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Introduction

When Hamilton (1964) published his theory of inclusive fitness it had no immediate impact in the social and behavioral sciences, even though ethnographers knew kinship to be a universally fundamental factor in human social organization, especially in egalitarian societies in which humans have spent nearly all their evolutionary history. In many ways, it was a theory that perhaps anthropologists should have devised: Anthropologists knew kinship fundamentally structured cooperation, identity, coalition formation, resource exchange, marriage, and group membership in traditional societies. It was not until 1974 with the publication of Wilson's *Sociobiology* (1975) and especially Richard Alexander's *The Evolution of Social Behavior* (1974) that evolutionary social scientists began to take note of the potential of kin selection as a powerful theory that could revolutionize the study of human social behavior. Alexander was the first to comprehensively demonstrate that ethnographic and psychological evidence provided strong support that hypotheses drawn from kin selection would be a productive area of investigation. His review of the anthropological literature on kinship, especially of the Human Relations Area Files (HRAF), was elaborated more fully in *Darwinism and Human Affairs* (1979). For example, Alexander's prediction that paternity uncertainty would skew nepotism matrilaterally (1974, pp. 373–374; 1979, p. 169) is now well documented. In addition, he provided important preliminary evidence that suggested that kin selection would help us understand food transfers and cooperative economic activities (Alexander, 1979, pp. 144–161), and that kin selection and reciprocal altruism would be closely linked (1979, pp. 52–58).

Meaning and Measurement in Kin Selection

What has become known as Hamilton's rule is at the heart of kin selection theory and it states that helping or cooperative behavior between any two individuals can evolve so long as benefit to the recipient's fitness is greater than the cost to the donor, devalued by the coefficient of relatedness between donor and recipient, or $Br - C > 0$. Although the general implications of the theory are relatively easy to comprehend, there have been a number of misunderstandings of its technical elements. Chief among them is that belief that relatedness refers to the proportion of genes shared, when, in reality, it is the probability that two individuals have genes in common as a consequence of immediate descent. This error and others are discussed by Dawkins (1979) and Queller (1996), whereas Park (2007) reviews erroneous or problematic characterizations of kin selection in social psychology text books. There is a growing literature on joint or coordinated behavior that may appear to be examples of kin-based nepotism but, in fact, may be instances of reciprocal altruism, mutualism, coercion, or manipulation (Clutton-Brock, 2009).

The Status of Kin Selection in Nonhumans

Cooperation and helping behavior among kin is well documented in a variety of animal species especially those that live in small, stable breeding groups with high degrees of relatedness. In a general review of kin selection in nonhumans, Griffin and West (2002, p. 1) assert:

> Hamilton's inclusive fitness theory represents one of the most important developments in evolutionary biology. In particular, the idea that individuals benefit from the reproduction of relatives (kin selection) has been extraordinarily successful in explaining a wide range of phenomena, especially cases of supposed altruism.

The evidence for kin selection in primates, largely through maternal links (reviewed by Silk, 2009), has been documented in baboons, macaques, vervets, gorillas, and red howlers. Kinship is crucial for social networks, grooming, coalitions, and dominance relationships.

In chimpanzees there is some evidence of reciprocal altruism in a variety of behaviors such as grooming, coalitionary support, and meat and sex exchanges (Gomes & Boesch, 2009). However, only very recently has kin selection been reasonably well established as a mechanism for cooperation among chimpanzees. Langergraber, Mitani, and Vigilant (2007) showed that maternal brothers were more likely to associate, groom, maintain proximity, support one another in conflicts, share meat, and jointly patrol. These patterns were not found for paternal brothers because of promiscuous mating among chimps. However, in a study based on 14 years of observation Lehmann, Fickenscher, and Boesch (2006, p. 931) found that chimp fathers spent more time playing with their own offspring and conclude that "our data show for the first time that wild chimpanzee males can recognise their own offspring." However, consistent with Langergraber et al. (2007), they found affiliative matrilateral links to be far stronger.

Reciprocal Altruism and Kin Selection

In many instances, reciprocal altruism (Trivers, 1971) is an alternative or even complementary model to explain cooperation. The general difference is that relatedness is zero and the payoff to the helper occurs in the future. Clutton-Brock's (2009) review of reciprocal altruism in nonhuman species shows that we have few examples of nonhuman intra-specific reciprocal altruism even though allogrooming in primates come close. Clutton-Brock draws several important conclusions: (a) most cases of purported reciprocal altruism can be explained as either examples of mutualism (simultaneous gain by both interactants) or manipulation, and (b) apparently convincing cases of reciprocal altruism may involve kin selection. He concludes that reciprocal altruism exists in humans because of language to communicate long-term intensions of interactants and "social norms" that prevent or discourage cheating.

Human Evolutionary History and Why Kin Selection Should Be Important

Humans, until quite recently, lived for much of their history in hunting and gathering bands of about 50 individuals (Binford, 2002). Hill et al. (2011) have recently investigated the degree to which kin relatedness structured bands in a comparative analysis of 32 hunter-gatherer societies. On average only about 10% of an adult (age >15) individual's primary adult kin (parents, siblings, or offspring) will be coresidents and about 25% of coresidents will be made up of close and distant kin. Mean relatedness of all adult Ache and !Kung band members to one another is 0.054 (slightly less than a half cousin). These measures should be viewed as underestimates because measuring relatedness only among adults hides the fact that an individual's subadult grandchildren and nephews and nieces are related by 0.25 were not counted, even though in hunter-gatherer groups subadults comprise about 50% of band members. Quarter relatedness kin ties are important because, as will be shown later, kin altruism tends to flow from senior (aunts, uncles, and grandparents) to junior kin (nephews, nieces, and grandchildren) as a consequence of differences in reproductive value. Hill and colleagues do note that historical factors such as pacification and the influence of colonial power and trade relations at the time kinship data was recorded could have altered the kin structure in these bands. Be that as it may, because of this alleged low level of relatedness, the authors declare, "These patterns produce large interaction networks of unrelated adults and suggest that inclusive fitness cannot explain extensive cooperation in hunter-gatherer bands" (Hill et al., 2011, p. 1286). They are unclear what extensive cooperation is and who one could rely on for critical cooperation. A similar but more detailed analysis was done on the Hadza drawing this conclusion "Although the Hadza have a preference for kin as both campmates and gift recipients . . . the Hadza also actively form many ties with non-kin" (Apicella et al., 2012, p. 500).

Approaches to the Study of Kin Selection

Evolutionary psychology and behavioral ecology are the two broad approaches taken in the study of kin selection in humans, although there can be considerable overlap. In part, the differences revolve around the kinds of questions asked, which often lead to different methodological approaches. Evolutionary psychology generally focuses on elucidation of mental modules that produce attitudes, expectations, orientations, and emotions toward kin and how kin are recognized. Most of the work is done through surveys and experiments. In contrast, behavioral ecologists who are mostly anthropologists observe behavior and fitness outcomes or associated proxies in naturalistic settings. The emphasis is on what subjects actually do and the reproductive impact of behavior. In many instances researchers in both camps overlap methodologically especially in the use of survey instruments to collect nonobservational, informant-generated data such as reproductive histories on fertility and survivorship, bequests in wills, and characterization of patterns of interaction with kin.

Another general contrast is the behavioral ecologists' study of traditional non- Western populations who live in social conditions that more closely approximate the environment of evolutionary adaptedness. In contrast, evolutionary psychologists more frequently study Western, educated, industrial, rich, and democratic or WEIRD peoples (Henrich et al., 2010). In some instances there is a point of tension over evolutionary predictions can be best tested by demonstrating the design features of mental modules in terms of how they lead to adaptive behaviors or how these behaviors actually affect measurable proxies of fitness such as growth, survivorship, and fertility (see Daly & Wilson, 1999 and a response by Smith, Borgerhoff Mulder, & Hill, 2001). Notwithstanding, both approaches are complementary because they work at different levels of analysis such that both approaches are required to gain a complete picture of the dynamics of kin selection or any evolved human behavior. The balance of this chapter is organized by topics covered by researchers in the study of kin selection. I begin with topics that have been dominated by evolutionary psychologists and then move to topics that increasingly are dominated by behavioral ecologists.

The Evolutionary Psychology of Kinship

As recently as 1997, Daly, Salmon, and Wilson (1997) declared that psychologists had made few contributions to the study of kinship even though their research agenda encompasses interpersonal relationships. As Daly and Wilson (2005) now note, this situation has improved significantly with considerable research on kin recognition, emotional closeness, empathy, and kin support reviewed next.

Kin Recognition

Kin recognition is widely studied in animals and reveals that multiple mechanisms are employed such as olfaction, cosocialization, habituation, and phenotypic matching (Park, Schaller, & van Vugt, 2008). For nepotism to function effectively, an organism has to be able to reliably distinguish between close, distant kin, and nonkin. All cultures have culturally based kinship classification schemes that distinguish between near and distant kin (based on genealogical closeness) and specify mutual expectations about helping behavior, coalition membership, marriage, mutual rights and obligations, and affective ties. Jones (2004, p. 214) notes that universal features of kinship terminological systems include genealogical distance, social rank, and group membership. From an evolutionary psychological perspective, Lieberman, Tooby, and Cosmides (2007) argue that humans have special mental circuitry to detect cues of kinship and compute them through a kinship estimator that gives us an idea of how close or distant the relationship is. This estimator generates appropriate emotions such as disgust in relation to contemplation of sex with close kin to a willingness to assist kin depending on their degree of relatedness. Lieberman, Oum, and Kurzban

(2008) argue that kinship along with sex and age may be universal social categories people employ to guide their social interactions.

Phenotypic Matching The degree to which individuals are phenotypically similar may be a signal of genetic kinship. The research to date focuses on facial similarity, attitude similarity, and common surnames. One study uses self-assessed overall physical similarity (Bressan & Zucchi, 2009) based on 12 physical traits, whereas all other studies are based on single phenotypic attributes such as facial similarity. Very useful reviews of this literature can be found in Park et al. (2008) and Arantes (2012).

Facial Similarity Considerable research has been done on facial similarity although much of it focuses on mate choice and paternity determination (DeBruine, Jones, Little,& Perrett, 2008). In an interesting marriage of behavioral economics and evolutionary psychology, several studies of facial similarity show enhanced cooperation in a public goods game (DeBruine, 2002; Krupp, DeBruine, & Barclay, 2008) and perceptions of trustworthiness (DeBruine, 2005), and altruism toward children who resemble adult subjects (DeBruine, 2004).

Association Patterns The widely known Westermarck hypothesis (see Wolf & Durham, 2004, for a review) posits a relationship between intimate patterns of childhood association (or cosocialization) leading to an absence of sexual attraction and even disgust at the very idea of sexual relations among individuals who have been reared together as siblings or as if they were siblings. Lieberman, Tooby, and Cosmides (2003, 2007) argue that sibling childhood association (or cosocialization) and maternal perinatal association are key elements of kin recognition that not only lead to incest avoidance but also to sibling altruism. The addition of maternal perinatal association (observing one's mother caring for an infant) is an important advance because it is a mechanism that prevents older siblings who might spend little or no time growing up with younger siblings from having a sexual interest in them. It is unclear whether the maternal perinatal association can be extended to account for grandparental altruism and whether there are other associative cues for kin identification.

Emotions Underlying Kin Altruism

A number of researchers have attended to the possible emotional mechanisms such as emotional closeness, emphatic concern, and empathy that underlie kin relationships. It is an area that has been less well studied compared to research on willingness to help, patterns of interaction, and actual patterns of help. According to Park and Schaller (2005), the altruistic mechanisms that trigger assistance to friends and kin may be very similar, and there may be sexual differences in how these mechanisms are activated (Ackerman, Kenrick, & Schaller, 2007).

Korchmaros and Kenny (2001, p. 262) use a measure called emotional closeness defined as "a sense of concern, trust, and caring for another individual and enjoyment of the relationship with the individual." They asked college students to choose which of their family members they would most likely provide with life-saving assistance. They found that emotional closeness and kinship independently predicted altruism, and kinship was strongly associated with emotional closeness. A later study by Neyer and Lang (2003) found that measures of subjective closeness (those who one could not live without) and support received on a regular basis (daily assistance, encouragement, and social support) was significantly correlated with kinship even after controlling for proximity and age. Maner and Gailliot (2007) posit that empathic concern (concern for the welfare of others) more strongly motivates altruism toward kin compared to strangers. Finally, Jeon and Buss (2007) show that empathic concern and emotional concern are correlated and both have independent effects on kin altruism toward cousins.

Kruger (2003) examined the psychological constructs of oneness (a sense of self– other overlap) and empathy representing something akin to the concept of emotional closeness. His research failed to show that subjects felt these emotions more strongly toward kin than toward friends. However, he did find that subjects strongly expected assistance from kin. Park et al. (2008, p. 220) importantly note that empathy ought to be the appropriate emotion to elicit because it is a demonstrated mediator of altruism. They note that "A subjective sense of closeness is not an emotion, per se" (Park et al., 2008, p. 219). At this point, which emotions influence altruism toward kin are poorly understood.

The work of Curry, Roberts, and Dunbar (2013) and Pollet, Roberts, and Dunbar (2013) invokes the concept of a "kinship premium" and points to a deeper understanding of how kinship is an independent factor in altruism. Both studies replicate previous research showing that emotional closeness is important to maintain helpful relationships (such as willingness to donate a kidney or travel a great distance to maintain contact) among friends and kin through reciprocation. However, both studies showed that close kinship (but not distant) had an independent contribution to altruism, hence the "kinship premium."

Willingness to Help

A number of studies have focused on willingness to help kin and friends. Perhaps the first study of kinship and willingness to help is found in Essock-Vitale and McGuire's survey (1980, p. 1985) of 300 women in the Los Angeles area. They found that close kin were more likely to help than distant kin and close kin bias increased with the cost of the assistance. In addition, help from friends was balanced in returns, whereas this was not the case for kin. These patterns have been replicated and elaborated in subsequent research. The pattern we see emerging is that, although friends may help more frequently as a consequence of proximity, kin become more important as the costs or benefits to helping increase.

Several studies show that, on a daily basis, we may depend on nonkin more frequently, but when the benefit for help to the recipient or the cost to the donor increases, then we increasingly rely on kin. Burnstein, Crandall, and Kitayama (1994) did the first such study and found that when the costs and benefits to kin were great (based on hypothetical scenarios of saving someone in a burning house at some risk to themselves compared to helping them find a lost personal item and being late to a meeting as a result) close kin were more likely to be helped. Fitzgerald (2009) replicated these results by distinguishing between everyday altruism (driving someone to the store), extraordinary altruism (giving a large loan), and life-threatening altruism (risking one's life).

Stewart-Williams (2007, 2008) administered surveys to undergraduates about their helping and exchange behavior toward friends, kin (siblings and cousins), and mates. For siblings, cousins, and acquaintances, greater relatedness was associated with more frequent levels of helping. Friends were an exception because they received as much or more help than kin. However, as shown in other studies, as the cost of helping increased, kin became strongly favored over friends, even though subjects felt closer to friends and mates. He contrasts his second survey (2008) with the results from Neyer and Lang (2003) who found that individuals in their sample felt closer to kin than friends and received more help from kin. He speculates that the difference in results are likely a consequence of age differences in subjects. The older subjects in Neyer and Lang (2003) had married, whereas Stewart-William's subjects were college students. These different results may reflect life historical changes in the development and maintenance of helping relationships. It may also reflect differences in mobility and wealth, as well as mature adults probably have established long-term friendships and familial relationships in contrast to college students who have just left home and are rapidly acquiring a new set of relationships.

Sex Differences in Nepotism

It seems reasonable to predict that men and women may have different strategies when it comes to nepotistic effort. One would hypothesize that these differences are determined by local reproductive opportunities. For example, where marriage is dependent on accruing cattle to pay bride price, men might use that wealth for themselves instead of assisting a son or nephew (Borgerhoff Mulder, 1987; Mace, 1996). In contrast, additional mating effort for women may have a much lower payoff, leading them to allocate more energy to parental and kin effort. This is especially true for women after menopause, which informs Hawkes' (Hawkes, O'Connell, & Blurton Jones, 1989) grandmother hypothesis. The same sort of life historical change may occur for men, especially in societies where polygyny is uncommon or prohibited (Winking, Kaplan, Gurven, & Rucas, 2007).

Salmon and Daly (1996) refer to Western women as "kin keepers" because, compared to men, they have greater interest in the welfare and activities of their kin, are more likely to identify themselves in kinship relation terms, more likely to maintain contact, felt closer to kin, and can recall more relatives (see Chagnon, 1988 for non-Western exception). However, both males and females were just as likely to nominate a kinsperson as the most significant person in their lives. These differences and others are also documented by researchers who take a nonevolutionary approach (see Dubas, 2001, p. 480 for a review). Benenson et al. (2009) note that the cross-cultural literature shows that men from childhood to adulthood form larger and more inclusive and interconnected nonkin networks than women, whereas women focus more strongly on maintaining family ties. Neyer and Lang's (2003) research measured these differentials in different age categories. As demonstrated in other studies (Essock-Vitale & McGuire, 1985; Euler & Weitzel, 1996), women felt closer to kin than men, and women were more likely to assist kin; these differences became more pronounced in middle and old age, which has implications for understanding menopause as a possible adaptation. In the grandparental solicitude literature, the female of a grandparental pair always engages in more altruistic acts toward grandchildren than her male counterpart

(Euler & Weitzel, 1996). Females are much more likely than males to engage in the care of young, dependent kin through direct care, such as holding, feeding, babysitting (Huber & Breedlove, 2007) or economically through food production. Perhaps the most dramatic sex difference in nepotism is seen in alloparental care by siblings (Hames & Draper, 2004) and in the extensive grandmothers' literature.

Behavioral and Ethnographic Approaches to Kin Selection

This section reviews research by anthropologists, psychologists, and others who evaluate kin selection hypotheses in naturalistic or seminaturalistic settings, measure the consequences of kin altruism through fitness differentials or their proxies, or measure actual instances of kin altruism. A striking feature of this literature is the enormous range of human behavior that kin selection theory can help us understand ranging from the evolution of homosexuality, labor and food exchanges, and political coalitions.

Homosexuality

Decades ago Wilson (1975, p. 279) speculated that homosexuality is maintained via kin selection. Given that male homosexuals in the West have about one-tenth the fertility of heterosexuals (Vasey & VanderLaan, 2009; King et al., 2005) it would seem that investment in kin would be their only road to fitness. In the West, evidence for high kin investment by gays is negative (Rahman & Hull, 2005). However, Vasey and VanderLann's meticulous examination of the transgendered androphiles in Samoa clearly demonstrates that an EEA-like culture may make a difference in altruism of androphilic males toward kin. The Samoan status *fa'afafine* means "in the manner of a woman" and it represents a third gender. Vasey and VanderLann (2009) show that Samoan *fa'afafine* invest more heavily in closely related younger kin (siblings, nephews, and nieces) compared to heterosexual kin who have no children. It is important to understand that *fa'afafine* are what Vasey and VanderLaan term transgendered androphilic males who are present in many ethnographic tribal and traditional populations in contrast to what they call sex-gender congruent androphiles (or egalitarian homosexuals) found in the West. *Fa'afafine* are expected to excel in feminine tasks such as the care, nurturing, and support of children and devotion to the home and domestic tasks. VanderLaan, Ren, and Vasey (2013) argue that the transgendered form is the norm in egalitarian populations, and it is in that social context that this behavior is adaptive.

Economic Cooperation: Food and Labor Exchange

A considerable amount of research has been done in evolutionary economic anthropology on how kin selection might influence interhousehold transfers of food and assistance. Although much of the research has entertained multiple hypotheses of transfers such as reciprocal altruism, costly signaling, tolerated scrounging, as well as kin selection (see Gurven, 2004, pp. 545–546 for definitions), I largely focus on the rather mixed research results relative to kinship. If we begin with Gurven's (2004, p. 558) comparative survey, food transfers appear to be more frequently regulated by reciprocal altruism than kin selection among foragers and other subsistence-based peoples. Although there is ample evidence, reviewed later, that kin selection can be important in particular ethnographic instances, it is becoming increasingly clear that food transfers are regulated by a variety of mechanisms.

Studies showing relatedness is the likely mechanism to account for food exchange is documented among the Ifaluk (Betzig & Turke, 1986), Hiwi (Gurven, Hill, Kaplan, Hurtado, & Lyles, 2000), Dolgan (Ziker & Schnegg, 2005), in a mixed tribal Peruvian community (Patton, 2005), and among settled Ache (Gurven, Hill, & Kaplan, 2002). These studies show that kinship predicts the frequency of exchange between households. Kinship also is negatively correlated with imbalance in exchange. That is, close kin tolerate greater one-way flows of resources with little or no reciprocation, whereas distantly related households seem to be in balance, suggesting a tit-for-tat form of reciprocal altruism. In contrast, research on the Yanomamö (Hames, 2000), Ye'kwana (Hames & McCabe, 2007), Tucker on the Mikea (Tucker, 2004) and forest Aché (Kaplan & Hill, 1985) show that relatedness does not predict transfers, whereas reciprocal altruism does. Noting these complex results, Allen-Arave, Gurven, and Hill (2008) persuasively argue that the Ache tend to set up reciprocal relations with close kin because they are better known, likely to be near-neighbors, and can be trusted to reciprocate.

In contrast to food transfers, cooperative labor has received relatively little recent study even though it was one of the first issues economic anthropologists examined to test kin selection predictions. These studies examine whether close kin are more likely to engage in joint labor such as working in each other's gardens or to work together as boat crews in marine hunting. Hames (1987) used an observationally based study of labor exchanges between Ye'kwana households and found strong support for kinship in a variety of ways. He found that mean relatedness between households predicted how frequently individuals would work in one another's gardens, that close kin were likely to have large imbalances in their labor exchanges while distant kin seem to pursue a closely regulated tit-for-tat strategy, and that those households that had more kin in the village were more likely to engage in cooperative garden labor.

A major problem in many of these economic studies is that the problem that food sharing or cooperative labor is designed to overcome (Hames & McCabe, 2007) is not addressed before predictions about the mode of exchange (e.g., kin selection or reciprocal altruism). For example, one might predict that food exchange is designed to reduce the variance in daily intake of critical food resources (Gurven, 2004, p. 544). Consequently, in small bands, one would predict that all hunters would contribute, regardless of their relatedness, and reciprocal altruism would be the mechanism. In contrast, if sharing were designed to help those who fell on hard times because of garden failure (Hames, 1987) or physical incapacitation (Sugiyama & Chacon, 2000), then strong kin biases would be predicted.

Inheritance

In the modern context, allocating all of one's worldly assets in a last will and testament is the ultimate opportunity to benefit kin. In many instances it is likely to be the largest investment individuals can make in kin and offspring. Straightforward predictions would be that close kin would receive more than distant kin and that reproductive value would also be important such that younger kin (nephews and nieces and grandchildren) would receive more than equally related older kin, such as grandparents, aunts, and uncles, and offspring should receive more than siblings of a testator. These predictions were generally borne out in analyses of wills in British Columbia (Smith, Kish, & Crawford, 1987) and California (Judge & Hrdy, 1992). In a series of laboratory studies Webster (2004) and Webster, Angela, Crawford, McCarthy, and Cohen (2008) students were asked to allocate fictional lotteries to blood relatives along with an examination of 1,240 probated wills with 4,819 beneficiaries in British Columbia. Although there was a strong correlation between relatedness and proportion of estate given, several new results emerged. First lineal relatives were biased over collateral relatives. This bias occurred even after controlling for age, since lineal kin of equal relatedness tend to be younger than collaterals and thus have greater reproductive value. Second, wealthy benefactors more strongly adhered to relatedness than poor benefactors. And third, among the wealthy group, younger relatives were favored over older relatives, whereas among the less wealthy, older kin were favored over younger. Why there is a bias toward lineals over collaterals is unknown, and Webster et al. (2008) pose a number of different hypotheses, such as paternity certainty and differences in the number of lineal and collateral kin. Finally, female testators more closely adhered to relatedness than males, a finding paralleling Judge (1995).

Politics and Coalitions

In perhaps the first use of inclusive fitness theory from a behavioral ecological perspective, Chagnon found that village fissioning was linked to biological kinship (1975). The problem revolved around how a village could maintain large size giving them an advantage in a milieu of chronic intervillage warfare. Within-village disputes are normal in any society, but in egalitarian societies, dispute-settlement mechanisms employ the authority of senior kin and the strength of their kinship ties to amicably settle disputes. As Yanomamö villages grow, disputes increase and mean village relatedness declines, thereby reducing the effectiveness of kinship in dispute settlement. After fissioning, new villages have greater mean relatedness than in the prefission village, and disputes are rarer and are more easily reconciled when they surface.

Using a filmed analysis of an axe fight among 30 Yanomamö in the village of Mishimishimaböwei-teri, Chagnon and Bugos (1979) showed that the side selected by the participants corresponded to their degree of relatedness to the two principle combatants, and members of each faction were more closely related to themselves than they were to the other faction. A later reanalysis by Alvard (2009) using more sophisticated statistical tools showed that the initial results stood up and, in addition, showed that lineage membership disappeared when relatedness was controlled for and that affinal links also played a role in coalition alignment.

Adoption, Fosterage, and Step-Relations

In a series of articles on anthropological populations by Silk for Oceania (1980), the Arctic (1987), and in Africa and elsewhere (1990) she tested a variety of standard cultural anthropological hypotheses (need for labor, sex-ratio balance) and found that close kin are the most frequent adopters. Silk also found biological parents monitor the welfare of their adopted children, place their children in households that are wealthier than theirs or offer advantageous social ties, and children are given up for adoption when parents feel they cannot adequately care for them. Although these patterns appear to fit derivable inclusive fitness predictions, often, adopted children are not treated as well as biological children. Realizing this, biological parents apparently strive to give their children to the closest biological kin available to mitigate this problem and actively monitor their treatment.

Adoption is an area of research that has direct social policy implications because in the United States, Canada, Great Britain, and elsewhere foster care and adoption institutions now bias placement with kin (Daly & Perry, 2011), and, in the United States, federal law encourages kin fostering (Herring, 2005). Such laws and policies encouraging kin placement were developed without reference to inclusive fitness theory. Herring, Shook, Goodkind, and Kim (2009) review a number of studies querying whether foster care placement with kin generally leads to better outcomes compared to placement with nonkin. Overall, as reviewed by Herring et al. (2009), a number of studies consistently, but not invariably, find that kin placements are more stable (i.e., they last longer) than nonkin placements. Of course, stability does not necessarily mean good treatment or outcomes (Perry, Daly, & Kotler, 2012).

Some researchers have examined the psychological consequences of kin versus nonkin fostering. Lawler (2008) examined foster-care outcomes using measures of emotional availability, for children who had been diagnosed with disruptive behavior, and found no difference between kin and nonkin fostered children. Testa (2004, cited in Herring et al., 2009, p. 10) used the construct of permanence to study the well-being of fostered children. Permanence consists of three components: “intent that the family relationship lasts indefinitely, continuation of the relationship despite geographic moves and temporal change; and belongingness. . . .” The concept of permanence was strongly correlated with kinship and increased with closeness of kinship. Despite these positive results, many studies do not control for important confounds such as income, education, and school and neighborhood environments that have independent effects on adoptee outcomes (Perry et al., 2012).

Pollet and Dunbar (2007) examined a large public database of 13,935 families compiled in 1910. They predicted that childless couples would be more likely than couples with children to have a household with a nephew or niece in them. Given that nephews and nieces had much higher reproductive value than other close kin (e.g., siblings), such households would better deploy their kin effort to younger categories of kin. After controlling for a variety of factors, they found that childless couples were 3.5 more times likely to have a nephew or niece in their household. Due to limitations in the database, there is no indication that any of these nephews and nieces were legally adopted but, given that they live in the households of their aunts and uncles, one can regard this as adoptive behavior.

Alloparenting: Helpers at the Nest and the Grandmother Hypothesis

There is now a large literature on alloparental care or cooperative breeding that encompasses helpers at the nest (care by siblings) and the grandmother hypothesis. Important reviews have been made by Sear and Mace (2008), Coall and Hertwig (2010), and Sear and Coall (2011) on the grandmother hypothesis, whereas Hames and Draper (2004), Hrdy

(2005), and Kramer (2012) cover the more general topic under the rubric of cooperative breeding. Most reviews examine the factors of paternity certainty, genetic relatedness, reproductive value, and sex biased investments. The potential utility of alloparents stems from a combination of derived life-history traits in humans including short interbirth, "reproductive stacking," or parents caring for multiple, dependent offspring, and long dependency where subadults are typically unable to produce as much as they consume until they reach the age of 16 years or more (Kramer, 2010).

The earliest evolutionarily informed research on human alloparenting (Turke, 1988) was inspired by the avian "helpers at the nest" literature and was firmly grounded in kin selection theory. Turke documented the positive effects of older siblings, particularly girls, on a mother's fertility or the survivorship of her children, behavioral measures of child care, and labor effort of older siblings. Hames (1987) showed a moderate correlation between alloparental relatedness and time expended in childcare among the Ye'kwana. This pattern of heavy investment in allocare by close kin is also noted in hunting and gathering groups such as the Efe (Fouts and Brookshire, 2009), Hadza (Crittenden and Marlowe, 2008), and the Martu (Scelza, 2009). Research by Ivey (2000) on the Efe shows that relatedness is a consistent and powerful predictor of allocare and similar findings are made for the Toba (Valeggia, 2008), Aka (Meehan, 2005), Hungarian Gypsies (Bereczkei, 1998), and Maya (Kramer, 2008). The dominant alloparents in roughly rank-order providing direct care were female siblings, grandmothers, aunts, cousins, and distant or nonkin.

The focus on the grandparental dimension of alloparenting was inspired by Williams' queries on menopause (1957) and became a well-researched area following Hawkes' innovative research on Hadza grandmothers (Hawkes et al., 1989) that revolve around grandmothers as reliable investors in conjunction with the evolution of longevity and menopause. The overwhelmingly consistent pattern in grandparental investment is maternal grandmothers invest most because they have no uncertain links to their grandchildren, followed by maternal grandfathers and paternal grandmothers who have one uncertain link to their grandchildren, and paternal grandfathers who have two uncertain links. However, socioecological differences do matter. For example, among Greeks paternal grandparents engage in more caretaking than maternal grandparents in rural farming communities where farmland is inherited patrilineally, residence is patrilocal, and paternal grandparents may co-reside with their son and daughter-in-law (Pashos, 2000).

The now voluminous grandparental research can be divided into three kinds of studies: (1) biological and reproductive outcomes; (2) investments, or what alloparents do for kin, and; (3) solicitude and other psychological factors that lead grandparents have greater interest, empathy, or feel closer to grandchildren. In addition, I note studies examining investment from aunts and uncles to nephews and nieces.

Outcomes Outcome research looks at the demographic consequences of grandparents on the fertility of their children and/or survivorship and growth and development of their grandchildren. Sear and Mace (2008) and, more recently, Sear and Coall (2011) summarized the demographic outcomes research. Sear and Mace provide an extensively detailed and critical analysis of studies that document how the presence of four types of grandparents as well as older siblings on child survival. In a comparative analysis of 45 studies, they found that presence of maternal grandmothers improved child survivorship in 69% of studies, whereas paternal grandmothers improved survivorship at a lesser 53% rate. In rare cases, grandmothers were found to actually decreased survivorship. They suggest two reasons why maternal grandmothers were more helpful than paternal: (1) they tend to be younger since females reproduce earlier than males, and (2) maternal grandmothers may have higher rates of paternity certainty. In contrast, maternal grandfathers had no effect on the survivorship of grandoffspring in 83% of the cases, whereas paternal grandfathers had no effect in 50%, a negative effect in 25%, and a positive effect in 25%. The effects of other relatives such as siblings are generally positive (Sear & Coall, 2011). The effects on survivorship tend to be greatest when the child is less than 5 years of age. Since survivorship during this period is highly sensitive to forms of direct care such as child tending, monitoring, and feeding, and women dominate these activities, grandmothers are likely instrumental. However, grandfathers may be valuable later in life when their social influence may be critical to marital and economic success. Finally, see Strassmann and Garrard (2011) for limitations of Sear and Coall's (2011) meta-analysis.

Investments Early research by Hawkes et al. (1989) showed that food production by grandmothers had positive effects on grandoffspring weight maintenance during food-scarce periods of the year. Gibson and Mace (2005) present time-budget data to show that maternal grandmothers spent more time in their daughter's households and were more likely to do heavy domestic labor thus reducing their daughter's labor load. In a more direct accounting, Meehan, Quinlan, and Malcom (2013) found that kin, largely grandmothers, significantly reduced a mother's energetic expenditure by as much as 216 kcal/day. In an interesting study of birthing, Huber and Breedlove (2007) made a distinction between direct care of the mother (assisting in the birthing process) and indirect care (food preparation and other activities to assist the mother after the birth). Using the HRAF Statistical Cross Cultural Sample of 60 societies, they found that relatedness, sex, and paternity certainty affected rendering of assistance. In the area of direct care, aunts provided more care than uncles, grandmothers more than grandfathers. The same pattern held for indirect care except that there was no difference between grandmothers and grandfathers.

Most grandparental research shows that although all grandparents invest, the investment magnitude generally follows female and paternity certainty links noted earlier. Euler and Michalski (2007) summarize numerous studies on contract and interaction frequencies, childcare, gifts received, and adoption. Nearly identical patterns were found for aunts and uncles by Gaulin, McBurney, and Brakeman-Wartell (1997) and their investments in nephews and nieces.

In a large and detailed study, Pollet, Nettle, and Nelissen (2006) found that contact frequency, investment in grandchildren shortly after birth, gifts, and provisioning of essentials was greater for maternal grandparents than paternal grandparents. However, there was no difference between the grandparents in loans, money for childcare, or assisting with household costs. They also noted that frequency of contact was an excellent proxy for financial investment.

Solicitude and Contact A number of studies such as Euler and Weitzel (1996) and Euler and Michalski (2007) show emotional and cognitive differences mirror the investment difference among grandparents. That is, MGM>MGF>PGM>PGF pattern was found in emotional closeness, favorite grandparent, relational closeness, grandparental mourning after the death of a grandchild, and emotionally closest grandparent. A variety of studies have shown matrilateral bias by aunts and uncles toward nephews and nieces (Gaulin et al., 1997). For example, McBurney, Simon, Gaulin, and Geliebter (2002) found matrilateral aunts and uncles had a greater concern for the welfare of their nephews and nieces than patrilateral aunts and uncles in an eastern U.S. sample with high paternity certainty. In addition, Kurland and Gaulin (2005, p. 461) showed the same matrilateral bias in terms of frequency of contact and doing favors for one another for full, half sibs, and cousins. Jeon and Buss (2007) using a formal model predicted that cousins linked though mother's sisters would be most altruistic, whereas those through father's brothers would be least altruistic. Links through mother's brother and father's sister would be intermediate. They found that measures of emotional closeness, empathic concern, and the frequency of contact followed the rank ordering in their model.

Summary, Trends, and Conclusions

Kin selection has been a potent force in our life history as a species. It plays a significant role in nearly all human social domains from care for subadults, costly investments, food and labor allocations, politics, and daily social interaction, to the ultimate altruistic act of designating recipients of last wills and testaments. In proportion to their degree of relatedness, kindreds feel emotionally close, are concerned about one another's welfare, and are willing to help them at great costs to themselves. Evolutionary anthropologists and psychologists are in the lead of behavioral scientists studying kinship. The following is a summary of what we know so far about kin selection.

Women More Frequently Deploy Nepotism Than Men

Kin investment by post- and prereproductive females provide two lines of clear evidence that females more than males use kinship to enhance their fitness. Demographic analysis of hunter-gatherer life history shows that, on average, women who reach the age of 45 will live an additional two decades (Gurven & Kaplan, 2007). Given that direct reproduction ceases as a consequence of menopause the only avenue open to females is indirect reproduction through the enhancement of the survival and reproduction of their offspring and grandoffspring, and there is considerable evidence for kin effects. Since men do not go through menopause and have options of serial monogamy and polygyny, direct reproduction may be a better option than kin investment in many sociocultural circumstances. However, where polygyny is limited, direct reproduction by men may end for the vast majority with their wives' last reproduction (Winking et al., 2007). Some of the grandparental literature show grandfathers enhance the survivorship of their grandchildren. The second line of evidence comes from the alloparenting literature documenting that girls are much more likely than boys to care for their siblings and other close kin and the presence of girls is more likely to reduce interbirth intervals for their mothers and the survivorship of their younger siblings. Beyond menopause and subadult female alloparenting, there is other evidence such as the kin keeper literature that shows that females are much more likely to keep track of kin and are more concerned about their welfare than men.

Kin Selection and Reciprocal Altruism

In the modern context there is considerable research that reveals we rely on friends for everyday forms of assistance with strict balancing, whereas kin are much more likely to assist when the cost is high and balance or reciprocation is not required. It is reasonable to conclude that people use reciprocal altruism for cheap, chronic, and easily tracked altruism; in contrast, they use kin selection for high cost/benefit altruism. Whether this is true in nonstate societies is unclear. In these societies, close kin are frequently coresident for one sex or the other. The flow of everyday assistance in goods and services shows reciprocal altruism is somewhat more important than kin mediated assistance (Gurven, 2004). For example, among the Ye'kwana, garden labor exchanges are strongly determined by kinship ties (Hames, 1987) but meal sharing is based on reciprocal altruism and not kinship (Hames and McCabe, 2007). The difference may be that meal sharing is a regular, nearly everyday event, easy to track, and not very costly (mainly food preparation). However, garden labor (clearing, planting, weeding, and harvesting) is arduous and seems to be a form of insurance for garden failure; if a family's gardens fail they can make up shortfalls by taking food from a kinsperson's garden.

Kin Altruism Flows Downhill

The ability of a recipient to parlay assistance into fitness is a crucial factor in the allocation of altruism. Many factors influence these decisions such as current and future needs, phenotypic quality, the ability of other kin to profit from the investment, and reproductive value. Age is a rough index of reproductive value and where research takes this into consideration assistance flows from older individuals to younger individuals. This is obviously evident in the grandmother- and alloparental-care literature as well as research on beneficiaries in wills, adoptions, and gifts.

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