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Culture, Altruism, and Conflict Between Ancestors and Descendants

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Introduction

The human adaptive complex, Lancaster and Kaplan (2009:95) explained, includes, among other things, a unique life history of development, aging and longevity and intergenerational resource transfer. Resource transfer from parents to offspring involved food and other tangible resources; however, it also involved the transfer of intellectual and strategic resources, including social and ecological skills that were transmitted or transferred as traditions (i.e., behavior – words or actions – transmitted from parents to offspring). This transmission, however, extended far beyond what Lancaster and Kaplan (2009:95) predicted – a “three-generational system of downward resource flow from grandparents to parents to children” – to very distant generations of descendants.

This enduring transfer, with one generation transferring intellectual and strategic resources to the next over many generations, has a number of requirements. Traditions are fragile; if one generation fails to repeat a tradition, it can be lost forever. Several things must be in place if this system is to endure; rules must be in place to not only tell children that they must cooperate, and with whom they must cooperate, but rules must also encourage those children to transmit what they learned to their own offspring. These rules will include moral injunctions – cooperate with distant kin as if they were close kin – and the acceptance of a hierarchical relationship between parent and child, with the child willing to learn and the parent willing to guide. Further, one’s kin must be identifiable as kin, that is, as an individual with whom one is taught to cooperate. In regard to implications, individuals who accepted these conditions and who shared a common ancestor were likely to share traditions – the same moral rules and similar body decoration, or “tags” (Holland 1993) – inherited from that ancestor, transmitted to them through their parents, grandparents, and other close kin. As the ethnographic record makes clear, individuals who inherit ancestral names or body decorations were regularly encouraged by moral traditions, in their interrelationships with the arts, storytelling and the plastic arts, to behave altruistically towards one another, to treat one another as if they were close kin (e.g., Murdock 1949; Evans-Pritchard 1940; Coe 2003; Steadman and Palmer 2008).

In this manner, altruism could come to be extended to individuals who shared descent, but whose relationship was far beyond the degree of relatedness (.125 or first cousins) that typically has been assumed to be the distance after which kin selection is ineffective. This, in an important sense, would extend “conflict” beyond the parent-child conflict, predicted by Trivers (1974) to an ancestor-descendant conflict in that individuals were told – in traditions coming from their ancestors – to disregard their own self-interest and to give preferential treatment not only to siblings but to both close and distant kin who were identified as co-descendants of that common ancestor.

Based on the concept of “ancestor-descendant conflict,” this paper presents a mathematical model for a new theoretical explanation of these characteristics. The concept of “ancestor-descendant conflict” is a multi-generational diachronic extension of Trivers’ concept of “parent-offspring conflict.” These multi-generational consequences of traditional parent-offspring conflict may explain why human kinship altruism extends to far more distant cousins than would be predicted by kin selection (Bernstein 2005). It leads to an extension and revision of Hamilton’s rule, or formula, “ $C < Br$ ” and constitutes a testable evolutionary explanation for why, in the ethnographic record, we regularly see human altruism extended to individuals who are only distantly related but who share ancestry.

Background

Hamilton’s formula ($C < Br$) states that altruism should only be favored by natural selection when the costs to the altruist are less than the benefits to the receiver, times their degree of genetic relatedness. This is conventionally taken to predict that unreciprocated altruism among kin is likely to be favored by natural selection only when it occurs between relatively closely related kin because r becomes insignificant past the relatedness of first cousins where $r = .125$. For example, Alexander claims that for “most people in a modern technological society, . . . the significance of distinguishing relatives decreases beyond some level, such as that of first cousins, because of low relatedness. . . . [This is] obviously consistent with a Darwinian model.” (1979:148, 149)

The problem for current Darwinian explanations of human kinship is that the ethnographic data from traditional societies are obviously inconsistent with a Darwinian model because not only are humans in every known traditional society able to identify kin far beyond first cousins, but that “extensive extra-familial nepotism” (Alexander 1979:211) also appears to be universal. Quoting Murdock (1949:14), Alexander (1979:156) describes this pattern by stating that universally

some of the intimacy characteristic of relationships within the nuclear family tends to flow outward along the ramifying channels of kinship ties [When an individual] needs assistance or services beyond what his family can provide, he is more likely to turn to his secondary, tertiary, or remoter relatives than to persons who are not his kinsmen.

In a recent overview of evolutionary explanations of kinship altruism, Bernstein elaborates on exactly why this feature of human kinship found in traditional societies is “surprising” to an evolutionist:

Because the return to fitness of altruism toward distant distant kin [i.e., kin far more distantly related than first cousins] is miniscule, typically less than helping an unrelated person with whom another has a profitable exchange, it may be surprising that such groups often have norms obliging members to favor these distant distant relatives over nonkin If altruism is prescriptive even on occasions when the degree of genetic relatedness is very small, the altruist’s fitness will decline depending on the frequency of such occasions. (Bernstein, 2005:529)

Bernstein suggests that such puzzling altruism can be ignored because it primarily occurs in situations such as famine and war (Bernstein 2005:529). Even if this is true, it still begs the question of why such altruism, and the norms obliging individuals to engage in such altruism, should occur at all. It also begs the question of why Alexander pointed out that such extension of altruism appears to be universally found in traditional societies. Thus, we are still left with an unsolved puzzle.

This puzzle of the existence of altruism not predicted by the standard evolutionary explanations of kin selection, reciprocal altruism, and indirect reciprocal altruism, has been widely noted by evolutionists (see Henrich et al. 2004). Further, the answer to this puzzle has usually been seen as involving culture in some way (see Richerson and Boyd 2005). There is, however, a fundamental difference between these approaches and our own explanation. Other approaches assume culture to be a *group* phenomenon. In some versions, this only means that the question is framed in terms of the question: How could a cultural behavior (e.g., like being altruistic to a non-reciprocating person who is not close kin) spread within a population through “population processes” (Henrich and McElreath 2003:124)? In stronger versions, the answer is through a process of cultural group selection (Richerson and Boyd 2001; 2005). In contrast, our “ancestor-descendant conflict” model is not framed within either form of group. Not only does it not require group selection, it does not require the assumption of a population. Instead it focuses on individual ancestors, and how their genes influencing them to start certain traditions could increase faster in subsequent generations than individual ancestors who did not start such traditions. This is why our approach requires a fundamentally different mathematical formula.

We now present the concept of “ancestor-descendant conflict,” and the mathematical formula upon which it is based. This concept arose when Lyle Steadman’s proposal that cultural traditions are descendant-leaving strategies (Steadman and Palmer 1995; Palmer and Steadman 1997) led us to a consideration of the unrecognized consequences of “parent-offspring conflict” (Trivers 1974) in a species in which offspring have routinely replicated the behaviors of their parents, and are frequently encouraged by their parents to do so.

Parent-Offspring Conflict

Theoretical basis

As the name suggests, our concept of “ancestor-descendant conflict” is a multi-generational diachronic extension of Trivers’ (1974) concept of “parent-offspring conflict.” Before examining the multi-generational consequences of what happens when different outcomes of parent-offspring conflict become traditional, we first summarize the aspects of parent-offspring conflict relevant to our model.

As originally stated by Trivers (1974), the existence of parent-offspring conflict means that “. . . parents are expected to attempt to mold an offspring, against its better interests. . . .” This attempted molding is the result of the simple biological fact that:

The mother is equally related to [all of] her offspring. However, the offspring is completely related to itself [i.e., related to itself by 1.0], but only half as related to its full siblings [i.e., related to full siblings by 0.5]. A Hamiltonian offspring should

value its personal fitness twice as much as it values any full sib's fitness. (Kurland and Gaulin 2005:452)

Therefore,

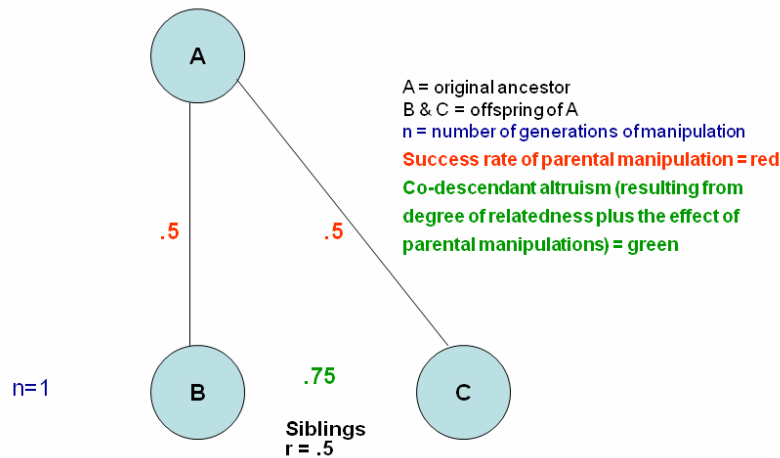
Each child should, in theory, see itself as twice as valuable as its sibling [i.e., an offspring values itself 1.0 and values a full sibling 0.5], while the parent, being equally related to the two, values them equally. Hence another Darwinian prediction: not only will siblings have to be taught to share equally [i.e., taught to value a sibling as much as itself, or 1.0 instead of 0.5]; parents will, in fact, try to teach them [to value each sibling as much as itself, or 1.0]. (Wright 1994:166)

This generates the prediction that natural selection would favor parents who could *manipulate their offspring to behave as if each of the parent's other offspring were related to them by 1.0 (i.e., value their siblings as much as they value themselves)*. Although the chances of such total victory by a parent has long been the subject of debate (Trivers 1974; Alexander 1974), and the outcome of parent-offspring conflict may be likely to be some degree of compromise, it seems likely that parents who were more successful in this manipulation would be favored by natural selection over parents who were less successful. This is because the increased altruism between offspring would increase the parent's total fitness.

An illustration

To illustrate this aspect of parent-offspring conflict, and eventually how it can be extended into ancestor-descendant conflict, we provide Figure 1. The triangular form of the diagrams used in this paper has been chosen to illustrate that kin are identified as individuals linked by one or more birth links through a common ancestor who forms "the apex of a triangle of descent" (Evans-Pritchard 1940:200). To simplify, we assume that every child has one parent, and we have chosen to portray females, mothers and their daughters, represented by circles. All calculations of "r" are based on full siblings. Thus, the offspring in Figure 1 would maximize their inclusive fitness by valuing a full-sibling .5 as much as themselves, but their mother would maximize her evolutionary success by manipulating all her offspring to value their full siblings 1.0 as much as themselves. For the sake of simplicity, our example will illustrate parent-offspring conflict that results in an "even" compromise resulting in siblings acting as if they value their full siblings .75 as much as themselves. *In such a case, the parental manipulation can be said to have a success rate of .5. Or, put differently, the offspring can be said to have accepted .5 of the parent's attempted manipulation.* This parental manipulation would obviously not actually increase the degree of relatedness between the offspring (i.e., "r"), but would instead influence the offspring to act "as if" they were related by .75 instead of .5 in regard to altruism toward their sibling. Figure 1 illustrates this 50/50 outcome to parent-offspring conflict.

Figure 1: The effect of a parental manipulation success rate of .5 on the amount of expected altruism between siblings.



Thus, the altruism between codescendants equals the sum of the degree of genetic relatedness (.5 in this example) plus the increase in altruism resulting from ancestral influence (.25 in this example where the ancestor is 50% successful in her attempt to raise the altruism from .5 to 1.0). It is important to note that the inclusion of social learning within the proximate causation of the offspring's altruistic behavior does not exclude the genetic component of proximate causation because all phenotypic traits (including altruistic behaviors towards kin) are the result of gene-environment interactions.

The conventional view of the effect of parent-offspring conflict on altruism between kin only extends forward in time to the altruism among siblings as shown in Figure One. Trivers (1974), however, realized that the influence of parents can extend far enough in time to alter "the later adult reproductive role of the offspring." We now extend this thinking still further by examining the previously unexplored consequences of parent-offspring conflict for future generations of co-descendants when the parental manipulation of offspring becomes traditional (i.e., is copied by offspring from their parents), transforming parent-offspring conflict into ancestor-descendant conflict. By doing so, we can examine how a parent who started a *tradition* of parental manipulation of offspring to be more altruistic toward that parent's other descendants could increase that parent's number of descendants, and thus increase the numbers of copies of that parent's genes, in *distant future generations*. This focus on distant generations of descendants as a measure of evolutionary success is completely compatible with the observations by West-Eberhard (1975:186) that "[i]nclusive fitness can include effects on future generations but does not specify how many generations should be included," and by Dawkins (1982:184) that "[i]deally we might count the relative number of descendants alive after some very large number of generations."

Ancestor-Descendant Conflict

Theoretical basis

One of the most incontrovertible facts of human behavior has been that much of an individual's behavior is replicated by that individual's descendants in the next generation, and so on and so forth, through subsequent generations (Palmer 2010). As Campbell (1975) pointed out, this intergenerational "retention and duplication" of behavior is why human behavior has tended to be traditional, and why Kroeber (1948) observed that "cultures are ... inclined to be persistent ...[e]ven in times of the most radical change and innovation there are probably several times as many items of culture being transmitted from the past as there are being newly devised." This fact is routinely recognized by recent evolutionists, but they frame it as a *group* phenomenon. Thus, instead of focusing on individual ancestors influencing their offspring to influence their own offspring, they have created a wide variety of concepts to explain which group members will or will not be imitated (Alvard 2003; Richerson and Boyd 2005). The problem with this focus on culture as a property of abstract *groups*, is that this does not match the actual patterns of interactions between individuals described in the ethnographic record (Palmer et al. 1997).

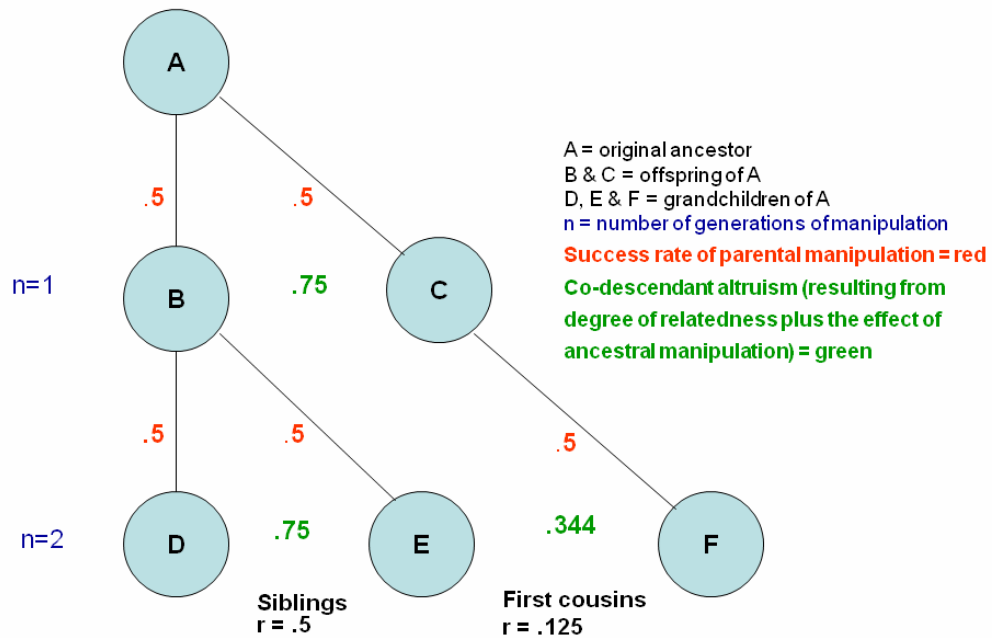
This focus on persistent patterns of behavior being passed from individual ancestors to their descendants (i.e., traditions) as descendant-leaving strategies led us to consider the potential *multi-generational* behavioral consequences of parental success in manipulating his or her offspring to be more altruistic toward the parent's other descendants. These consequences are only recognized when one stays focused on individuals, instead of abstract groups, and expands the conception of "parent-offspring conflict" into the concept of "ancestor-descendant conflict" by considering what happens when the parental manipulation becomes *traditional*. Parental manipulation becomes traditional when the parental manipulation of offspring that increases the altruism of the offspring toward each of the parent's descendants *is copied by offspring and directed toward their own offspring*, and so on and so forth through subsequent generations (see Steadman and Palmer 1995).

An oversimplified example of how parent-offspring conflict could have been transformed into ancestor-descendant conflict is the following three-part exhortation by a parent to his or her offspring: "1) treat all of my other descendants as if they are as valuable to you as you are to yourself, 2) tell your offspring to also treat all of my descendants as if they are as valuable to them as they are to themselves, and 3) also tell your offspring to tell their own offspring these things." We describe the evidence for the actual existence of such exhortations later in this paper.

An illustration and formula

The consequences of such a request producing the retention and duplication of a parental manipulation success rate of .5 for the degree of altruism between co-descendants two generations removed from their common ancestor (A) are illustrated in Figure 2. These three co-descendants are the siblings (D and E) and their first cousin (F).

Figure 2: The “Ancestor-Descendant Conflict Formula” shown through two generations at a parental manipulation success rate of .5.



Here, the altruism in this second generation expected between the siblings “D” and “E” remains the same .75 as it was between siblings “B” and “C” in the first generation, and as it will for all subsequent generations of siblings. This is because each parent in these examples, whether or not they have been influenced by their own parent, attempts to manipulate their offspring to act as if they are 1.0 related to each of their siblings, but they are only 50% successful in raising the offspring’s altruism to this level from the level of .5 expected as a result of their degree of genetic relatedness being .5.

The key to the ancestor-descendant conflict formula is its ability to predict the degree of altruism between *cousins* (*first cousins in the current example*) as well as siblings. For example, the altruism in the second generation expected between “E” and her first cousin “F” can be predicted by a simple formula. In this formula, “n” equals “2” because the individuals are two generations removed from their common ancestor “A,” and “r” = .125 because this is the degree of genetic relatedness between “E” and her first cousin “F.” Through the previously described exhortation, “A” attempts to manipulate “B” to manipulate “E” to act as if “F” is related to “E” by 1.0. “B,” however, only accepts .5 of this manipulation, and “E” in turn only accepts .5 of “B’s” attempt to manipulate her. Thus, “E” is only influenced by .5 of .5 of “A’s” attempt to manipulate “E” to treat “F” as if “F” were related to her by 1.0. Thus, the formula presented below shows the altruism resulting between first cousins as the result of both their genetic relatedness and the *indirect* influence of their common ancestor “A” transmitted through the behavior of “B.” In this example, the formula predicts that the amount of altruism shown by “E” toward her first cousin “F” will be .344, due to both the altruism expected because of their genetic relatedness (.125) and the altruism resulting from “B’s” manipulation of

“E’s” behavior (.219), that is itself the result of “A’s” manipulation of “B’s” behavior. The formula can be written:

$$A_n = r_n + S^n(1-r_n)$$

Where

- A_n = The amount of altruism
- n = The number of generations from common ancestor
- S = The success rate of parental manipulation
- r_n = The degree of relatedness

As in parent-offspring conflict, the ancestor-descendant conflict formula states that the amount of altruism (A_n) expected between co-descendants will be equal to r plus the amount of altruism resulting from the effect of parental manipulation. However, *in order to apply to subsequent generations*, the ancestor-descendant conflict formula states that the amount of altruism will be the result of r plus the success rate of ancestral manipulation (S) *raised to the power of the number of generations (n) separating the co-descendants from the common ancestor*, times the amount of potential increase in altruism ($1-r_n$). In this example

$$\begin{aligned} n &= 2 \\ S &= .5 \\ r &= .5 \end{aligned}$$

Therefore, the amount of altruism (A_n) between “E” and “F” will be

$$\begin{aligned} A_2 &= .125 + \{.5^2 (1-.125)\} \\ A_2 &= .125 + \{.25 (.875)\} \\ A_2 &= .125 + .219 \\ A_2 &= .344 \end{aligned}$$

This two-generational tradition of a .5 compromise outcome to parent-offspring conflict extends the amount of altruism far beyond what is predicted by kin selection alone because first cousins are now expected to be far more altruistic toward each other than they would be on the basis of genetic relatedness (.344 compared to .125). This .344 figure is a result of a cost and benefit analysis as is the .125 figure in Hamilton’s formula. The .125 figure means that selection will favor genes that cause altruism toward a first cousin when the costs to the altruist are less than one-eighth of the benefits to the recipient. That is, altruism should occur when the benefits are eight times as great as the costs. The .344 figure means that selection will favor genes that cause altruism toward a first cousin when the costs to the altruist are less than 344/1000 of the benefits to the recipient. That is, to state it simply, altruism should occur when the benefits are nearly three times as great as the costs. The larger, .344, figure is the result of considering the costs to the altruist and benefits to the recipient *and* the costs and benefits to the common ancestor who started the tradition.

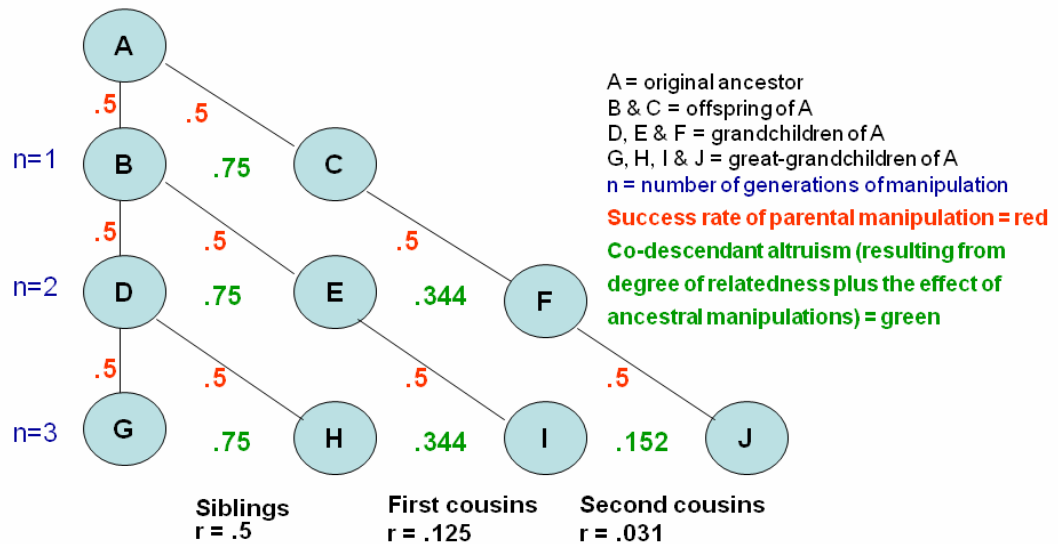
The consequences of ancestor-descendant conflict, however, are just beginning to become apparent. Before applying the formula to more subsequent generations, it is advantageous to rewrite the formula so that some of its properties become clearer.

For the rest of this paper we will state the formula as $A_n = S^n + r_n (1-S^n)$. This more clearly shows that when we compute the amount of altruism among co-descendants who are n generations from their most recent common ancestor, there are two factors that we must consider: kin selection (r_n), and the success rate of parental manipulation among the individuals' ancestors (S) and that these two factors are not independent. It is, in fact, their combined or coupled influence that increases the effect of each factor on succeeding generations. Writing the formula as $A_n = r_n + (1-r_n) S^n$ we see that the influence of kin selection on altruism, r_n , must be increased by the amount $(1-r_n) S^n$. Writing $A_n = S^n + (1-S^n) r_n$ we see the success rate of parental manipulation on altruism, S^n , must be increased by the amount $(1-S^n) r_n$. The terms $(1-r_n) S^n$ and $(1-S^n) r_n$ measure, respectively, the increase of r_n and S^n caused by the coupling of these two quantities.

The formula can also be interpreted in terms of probabilities. That is, " r_n " is a measure of the probability that two individuals that are n generations removed from their common ancestor will behave altruistically toward each other due to their kinship. " S^n " is a measure of the probability that two individuals who are n generations removed from their common ancestor will behave altruistically toward each other as a result of the success rate of parental manipulation among their ancestors. Thus, " A_n " is the probability that two individuals who are n generations removed from their common ancestor will behave altruistically toward each other as a result of either kin selection or the influence of ancestors through parental manipulation. Thus, the formula $A_n = r_n + S^n - (r_n)(S^n)$ is a probabilistic relation that says two things. First, it says that the probability of altruism due to kin selection or ancestral influence through parental manipulation is the probability for kin selection, r_n , plus the probability of ancestor influence through parental manipulation, S^n , minus the probability of altruism due to both factors; the second thing the formula says is that the probability due to both factors is just the product of the individual probabilities $(r_n)(S^n)$.

Figure 3 shows the consequences of this same .5 degree of parental manipulative success, being copied to a third subsequent generation.

Figure 3: The “Ancestor-Descendant Conflict Formula” shown through three generations at a parental manipulation success rate of .5.



In this example, the altruism expected between siblings, and between first cousins remains the same in the third generation as it was in previous generations. The altruism (A_3) expected between second cousins is again generated by the formula.

$$A_3 = S^3 + r_3 (1-S^3)$$

$$A_3 = .125 + .031 (1-.125)$$

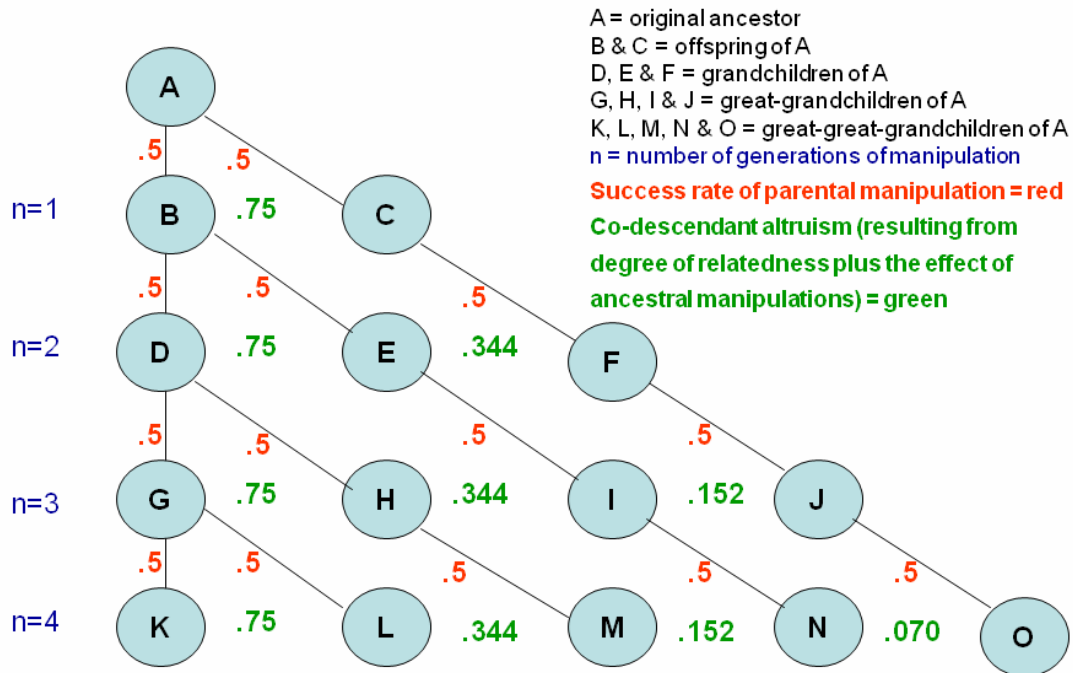
$$A_3 = .125 + .031 (.875)$$

$$A_3 = .125 + .027$$

$$A_3 = .152$$

In this example, “I” is only related to her second cousin “J” by .031. Through the previously described exhortation, “A” attempts to manipulate “B” to manipulate “E” to manipulate “I” to act as if “J” is related to “I” by 1.0. “B,” however, only accepts .5 of this manipulation, and “E” in turn only accepts .5 of “B’s” attempt to manipulate her, and “I” in turn only accepts .5 of “E’s” influence. Thus, “I” is only influenced by .5 of .5 of .5 of “A’s” attempt to manipulate “I” to treat “J” as if “J” were related to her by 1.0. Thus, the formula shows the altruism resulting between second cousins as the result of both their genetic relatedness and the *indirect* influence of their common ancestor “A” transmitted through the behavior of first “B” and then “E.” The amount of altruism shown by “I” toward her second cousin “J” will be .152, due to both the altruism expected because of their genetic relatedness (.031) and the altruism resulting from “B’s” manipulation of “E’s” behavior (.121), that is itself the result of “A’s” manipulation of “B’s” behavior. Figure 4 extends this traditional parental manipulation through a fourth generation.

Figure 4: The “Ancestor-Descendant Conflict Formula” shown through four generations at a parental manipulation success rate of .5.



In this example, the altruism expected between siblings, first cousins, and second cousins remains the same, and the altruism between third cousins “N” and “O” is .070.

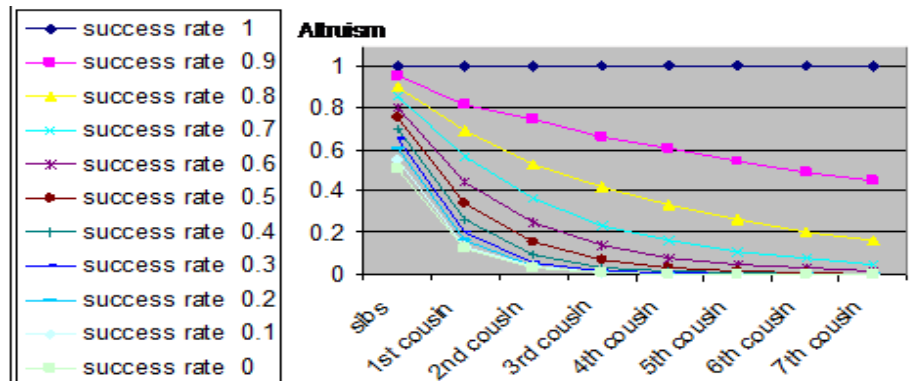
$$\begin{aligned}
 A_4 &= S^4 + r_4 (1-S^4) \\
 A_4 &= .063 + .008 (1-.063) \\
 A_4 &= .063 + .008 (.938) \\
 A_4 &= .063 + .007 \\
 A_4 &= .070
 \end{aligned}$$

There is, of course, no reason to assume that offspring will always accept .5 of their parent’s manipulation as we model in these examples. The attempted manipulation of offspring may have a rate of success ranging anywhere from 0.0 to 1.0. It is also important to remember that the amount of altruism resulting from any rate of successful manipulation can be calculated for an infinite number of generations.

As the success rate decreases and approaches 0, the expected amount and extent of altruism among descendants will more closely approximate the predictions based only on “r,” and thus becomes more consistent with the predictions generated by the concept of kin selection. In so doing the results of the model become more congruent with the limited extent of kinship altruism characteristic of modern, *non-traditional*, technologically complex societies, where traditions have come to exert less influence on behavior, but less consistent with the extent of altruism described in ethnographic descriptions of *traditional* societies. Conversely, as the success rate increases and approaches 1.0, the expected amount and extent of altruism among descendants diverges

more greatly from the expectations based on kin selection, but becomes more consistent with the extent of altruism found in *traditional* societies (see Figure 5).

Figure 5: Table showing the amount of expected altruism (ranging from 0.0 to 1.0) among different co-descendants (siblings through seventh cousins) resulting from success rates of parental manipulation ranging from 0.0 to 1.0.



Predictions and Ethnographic Evidence

The model we propose can be expanded and refined to incorporate many additional variables (see “Discussion”), but even in this simplest of forms it generates numerous predictions that can be easily tested against ethnographic evidence. Space does not allow for anything approaching a complete review of the ethnographic descriptions of kinship altruism in traditional societies, as this literature makes up a large part of the accumulated work of cultural anthropologists. Thus, we now only present some of the key findings and representative statements directly relevant to the following key predictions generated from our concept, “ancestor-descendant conflict.” In all of these predictions, references to “traditional societies” will refer to societies where a large amount of cultural (i.e., socially learned and replicated) behavior is traditional (i.e., has been socially learned from parents and/or other ancestors, replicated, and then socially learned and replicated by offspring, often for many generations). The determination of the existence of traditions has always been a cornerstone of cultural anthropology. The categories of behavior most often evaluated in terms of their traditionalness include language, religion, rituals, diet, and dress (Coe 2003). The measurement of the traditionalness of different societies in order to test the following predictions would simply entail a continuation of this longstanding anthropological practice.

Prediction 1): Altruism toward kin more distantly related than predicted by Hamilton’s Rule (i.e., kin more distantly related than first cousins) will be universal in traditional societies. This prediction is supported by the previously presented statement by Murdock (1949).

Prediction 2): Altruism toward kin more distantly related than predicted by Hamilton’s Rule (i.e., kin more distantly related than first cousins) will *not* be universal in nontraditional societies. This prediction is supported by the previously presented

statement by Alexander (1979). Large amounts of ethnographic evidence support the further prediction, generated by the combination of predictions one and two, that there will be a positive correlation between the degree to which a society is traditional and the extent of its altruism directed toward distant kin.

Prediction 3): Verbal rules prescribing altruism toward distant kin will be universal in traditional societies where kinship altruism extends beyond the limits predicted by Hamilton's rule (i.e., kin more distantly related than first cousins). As previously stated by Bernstein (2005), there is a general pattern that traditional societies do indeed exhibit *prescriptive norms obliging distant kin altruism*. This is such a common feature of traditional societies that Fortes (1969:232) coined the "prescriptive" nature of this altruism the "axiom of kinship amity." A typical example of such a prescriptive rule obliging individuals to act altruistically toward distant kin is found in the description among the Ndembu of the "moral man" who is one who "honours his kinship obligations" (Turner 1979:374), and Middleton's statement that Lugbara state "The rules of social behaviour are the 'words of our ancestors'" (Middleton 1960; quoting the Lugbara of Africa). Despite this supporting evidence, further research focused on this specific prediction will be needed before this prediction can be fully evaluated.

Prediction 4): Traditional rituals encouraging both the acceptance of the influence of ancestors and altruism toward distant kin will be universal in traditional societies. Traditional rituals encouraging both the acceptance of the influence of ancestors and altruism toward distant kin will be universal in traditional societies. Prediction 4 is consistent with the finding by Steadman and Palmer (Steadman et al., 1996) that not only has ancestor worship been widely reported in many traditional societies, but supernatural claims about dead ancestors still influencing the living are found even in the ethnographic descriptions of all societies previously coded as lacking ancestor worship.

Prediction 5): Although there will always be some variability in the effectiveness of traditions in promoting altruism among co-descendants, when viewed over historical time, there is predicted to be a general pattern. This is the prediction that the deterioration of traditions will be followed by a contraction in the extent of distant kin altruism, producing the previously described correlation between traditionalness and distant kin altruism. That is, there will be less altruism toward distant kin *just because they are kin*. This is not the same as predicting there will be less altruism toward other people living in the same community or region. Hence, measures of altruism that are only focused on other community members in general (e.g., Henrich et al. 2004) instead of specific degrees of distant kin do not constitute a test of this prediction. Although there are instances when kinship has been temporarily emphasized in the face of tradition loss, as when people from traditional societies migrate to cities and rely almost exclusively on distant kin during the initial phases of the migration (Ferraro 1973), migration and other forms of tradition loss typically create "fewer kinship ties with [genealogically] *distant* relatives" (Goode 1963:1; emphasis added). For example, in his ethnography of an Irish community "in the midst of rapid social change from a traditional peasant organization to part of an industrial system," Leyton (1975:98) describes how "the kinship system and other traditional values . . . are impossible to sustain." He then emphasizes, that far from

this being a unique occurrence, it is occurring all over the world, as among the Nupe where “kinship relations . . . have been overwhelmed” and the Tallensi where the sentiment of kinship “dissolves” due to the loss of traditions.

Prediction 6): Highly traditional societies will exhibit a correlation between kinship distance and altruism even among very distant kin. As Palmer and Steadman (1997) point out, this is a crucial prediction because it is not predicted by any of the other standard evolutionary explanations of altruism: kin selection, reciprocal altruism, indirect reciprocal altruism, or multilevel selection. Much of the abundant ethnographic evidence consistent with this prediction comes from descriptions of segmentary opposition. Segmentary opposition occurs when

(descendents of) close kin stand together against more distant kin: (descendents of) brothers are allied against (descendents of) cousins, cousins against second cousins etc. Thus, even very distant kin will automatically put their conflicts to the side and unite against any threat from groups of non-kin . . . (Anthrobase Online Dictionary of Anthropology, 2009)

Sahlins (1961) points out that such a pattern of behavior, where the “closer the kin relation, the greater the sociability . . . the more distant, or more nearly unrelated, the less,” is one of the “very widespread—nearly universal—features of human social organization.” Palmer and Steadman (1997) provide numerous examples of the favoring of distant cousins over even more distant cousins from many parts of the world, including Africa, China and European peasant communities.

Another finding very consistent with our approach is that the genealogical distance at which distant kin are favored over still more distant kin and non-kin also appears to correlate with the degree of tradition loss. In extremely traditional societies, such as some of those in Africa when first studied by anthropologists, altruism flows outward along the ramifying channels of kinship to truly astonishing distances. This is illustrated by Fortes’ (1969:237) observation that the axiom of kinship amity “applies to all of the Tiv” where “the whole population of some 800,000 traces descent by traditional genealogical links from a single founding ancestor” (Keesing 1975:32-33). In contrast, in European peasant communities, in the midst of losing traditional patterns of behavior, the correlation between kinship distance and altruism extends further than the predictions of kin selection, but far less than among the Tiv. For example, in his section entitled the “Gradation of Obligation,” Leyton writes that

The kindred, however, is not an undifferentiated block. Obligations of equal strength are not extended to all members of a man’s kindred, but are determined according to the ‘closeness’ of genealogical relationship . . . with a gradual reduction in the strength of these obligations occurring as one nears the group’s peripheries. The individual feels obliged to perform acts for a brother’s son that he would not perform for a full cousin and so on. (Leyton 1975:44)

Leyton also emphasizes that the exact number and type of kin included in the reference “so on” varies between classes. In fact he appears to describe a community where traditions among one part of society have disintegrated to the point where the correlation between kinship distance and altruism starts to approach the pattern predicted by kin

selection. This is seen in the statement by one of Leyton's informants that among the upper classes, in contrast to the more traditional lower classes, "second cousins are just a little step above people you'd meet on the streets." (Leyton 1975:44)

Although much further testing of the predictions of our model can be performed with ethnographic data, including predictions generated by refinements in our model described below, it is clear that our predictions are supported by a great amount of ethnographic evidence. More specifically, the ethnographic evidence appears to suggest that our species has engaged in a large range of traditions of parents encouraging their offspring to be altruistic toward co-descendants, and that the success rates of these manipulations has varied from being high enough to extend to hundreds of thousands of co-descendants (i.e., success rates $> .9$) to modern "nontraditional" societies where traditions of parental manipulation of altruism toward distant co-descendants have essentially ceased to exist.

Discussion

Cronk and Gerkey (2007, see also Coe 2003) point out that the study of kinship altruism begins with, but cannot be limited to, Hamilton's rule. We have argued that to understand kinship altruism we need to understand its structure in traditional societies. We have modified and expanded Hamilton's rule to incorporate the influence of parental manipulation becoming traditional. The new rule states that the altruism expected among co-descendants is based on the formula $A_n = S^n + r_n (1-S^n)$. The revision is necessitated by the ethnographic evidence of nepotism far beyond the range of kin predicted by Hamilton's rule. Although ancestor-descendant conflict is almost certainly going to be most pronounced among humans, it may influence behavior in any species where parental behavior is to some extent traditional (Avital and Jablonka 2000).

Real life is obviously more complicated and variable than the examples used to demonstrate our model. As stated, however, the model generates the previously discussed testable predictions about correlations between the extent behavior is traditional and the extent and amount of altruism between kin. These predictions could be further tested through comparisons at both the societal and individual level. The model also directs future research toward identifying the specific behaviors that increase or decrease the success rate of parental manipulation. Such factors may range from ancestor worship, or holding ancestors in high honor, to residential rules and life histories increasing or decreasing the amount of contact between generations. Future refinements to the model include adjustments to reflect different degrees of manipulative success between mothers and fathers, and thus, different types of matrilineal and patrilineal ancestors (e.g., father's mother's mother, mother's father's father). This could then be used to predict differing degrees of altruism between half-siblings and half-cousins, as well as the effects of patrilocality and matrilocality. The influence of grandparents on their grandchildren could also be made higher than in subsequent generations to reflect greater success in manipulation resulting from the overlapping of life spans. The rates of manipulative success could also decrease after any given generation to model what might happen in a traditional society that comes into contact with a larger culture at some point in history.

It also will be of interest to eventually use this proposed mathematical model to develop evolutionary matrices and computer models that explore which degrees of

parental manipulation would be evolutionary stable strategies. This could be done by having different initial ancestors start traditions involving different degrees of successful parental manipulation in environments varying in the amount of distribution and amount of resources. Although we assume that such further applications and tests of our model will lead to major refinements and revisions, we are confident that a focus on the traditional aspect of human behavior will contribute to more powerful evolutionary explanations of human behavior for the simple reason that during much of human evolution, human behavior has been highly traditional.

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