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The Role of Biological Evolution in the Persistence of Religion:

Does Religion have Adaptive Value?

Zoe Fu-Chen

Abstract

Religion, a shared social system that connects people with a supernatural power, exists in human populations worldwide. Scientists have long debated whether religion is a cultural or evolutionary phenomenon; that is, whether religion is a learned set of values, beliefs, and behaviors, or instead the result of gene variants that have increased in frequency over time. In this paper, I argue that natural selection, the process by which the frequency of certain genes increases over generations due to their reproductive benefit, has played a role in the persistence of religion. I begin by providing background on the definitions of religion, biological evolution, and adaptation, which are necessary to clarify before analyzing the role of biological evolution and adaptivity in religion. I then explain and provide evidence for how religion meets the three conditions of natural selection. Finally, I present multiple adaptive hypotheses to explain how religion might increase fitness. This work clarifies scientific understanding of how natural selection impacts religion and expands on existing adaptive hypotheses that explain how religion might increase biological fitness.

Background

Defining Religion

"Religion" derives from the Latin term *religare*, meaning 'to bind together' or to 're-bind.' Religare connotes a bond between worshiper and higher power; defining religion itself, however, is a continuous source of debate. Academics of all disciplines have described religion in various– and sometimes wildly differing– ways. For example, the psychologist William James emphasized the individual experience in his definition of religion as "the feelings, acts, and experiences of individual men in their solitude, so far as they apprehend themselves to stand in relation to whatever they may consider the divine." In contrast, sociologist Émile Durkheim believed religion was "a unified system of beliefs and practices relative to sacred things… which unite into one single moral community called a Church, all those who adhere to them." Some scholars assert religion is an invented construct and therefore does not exist (Asad 1993); still others contend that religion, being a fundamentally Western and Christian-centric concept, is limited in its applicability outside this domain (Bell 2006). Although the category of religion certainly has its flaws, I argue that it is still useful as a lens of analysis. Across human populations worldwide, we see social systems with a belief in the supernatural. Categorizing these phenomena as religion provides the framework for us to note, analyze, and make sense of this recurring pattern. For the purposes of this paper, I will define religion as a shared social system that connects people with a supernatural power, religious as belonging to a religion, religiousness as the state of being religious, and religiosity as the degree to which an individual values religion in their lives.

Biological Evolution

In 1858, naturalists Charles Darwin and Alfred Russel Wallace both proposed nearly identical hypotheses to explain the variation observed in the natural world. The hypothesis, variously termed descent with modification, theory of natural selection, or descent with modification by means of natural selection, postulated that the exponential growth of populations in the face of limited resources caused a struggle for existence, leading to the preferential survival of organisms with survival-increasing variants. These variants were then inherited by offspring; over long periods of time, this preferential survival of organisms with certain traits led to organismal improvement and eventually speciation (Darwin & Wallace 1858, Darwin 1859, Oldroyd 1986, Kutschera & Niklas 2004).

At the time, neither Darwin nor Wallace could explain why variations existed or the manner in which they were inherited. In addition, although Darwin acknowledged that modification occurred by means other than natural selection, he did not attempt to explain how those alternative methods of modification might function. Major advancements in biological science, such as the discovery of DNA in 1869 and in 1953 (Lamm et. al. 2020), the development of the principles of inheritance around 1865 (Mendel 1865), and the emergence of the field of genetics in the early 20th century (Gayon 2016) have since greatly increased our understanding of how natural selection, as well as the other forms of what is now known as evolution, operate to change biological variety over time. Today, we understand biological evolution to be the change in the frequency of gene variants in a population (defined as a "group of individuals of the same species living and interbreeding within a given area," Tarsi & Tuff 2012) over successive generations. Biological evolution operates by four distinct mechanisms: mutation, genetic drift, gene flow, and natural selection.

Mutation, a random change in an organism's DNA sequence, is the foundational source of genetic variation needed for evolution to occur. Mutations occur irrespective of their impact on an organism's fitness, defined here as survival to reproduction and reproduction. Therefore, they can be fitness-increasing, fitness-decreasing, or have no effect on fitness. De novo mutations, new mutations that occur during the production of egg and sperm cells, are the main source of heritable genetic variation. Although some mutations are caused by environmental factors (induced mutation), they are rare compared to de novo mutations and are not always heritable.

Genetic drift is the “change in frequency of an existing gene variant in a population due to random chance” (NIH, n.d.). These random changes in gene frequency can result in the loss or fixation of genes in a population, regardless of the gene’s effect on fitness. The effects of genetic drift are magnified in small populations because gene frequency in successive generations is more likely to be impacted by random chance events (ex. chance death or chance reproduction) than in large populations.

Gene flow is the movement of gene variants from one population to another. This movement of gene variants can occur through active dispersal pathways such as migration, or passive dispersal pathways such as pollination or water column movement. The introduction of new gene variants to a population can then impact gene frequency.

Lastly, natural selection is the process by which, over successive generations, a “non-random difference in the reproductive output” of organisms leads to an increase in the frequency of gene variants that confer a fitness benefit (Gregory 2009). Three conditions are necessary for natural selection to occur (Endler 1986). First, there must be a variety of traits in a population. Second, these traits must have a genetic origin. Third, there must be a non-random difference in the fitness of organisms with certain genetic variants compared to organisms with alternative variants. When these three conditions hold true, natural selection will occur, and the frequency of fitness-increasing gene variants that express fitness-increasing traits will increase over multiple generations.*

These fitness-increasing traits are called adaptive traits, and the fitness-increasing benefit they confer is known as adaptive value. Both the biotic and abiotic environment play a large role in determining the adaptive value of a gene variant. A gene variant that provides adaptive value in an environment with a high proportion of grasses, for example, may not provide adaptive value in an environment with a high proportion of trees. Similarly, a gene variant that provides adaptive value in cold environments may not provide adaptive value in warm environments.

*Note: A “struggle for existence,” or existing environmental pressures such that only some organisms will survive to pass on their genetic material to the next generation, is often included as a necessary condition for natural selection. However, natural selection can take place without environmental pressures. For example, imagine that an organism carries a germline mutation that increases clutch size. The female offspring of this organism will inherit this mutation and will themselves have increased offspring and so on and so forth, thus changing the frequency of this mutation in the population over generations irregardless of environmental pressure. Outside of artificial conditions, however, there are nearly always extrinsic pressures– for example, resource scarcity, competition, or environmental harshness– that impact an organism's reproductive outcomes and thus population gene variant frequencies. Therefore, although environmental pressures are not strictly necessary for natural selection to occur, they do influence the process of natural selection.

Biological evolution occurs on both a small, population-level scale (microevolution), and a large, species-spanning scale (macroevolution). Biological evolution can happen very slowly over thousands of years, or very rapidly over the course of just a few generations (Altizer et. al. 2003, Ellner et. al. 2011, Koch et. al. 2014). Often, multiple of these evolutionary mechanisms interact to result in the existing gene frequencies, and therefore existing traits, seen in organisms. However, natural selection is the only mechanism by which gene variants with adaptive value increase with frequency due to their adaptive benefit.

The Fallacies of Adaptivity

The term “adaptive” specifically describes gene variants and their resulting traits that have undergone the process of natural selection. However, “adaptive” is frequently used outside of this original biological evolutionary context, both informally and in academic settings, to describe any trait or process that increases fitness. As noted by Stephen Gould and Richard Lewontin in the famous “Spandrels of San Marco” article (1979), misunderstanding around the meaning of “adaptive” results from lumping three distinct phenomena under one term. In addition to its evolutionary meaning, “adaptive” is used to describe phenotypic plasticity or physiological adjustments in response to the environment, such as acclimating to a cold climate after living in a warm climate. “Adaptive” is also used to describe beneficial cultural traits, such as the trash-opening behavior that spread through a population of sulphur-crested cockatoos (*Cacatua galerita*) in Sydney, Australia. The many usages of “adaptive” can cause the misattribution of biological adaptation to contexts where it is not applicable. While ability to thermoregulate is a biologically adaptive trait (Boyles et. al. 2011), the acclimatization itself– physiologically adjusting from living in a warm environment to a cold environment– is not an example of evolution or biological adaptation taking place because the change occurs within a single lifetime and is a reversible, short-term response to the environment. Similarly, cockatoo trash-opening likely increases cockatoo survival by supporting easy access to food, but is not an evolutionary adaptation because the behavior is developed within one lifetime and has no genetic basis. In short, just because a trait increases fitness does not necessarily mean that it has undergone natural selection. I will be using the term “adaptive” in a strictly biological evolutionary sense.

Figure 1. A sulphur-crested cockatoo opens a trash can. While fitness-increasing, this behavior is not a biological adaptation because it is learned and lacks a genetic basis.

Credit: Barbara Klump / Max Planck Institute of Animal Behavior

Religion and the Three Conditions of Natural Selection

To demonstrate that religion is an adaptive trait, we must first establish that it meets the three conditions of natural selection. Therefore, at least one human population must have 1) variation in religiousness, 2) gene variants responsible for this variation in religiousness, and 3) a non-random difference in the fitness of organisms with gene variants expressing religion compared to organisms with alternative gene variants.

Condition I: Variation

Around 84% of the global population affiliates with one of the estimated 10,000 religions worldwide (Pew Research Center 2012, Johnson & Grim 2013). Non-affiliated individuals account for 16% of the global population. Religiosity also occurs on a scale, with some individuals self-identifying as highly religious and others as minimally religious (Huber & Huber 2012). Thus, there is high variation of religious phenotype both in terms of religious affiliation and religiosity.

Condition II: Heritability

Although there are undoubtedly extrinsic factors resulting in an individual's participation in religion, genetics also play a role. (To be clear, gene variants themselves do not result in religiousness. Rather, gene variants influence cognitive processes or mechanisms that can then predispose an individual to religion. Religion is still considered heritable because, although it is not direct, there is a correlation between gene and trait.) Twin studies are often used to determine the degree to which a trait is influenced by genetic factors compared to environmental factors. Monozygotic twins are conceived from a single egg and sperm and share approximately 100% of their DNA, while dizygotic twins are conceived from two eggs and two sperm and share approximately 50% of their DNA. If monozygotic twins have greater similarity in a trait than do dizygotic twins, then the trait likely has genetic influence. Twin studies show that monozygotic twins score more similarly to each other on measures of self-reported religiosity than do dizygotic twins. Therefore, genetics likely contribute to religiosity (Waller et. al. 1990, Koenig et. al. 2005, Bouchard et. al. 1990, Hvidtjørn et. al. 2013). In addition, studies have found that environmental factors have greater effect on childhood religiosity than adult religiosity, while genetic factors have a smaller effect on childhood religiosity and a greater effect on adult religiosity (Waller et. al. 1990, Kendler et. al. 2009, Koenig et. al. 2005; Koenig et al. 2011). Although no specific gene has been identified as contributing to a religious phenotype– given religion's complexity, there is likely a confluence of contributing genes– evidence suggests that religion has heritability.

Condition III: Non-Random Difference in Fitness

Religious affiliation is associated with greater survival and reproduction than non-affiliation. Participation in religious services is associated with reduced mortality in multiple countries (Christopoulos 2023, Hill et. al. 2020, Yeager et. al. 2006). In addition, women of all listed religious denominations gave birth to greater numbers of children than unaffiliated women in the 2002 Swiss Census (Blume 2009). Pew Research surveys also indicate that women with a religious affiliation have higher average birth rates than unaffiliated women (Pew Research Center 2015). Lastly, women who report that religion is important in their lives have higher intended and actual births than women who report that religion is of minimal to no importance (Hayford 2009).

Evidently, religion is an extremely complex phenomenon that cannot be understood exclusively through gene expression. However, evidence shows that nearly all behaviors have a genetic component and are the result of gene-environment interaction (Rutter 2006). Many complex traits that are not solely genetic, such as birdsong or parental care, are still shaped by biological evolution (McEntee et. al. 2021, Fitzpatrick et. al. 2021). Given the variation and heritability of religion in addition to the greater fitness of religious individuals compared to non-religious individuals, it is appropriate to assume that natural selection has played a role in its persistence.

Adaptive Arguments

If religion is in part a product of natural selection, then it must have adaptive value. Therefore, some component(s) of religion must be responsible for the observed increased fitness of religious individuals. As previously noted, religion is an extremely multifaceted and varied trait. There is enormous variation in both the beliefs and practices of individuals belonging to different religions as well as in the beliefs and practices of individuals within the same religion. Given its complexity and diversity, religion as an overarching category most likely has multiple fitness increasing components as opposed to a singular adaptive benefit. In addition, because environmental conditions can influence the adaptive value of a trait, and different religions arose in a variety of ecological conditions around the world, each religion may have environment-specific means of increasing fitness. Therefore, adaptive arguments for religion attempt to explain not the entirety of religion's adaptive value, but the ways in which specific components of certain religions may increase fitness, and, when applicable, how these components increase fitness in certain environments.

In this section, I briefly discuss the hypothesis that ancestor worship increases inclusive fitness, followed by the hypothesis that shared religious membership increases mate compatibility and therefore fitness. However, the majority of research on the adaptive value of religion has focused on the adaptive benefit of cooperation in religious groups. As such, the main focus of this section is to explain 1) how cooperation in religious groups may increase fitness and 2) how religious groups facilitate high levels of cooperation.

Hypothesis: Ancestor worship decreases conflict among kin, leading to inclusive fitness gains.

Reproduction is the most direct way for an organism to propagate their genes into the next generation. However, by assisting in the reproduction of genetic relatives, an organism can still effectively pass on some of its genetic material and thereby increase its fitness without directly reproducing. The greater the relation to kin, the higher the inclusive fitness gain. (The biologist J.B.S. Haldane famously quipped that he “would lay down my life for two brothers or eight cousins.”) This non-direct fitness increase is known as inclusive fitness, and is formally defined as “the number of related individuals produced, multiplied by the degree of relatedness of those individuals” (Hamilton 1964). Therefore, cooperation and mutual assistance among kin is often adaptive because it can increase inclusive fitness (West & Gardner 2013).

Some religions feature ancestor worship, in which ancestors are believed to have a continued existence beyond death and can influence the living. Religious ancestor worship may foster cooperation among living relatives, thereby increasing inclusive fitness (Crespi & Summers 2014). For example, venerating a deceased family member may increase positive feelings among living kin by serving as a reminder of connectedness, which may then reduce conflict and lead to greater survival, thereby allowing for greater future reproduction. If ancestor veneration leads to reduced conflict, parental inclusive fitness may be particularly increased, as the mediation of offspring conflict can reduce death rates and thus allow more parental genetic materials to be propagated into the next generations (Crespi & Summers 2014, Coe et. al. 2010).

Hypothesis: Religious membership increases perceived or actual similarity, thus increasing marital compatibility and reproduction.

As a social system, religion ties individuals to each other even if they lack a personal connection. In humans, both perceived and actual similarity has been shown to increase attraction (Philipp-Muller et. al. 2020, Byrne 1961, Kalmijn 1994, McPherson et. al. 2001, Montoya et. al. 2008). Thus, it is plausible that, for some religions, the shared experiences and beliefs associated with religious membership creates perceived and/or actual similarity among individuals of the same religion, increasing romantic attraction, coupling, and reproduction in intrafaith couples. Indeed, studies show that religious homogamy is positively correlated with marital satisfaction (Hunt & King 1978, Marks 2005, Heaton & Pratt 1990). Marital satisfaction may increase the probability of having an additional child compared to marital non-satisfaction (Myers 1997). In addition, marital satisfaction has been found to correlate with a desire for more children (Beaujot & Tong 1985). Thus, high rates of marital satisfaction among religious individuals may play a role in the observed higher fitness of religious individuals compared to non-religious individuals.

Hypothesis: Religion increases fitness by promoting mutually beneficial non-kin cooperation.

Cooperation, the "simultaneous or consecutive acting together of two or more individuals by same or different behaviors," is itself an extremely complex phenomenon (Taborsky et. al. 2016). Cooperation persists only when it provides a net-fitness benefit. Evolutionary theory and observation suggest that cooperation among kin can be adaptive, as it can yield indirect fitness benefits (Komdeur & Hatchwell 1999). Persistence of cooperation among non-kin is not as straightforward, as it provides no indirect fitness benefit. However, even specific types of cooperation among non-kin have been shown to increase fitness, providing the correct conditions. Reciprocal altruism occurs when an organism engages in an altruistic act for a receiver with the expectation that it will receive an altruistic act from the receiver at another time. Vampire bats (*Desmodontinae spp.*) that shared regurgitated blood for other bats were more likely to receive blood at a later time and show increased fitness (Carter et. al. 2013, Wilkinson et. al. 2016). In addition, female vampire bats who engaged in "social bet-hedging," in which they shared blood with many non-kin bats (and therefore invested in quantity of relationships over quality), suffered smaller food losses later (Carter et. al. 2017). Social bonding can also increase fitness– stronger social bonds between non-kin male macaques were associated with greater reproductive success (Schülke et. al. 2010).

Figure 2. Vampire bats that share blood with another roost member are more likely to receive blood upon future need. This reciprocal altruism leads to long-term fitness benefits.
Credit: B.G. Thomson / Science Source

Studies indicate that religion promotes intra-group cooperation (Valencia Caicedo et. al. 2023, Anderson & Mellor 2009). For example, members of religious Israeli kibbutzim were more cooperative than members of secular Israeli kibbutzim during a common-pool-resource game (Sosis & Ruffle 2004). In addition, religious players had greater sustained cooperation in a public-goods game than non-religious players (Anderson & Mellor 2009), and religious communes often survive longer than secular communes (Sosis 2000, Sosis & Bressler 2003). However, very little research has been conducted on the link between cooperation and fitness in religion or the occurrence of specific forms of cooperation in religion. Given that some forms of cooperation increase fitness, I hypothesize that religion's promotion of overall non-kin cooperation increases the frequency of fitness-increasing forms of cooperation.

Because they are predisposed to intra-group cooperation, religious members may then be more likely to engage in reciprocal altruism for resources such as food, money, shelter, or childcare, and thereby increase fitness. In addition, religion may be a proxy for social bet-hedging. As members of a religion, religious individuals have access to a social network with a level of established trust. If religious individuals act altruistically for many other members, they can expect help in return when in need, and thus increase their survival. In addition, religious community and the frequency of religious events provide opportunities for social bonding, which may be fitness-increasing.

It is also possible that cooperation among religious members does not directly increase fitness, but does so indirectly by maintaining group longevity. Cooperative behavior can directly benefit fitness, such as in the case of blood-sharing vampire bats. In other cases, however, cooperative behavior indirectly affects fitness by enabling other fitness-increasing behaviors to occur. For example, individual vigilant behavior of prey species, which involves scanning surroundings for predators, decreases as group size increases; this indirectly increases fitness by allowing prey to allocate more time to foraging (Roberts 1996, Wang et. al. 2021). Similar to the foraging increase facilitated by prey group cooperation, the increased degree and maintenance of cooperation observed in religious groups may indirectly increase fitness by enabling the existence of other fitness-increasing behaviors– although what these behaviors might be are not entirely clear.

Having presented evidence that religion may increase fitness through high levels of cooperation, the following two sub-hypotheses explain how aspects of religion may function to increase member cooperation to greater levels than observed in non-religious communities and individuals.

Sub-Hypothesis: Religious ritual increases intragroup cooperation by serving as an honest signal of commitment.

Religious ritual is repeating or patterned behavior that occurs in conjunction with a religion (George & Park 2013). Many religions include rituals that demand investment of time, energy, and money and sometimes put individuals at risk of bodily harm. For example, members of the Church of Jesus Christ of Latter-Day Saints participate in tithing, in which they are required to donate ten percent of their income to the church. In preparation for the annual Tamil Hindu Thaipusam festival, participants may fast 48 days in advance, adopt a celibate lifestyle, bathe in cold water, or sleep on the floor (Xygalatas et. al. 2021); during the Kavadi ceremony, participants pierce their faces and backs with skewers and hooks (Ward 1984). Many Muslims pray five times a day (Sayeed & Anand 2013), and many Christians attend church weekly (Pew Research Center 2016). Behavioral ecologists refer to these types of behaviors as “costly behaviors” because they impose a significant energetic, time, physical, or resource cost on the individual such that, in theory, reproductive output is compromised.

Evolutionary theory predicts that genes encoding for costly, fitness-decreasing traits should decrease in frequency over generations due to natural selection. However, some traits that appear costly at face-value incur a net-fitness benefit. Once such type of trait is known as an honest signal, which is a form of phenotypic communication that provides accurate information about a signaller to a receiver. Because the signal is too costly to be faked, the receiver recognizes the signal to be "honest," which then benefits the signaller. For example, when pursued by a predator, the springbok (*Antidorcas marsupialis*) will sometimes jump in the air in a behavior known as stotting before running away. Although stotting expends energy that could be used to escape, it signals to the predator that the springbok is healthy and strong and therefore not worth pursuing. Thus, the springbok survives and can consequently reproduce. Stotting is too costly to be faked because a springbok in poor condition does not have enough energy to both stot and outrun the predator.

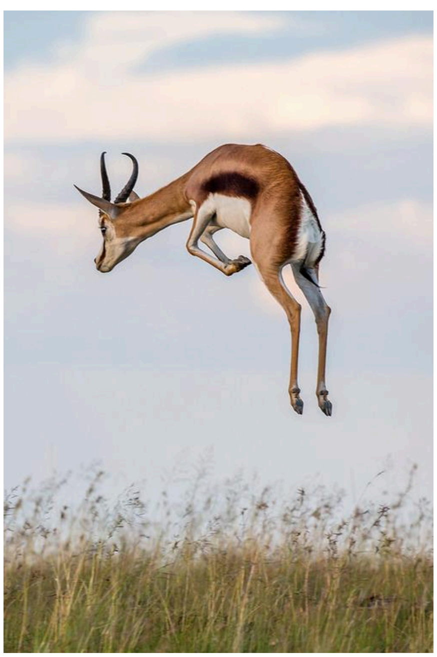

Figure 3. The springbok's stotting is an honest signal to the predator that the springbok is in good condition and therefore not worth pursuing.

Credit: Prakash Srinivasan

Like stotting, religious ritual may serve as an honest signal of an individual's investment in a religious group, thereby improving trust and cooperation (Sosis 2004). The high cost of participating in religious rituals disincentivizes and prevents "cheating" from individuals who are uncommitted to the religious group but want to take advantage of group resources, such as money or childcare. Participation signals true commitment to the group– only individuals who are dedicated to the religious group will choose to attend regular religious functions, donate money, or pierce their body. Thus, religious rituals may effectively filter out non-committed individuals, leaving only those committed and willing to cooperate. Several studies have corroborated this hypothesis. Religious individuals partaking in the pilgrimage to Santiago de Compostela, a historically Catholic pilgrimage route to the tomb of the Apostle St. James, were rated more trustworthy by Christian individuals. Trustworthiness rating was positively correlated with distance walked (Chvaja et. al. 2023). Studies have found that trust increases willingness to cooperate (Acedo & Gomila 2013, Acedo-Carmona & Gomila 2014); as such, a higher trustworthiness is likely a positive indication of willingness to cooperate. In addition, individuals belonging to the African diasporic religion Candomblé who engaged in greater amounts of honest signaling provided and received more cooperation from other Candomblé members in a public-goods game (Soler 2012). Christian and Muslim individuals engaging in honest signaling, such as donating to religious charities or following religious dietary restrictions, were rated as more trustworthy by Christian individuals than Christian and Muslim individuals who did not engage in signaling (Hall et. al. 2015).

Sub-Hypothesis: A belief in moralizing gods encourages cooperation.

Many religions feature moralizing gods or supernatural powers that instruct believers on what is right or wrong. In religions that include them, the perceived monitoring of moralizing gods, as well as the fear of punishment, may increase cooperation and suppress free-loading of resources (Potz 2023). For example, individuals who attributed punitive qualities to gods cheated less than individuals who perceived gods to be loving (Shariff & Norenzayan 2011), suggesting that the fear of supernatural punishment may disincentivize transgressive behaviors that are not conducive to cooperation. This perceived monitoring of gods may be maintained not only through explicit religious beliefs, but also through interaction with religious settings, objects, or topics that may subconsciously remind an individual of their belief in moralizing gods (Potz 2023). Religious priming (exposing individuals subconsciously to a religious stimulus) involving supernatural punishment also increased cooperation during a trust game more than priming individuals with non-religion related subjects (Hadnes & Schumacher 2012). In addition, a belief in moralizing gods may further maintain group cooperation by encouraging the punishment of infractions. When primed with religious concepts, individuals who had previously donated to a religious organization increased their punishment of transgressions in a game (McKay et. al. 2011). Thus, a belief in moralizing gods likely enhances cooperation by increasing cooperative behavior, decreasing transgressive behavior, and motivating individuals to punish non-cooperative acts.

Moralizing gods– specifically punitive gods– may be particularly adaptive in ecologically harsh and resource poor environments. Studies show that group living is most common in ecologically poor or uncertain conditions, in which the fitness benefits of group living are more likely to outweigh its costs than in good conditions (Ebensperger 2014, Guindre-Parker &

Rubenstein 2020). A belief in moralizing gods is associated with societies living in ecologically harsh and resource-poor environments (Snarey 1996, Botero et. al. 2014, Međedović 2020). Thus, a belief in supernatural punishment may enhance the viability and longevity of group living in ecological harshness by encouraging individuals to cooperate and to punish transgressions more than would a belief in a loving god or no belief in a god. Although this hypothesis has been little studied thus far, it has received support from Jackson et. al. 2021, which found that a belief in punitive gods increased group tightness and cooperation.

Discussion

Religion's partial heritability, trait variation, and differential fitness provide strong evidence that natural selection has played a role in its persistence; therefore, it is highly likely that religion possesses biologically adaptive value. However, moving beyond an assessment of religion's fulfillment of natural selection criteria to thoroughly analyzing how components of religion may be adaptive is challenging. Religion is shaped by the interplay of genetic and cultural factors, and it is difficult to disentangle their effects when considering adaptive value. As discussed earlier, some fitness-increasing traits are not products of natural selection– for example, the trash opening behavior of the sulphur-crested cockatoos. Although we can hypothesize about which particular components of religion are responsible for its observed fitness benefit, it is difficult to determine whether the components of religion we believe may be adaptive are products of natural selection rather than non-biological, but fitness-increasing, cultural transmission. Of the adaptive hypotheses I discussed, I speculate that non-kin cooperative behavior in religious groups is the most likely to have been significantly influenced by natural selection. Adaptive cooperative behavior is observed across many species and primarily functions to increase fitness; as such, it is very possible that a significant part of religion's adaptive value lies in its facilitation of fitness-increasing cooperative behavior. In contrast, ancestor worship primarily functions to honor the dead and may be affected by genetics, but fitness benefits accrued from engaging in this practice are indirect and likely minimal. Given the small fitness differential between individuals who engage in ancestor worship compared to those who do not, cultural transmission likely plays a much larger role in the persistence of ancestor worship than does natural selection. In addition, mate compatibility arises not from religion specifically, but from perceived or actual similarity due to same-group belonging. Thus, mate compatibility may be a by-product of religion rather than a biological adaptation that contributes to its persistence. To better understand the effects of natural selection on religion, further research should investigate 1) the genetic basis of honest signaling, belief in moralizing gods, and ancestor worship, 2) the link between non-kin cooperation and fitness in religious groups, and 3) the presence and fitness benefits of religion in differing ecological conditions. Important parameters to consider for use in modeling include genetic relatedness, religiousness and/or religiosity, and ecological conditions.

Glossary

Adaptive trait: a heritable trait has increased in frequency over successive generations due to the fitness benefit it provides

Adaptive value: the fitness increase provided by adaptive traits

Biological evolution: the change in the frequency of gene variants in a population over successive generations

Cooperation: the simultaneous or consecutive acting together of two or more individuals by same or different behaviors (borrowed from Taborsky et. al. 2016)

Cultural transmission: the transmission of cultural elements between individuals

Culture: learned values, beliefs, and behaviors

Fitness: survival to reproduction and reproduction

Natural selection: the process by which the frequency of certain gene variants increase over successive generations due to their reproductive benefit

Population: a group of individuals of the same species living and interbreeding within a given area (borrowed from Tarsi & Tuff 2012)

Religion: a shared social system that connects people with a supernatural power

Religiosity: the degree to which an individual values religion in their lives

Religious: belonging to a religion

Religiousness: the state of being religious

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