also been used — reviewed in Solomon & French (1997)). When communal breeding includes infant care that is clearly costly and is provided to both an individual's own young and to the alien young of a co-nesting parent, then the question arises as to whether the caregiver can discriminate between its own and the alien young. If a parent provides significant (but not necessarily equal) care to both types of young, then such indiscriminate care does not necessarily mean that the parent is unable to recognize its own offspring because the benefits of indiscriminate care may outweigh the costs (Lewis & Pusey 1997). Infanticide, for example, is common in many populations of house mice (*Mus musculus*) and females that nest communally suffer less infanticide than single-nesting females (Manning *et al*. 1995, Dobson *et al*. 2000). This result suggests that even if mothers can recognize their own young, it may not be in their reproductive interests to provide discriminative care if doing so would result in other females rejecting them as co-nesting partners. Indeed, if a fitness-neutral assay showed that co-nesting females could discriminate between their own and alien young and yet provided indiscriminate care (e.g. Jesseau 2004), then it would be reasonable to conclude that the benefits of communal breeding outweighed the costs of indiscriminate care. That is, a study of the proximate ability to recognize offspring would imply that communal breeding has a functional net benefit.

In mammals, one of the potential costs of communal breeding is that it renders mothers vulnerable to milk theft by alien young (Lewis & Pusey 1997, Hayes 2000), which could be quite costly for mothers given the energetic expense of lactation (König *et al*. 1988). Accordingly, I suggest that recognition studies in mammals which breed communally would be valuable because functional reasoning leads to a clear prediction that could be tested: mothers should be able to discriminate between their own and alien young. However, if two or more mothers give birth synchronously in a common nest, it is not obvious how they could distinguish among infants and nurse their own offspring exclusively. Mother–offspring recognition in mammals is generally mediated by the prior association mechanism (Holmes 1990), yet this mechanism would seem inadequate in communally-nesting species given that nest sharing would seem to deny mothers the opportunity to learn the kin labels of their own offspring that reside in a communal litter. Phenotype matching might allow mothers to identify their own young, and I suggest that it would be instructive to investigate mother–offspring recognition in communally-nursing species to learn whether mothers can identify their own young (Jesseau 2004) and, if so, whether phenotype matching explains this unexpected recognition ability.

Concluding remarks

As I proposed in my Introduction, W. D. Hamilton set in motion empirical research programs for several behavioral ecologists when he published his ideas on inclusive fitness theory (Hamilton 1964), and, in fact, kin recognition studies may be a quintessential example of a cottage industry that sprung from abstract theory. As E. O. Wilson (1987) wrote, "… rarely in the history of biology has a domain of empirical knowledge followed so closely and fruitfully upon an abstract theoretical idea." (p. 7). As a participant in this cottage industry, what I have tried to do in this review is examine some of the empirical work and conceptual issues that characterized early research on kin recognition. At the organismal level, we have learned much about how and why kin are recognized in a surprisingly diverse array of organisms, although the genetics and neurophysiology of kin recognition mechanisms continue to exist largely as black boxes.

The ability to identify relatives is one of several forms of recognition that can be linked theoretically to more general issues and problems in the study of recognition systems (Sherman *et al*. 1997, Starks 2004). I want to suggest, however, that for social creatures like us for whom nepotism is a central and defining attribute there is something which is truly "special" about kin recognition. An anecdote cannot provide strong evidence to support my claim for the "special" status of kin recognition, but nevertheless I want to conclude by describing a recent event that reminded me of why I have long been intrigued by kin recognition problems, including our own abilities to recognize relatives. I occasionally eat lunch in a restaurant specializing in Chinese food that is staffed by native speakers of Mandarin, which I hear infrequently and definitely do not speak. During a recent lunch, I overheard Li Ming, the woman who always takes my order, chatting in Mandarin with diners at another table hidden behind a partition and thus not visible to me. Then, the impossible happened — Li Ming came out of the kitchen, which I could see directly in front of me, while the conversation in Mandarin continued behind the partition. I later learned that Li Ming's sister was visiting from China and helping out in the restaurant, thus explaining my "impossible" experience. As I said, my anecdote hardly makes a compelling case for the "special" status of kin recognition, but what does it mean if the vast majority of you who read my anecdote have had a similar experience and were as flabbergasted by your experience as I was by mine?

Acknowledgements

I thank Phil Starks for inviting me to contribute to this special edition of the journal on recognition system research, although I must question his email characterization of me as "… our recognition system 'old man' — our silverback." I thank George Gamboa, who has studied kin recognition for as many years as I have, and Mark Hauber for their helpful comments on an earlier version of my paper. I thank Paul Sherman whose invitation to visit his ground squirrel study site at Tioga Pass, California, lead to several fruitful years of collaboration and intense discussions. Finally, I extend a special thanks, first, to Hannah Wu, who convinced me that my skepticism was unjustified and that it would be valuable to study kin recognition in pigtailed macaques during our graduate student experience at the University of Washington and, second, to all of the undergraduate and graduate students from the University of Michigan, who worked with me in the laboratory or field as assistants and friends during our research on ground squirrels' kin recognition abilities.

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