Why Traditional Ethical Codes Prescribing Self-Sacrifice Are a Puzzle to Evolutionary Theory: The Example of *Besa*

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Abstract

Traditional codes of ethical behavior have been passed down from one generation to the next in all known cultures, suggesting that such traditional codes of how to behave and how not to behave may have been evolutionarily advantageous. In accordance with this view, many aspects of ethical codes appear to be easily accounted for by evolutionary theory. Others, however, do not. Foremost among the aspects of ethical codes that are puzzling to evolutionary theory are those encouraging forms of sacrifice for others that are not readily explainable by conventional evolutionary explanations of altruism. This paper illustrates this with the example of *besa*, a key concept in the traditional Albanian code of ethics (the *Kanun*) that emphasizes the promise to engage in various forms of altruism. It then presents an alternative evolutionary explanation of altruism based on the concept of traditional parental manipulation that may help explain the concept of *besa* and other aspects of traditional ethical codes.

Introduction

Scholars from various disciplines have been successful in demonstrating how many aspects of folklore from around the world make evolutionary sense in that they reflect evolutionary concepts relevant to aspects of human behavior ranging from mating strategies to foraging techniques. This folklore includes codes of ethical behavior as "all known societies have oral texts that validate a moral order" (Maddox, 2005, p. 1668). In regard to these codes, conventional evolutionary theory generates the general prediction that "people tend to pass the sorts of moral judgments that help move their genes into the next generation" (Wright, 1994, p. 146). While many aspects of traditional codes of ethics may conform to this prediction, some of the traditional behaviors parents influence their offspring to engage in do not. That is, some aspects of traditional codes of ethics promote behaviors that would be "unfit" in the sense of reducing the fitness and inclusive fitness of the individuals who engage in them. Among these puzzling aspects of traditional codes of ethics are exhortations to engage in forms of altruism that do not appear to coincide with conventional evolutionary explanations of altruism. An example of such behavior would be sacrificing one's life to save the life of someone who is not closely related under circumstances where the act is not likely to evoke any form of future benefits to the altruist's inclusive fitness. Many generations of Albanians have been swearing a traditional sacred oath, known as *besa*, to engage in a traditional ethical code of behavior (referred to in this paper as "the *Kanun*", but actually consisting of a number of slightly different *kanuns* in different regions of Albania) that includes exactly this form of altruism.

A Short History of Evolutionary Explanations of Altruism

Darwin's (1871) explanations of human altruism involved both individual selection and group selection (p. 161), but he was also aware of potential problems with group selection (p. 163). However, a century of

failed attempts to explain many forms of altruism with individual level selection led to widespread acceptance of group selection by the early 1960s (Wynne-Edwards, 1962). This was, however, quickly followed by a rejection of group selection and a return to attempts to explain altruism with individual level selection enhanced by the concept of kin-selection (i.e., inclusive fitness) (Hamilton, 1964) and an increased emphasis on reciprocal altruism (Trivers, 1971; Williams, 1966). In the 1980s explanations of altruism started to also emphasize indirect reciprocal altruism where the altruistic act enhances the altruist's reputation and thereby evokes reciprocity from someone other than the original receiver (Alexander, 1987).

Kin selection and reciprocal altruism provided explanations for many altruistic behaviors, but their inability to explain certain occurrences of altruism led to continuing attempts to find better explanations. Much of this effort has gone toward trying to determine if extremely complex patterns of indirect reciprocal altruism might account for additional forms of altruism (Atkisson & Smaldino, 2015), including the possibility that some forms of altruism might be explained as a form of costly signaling (Palmer & Begley, 2015). There have also been sophisticated attempts to calculate if limited dispersal can influence the degree of relatedness among members of a population in a way that might account for certain forms of altruism, as well as attempts at resurrecting various versions of multi-level selection (West, El Mouden & Gardner, 2011; Wilson, 2015). Many evolutionists also used the "Price equation" (Hamilton, 1975; Price, 1972) to conceptualize kin selection, reciprocal altruism, and group selection as "simply three systems of gene-tracking and fitness accounting from three different perspectives," and therefore, "any solution [explanation of altruism] can be reformulated from each perspective to yield the identical answer [explanation]" (Henrich, 2004, p. 10). When encountering acts of altruism that represent a puzzle because they cannot be solved by this fitness accounting (i.e., shown to increase the inclusive fitness of the altruist), another option is to attempt to explain them by cultural group selection (Soltis, Boyd & Richerson, 1995). However, both the reality of cultural group selection and its relationship to inclusive fitness remains open to debate (West, El Mouden & Gardner, 2011, p. 248). Another option is to question the actual existence of the act of altruism *claimed* to have taken place. For example, Schloss (2004) wrote, "If individual reproductive benefit were the only source of human moral beliefs and cooperative behavior, we would expect rhetorical affirmations of altruism to be largely uncoupled from genuinely sacrificial behavior" (p. 13). The remaining option is to explain away puzzling acts of altruism as merely rare aberrations (Teehan, 2010, p. 41). Despite the ability of these options to explain many aspects of human behavior, they do not appear to be able to account for some parts of traditional codes of ethics to which the oath of *Besa* is taken.

Besa: A Traditional Oath

The word *besa* is usually translated as "an oath, promise, a binding word of honor" (Mustafa, Young, Galaty & Lee, 2013, p. 104), and usually refers to taking an oath to follow the *Kanun,* a traditional code of ethics primarily found today in Albania and places to which Albanians have migrated (Boman & Krasniqi, 2012; Camaj, 1989; de Waal, 2005; Trnavci, 2010). Our argument concerning *besa* requires establishing that taking this oath to follow the *Kanun* is both traditional and involves forms of sacrifice puzzling to conventional evolutionary theory.

Establishing that *besa* is traditional requires challenging a trend in anthropology and folklore to deny the existence of long-lived traditions (i.e., behaviors transmitted from parents to offspring for many generations). We acknowledge that it is often impossible to know exactly when different parts of a traditional code of ethics originated, as well as how and when different parts may have been modified during transmission or even invented (Hobsbawm & Ranger, 1983) and then falsely asserted to have been transmitted from earlier generations of ancestors. However, it is important to recognize the evidence of actual traditional transmission of behaviors (Mathew & Perreault, 2015; Fragaszy, 2003), and to realize that falsely claiming something to be a tradition would not prove to be "a particularly useful ideological resource"

(Schwandner-Sievers, 2001, p. 97) if behaviors actually transmitted for many generations were not seen as being important and influential. What is needed is a theory that can account for not only the breaking, manipulating, rejecting, and inventing of traditional codes of behavior, but also for the existence of traditional codes of behavior (Palmer, 2010; Palmer, 2013a; Palmer, Begley, Coe & Steadman, 2013).

There is no question that offspring, at the bequest of their parents, have taken the oath of *besa* to follow "a detailed guide to how to behave in many, indeed most, possible forms of human interaction" (Schwandner-Sievers, 2002, p. 7), and required their own offspring to take the same oath of *besa* when the time comes for them to do so. The question is over how many generations this behavior has been transmitted from one generation to the next, and how much the behaviors regarding religion, family, marriage, house and property, hospitality, work, speech, honor, punishment, and law (Fox, 1989; Mustafa, Young, Galaty & Lee, 2013) stipulated in the *Kanun,* have changed over those generations.

Precise answers to these questions are impossible because "it is impossible to be too definite" about the origins of Albanians (Iseni, Iseni & Beadini, 2013, p.50; see also Kola, 2013; Tarifa, 2008), and various claims about these origins have been used in debates over Albanian identity, borders, and other political issues (Galaty, Lafe, Lee & Taflica, 2013, p.7; Schwandner-Sievers, 2001; 2002; 2003; 2004; 2008; Vickers, 1995). There has also been debate over the number of generations individuals have taken the oath of *besa* to follow the *Kanun*. At one extreme, Vickers (1995) claimed that this tradition has been "inherited from the Illyrians...[and] transmitted orally down through the generations" (pp. 5-6). Fox even speculated that it "may indeed date back to remote antiquity, to the era before the vast migrations of the Indo-European people" (Fox, 1989, p. XVI), and suggested that it may share a common origin with aspects of the traditional codes of ethics found in surrounding areas (Fox, 1989, p. XIX; see also Pollo & Puto, 1981). At the other extreme, much of the work since the end of Communism has largely ignored or denied the existence of traditional forms of behavior in Albania because this work "has been informed directly by recent social theory, postcolonial theory in particular, which tends to de-emphasize further the study of tribalism, focusing instead on the individual agency of northern Albanian themselves" (Galaty, Lafe, Lee & Taflica, 2013, p. 7; see also Schwandner-Sievers, 2001, p. 98).

In evaluating these two positions it is important to note that even scholars, such as Galaty, Lafe, Lee & Tafilica (2013), who accurately criticized the notion of Albanians being so traditional that they represent a "people stranded in time" (p. 6), described many aspects of Albanian culture as traditional and emphasize that in Albania "there is continuity in change" (p. 2; see also Schwandner-Sievers, 2001). Further, the aspects of culture continuing many generations include "oral traditions passed from father to son" (Lee, Lubin, & Ndreca, 2013, p. 45), and these include "localized forms of traditional law" (Mustafa, Young, Galaty & Lee, p. 104). Further, it is agreed that the tradition of taking the oath of *besa* to follow traditional laws is much older than the period of 1389-1429 when Lek Dukagjin (1410-1481), chief of the the Dukagjin family, and the leaders of other prominent families, are said to have "laid down the northern tribal laws and customs known as the *Kanun"* (Lee, Lubin and Ndreca 2013, p. 46; see also Bardhoshi, 2012, p. 67; Mustafa, Young, Galaty & Lee, 2013, p. 100; Jacques, 1995; Elsie, 2001; Vickers & Pettifer, 1997; Hasluck, 1954).

In light of this evidence, it is clear that details of the Albanian Kanun have at times been modified (i.e., "adapted to circumstances" Schwandner-Sievers, 2001, p. 97) as it has been transmitted from one generation to the next, and this has led to a variety of similar *kanuns*. It is also clear that "Albanian traditions have been invented and revitalized" in recent political debates (Schwandner-Sievers, 2008, p. 54). However, it is also clear that taking the oath of *besa* to follow the *Kanun* qualifies as a tradition because for many generations it "was transmitted orally from one generation to the next" (Vickers & Pettifer, 1997, p. 132). Further, despite dramatic changes in other aspects of Albanian culture:

> The *Kanun* is by no means a relic of the past. Many of its precepts continue to play an important role in the lives of Albanians throughout the world, even in Albania itself where the communist

> regime has attempted, since its violent inception, to suppress or extricate any laws and customs other than its own. (Fox, 1989, p. XIX; see also Voell, 2012, p. 150; Bardhoshi 2012, p.69).

Mustafa, Young, Galaty & Lee (2013) also referred to the "ongoing reliance on the *kanun*" (p. 105; see also Boman & Krasniqi, 2012), and Voell (2012) reported that children currently living in Albania "still knew about the importance of their own cultural traditions" (p. 147). Thus, taking the oath of *besa* to follow the *Kanun* can be seen as a tradition spanning the transition from traditional cultures to the modern nation state (Lubonia, 2002; see also Begley, Coe & Palmer, 2015).

Besa: An Oath to Sacrifice for Others

The best known aspects of the *Kanun* concern how the oath of *besa* is applied to blood feuds and hospitality. Both of these examples of *besa* are promises to sacrifice for others when certain events occur. The importance of making sacrifices to maintain honor in blood feuds is frequently depicted in novels, movies, and plays (e.g., Romano & Miceli, 2016); and often emphasized in explanations of the entire Kanun (Mustafa, Young, Galaty & Lee, 2013). The relationship of blood feuds to evolutionary theory and the transition from traditional to state societies is discussed by Begley, Coe, and Palmer (2015). Here we focus on the aspect of *besa* related to hospitality because it is the aspect most puzzling to evolutionary explanations of human behavior.

In the section on social honor and degree of relationship, the *Kanun* states that "after you have said, 'Welcome,' he [the guest in your house] must have no fear and know that you are ready to defend him against any danger" (Fox, 1989, p. 132). The gravity of the obligation to defend a guest is revealed in the stipulation that "if someone mocks your guest, or abuses him, *you must defend your guest's honor, even if your own life is in danger* [emphasis added]" (Fox, 1989, p. 136; for an example of a blood feud resulting from the killing of a guest, see Mustafa, Young, Galaty & Lee, 2013). The importance of this pledge to sacrifice one's life to protect a guest is described by Dharssi and Krieger (2010):

> Meaning "to keep the promise," Besa is a code of honour that holds a central place in Albanian culture. It is linked to an Albanian folk principle of taking responsibility for others in their time of need. According to one Albanian saying, "Albanians would rather die than break Besa." (p. 18)

Besa also obligates people to be willing to kill their own close kin in order to protect a guest, as Hasluck (1954) recounted, "Children in *Shalë* [a valley in northern Albania] were taught with great pride that once a tribesman killed his brother for killing a guest, for an Albanian's duty to his guest transcends the claims of blood relationship" (p. 211).

Besa: An Evolutionary Puzzle

From an evolutionary perspective, the first puzzling aspect of pledging *besa* to follow the *Kanun's* prescriptions concerning the protection of guests is that this entails sacrifice for all guests who are members of one's *fis*. This is a puzzle because a *fis* is a category that includes many kin far more distantly related than the range of kin where such acts of sacrifice could possibly be accounted for by kin-selection.

Scholars have struggled over whether a *fis* is a lineage, clan, or tribe. For example, Fox (1989) settled on the term clan (p. XX), and Mustafa, Young, Galaty & Lee (2013) differentiated between two types of *fis*. They referred to a small *fis* (*fis i vogël*) as a patrilineage, and describe it as a "line of descent that includes cousins, both immediate and distant" (p. 89). They then stated that "the *fis i madh* ('big *fis'*)" is a "wider lineage network composed of all those individuals who trace descent from a single, probably mythical, ancestor, sometimes glossed as 'tribe'" (p. 90). Although it might be convenient to refer to a large *fis* as a tribe, it is misleading because a *fis* is exogamous and thus this category of people does not approximate either a breeding population or a self-contained "people" or "culture." Instead, a *fis i vogël* appears to co-

incide with what anthropologists typically call a lineage, and *fis i madh* a clan, because these terms refer to smaller and larger categories of individuals defined by having the same descent name. The "growth and elaboration of patrilineages" (Mustafa, Young, Galaty & Lee, 2013, p. 87), which transforms a *fis i vogël* into a *fis i madh,* has been observed in traditional cultures throughout the world where "...large lineages or clans grow up over time as the descendants of the original ancestor/ancestress accumulate" (Fox, 1967, p. 122). The potential multi-generational duration of this process is indicated by the Albanian saying "blood goes endlessly" (Gjeçovi, 1993, p. 122), and the extent to which this potential has been realized is indicated by Whitaker's (1968) observation that "the genealogies of individual persons would be carefully remembered, showing a link by male descent with the founder of the clan, who might have lived thirteen or fourteen generations earlier" (p. 254). The concept of *fis* also appear to exhibit the segmentary opposition (Evans-Pritchard, 1940) typical of such descent name categories whereby lineages, clans, and still larger categories of multiple clans claimed to have a common ancestor, unite in opposition to outside threats: "Sometimes *fis* would join together into larger confederacies (*farë e fis*), (Mustafa, Young, Galaty & Lee, 2013, pp. 90-91). Indeed, "the historical process that led to the current structure of the Shala *fis* presents an excellent example of tribal segmentation, whereby through time, larger social units grow and fission along kinship lines" (Mustafa, Young, Galaty & Lee, 2013, p. 106).

The important point is that kin selection cannot account for the vast majority of kin to whom individuals pledge to sacrifice for by taking the oath of *besa.* This is because even the smaller *fis* include both immediate and distant cousins, while the large *fis* include far more distantly related cousins, and confederations of *fis* include cousins who are still more distantly related. Indeed, there is emphasis placed on the obligation to sacrifice in order to protect a guest who is not close kin, and may not even be distant kin. Fox (1989) stated that "the guest (*mik*) [*miq*] usually belongs to a different brotherhood, village, or clan" (p. 136), and Mustafa, Young, Galaty & Lee (2013) referred to *miq*, not as kin, but as "friends of the family" (p. 105).

The oath to be willing to die to protect a very distantly related, or even unrelated, guest could, in some instances, be potentially explained by reciprocal altruism. Indeed, Fischer (1984) stated "*Mik* means linked through reciprocity" (p. 110). However, the *Kanun* stresses that hospitality requiring such sacrifice was not to be restricted to likely reciprocators. Jacques (1995) described how *besa* requires extreme sacrifice for not just those who may reciprocate, but even to those with whom one has a hostile relationship: "Hospitality was a sacred obligation, the host being required to avenge harm to one's guest....The *besa* or *besa-besën* (word of honor) was an oath or pledge to keep one's word, and when extended...to blood enemies was absolutely sacred and inviolable" (p. 176).

Besa's encouragement of extreme sacrifice for individuals who are neither close kin nor likely reciprocators might be explainable by some form of group selection. However, the group that might be benefiting from this sacrifice is not readily apparent. Neither the small or large *fis* constitute promising candidates for group selection because neither category forms a residential group. Although some of the members of a small *fis* may live in the same place, others do not (Mustafa, Young, Galaty & Lee, 2013, p. 89). Exogamy also means that "all villages are inhabited by several lineages..." (De Rapper, 2012, p. 85), and larger geographic areas will have members of different large *fis* (Galatay, Lafe, Lee & Tafilca, 2013, p. 26; see also Voell 2004; Bardhoshi, 2012). Further, the emphasis placed on the willingness to sacrifice for the benefit of "enemies" would appear to go against the hypothesis that the sacrifice benefitted even a temporary "trait-group" (Wilson, 2015, p. 152) of cooperating individuals.

Thus, the oath of *besa* in this context entails promising to sacrifice one's own life, and/or the lives of one's family members, in order to protect someone who may be neither close kin nor a co-member of any form of salient group, and to do so without consideration of future benefits resulting from direct or indirect reciprocity. That is, the exhortation to make such a sacrifice is not contingent on any of the conditions predicted by evolutionary theory. Instead, it is only contingent on the act being prescribed by ancestors as

the "right" and "honorable" way to behave. This is consistent with the observation that "one of the guiding principles [of *besa*] is...sacrifice for the sake of honor" (Schwander-Sievers, 2002, p. 7).

Another possible evolutionary explanation is that all of the talk about *besa* was just talk. That is, there was a tradition of talking about sacrifice, but actual acts were so rare that they do not warrant an explanation. This might be a plausible explanation if the evidence of actual acts of altruism resulting from *besa* was confined to stories of such acts (Durham, 1909, p. 171; Gawrych, 2006, p. 12). There is, however, much stronger evidence. During World War II at least several thousand Albanians hid Jews, and others, from the Nazis, and often claimed that it was their oath of *besa* that led them to do so (Nidam-Orvieto & Steinfeldt, n.d.; Gershman, 2008; Perez, 2013; Paldiel, 2008). These acts of altruism occurred despite the fact that "the German army...issued orders...to kill the relatives of those who resisted their forces" (Vickers, 1995, p. 152).

Although it is impossible to know exactly how many Albanians risked the lives of themselves and their families to rescue Jews, the Yad Vashem organization of Israel received a list of 3,280 Jews claimed to have been saved by Albanians during WWII. Further, as of 2015, 73 Albanians have been awarded the title of "Righteous Among the Nations" by Yad Vashem. This is particularly significant because the criteria required to be awarded this title effectively eliminates the possibility of the behavior being explainable by conventional evolutionary explanations of altruism:

> A person can be considered for the title of "Righteous Among the Nations" when the data on hand based on survivor testimony or other documentation, clearly demonstrates that a non-Jewish person risked his or her life, freedom, and safety, in order to rescue one or several Jews from the threat of death or deportation without exacting monetary compensation or other rewards. (Yad Vashem Web Page)

This single sentence stipulates that the altruism had to involve extreme sacrifice (i.e., risking of life, freedom, and safety), had to benefit someone who was neither close kin nor of the same group (i.e., a non-Jew had to sacrifice to benefit a Jew), and could not be done to reap benefits from reciprocation of any kind (i.e., monetary compensation or other rewards). Thus, it essentially stipulates that the title of "Righteous Among the Nations" is only awarded to individuals who behaved contrary to the predictions of conventional evolutionary theory (Palmer, 2013b). Further, there had to be evidence that this altruistic behavior actually took place and was not "just talk".

Although it might be argued that this number of individuals, as well as the total number of people awarded the title of Righteous Among the Nations (25,685 as of January 1, 2015) may be consistent with the rare aberration argument, this explanation cannot account for why the Righteous Among the Nations and other altruists are so often portrayed to be moral exemplars that inspire others (Palmer, 2013b). More generally, it cannot account for why traditional codes of ethics requiring apparently unfit forms of sacrifice (e.g. sacrificing one's life in battle) may be wide spread, if not universal (Palmer, Begley & Coe, 2013; Palmer, Begley, Coe & Steadman, 2013). Hence, the consideration of an alternative hypothesis about altruism that explicitly incorporates the traditional encouragement of altruism is warranted.

An Alternative Evolutionary Explanation: Traditional Parental Manipulation

To find a new explanation of altruism capable of accounting for traditional codes of ethics, we start by returning to a largely unused third explanation of altruism first put forth in the mid-1970s. The parental manipulation explanation of altruism (Alexander, 1974; Dawkins, 1982; West-Eberhard, 1975) is based on the concept of parent-offspring conflict. 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" and in favor of the interests of the parent (p. 249). This attempted molding, or manipulation, is the result of the simple biological fact that a parent is equally related to all of his or her offspring, but the off-

spring is completely related to itself (r = 1) and only half related to a full sibling (r =0.5) (where "r" stands for degree of relatedness within the range of 0 to 1). Therefore, evolutionary theory predicts an "offspring should value its personal fitness twice as much as it values any full sib's fitness" (Kurland & Gaulin, 2005, p. 452), but parents should try to influence offspring to value a full sibling as much as it values itself (Wright, 1994, p. 166). This is because both siblings are equally valuable to the parent in terms of genetic relatedness because both offspring are equally related to the parent. This prediction is supported by the apparently cultural universal of encouragement of altruism toward kin, labelled by anthropologists as the "axiom" of "kinship amity" Fortes, 1969, pp. 231-232).

During the 1970s, evolutionists recognized that "humans are parental manipulators par excellence" (Alexander, 1974, p. 367) and that a human parent could suppress selfish behavior even in their adult offspring, and even after the death of the parent (Alexander, 1974, p. 368; Trivers, 1974, p. 262; West-Eberhard, 1975, p. 18). However, these insights only scratched the surface of the potential behavioral consequences of parental manipulation because they only considered the influence of parental manipulation on the next generation of descendants. Two decades later, Voland and Voland (1995) suggested that "the conscience evolved within the context of parent/offspring conflict over altruistic tendencies" (p. 397) and functioned to reduce the "selfish impulses" of offspring (p. 401). Then Voland and Voland (1995) came tantalizingly close to recognizing the full consequences of parental manipulation when they referred to the possibility of offspring being "raised to 'voluntarily' stake at least part of their reproductive fitness for the maintenance and welfare of their families and thus to the long term advantage of their *lineage* [emphasis added]" (p. 407). The use of the word "lineage" is crucial because it refers to a chain of ancestors and descendants, and therefore implies a time-span much longer than one individual's entire lifespan.

The failure to follow up on this insight is unfortunate because recognizing that this manipulation can be extended past a single generation leads to a profound new prediction about how individuals should be expected to behave. If individuals who influenced all of their offspring to "treat each other as if you valued them as much as yourself" (i.e. r=1.0) have been favored by natural selection over individuals who did not influence their offspring to behave this way toward their siblings, then individuals who had grandchildren influenced to treat all of their co-descendants as if they valued them as much as themselves (i.e. r=1.0) would have been favored over individuals who did not have their grandchildren influenced to behave this way toward their siblings *and first cousins*. Further, individuals who had all of their *great-grandchildren influenced* to "treat each other as if you valued them as much as yourself" (i.e. r=1.0) would have been favored over individuals who did not have their great-grandchildren influenced to be this way toward their siblings, first cousins, *and second cousins*, and so on, and so forth. This leads to the conclusion that selection would have favored individuals who were most success at influencing the social behavior among the most distant generation of their descendants (Steadman & Palmer, 2008; Coe, Palmer, Palmer & DeVito, 2010; Palmer & Palmer, 2015).

The question is then: How could individual humans possibly influence descendants born many generations after their own death to be willing to sacrifice for their distantly related co-descendants? The answer is as simple as it has heretofore been unappreciated: through transmitting traditional behaviors that influenced each generation to be willing to make such sacrifices *and* to replicate that transmission to the next generation. Such a multi-generational approach is fully compatible with the view that natural selection can be most accurately measured over a large number of generations than in terms of the number of surviving children or grandchildren produced (Alexander, 1974, p. 346; West-Eberhard, 1975, p. 29; Dawkins, 1982, p. 184). It is also consistent with evidence of cultural traditions often enduring many generations (Palmer, 2010; Mathew & Perreault, 2015), and with examples where explicit emphasis is placed on replicating the traditional code of ethics to each generation. For example, Sosis (2008) wrote:

> Arguably the central Jewish prayer, the V'ahavta (the first paragraph of the shema), which is placed inside the mezuozot (hung on Jewish doorposts) and tefillin (phylacteries), emphasizes the importance of teaching the Torah's laws to children. Ironically, this is the first prayer that Jewish

> children learn, so children are thereby taught the importance of teaching Jewish ways to their children. (p. 214)

The final question that needs to be addressed is: How could selection favoring the ability to influence distant generations of descendants to sacrifice for their genealogically distant co-descendants, lead to a code of ethics specifying similar actions to be directed toward individuals who were not co-descendants. We suggest that the traditions exhorting sacrifice for others occurred during a period when all individuals consistently were co-descendants. That is, "we were made for a world...in which all activities were enmeshed in webs of kinship..." (Cronk, 1999, p. 119). In such an environment there would not be selection to make the distinction between kin and non-kin and to restrict the altruism to only kin. This allowed for traditional codes of ethics to be modified relatively easily to encourage sacrifice for even unrelated individuals in other groups who are unlikely reciprocators.

Conclusion

Although the tradition of pledging *besa* to follow the *Kanun* is unique in its details, we propose that following the lineages of all living humans into the past would lead to ancestors who influenced the behavior of many generations of descendants through transmitting traditional codes of conduct. That is, the saying of the Lugbara of Africa that "the rules of social behaviour are the 'words of our ancestors'" (Middleton, 1960, p. 27), would apply to all of our ancestors. Further, the fundamental values to which one pledged *besa* also appear to be universal. For example, Turner (1975), who reported that among the Ndembu, the "moral man" is one who "honours his kinship obligations" and "respects and remembers his ancestors," also reported that these "moral values and...ethical code...would be recognized as valid by all human groups" (p. 238).

We propose that focusing on the traditional nature of these codes will significantly contribute to the explanation of forms of human altruism puzzling to conventional evolutionary explanations. Further, this approach may also help to account for the many other forms of behavior that often accompany the transmission of traditional codes of behavior. For example, the behaviors prescribed in the *Kanun* were not simply transmitted from parents to offspring as simple instructions of how to behave. Instead, the tradition was made more interesting, and thus more influential, through being transmitted in stories, songs, and plays, and these accompanying behaviors often emphasized the importance of keeping one's *besa* to sacrifice for others as prescribed by the *Kanun*. Whitaker (1968) explained how "traditional Albanian epic songs (këngë trimnijë)...reveal the Canon of Lekë Dukagnini in operation" (p. 265), and Mustafa, Young, Galaty & Lee (2013) observed that the pledge of *Besa* to follow the social behavior require by the *Kanun* is "informed by cultural narratives so immense and unique to the people of the valley that entire books have been written about them" (p. 85). For example, the play "*Besa yahud Ahde Vefa* (*Pledge of Honor or Loyalty to an Oath)"*, written by Şemseddin Sami Bey Frashëri and first performed on stage in Istanbul in 1874, emphasized the oath to engage in sacrifice that would appear to be evolutionarily "unfit" because the hero righteously sacrifices both his own life and that of his son in order to keep *besa*. The author of this play, Şemseddin Sami, observed: "Albanians are very strong in defending their ancestors' morals [*ahlak*], customs [*adat*], honor [*namus*] and race/nationality [*cinsiyet*] as well as in [fulfilling] their oath that they call besa" (as quoted in Gawrych, 2006, pp. 97-98). To this observation, we add that his play probably helped transmit the tradition of *besa* to future generations, and that many forms of folklore, literature, and art in other cultures also facilitated the transmission of traditions encouraging sacrifice for others.

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COMMENTS

on Palmer and Palmer

Parental manipulation vs. multi-level selection: Equivalent or Alternative Hypotheses?

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The example of *Besa* discussed by Palmer and Palmer (hereafter PP) is one of many examples in which individuals are expected to abide by the commandments of their moral community, even when it entails sacrifice to self and kin. They focus on a norm of protecting guests in one's home, but they could have equally focused on the story of Abraham's willingness to sacrifice his only son, Isaac, for no reason at all other than obedience to his God.

These acts of obedience to one's moral community are puzzling against the background of inclusive fitness theory, as it was originally formulated in the 1960's. The original formulation assumed that behaviors are coded directly by genes and calculated an "inclusive fitness" based on fitness effects on self and others, weighted by the probability or sharing genes identical by descent. According to this logic, individuals should never help unrelated individuals or more distantly related kin at the expense of more closely related kin. Other theories are required to explain such behaviors, such as reciprocal altruism, group selection, or parental manipulation.

A lot has happened since the 1960's, which is only partially reflected in the target article. Inclusive fitness theory has gone way beyond the narrow interpretation of genes that are shared through identity by descent. The coefficient of relatedness (r) is now interpreted more broadly as a correlation coefficient between the phenotypes of the actor and recipient (see Birch and Okasha 2014 for a recent review). Take the case of parental manipulation as an example. For simplicity, imagine that parents are able to completely

control the behaviors of their offspring toward each other. Sibling interactions are therefore phenotypically uniform within each family but differ between families, leading to a phenotypic coefficient of relatedness of r=1. In the language of multi-level selection theory, there are no fitness differences among siblings within families and there are fitness differences between families, so parental manipulation is a case of pure between-family selection.

This hypothetical example illustrates the concept of equivalence, or theoretical frameworks that offer different perspectives on the same causal process, as opposed to invoking different causal processes (Wilson 2015, ch 3). Non-equivalent frameworks invoke different causal processes and deserve to replace each other on the basis of empirical evidence, in the standard scientific fashion. Equivalent frameworks deserve to coexist to the extent that they offer useful insights by virtue of their different perspectives. It is a great mistake to argue equivalent frameworks against each other, as if one can be right and the other wrong. Instead, it is important to develop an ability to translate between equivalent frameworks, similar to translating between different languages.

PP briefly allude to equivalence in their target article (citing Henrich 2004, p. 10) but treat their own parental manipulation hypothesis as non-equivalent. Either way, I find their hypothesis highly implausible. A causal mechanism is required to explain how parents influence the phenotype of their offspring beyond sharing half of their genes. The mechanism might be epigenetic or behavioral. A causal mechanism is also required to explain how ancestors influence the phenotypes of their distant descendents. Insofar as the mechanism is behavioral, then PP's hypothesis invokes the transmission of behaviors across generations, which is cultural evolution. In their reply, I hope that PP will spell out how a cultural norm such as *besa* can evolve by ancestor manipulation, *compared to alternative norms*. Evolution is a comparative process. Presumably there were other norms that died out in competition with the besa norm. At what scale did the competition occur? Between individuals within socially defined groups? Between socially defined groups? I will be surprised if this line of inquiry does not end up identifying a form of cultural group selection.

Even when we follow PP's logic, an add-on is required to explain the "puzzle" of *besa*. The norm must have evolved during a historical period "when all individuals were consistently co-dependents". No evidence is provided in support of this claim, which remains a speculative "just-so" story.

I conclude this commentary with a few observations.

1) A norm such as *besa* is not a puzzle. It is the nature of morality that individuals are expected to subordinate their self-interest to the interest of their moral community. Subordinating self-interest includes subordinating interest in genealogical relatives.

2) To the best of our current knowledge, the genetic and cultural traits associated with morality evolved by between-group selection. Very simply, groups that manage to function in a well-coordinated fashion and avoid disruptive self-serving behaviors among their members outcompete other groups. This was Darwin's hypothesis and its modern exposition can be found in books such as Boehm (1999, 2011) and Turchin (2005, 2015).

3) Parental manipulation is not an alternative hypothesis. It assumes that evolution takes place in a multi-group population. Parental manipulation influences the partitioning of behaviors within and among groups, and so on. PP need to demonstrate their grasp of equivalence by translating their model into the language of multi-level selection theory.

4) The specific norm of *besa* makes good functional sense for a segmented society subject to chronic feuding. While I am not familiar with the details of Albanian society, it is probably similar to the feuding

Montenegrin society described by Boehm (1984) and to Evans-Pritchard's (1940) original account of segmentary opposition among the Nuer. In these societies, segments shift back and forth between competition and cooperation depending upon the scale of the common threat. Conventions and norms are required for segments of the society to resolve their conflicts other than by endless feuding. The leopard skin chief performed this function in traditional Nuer society (Evans-Pritchard 1940; discussed from a multi-level cultural evolutionary perspective in Sober and Wilson 1998 p. 186-191). Chosen from an unimportant lineage, he was given sacred status to arbitrate homicide disputes. Without this convention enforced by norms, it is almost certain that Neur society would have disintegrated into smaller social units that would be unable to unite in the face of common threats. In other words, between-group selection is a strong and observable force capable of explaining the cultural evolution of the social convention. I can well imagine that *besa* performed a similar function in Albanian Society. Currently opposed segments would need to mend their differences to unite in the face of a common threat. This would require meeting in each other's homes and protecting visitors from one's own kinsmen bent on revenge. In this fashion, the norm of *besa* can be explained at face value as a group-level adaptation without turning it into a puzzle.

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Self-Sacrifice for Unrelated Individuals: Further Considerations

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Self-Sacrifice for Unrelated Individuals: Further Considerations

Palmer and Palmer (this issue) argue that existing evolutionary accounts of altruism (i.e., kin selection, reciprocal altruism, and group selection) do not explain certain aspects of traditional ethical codes, such as self-sacrifice for unrelated individuals. They also assert that the "rare aberration" argument (e.g., Teehan, 2010) cannot account for why altruists are portrayed to be moral exemplars, and offer examples of self-sacrifice to refute the argument that actual acts of self-sacrifice are so rare that they do not warrant an explanation. Finally, Palmer and Palmer present an alternative explanation based on parental manipulation that may account for some occurrences of altruism, including self-sacrifice for unrelated individuals prescribed by the *Kanun*.

Palmer and Palmer seem to offer a reasonable, alternative, evolutionary explanation for why some traditional codes of ethics advocate self-sacrifice for unrelated individuals. However, self-sacrifice for unrelated individuals may be motivated by several, non-exclusive reasons. In this comment, we identify and address theoretical concerns, including: 1) the actual occurrence of self-sacrifice for unrelated individuals, 2) the rare aberration argument, 3) parental manipulation as an alternative explanation for self-sacrifice, such as prescribed by the *Kanun*, and 4) modifications of traditional codes of ethics to encourage sacrifice for unrelated individuals.

Actual occurrence of self-sacrifice for unrelated individuals

Palmer and Palmer comment that "all of the talk about *besa* was just talk" (e.g., Schloss, 2004). They argue that this is unlikely to be correct, given the evidence that self-sacrifice does occur. They point out the thousands of Jews who claimed to have been saved by Albanians during World War II. However, we are not convinced that the evidence presented by Palmer and Palmer is sufficient to refute the aberration argument. The authors assert that "it is impossible to know exactly how many Albanians risked the lives of themselves and their families to rescue Jews". We rather state the opposite: It is impossible to know exactly how many Albanians *did not* risk the lives of themselves and their families to rescue Jews.

It is probable that there are far more Albanians who *did not* help Jews than who *did* help them – simply because humans are built by ruthlessly selfish genes (Dawkins, 1976). In fact, history is rife with stories of selfish behavior. During the Cold War, Americans who turned in supposed communists gained the benefits of being considered patriots and moral exemplars. It is not surprising that some Americans sold out even their relatives. Recently, many Europeans refused to host Syrian refugees, for the sake of their own social welfare. Therefore, self-sacrifice for unrelated others may be infrequent enough that it qualifies as an aberration, an error of evolved machinery of the mind. When it has occurred, it seems to be confined to very specific cases (e.g., "Righteous among the Nations"), and often entails very specific behaviors – maybe even a rare aberration, as suggested by previous evolutionary scholars (e.g., Teehan, 2010).

Self-sacrifice as rare aberration

One of the explanations for this sort of altruism is that such behaviors reflect the outcome of an evolutionary "glitch" (i.e., a rare aberration; Teehan, 2010). Palmer and Palmer state that such an argument cannot account for why such people are "so often portrayed to be moral exemplars that inspire others". More generally, and according to Palmer and Palmer, it cannot account for why such "traditional codes of ethics requiring apparently unfit forms of sacrifice (e.g., sacrificing one's life in battle) may be wide spread, if not universal". However, apparently maladaptive forms of sacrifice (such as sacrificing one's life in battle) might have selfish motives, such as the promise of compensation (e.g., pension, prestige); and those who sacrificed themselves for the sake of the others may be considered moral exemplars simply because such anomalous behaviors – the pure altruistic behaviors – benefit others.

Because altruistic behaviors benefit others, individuals who perform them are often regarded as heroes and moral exemplars; and because they benefit others, many forms of folklore, literature, and art facilitate the transmission of traditions that encourage sacrifice for others. This does not mean that individuals are seeking to become moral exemplars by sacrificing themselves for others. It also does not mean that all individuals who took the oath of *besa* to follow the *Kanun* are in fact prone to perform such acts. Therefore, we are not convinced that the rare aberration argument cannot be among the valid evolutionary explanations for such acts of self-sacrifice.

Parental manipulation as an alternative explanation

Palmer and Palmer offer parental manipulation (Trivers, 1974) as an explanation for self-sacrifice for individuals who are neither close kin nor a co-member of a social group. According to Palmer and Palmer, parents are expected to encourage an offspring to value full siblings as much as himself or herself – as parents are equally related to all their offspring. Similarly, grandparents are expected to encourage a

grandchild to value cousins as much as himself or herself – as grandparents are equally related to all their grandchildren. We argue that it may not have been ancestrally advantageous for parents to encourage an offspring to value cousins as much as himself or herself, because the offspring's cousins are less related to the parents than is the offspring. Similarly, it may not have been ancestrally advantageous for grandparents to encourage a grandchild to value *second cousins* as much as himself or herself, and so on. Therefore, parental manipulation, if extended past a single generation, embodies an intergenerational conflict of interests. The question is: What are the ancestral advantages for parents to encourage an offspring to value co-descendants (with the exception of full siblings) as much as himself or herself, if such co-descendants (e.g., first or second cousins) are not equally related to parents as the offspring is?

Modifications of traditional codes to encourage sacrifice for unrelated individuals

Palmer and Palmer suggest that the "traditions exhorting sacrifice for others occurred during a period when all individuals consistently were co-descendants" and "this allowed for traditional codes of ethics to be modified...to encourage sacrifice for even unrelated individuals in other groups who are unlikely reciprocators". They argue that, in ancestral environments, individuals interacted most often with genealogically close co-descendants; in the modern world, because we live in larger social groups, individuals are less likely to be genetically related to members of the social groups to which they belong.

Such differences between ancestral and modern environments did not modify human proneness to sacrifice the self for others (i.e., co-descendants), but may have led to the modification of traditional codes of ethics, to encourage sacrifice for unrelated individuals. However, it is not clear *why* traditional codes of ethics may have been modified to encourage sacrifice for unrelated individuals. If the mechanism underlying such codes of ethics is *specifically* the proneness to perform self-sacrifice for co-descendants, then why have such codes of ethics – which can be modified during transmission – not been modified accordingly, i.e., to *specify* sacrifice for genealogically close co-descendants rather than for unrelated individuals?

Conclusion

In an engaging and fascinating paper, Palmer and Palmer seem to identify a reasonable, alternative, evolutionary explanation for why some traditional codes of ethics encourage self-sacrifice for unrelated individuals. However, we argue that some existing evolutionary explanations are plausible, and that Palmer's and Palmer's explanation is not in conflict with them. For instance, as suggested by Palmer and Palmer, individuals might follow this code of ethics because it is consistent with the proneness to self-sacrifice for others. However, some individuals might take the oath of *besa* to follow the *Kanun* because they secure the benefit of social acceptance, and they did not expect and neither did they intend to sacrifice themselves for unrelated individuals. Also, individuals might follow *besa* as a culturally-supported aberration to perform extreme altruistic behaviors – behaviors that made them moral exemplars because of the bevy of benefits bestowed on others.

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Cultural Power and Manipulation

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Evolutionary theory for human cultural evolution is based on an apparent paradox: each individual is expected to strive to maximize their own inclusive fitness, but the moral codes of most, if not all human cultures, exhort their members to be altruistic and self-sacrificing. Several conceptual frameworks purport to explain this foundational human hypocrisy.

First, as proposed by Darwin (1871), competition between groups can select strongly for self-sacrificial cooperation in the general service of defense, where self and group interests commonly coincide. Lahti (2005) extended this argument, suggesting that shifts across time and cultures in the relative strengths of within versus between group conflicts drive fluctuating selection for moral and religious beliefs and behavior, and maintain conditionality of expression and intensity in altruism. This Darwinian, and now Hamiltonian, framework depends on biological and psychological kinship (Bailey 1998) being greater within than between groups, and within-group altruistic or mutualistic benefits from cooperation.

Second, as proposed by Freud (1930/2002), unconscious self-interests conflict with conscious moral sentiments (and their institutional agents) within the psyche, with ongoing discontents as outcome. This view provides a general psychological mechanism, compatible with cultural-evolutionary theory, for the development and expression of human striving under cultural, within-group constraints. Such mechanisms are important because they indicate the otherwise-invisible hand of adaptation due to specific forms of selection in the past (Tooby and Cosmides 1995); they are supported, for example, by common human inabilities to rationalize moral decision-making (Haidt 2001).

Third, as proposed by Palmer and Palmer, self-sacrificing and altruistic behaviors within groups can be manipulated – that is – imposed upon individuals, by parents, ancestral lineages, and resultant cultural traits such as moral codes. The key process here is the generation and perpetuation, by older individuals, of cultural phenotypes (such as morals and religious stories and beliefs) that foster increased cooperation among children and later descendants. Such cooperation benefits the perpetuators because it reduces competition between copies of their own alleles, in the same general way, for example, that producing a female-biased sex ratio reduces competition between a mother wasp's genes in the males of her brood (Shuker et al. 2005). Moreover, Palmer and Palmer suggest that self-sacrificing, ancestrally-manipulated cultural traits should also evolve towards more-effective cultural transmission, through explicit prescription of their teaching to the next generation.

Manipulation may work in any given case, but it also imposes costs on the manipulated individuals. Any given female in a wasp brood would have had higher inclusive fitness as a male, and any given child could have higher fitness if less controlled by parents. In wasps, the process works because mothers determine the sex of their offspring. In humans, the manipulation mechanism succeeds, in theory, because young human children can be so readily and thoroughly indoctrinated: having so much to learn when young creates a premium on uncritical acceptance of enculturation.

But are human children so culturally malleable for such fitness-salient traits as altruism and self-sacrifice? How much indoctrination is mutualistic rather than manipulative? From a genetic perspective, how much will intragenomic conflict between genes expressed during childhood or parenthood limit the evolution of such kin-conflictual traits (Bossan et al. 2013)? Most broadly, is manipulation, from parents, to ancestors,

to stories, to moral codes and religions, a necessary or sufficient mechanism to explain culturally-prescribed sacrifice?

The main importance of Palmer and Palmer's hypothesis should, in my view, be not manipulation *per se* but asymmetries in power, and this perspective generalizes and extends their argument as well as raising new and crucial questions. Power is control over a phenotype in another individual: control through asymmetries in physical force (dominance), knowledge (information), or leverage (possession of some resource that cannot be taken by force) (Lewis 2002, Watts 2010). It is the forms, agents, and strengths of asymmetries in power, combined with considerations from kinship and within and between-group structures, that must predominantly control the formation and perpetuation of cultural traits. Small-scale societies, which are often highly egalitarian, will differ profoundly in power asymmetries, structures and dynamics from societies with written codes or institutionalized religion, whose forms will be determined by who originated them, who benefits from them at any given time, and who, if anyone, can change them in what ways.

A focus on power in general, rather than just manipulation in particular as one of its mechanisms, is important because it tells us what aspects of culture to measure, and where to look for the causes of cultural phenotypes and changes, including apparently-paradoxical self-sacrifice. Most importantly, it is the combinations of kinship (both biological and psychological) with power, such as groups of self-perceived kin with common interests (Jones 2000) that should most-strongly structure societies and explain cultural traits such as moral codes. It is in this context in which we seek, and more or less succeed, to maximize our inclusive fitness, in ways both moral and not.

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Traditional Ethical Codes Prescribing Self-Sacrifice as a Puzzle to Evolutionary Theory

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"Much still to be learned, theoretically and empirically, about the evolutionary origins of Besa."

Palmer and Palmer shed evolutionary light on *besa*, an Albanian traditional oath that appears to be a culturally-mediated motivator of altruism with the potential to be aimed at non-kin. Although we can place *besa* alongside any number of other behaviors in contemporary societies that appear to direct altruism at non-relatives, the tradition is particularly interesting for a couple of reasons. First, *besa* is a broadly-adopted tradition in Albanian culture. Second, *besa* appears to require costly sacrifice from those who adhere to its ideals. As a target for understanding the nature of contemporary human altruism, I agree that *besa* is an interesting cultural tradition to try to explain.

As Palmer and Palmer point out, the first thing we need to do if we are going to study *besa*-inspired behavior as a difficult-to-explain form of altruism is to establish that it is indeed a form of altruism. If the tradition of *besa* has inspired many costly behaviors aimed at helping non-relatives, we have a paradox on our hands. The reason that altruism is considered evolutionarily paradoxical is that we expect – absent any other dynamics – that non-altruists will end up producing more offspring than self-sacrificing altruists. Is there evidence that *besa*-inspired behaviors have been costly? Unfortunately most of the evidence for the costs of *besa* emerges from the rhetoric of *besa*. Numerous psychological experiments have demonstrated that the stated rationale for a behavior does not always reflect the true underlying strategy of a behavior (Nisbett & Wilson 1977), so there is reason to question whether *besa* actually compels costly behavior. Perhaps *Albanians would rather die than break besa*, but the real question is *how often have Albanians died to avoid breaking besa?*

The most direct evidence that Albanians exhibit altruistic *besa*-inspired behaviors involves shielding Jews from the Nazis during World War II. Reasonably documented, this behavior can clearly be seen as *potentially-costly*. The risk associated with defying Nazi invaders is undeniable, but the altruistic nature of *besa* could be better understood if there were historical accounts of the frequency with which the shielding of Jewish guests led Albanians to be killed, imprisoned, or otherwise sanctioned by the Nazis. If *besa* is still an operating Albanian tradition – which it seems to be – then it must also be possible to measure its actual costs today; if we cannot demonstrate the costly nature of *besa*, we cannot label it an altruistic behavior. Ideally, data chronicling the actual cost of *besa* would involve direct observation of costly behavior rather than self-reporting, as people tend to bias depictions of their own behaviors to align with social norms (Sablosky 2014).

The stated rationale for a behavior is not always the actual reason why that behavior exists. An alternative explanation of *besa* is that while the tradition is framed socially in terms of self-sacrifice, it actually provides direct benefits to those who maintain the tradition. This is possible if *besa* is understood as an implied threat to do harm to those who dishonor one's home, including guests in that home. The implied threat in *besa* may be all that is necessary to prevent exploitation or attack by others (perhaps even by one's own kin), so maintaining one's adherence to *besa* could be a cultural version of aposematic signaling. As such, *besa* could belong to a larger family of honor traditions (Cohen *et al.* 1996) in human societies whose basic message is *don't tread on me*. The Albanian honor tradition of *besa* may also be a social-

inclusionary trait (Roughgarden 2009) whose benefits outweigh its costs; if demonstrating (sometimes even through an extreme act of violence against a relative who has transgressed) an adherence to *besa* is crucial to maintaining status in Albanian society, *besa*'s benefits may still outweigh its costs. Honor traditions can provide direct benefits to those who practice them and thus may not be evolutionarily paradoxical. In order for the "paradox of *besa*" to be taken seriously, more serious work needs to be done to establish that honoring *besa* leads to altruistic rather than directly self-serving behaviors.

Rather than arguing that evolutionary theory cannot explain *besa*, Palmer and Palmer suggest that the current toolkit employed by evolutionists is insufficient to the job. I am amenable to this idea, especially when it comes to explaining the evolution of very-recently-evolved human behaviors, which are invariably more a product of cultural rather than genetic evolution. Traditionally we evolutionists pull from a toolkit that was honed by studying the evolution of other species; because we share biological heritage with other animals, that toolkit works well for explaining many human behaviors. But today humans – and in particular human societies – exist in unprecedented forms. This suggests that some very unique theoretical tools may be required to explain the recent evolution of many human behaviors.

Palmer and Palmer seek to add to the evolutionist's toolkit by suggesting that some human behaviors are mediated by parental manipulation of descendants via culture (*put more simply*, a tradition). They propose that *besa* is a tradition which emerged because it allowed ancestors to control the behavior of their descendants, creating generations of altruists willing to aid weakly-related members of one's clan (*fis*). They suggest that their explanation is neither a form of kin selection (because members of one's integrated, inter-breeding *fis* are too distantly related) nor a form of group selection (because the *fis* does not represent a group with a fixed geographical location).

Whether or not Palmer and Palmer's ancestral tradition theory is substantially different from kin or group selection, it still has to clear the same hurdles as any theory explaining altruism. Primarily, the theory must provide an evolutionary mechanism that is robust to the universal threat to altruism: mutants who ignore rules promoting altruism and can therefore invade and prosper at the expense of the rule-followers. If it is in the interest of the clan but not individual members of the clan to altruistically sacrifice for the sake of the ancestral lineage, what prevents mutants resistant to the idea of *besa* from ignoring the tradition? Only a psychological predisposition to parental loyalty, or extremely well-policed cultural norms, would prevent the breakdown of *besa* as an honored tradition. And if either psychological or cultural mechanisms maintaining *besa* do exist, some other evolutionary mechanism must be maintaining these biological or cultural characteristics. The problem with Palmer and Palmer's theory is that it requires additional evolutionary mechanisms to maintain its own mechanism (high-fidelity trans-generational adherence to the prescripts of *besa*).

I do not doubt that in many cases vertical transmission of cultural ideas has occurred with reasonable fidelity across many generations. Palmer and Palmer's (2015) theory explaining the existence of *besa* predicts that the idea has been transmitted faithfully from parent to offspring for generations; interestingly, other evolutionary theories explaining *besa* might not require such fidelity. Uncovering historical evidence that *besa* has indeed been transmitted faithfully from parent to offspring for generations would provide some support for this theory.

The strongest evidence for *besa*-inspired altruism is accounts of Albanian protection of Jews from the Nazis. But by cultural definition – as well as genetic relatedness – Jews were outside of the integrated inter-breeding *fis* of Albanians, so at best this example of *besa* is applied in a manner that runs counter to the theory that *besa* serves to motivate altruism amongst a large, inter-breeding cultural group. That *besa* as a cultural idea has evolved to be applied so widely argues against its role as a means of promoting altruism within the *fis*.

Palmer and Palmer appeal to parent-offspring conflict to explain why parents would gain advantage by passing on the tradition of *besa* to their offspring. As a kind of explanation this could make sense, as it has been shown that parents can use manipulation to advance their own genetic fitness over the fitness of their offspring (Kapheim *et al.* 2015). However, it is not entirely clear what benefit parents derive from promoting the tradition of *besa*, as what it potentially fosters is altruism by offspring directed at distant kin; why such altruism is in the interest of parents needs to be better clarified. If inclusive fitness cannot explain this ancestor manipulation of descendants, what does?

Do the infrequent acts of extreme altruism that *besa* can promote increase the inclusive fitness of earlier ancestors? Possibly. Palmer and Palmer (2015) demonstrate in earlier work that a combination of inter-clan marriage and clan loyalty can create a very extensive in-group at which altruism can be aimed (for Albanians, the *fis*). It sounds as though the concept of the *fis* is ripe for genetic investigation: how related are individuals who identify as part of a *fis*? I don't doubt that such investigation would confirm that a *fis* is composed of many individuals who are only very distantly related; thus, I doubt genetically-assaying relatedness would resurrect kin selection as a sole explanation of *besa*-inspired behaviors. But just as it is important to quantify that *besa* compels costly – and therefore altruistic – behaviors, it is important to use available tools to establish that the affiliation with a *fis* cannot be explained simply based on kinship.

Which brings us full circle to the question of whether current evolutionary theory can explain *besa* as a form of altruism. Is the model of Palmer and Palmer really outside of the current toolkit of evolutionary theory? If the altruism required by adhering to *besa* is really the result of parental manipulation of descendants, then we can appeal to inclusive fitness as the explanation for this tradition. If inter-marriage between clans serves to integrate less-related individuals, then *besa* that compels altruism aimed at one's *fis* is really just a form of cultural group selection; if inter-clan marriages and adherence to *besa* are adaptive traditions, we would expect groups that maintain these traditions to outcompete groups with different traditions. Evolutionary theory's existing toolkit seems more than up to the job of explaining the existence of *besa*, especially if we include additional mechanisms that maintain social norms (*for example:* punishment, social partner choice, reputation).

What does seem novel to me in the tradition hypothesis forwarded by Palmer and Palmer is the combination of culturally-transmitted altruism-promoting norms, clan identity, and frequent inter-group mating. While I think that the mechanism they suggest can be understood by appealing to either inclusive fitness or multi-level selection, the details of their mechanism are interesting and potentially novel. The process by which humans have increased the scale of their societies seems intricately tied to various forms of social integration, and Palmer and Palmer nicely point out one scenario by which this social integration can emerge and compel altruistic behavior within a larger, weakly-related clan. I do not believe that group selection – especially cultural group selection – requires geographical location. For humans, groups can form so long as there are markers of identity and opportunities for exchange of altruism; human groups compete even within integrated societies. Palmer and Palmer's theory seems to me to portray an important but particular kind of group selection.

At this point their model of social integration via cultural tradition is a verbal and visual model. What they have proposed desperately begs for more sophisticated modeling that can properly simulate the fitness effects of inter-clan marriage and the cultural transmission of *besa*. Intuition about the actual dynamic behavior of mental or verbal models is notoriously bad: this is why evolutionary biologists build mathematical or agent-based models. It is possible that *besa* could be better understood through such modeling efforts.

Palmer and Palmer have illuminated an intriguing cultural practice and suggested an intriguing mechanism for its evolution. But before *besa* can better help us understand the nature of human altruism, we need to gather more evidence that *besa* actually compels altruistic behavior (and which clarifies at whom

that altruistic behavior is generally aimed). If *besa* does compel costly behavior, understanding the cultural evolution of the *besa* tradition requires rigorous modeling.

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How Universality Can Help Us Better Understand Evolutionary Explanations about Self-Sacrifice

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Although the authors discussed self-sacrificing focused on *Besa* and *Kanun* in the Albanian tradition, it is not uncommon among various other cultures or different times in human history. One of the highest levels of sacrifice – risking one's life to save the life of a stranger or even enemy – has been also widely found across regions and times. However, this does not mean that we can easily encounter self-sacrificing people anywhere at any time. These people are rare but from many different cultures. For instance, as Palmer and Palmer mentioned about Albanian rescuers of Jews in World War II practicing *Kanun* (self-sacrificing), there were also people in many European countries (including Belgium, France, Netherlands, and Poland to name a few) who willingly took life-threating risks to save the lives of Jewish people (See The International School for Holocaust Studies, 2016).

More recently, we have also heard the stories of heroes or heroines who first tried to help others escape when natural disasters hit or serious accidents occurred and were killed in the process. More specifically, in my doctoral research project studying South Koreans' conceptions of "a moral person," one respondent selected his moral exemplar as a young Korean man who lost his life while trying to save a drunken Japanese man who fell on the train tracks in a subway station in Tokyo, Japan (See Reitman, 2001). Considering the hostile relationship between Korea and Japan, we can easily understand that a Korean's sacrifice to save a Japanese person's life would be considered very surprising, and in turn, could be regarded as exemplary moral behavior.

If sacrificing one's life for the sake of others has been found in various cultures, we can conclude that the ethical code of *Kanun* is the Albanian version of widespread moral virtue, self-sacrifice. However, I agree that the Albanian ways of practicing *Kanun* appear to be unique; how seriously it has been highlighted (they make an oath, *Besa*, to bind themselves to the promise), how much it has been emphasized (as the highest ethical code), and how long and widely it has been pursued (it has been their cultural tradition) all

indicate that they execute *Kanun* most seriously in many cultures of the world. However, if we were to seek evolutionary explanations of self-sacrificing (*Kanun*), keeping our focus on the universal aspects of the phenomena would be more helpful. Note that evolutionary theories, generally speaking, have tried to explain behavioral outcomes of the entire human species, not a single culture. Then, what kind of statement sounds more plausible: (1) an evolutionary outcome is only applicable for one tribe or culture, or (2) a universal behavioral tendency can be the results of an evolutionary process. Moreover, from an evolutionary point of view, all people living on the earth now are the offspring of forefathers who survived the evolutionary selection process, broadly defined. Any evolutionary explanation, therefore, should be applicable for similar behaviors of any groups of people in the world.

Palmer and Palmer's evolutionary solution to the puzzle is persuasive and brilliant, but one big question still remains: Why have only a small number of people shown the behavior? As the authors also mentioned, not all Albanians who know *Kanun* and practice *Besa* actually take actions accordingly. Because those greatly altruistic people are rare, they appear to be morally outstanding, remembered by many others for a long time, and becoming moral exemplars for someone else. If they are so sporadic, is it still legitimate for us to claim that we, as humans, have sacrificial genes programmed in ourselves throughout the evolutionary process?

One day in June of 2015, an elderly man fell on the train tracks at a subway station in South Korea. Three young men instantly ran down onto the tracks and saved the old man's life and survived. When they were asked what made them instantaneously put themselves in life-threatening situation, they answered, "it seemed like an instinct. Before I could think or decide anything, my body seemed to immediately react like that when I saw the old man on the tracks." An immediate bodily reaction to take risks can be evidence showing that we might have been genetically coded to be altruistic and self-sacrificing. It is human nature to be deeply moved and angered by a picture of the dead body of a 3-year-old Syrian boy washed upon the shore after an unsuccessful attempt to escape his country threatened by war and violence. Looking at the scenes of people suffering from famine and disease, we tend to take actions like donating our money, energy, and time to help and save them in any possible way. Naturally being concerned about the survival of others is a common behavioral pattern of the human beings.

In conclusion, it is safe to say that humans more frequently exhibit more sacrificial characteristics than we may have thought. Many people may be ready to practice *Kanun* in their own ways if any situation requires them to do so. This understanding of universal characteristics of self-sacrifice would make the evolutionary explanations about it from Palmer and Palmer more appreciable and plausible. We are self-sacrificing human beings who have been programmed to behave so throughout the history of our species.

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Palmer's and Palmer's Reply to Comments

We are very pleased to see that, as anticipated in our paper, most of the reviewers' comments consist of arguments in favor of one or more of the conventional evolutionary explanations of altruism as a solution to the puzzle of traditional ethical codes prescribing seemingly unfit acts of self-sacrifice.

Wilson, predictably, finds our explanation "highly improbable" because he finds such codes easily explained by group (i.e., multi-level) selection. We have no hope of dissuading him, or his followers, from that position. We will only point out that a crucial, but rarely recognized, tactic in Wilson's group selection explanations is his recasting of whatever actual human behavior needs to be explained into "a group" phenomenon regardless of the inaccuracy of such a label. Given that any imaginable category of individuals can be referred to as if it was a group, this subtle tactic can give the unskeptical reader the impression that group selection is a plausible of explanation of any imaginable human behavior. In this case, Wilson uses his first sentence to recast the very ungroup like categories of individuals referred to in our paper (e.g., the categories of individuals referred to by the Albanian term *fis*) into a very group like "moral community." This recasting then becomes essential to his conclusion: "1) A norm such as *besa* is not a puzzle. It is the nature of morality that individuals are expected to subordinate their self-interest to the interest of their *moral community*" (our emphasis). We propose that if, and only if, such recasting in group terms is accepted, do all explanations of altruism become equivalent with, and *a priori* examples of, group selection.

Turning to Wilson's more specific criticisms, he is correct in pointing out that, due to length restrictions, we provided only one citation (Cronk 1999) to support our claim that there was a time in human existence "when all individuals were consistently co-dependents" (which we assume is Wilson's misquotation of our statement that there was a time when "all individuals consistently were co-descendants"). For the evidence upon which our assertion is based we direct interested readers to the extensive ethnographic examples cited in Palmer et al. (2016). We were far more puzzled by Wilson's assertion that we do not provide an alternative pattern of behavior proposed to have proved less successful than traditional parental manipulation. Not only does all of the evolutionary literature on parental manipulation imply a comparison of the evolutionary success of parents who manipulate their offspring in certain ways with those who do not, this comparison is explicit in our many statements that individuals who influenced their descendants in certain ways "would have been favored over individuals who did not."

In contrast to Wilson's assertion that the entire logic of our paper is flawed because the concept of alternative evolutionary explanations of altruism has been rejected, Lopes and Shackelford refer to our paper as a "reasonable, *alternative*, evolutionary explanation" (our emphasis). These authors focus primarily on the question, anticipated in our paper, of whether or not actual instances of unfit altruism are anything more than rare aberrations resulting from the general human tendency to seek the rewards that can be garnered from building a reputation for heroism. Thus, they question the proportion of Albanians protecting Jews during the Holocaust, compared to those who had the opportunity to do so but chose not to risk their lives and their families. Further, they suggest that those who did protect Jews did so to reap the rewards of heroism. However, evidence does not support either of these hypotheses. Although Sarner's (2007) claim that "one hundred percent of Jews in Albania [were] rescued from Holocaust" may be an exaggeration, there is actually very little, if any, evidence of Albanians choosing to turn Jews over to the Nazis instead of assisting them (Nidam-Orvieto & Steinfeldt, n.d.). The seeking of a heroic reputation is also hard to apply to the actions of the Righteous Among the Nations in any nation because the chances of reaping such benefits were greatly outweighed by the potential costs of rescuing Jews during the Holocaust.

Crespi brings up the very important point that just as parental manipulation consists of "conflict" between the interests of the parent and offspring, traditional parental manipulation consists of conflict between ancestors and descendants. Indeed, this is why the article presenting our mathematical formula to calculate the multigenerational consequences of traditional parental manipulation (Coe et al. 2010) calculates these for different outcomes of this conflict.

Jensen raises two important points. First, he provides a clear example of the assumption that one or more

of the conventional evolutionary explanations *must* somehow account for traditional ethical codes, even when this does not appear to be the case: "If inclusive fitness cannot explain this ancestor manipulation of descendants, what does?" Our answer, which we admittedly failed to expound upon sufficiently in this particular paper, is that even when traditional parental manipulation reduces the inclusive fitness of an individual offspring, it can increase the number of descendants over many generations and "natural selection can be most accurately measured over a large number of generations than in terms of the number of surviving children or grandchildren produced" (Alexander, 1974, p. 346; West-Eberhard, 1975, p. 29; Dawkins, 1982, p. 184). This is what leads to our "conclusion that selection would have favored individuals who were most successful at influencing the social behavior among the most distant generation of their descendants." Jensen also calls for the need to model how traditional parental manipulation could increase the number of descendants over many generations. We are in full agreement with this position, and invite Jensen, and other readers, to help us perform such modelling. In particular, we solicit potential ways to model the evolutionary success of alternative cultural traditions that measures evolutionary success over large numbers of generations, and conceives of selection taking place between individuals and avoids preconceived notions of selection taking place within or between groups. Until skeptics of our approach produce such models demonstrating that our explanation is inaccurate, the absence of models neither strengthens nor weakens our hypothesis.

Finally, we are also in full agreement with Kim's statement that the plausibility of our hypothesis would be greatly increased if it could account for all of the seemingly puzzling evolutionary codes of self-sacrifice that represent a "universal behavioral tendency," instead of only accounting for the Albanian code of ethics and the concept of Besa. Indeed, we attempted to emphasize that Besa is only used as an example of a universal behavioral tendency. We apologize for not making this point clearer, and we thank Kim for drawing attention to the species-typical scope of the puzzle our paper presents to evolutionary theory.

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