The Kin Selection of Religion

Bernard Crespi

Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada

Correspondence: Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada, tel 778 782 3533, fax 778 782 3496

Email address: crespi@sfu.ca (B. Crespi)
Abstract

I describe an integrative hypothesis for the origin and evolution of human religious cognition and behavior. The hypothesis is based on kin selection, which leads to reduced competition and increased cooperation within family and small-scale groups, and generates novel forms of psychological kinship that foster cooperation in larger scale groups. The 'concept of God' is represented by, and originates in the context of, one's circle of kin and one's ancestors, such that serving God and serving these individuals become synonymous. Kinship pervades, motivates and supports all of the major manifestations of religiosity, including ancestor worship, animism, totemism, monotheism, and culturally based moral codes. The primary selective pressures favoring religious phenotypes are social and ecological selective pressures within and between groups, mainly centered on food acquisition and intraspecific competition. Religiosity, as combined forms of morality and supernatural beliefs founded in kinship, represents group-specific adaptations that mediate cultural-group survival and reproduction as well as structuring opportunities and constraints for maximization of inclusive fitness. Religion originates in the setting of local, mainly biological kinship, but as groups increase in size, psychological kinship becomes more and more important. The kinship theory of religion is consistent with diverse data from anthropology, evolutionary biology, psychology, psychiatry, endocrinology, and genetics. It is not incompatible with most previous theories for aspects of the origins and evolution of religion, but it grounds them in basic, well-established evolutionary and behavioral-ecological theory.

*Keywords*: religious behavior, inclusive fitness, kinship
"There is something sacred about kinship, as most social anthropologists who have studied its operation in the field are prepared to admit" - Myers (1975)

The purpose of this chapter is to demonstrate that biological and cultural kinship form the core of human religious thought, behavior, and institutions. In doing so, I describe a simple model, centered on kinship, for how religion has evolved, step by step, under natural selection. This model can be broadly considered as a synthesis of Émile Durkheim's and Alfred Radcliffe-Brown's functionalist perspectives from anthropology, psychology, and sociology with empirical developments in evolutionary biology, behavioral ecology, endocrinology, and genetics over the past 50 years. It is founded predominantly on theory and ideas from Hamilton, Alexander, Trivers, Steadman, Coe, Palmer, and Lahti (Hamilton, 1964; Trivers, 1974; Alexander, 1974, 1987, 2013; Coe & Palmer, 2008, 2013; Palmer et al., 2008, 2010; Steadman & Palmer, 2008; Lahti, 2009). The ideas are straightforward and can be empirically tested. Their ramifications are important in that they conceptually unify the meanings of life in biology and spirituality, and provide an intuitive foundation for consilience between them.

I begin by explaining the causes of cooperation among animals, including humans, from basic behavioral-ecological and evolutionary theory. Next, I describe genetic relatedness, kinship, and inclusive fitness, and how they are associated with cooperative, and competitive, behavior. Third, I explicate the basics of behavioral ecology, the discipline whereby variation in ecology can be used to explain and predict variation in behavior, and the social systems that result. In the context of this article, religion can, most generally, be regarded as a social system that derives from culture-specific ecological and social adaptation, through the effects of natural selection. Fourth, I discuss the roles of human cognition and affect (emotion and mood) in the origins and evolution of religious thought, behavior, and institutions.
Fifth, in the spirits of Durkheim and Radcliffe-Brown, I describe a sequence of hypothesized stages in the evolution of religion, whereby this set of adaptations evolves, step by step, under selection, centrally mediated by effects of kinship. I conclude with a brief synthesis and suggestions for empirical tests.

The evolution of cooperation

As conceptualized here, religion involves cooperation (in a broad sense of the word) in the context of some combination of morality with the sacred or supernatural. Cooperation between two or more parties, whereby they provide benefits to one another, evolves under three possible conditions (Crespi & Choe, 1997; Lehmann & Keller, 2006). First, cooperation may be mutualistic. In a mutualistic system, both parties gain in the short or long terms from the cooperative interactions, such that eschewing them, or engaging in selfish or exploitative alternatives, are simply not favored. Plants and pollinators represent a simple example, as do humans engaged in trade. Mutualistic systems often evolve in situations where the two parties are phenotypically different in some way or ways that leads them to be able to provide complementary resources or services to one another. However, they may also evolve when two or more parties can jointly benefit from collective action, performing tasks with higher efficacy than could be otherwise be achieved.

Mutualisms are ecological, but also social, in that they evolve and are maintained only if one party cannot or does not 'cheat', exploiting the other by receiving benefits without providing gains in return. This situation is epitomized in the 'Prisoner's Dilemma' game, whereby two parties acquire more benefits by both cooperating with one another than by both cheating, but one party would gain even more (than by joint cooperation) by cheating while the other cooperated (Axelrod & Hamilton, 1981). Strategies in the game can evolve towards mutual cooperation, rather than joint cheating (a lack of cooperation), but only if
some means or mechanism exists to avoid or suppress cheating. This evolutionary game generalizes across many individuals to a 'tragedy of the commons', whereby a shared resource can be depleted if individuals each act in their self-interest rather than for the good of the group as a whole. In the study of religion, prisoner's dilemma and tragedy of the commons situations are usually represented in terms of the 'free rider problem', referring to individuals who gain the benefits of religious cooperation without paying their fair share of the costs (e.g., Wallis, 1991).

Hunter-gatherer groups, within which humans have spent the great majority of their selective, evolutionary history, are typically highly cooperative in mutualistic and egalitarian ways (e.g., Richerson & Boyd, 2001; Whiten & Erdal, 2012). Such cooperation is exemplified by extensive food sharing and cooperative, mutualistic divisions of labor, which have apparently evolved, at least in large part, in the ecological-economic contexts of selective pressures from starvation and malnutrition increasing the risks and effects of disease. As such, from an evolutionary-ecological perspective, human hunter-gatherers should be considered as a species of great ape that has evolved complex, cooperative social-ecological adaptations, specific to their local environment, and supported by large brains and cultural transmission of social and ecological adaptations (Crespi, 2014; van Schaik & Burkart, 2011). The more or less unique culture of each group can be conceptualized as an integrated set of 'cultural survival vehicles', adapted to local ecological and social conditions (Pagel, 2012; Palmer, 2010). These vehicles include, of course, different forms and manifestations of religion. More so than any other primate species, human adaptation is based around cooperating social groups, with most interactions being mutualistic.

Second, parties may cooperate due to manipulation or repression (Alexander, 1974; Frank, 2003). Under this model, one party exerts partial or full control over the behavior of the other, but also depends upon it, to some degree, for benefits. Examples include (1) lichens, comprised of fungi and algae, with the former in control of resources; (2) dominance in paper-wasp nests, where the queen behaviorally
suppresses worker reproduction and coerces individuals to work; (3) 'policing' in honey bee workers, whereby worker-laid eggs are eaten by other workers; and (4) humans engaged in jointly-beneficial ventures where one party is physically or socially dominant over the other. By this model, the parties are cooperating, though not as equals or free agents, and they are forced (with control taken away) or coerced (with costs actually or potentially imposed on non-cooperators) in some way to act more cooperatively.

Humans, like other primates, exhibit asymmetries in physical power, information, abilities related to food acquisition and group defense, social status, and skills, including social leverage through friendship and kinship ties (e.g., Lewis, 2002; Smuts, 1985); these and other variables can, in principle, mediate cooperation due to manipulation or repression. Most commonly, however, the repression of competition and coerced manipulation towards cooperation are some function of the moral codes specific to each culture. Such codes are enforced, pre- or post-emptively, by the group itself, or some subset of it, usually through aspects of religious cognition, behavior, and institutions. Generally, their role is to preclude or suppress behavior that is personally self-serving (with costs to others, or to the group more widely) or nepotistic (serving kin with costs to others, as described in more detail below) in ways that are detrimental to the interests of the group members, or relatively influential group members (Hughes, 1988). The supernatural or sacred nature of religious moral codes means that they can, in principle, be psychologically and culturally 'enforced' by agents beyond human control, which instantiates fairness and equality in ways that are not subject to dispute or human dominance, with beneficial sequelae to most individuals, most of the time, from moral adherence.

The third condition under which cooperation evolves is kinship (Hamilton, 1964). To a biologist, kinship is the sharing of alleles between two individuals due to descent of the alleles from a shared ancestor, such as their father or grandmother. Biological kinship is based on genetic relatedness; it is the probability that a specific allele in one individual (color it blue, conceptually) is also present in another
individual. Genetic relatedness values depend on the nature of inheritance regarding the (blue) allele concerned. If the allele is on an autosome, then relatedness from parent to offspring, or vice versa, is one-half, since meiosis leads to the random transmission of one allele or the other, at a locus, from one individual to the other (see Figure 1). Each additional meiotic link halves relatedness, to one-fourth for aunts and uncles with nieces or nephews, one-eight for first cousins, and so on. We usually consider 'distant' relatedness links, such as those beyond first cousins, as weak; however, from the standpoint of natural selection, links of even a few percent, corresponding to selection coefficients of this magnitude, can generate substantial effects across evolutionary scales of time.

In 1964, the eminent evolutionary biologist William D. Hamilton first demonstrated how genetic relatedness is expected to influence the evolution of behavioral interactions between relatives. Hamilton showed that individuals are expected to behave so as to maximize their 'inclusive fitness', which represents one's own reproduction plus one's effects on the reproduction of other individuals devalued by one's genetic relatedness to them. Individuals should thus commonly provide benefits to non-descendent (as well as descendent) kin, because doing so increases their inclusive fitness. This mathematical logic corresponds to a gene's eye view of natural selection; an allele may increase in frequency by having relatively beneficial effects on its bearer (compared to alternative alleles at a locus), and by having relatively-beneficial effects (through the behavior of its bearer) on kin, who probabilistically also bear copies of the allele identical by inheritance. Such natural selection involving kinship is sometimes called kin selection. The validity and universal applicability of inclusive fitness theory has been demonstrated in hundreds of studies (Abbot et al., 2011; Bourke, 2011); it is not controversial, and represents a simple extension of Darwinian evolutionary theory to the level of genes. For humans, the centrality of kinship systems to social and cultural behavior (e.g., Déchaux, 2008) attests to the long-term evolutionary
importance of inclusive fitness effects in our species, despite post-modernist attempts to discredit kinship studies through political criticisms of the biological and anthropological sciences more generally.

Kinship can favor cooperation via altruism, mutualism, or manipulation among kin. Altruistic behavior evolves under kin selection whenever an individual bears a cost in reduced personal reproduction that is outweighed by benefits to non-descendent kin. Mutualistic behavior is favored by kinship because it increases the fitness benefits from such cooperation, since aided individuals who benefit are kin. Additionally, kinship mediates the effects of cooperation by manipulation because, for example, subordinate individuals will be more likely to cooperate with, and help, a dominant individual who is kin than a dominant non-relative (Trubenová & Hager, 2012).

The strongest, most general prediction that one can make about behavior is that individuals are expected to (unconsciously) behave so as to maximize their inclusive fitness, barring mistakes and effects from evolutionary novelties (Alexander, 1979, 1987, 1989). Among humans, however, doing so most effectively need not always involve favoritism towards kin, or closer kin, at some cost to more distant kin and non-relatives. Indeed, if every individual in a large social group sought unilaterally and unswervingly to maximize their own inclusive fitness, the result would be pervasively expressed conflicts of interest, and likely social/ecological disaster. What is important to bear in mind here is that although kinship usually engenders some higher level of cooperation in any specific instance, variation in kinship represents one of the strongest factors potentially generating social/behavioral divisiveness within groups, unless mechanisms are in place to ameliorate its disruptive effects. Variation in kinship is important because when variation is greater, individuals are more favored to provide benefits to, and cooperate with, closer kin, and are less favored to help others (more distant kin and non-relatives). For example, at one extreme, we might have two sets of brothers in a group, with cooperative behavior restricted to within-
brother dyads. Towards another extreme, we might have a set of four cousins, who should cooperate with each other more or less equally compared to non-relatives.

To understand kinship effects, it is thus essential to take into account both cooperation and conflict. Consider two specific cases. First, a child is related to its mother, and its full siblings, by one-half. Our focal child is, however, related to their own (eventual) offspring by one-half, and to the offspring of their siblings (their eventual nieces and nephews) by only one-quarter. This means that the child will be favored to value itself, genetically, twice as highly as it values each sibling. Children in sibships are competing for limited resources from their parents. In this situation, each child 'wants' (i.e., has been subject to selection to take, or solicit) more resources from its mother (or father) for itself than for any sibling. Siblings thus compete with one another for parental resources, in a manner only partially constrained by their relatedness to one another (Bossan et al., 2013; Trivers, 1974). By contrast, the mother is equally related to each offspring, so her inclusive fitness is maximized, all else equal, by the same allocation to each. We have conflicting optima, and expect sib-sib and mother-offspring conflict.

Who wins, if anyone, in this situation? It depends on who is in control of what aspects of the interactions, and on the strength of kin selection on each party. If only the mother could, in some ways, use her privileged position as a primary source of childhood enculturation, and morals, to discourage or limit sibling competition, thereby reducing the degree to which copies of her genes interfere with their own transmission. This example illustrates how close kin are often also close competitors, and how all parties concerned can, in principle, benefit in inclusive fitness from reducing the level of wasteful competition between them.

As a second case, consider a hunter returning to his village with a large prey item. He might either distribute it among his kin, according to degrees of genetic relatedness combined with benefits gained by each relative, or distribute it equitably among all village members. The former distribution would
maximize his inclusive fitness, but only in the absence of a broader social network that provides mutualistic support by culturally-motivated egalitarian food sharing. The hunter may, indeed, suffer a run of bad luck in hunting later on; if he had been relatively selfish and nepotistic, he would be less likely to gain help from others in this situation, and if one's culture did not dictate sharing food more or less equally, the group as a whole would also be less likely to survive and prosper, relative to more-egalitarian groups.

This example applies to 'immediate return' food economies, as found in almost all hunter-gatherer groups. Such benefits from the 'moral' sharing of food are ecologically-based, and should be less pronounced in cultures with a higher predictability of food supplies.

To a biologist, these applications of inclusive fitness theory, in the context of genetically-based biological kinship, are straightforward. But anthropologists are well aware that biological genetic relatedness, and the actual kinship terms used by individuals in small-scale societies, are by no means always the same (see Figure 1). Why should this be so? A primary reason is that humans learn who their 'kin' are from being told by others, usually in childhood. This information need not be biologically accurate, and should indeed reflect the inclusive fitness interests of the controlling party or parties, and/or the summed interests of the group as a whole. Referring to mother's brother (or all father-aged males in a group) as 'father' may be genetically false, but it may, in some social and ecological contexts, be beneficial to both 'fathers' and 'offspring'. Similarly, calling some categories of cousins 'siblings' may usually be incorrect genetically, but doing so can serve to prevent inadvertent incest, as well as fostering closer kinship bonds between them. At an extreme, systems of 'universal kinship' have developed in many cultures, whereby everyone in a large cultural group has a designated kin relationship to every other member, and everyone outside of the group is non-kin (Barnard, 1978).
The key point here is that kinship is cultural and psychological, as well as biological (Bailey & Wood, 1998; Jones, 2000). Genetic relatedness, especially between parents and offspring, was the original context for the generation and maintenance of altruistic and mutualistic social bonds; it creates 'bonded' relationships, motivated by neurological and endocrinological reward systems, whereby individuals provide for one another. But because humans learn (and are told) who their 'kin' are, and are taught proper behavior towards kin and others in the group, kinship in our species is fundamentally psychological (Haig, 2011). Psychological kinship differs notably from biological kinship in that it is culturally malleable (e.g., Qirko, 2004) and can, in principle, promote close kin-like cooperation between any set of individuals in a group. Especially in matrilineal and patrilineal societies, links to shared common ancestors can also reinforce psychological kinship, because all individuals can trace themselves to the same 'parent' or 'grand-parent' (or more distant) kin, thus making the group a single, expanded, “nuclear family” of a sort, with everyone exhibiting the same level of psychological genetic relatedness to an ancestor and to one another (see, e.g., Shiels, 1975) (see Figure 1). Indeed, as noted by Wallwork, (1984), referring to the work of Durkheim:

The clan is a kinship group with self-sufficient religious, political and economic functions. Within it, solidarity is maintained by real or fictitious consanguinity. Actual blood relatedness lies at the basis of these ties, but real consanguinity is less important … than shared beliefs about a common origin. (p. 5)

How does inclusive fitness maximization work, then, under both biological and psychological-cultural kinship? Its operation should depend on the social ecology more or less specific to each cultural group. At one extreme, where ecological selection (mainly from food and disease) and social selection (mainly from competing groups, as well as from competition within groups) for group-wide cooperation are weakest, individuals should be most likely to strive to maximize their (biological) inclusive fitness,
subject to the effects of competition with other individuals also trying to do so. At the opposite extreme, where ecological and social selection make extensive within-group cooperation essential to survival, individuals should be selected to generally treat all others within the group as close kin in order to reduce the socially-divisive effects of genetic relatedness variation. In this general regard, perceptions and applications of kinship can be considered as culture-specific adaptations, as many anthropologists have described in their discipline-specific ways. However, despite such variability in kinship term usage across cultures, one still expects strong selective pressure for treating kin according to their genetic relatedness, so much as possible in any situation or culture; all individuals will indeed benefit from doing so, so any cultural norm that supports the general and successful ability to maximize inclusive fitness should also spread and be maintained if it does not also generate overly socially-divisive effects.

What does psychological kinship have to do with religion? As described in more detail below, it is my thesis that religion represents a form of kinship at its psychological and conceptual-institutional core, but a special kind—one that is grounded in the ideas of the sacred and supernatural, and thus is more effective than biological kinship at promoting cooperative acts.

**Behavioral ecology of human hunter-gatherers**

We have discussed kinship, and religion, in terms of adaptation. How, then, do adaptations evolve and generate diversity within and between species in traits such as social behavior, cognition, and aspects of culture?

Behavioral ecology is a scientific discipline that seeks to explain adaptive variation in behavior from variation in ecology, within and across taxa. For example, most passerine birds defend territories to ensure access to sufficient food for rearing offspring, and their mating systems are socially monogamous
because males benefit from helping to feed and defend the territory and offspring. The ecological situation (food for babies, and a territory that is defensible and contains such food) selects for the behavior (territorality) and the social system (monogamy). Where food is not defensible, as in many seabirds, territoriality does not evolve.

What is the behavioral ecology of humans? We are great apes with especially large brains that live in large cooperative and competitive social groups, who use tools extensively to procure food and transmit ecological and social information culturally. Despite these commonalities, and likely because of them, humans inhabit a vast diversity of ecological habitats, from rain forest to arctic, desert to high mountains. This ecological diversity is expected to generate behavioral and cultural diversity, as each group has evolved, under gene-based natural selection and cultural selection, a set of ecological adaptations that promote survival and reproduction under their particular conditions. Most of these ecological adaptations relate to procuring food, ameliorating abiotic forces, avoiding and surviving disease, and dealing with predators and competitors. Their diversity attests to the flexibility and effectiveness of cultural adaptations, and their key roles in producing the uniquely pronounced behavioral and social diversity of our species. So humans have myriad ecologies and consequent diversity in behavior and systems of sociality.

Humans also compete with one another, both within and between groups. We have discussed competition within groups, in the context of inclusive fitness maximizing; competition between human groups appears to have been at least as potent a selective factor in human evolution, although the pre-historical evidence for such competition is indirect (Alexander, 1989; Bowles, 2009). What is important about between-group competition in humans is that (1) it should strongly select for within-group unity and cooperation, and cultural adaptations for defense of the group as well as success in prevailing over other groups (Alexander, 1979; Lahti & Weinstein, 2005); (2) it should be at least as efficacious a selective
pressure in ecologically-favorable habitats as in harsh ones, since better environments can support higher population densities and generate stronger demographically-based group competition for the best lands; and (3) it may often involve human groups that treat one another as different species (as indeed they can be, culturally and with regard to interbreeding) and have the capacity to eliminate one another completely. Many small-scale groups thus refer to themselves in some way as 'The People', indicating that other groups are not considered to be human at all.

The upshot of these behavioral-ecological considerations is that the primary selective pressures affecting humans throughout most of their evolutionary history are expected to have been both ecological (especially food and disease) and social/ecological (other humans). The origins, evolution, and diversity of religious beliefs, behaviors, and institutions must be set in these selective contexts in order to understand their variable application and relevance for different cultural groups.

By what selective, evolutionary mechanisms would religious behavioral/ecological adaptations come about? Within the ecological and social contexts described above, religious adaptations would have evolved under both genetic and cultural selective processes, where 'culture' is conceptualized as human-generated cognitive information and material objects that are transmitted through social learning and physical inheritance. Most broadly, human 'culture' thus represents aspects of the environment—including other humans, and their ideas—that can be perpetuated vertically (i.e., across generations) and horizontally within groups, as well as horizontally between groups (Alexander, 1979). Like language, religious beliefs and behaviors thus evolve genetically as well as culturally; humans have evolved the genetic capacities for language (for example) and religiosity, but their expression depends on interactions between the effects of genes and the effects of environments. Genes 'for' religion, which are evidenced by statistical associations between allelic variation and variation in measures of religiosity, must therefore exist (e.g., Bradshaw & Ellison, 2008; Kandler & Riemann, 2013) since the cognitive capacity for religion
has evolved, but their effects always depend on the environment in which they are expressed. Genes 'for' religion should also, by the thesis described here, represent genes for perception, cognition, and behavior related to kinship and bonding. How, then, have they evolved?

**Human cognitive ecology**

The starting point for discussing the origin of religion must, of course, be what it is conceived to be, and what phenotypes were present just prior to its inception. As noted above, we are considering religion as some combination of morality with the sacred or supernatural. Morality here is indirect reciprocity, which evolved from mutualism and altruism among kin (Alexander, 1987) (Table 1), and the sacred or supernatural refer in some manner to gods and other immaterial presences, faith, magic, worship, and veneration. “Supernatural” and “religious” are usually contrasted with “natural” and “secular”; these distinctions need not exist as cultural divisions (and indeed do not exist in most small-scale societies), but phenomena must still vary, somehow, in religious relevance or import. I consider some degree of morality to be present initially, prior to its combining with the supernatural or sacred, in part because conceptions of 'fairness' have been demonstrated across multiple species of primate other than our own (e.g., de Waal, 2013).

Cognitive and emotional traits that can be considered as necessary though not sufficient for the origin of religious thought, some of which are unique to humans, include the following:

1. sharing of attention, since religion represents a group-level phenotype in most of its effects;
2. empathic connections or bonds with others, whereby feelings or thoughts link one individual with another in a fitness-salient way, or link two or more individuals together in shared fitness-salient experience;
(3) capacity to establish, maintain, and remember a social relationship with specific others even in their physical absence, or after their death;

(4) theory of mind, the belief that other individuals or entities have minds, mental states, awareness, motivations, and agency comparable in some way to our own;

(5) ability to infer meaning and purpose from events in the world;

(6) imagination, the ability to generate or form a mental concept or image of someone or something that is not real or present;

(7) social learning, which forms the primary basis for cultural transmission of narratives, cultural norms, and ideas;

(8) language, which, like shared attention and social learning, is required for the sharing and transmission of cultural phenotypes with abstract content; and

(9) self-awareness, which is required for conception of the 'self' as a 'mind' or entity separate in some way from the 'body'.

Such lists of hypothesized preconditions for religiosity have been discussed before (e.g., Wade, 2009), but they have seldom been considered together in the context of a stepwise evolutionary process at the origin of religious phenotypes.

It is essential to recognize, initially, that all of the nine phenotypes above evolved in selective situations entirely separate from religious ones. As in the evolution of other qualitatively 'new' traits, the novelty must arise from some process of change or divergence in function (such as fins to legs at the origin of amphibians), or some combination of traits with new, emergent properties (such as the tendency to combine two actions, or ideas, with synergistic effects)—and in both cases, the initial, small, novel change must be selectively favored. Of the phenotypes above, imagination, theory of mind, and self-awareness appear most relevant to the origin of supernatural aspects of religious cognition, because they
require something that is imagined and not material, comprising some element of 'mind' or 'agency' that is comparable to that of the self. The closest such entity may well be the 'spirit' of a close relative who has recently died, because they indeed still exist in an immaterial way as thought-patterns and memories in the minds of the living (Lahti, 2009), with an emotional bond, forged by close kinship, connecting the survivor to the deceased (Bowlby, 1999).

There is no good reason to believe that supernatural thinking and morality were connected with one another at the onset of supernatural thought; they presumably evolved in parallel at least initially (with morality present beforehand, as noted above), but then combined under some cultural and cognitive circumstances. Indeed, it is this combination that, under our definition, produced the first religious phenomena per se. What selective circumstances, then, might lead to these two phenotypes coming together?

At this nexus in our scientific narrative of religious creation, it is important to address—and dispel—a biologically-based conception of the origin of religion that I see as antithetical to evolutionary biology itself. Religion is thus seen by some researchers as arising as a spontaneous byproduct of other traits, as driven by the 'hyperactivity' of agency-detecting mental modules, as 'canalized' by evolved constraints on brain functions, or as maladaptive, non-adaptive, or delusional side effects of selection in other contexts (e.g., Atran, 2002; Atran & Henrich, 2010; Dawkins, 2009; Powell & Clarke, 2012). The primary difficulty with these arguments is that religiosity and religion represent central features of the cognitive and cultural landscapes of virtually all human societies, including hunter gatherers who are believed to resemble our ancestors over tens of thousands to hundreds of thousands or even millions of years. If religious cognition, rituals, and institutions were maladaptive, or neutral and under the radar of selection, their aspects could not have increased in frequency and it would certainly not be universal; this is precisely opposite to the pattern expected under basic evolutionary theory (Bulbulia, 2004). There is no
question, at least in my view, that humans have genetically evolved, adaptively, the capacity to conceive, enact, and experience religiosity and culturally-evolved forms of religion that serve core functions in human societies. The questions are how this evolutionary process occurred, and most importantly how to find out.

The origins and early evolution of religious thought and behavior

We have discussed 'religion' as an entity, but we must remember that it involves a mosaic of cognitive, behavioral and cultural elements, connected by commonalities that include the sacred, supernatural, magical and spiritual. It is the linking of these elements with cooperation and conceptions of morality or 'proper behavior' that constitute the origins of religion. As described above, the general, proximate mechanisms whereby cooperation can evolve include mutualism, manipulation or repression, and kinship. Our goal thus becomes, in part, generating plausible and testable scenarios for how these three processes can join the supernatural or sacred with morality, in the frameworks of typical human social interactions structured by maximizing of inclusive fitness.

The religious brood

Consider the most basic of primate or human groups: a mother with her offspring. We have discussed above how patterns of kinship within such a family generate mixtures of cooperation with conflict: The mother is equally related to each of her offspring, and thus is selected to treat each equally in provision of resources (all else equal), but each offspring is selected to seek to obtain more resources than its sibling does, and more than the mother is selected to provide it. The system resembles a multi-way tug of war, in
that relatedness values of one-half promote cooperation, but individuals are also unrelated for half of their genes, which promotes competition. Such competition is socially 'wasteful' because energy and time are expended in the conflicts (e.g., fighting among siblings, tantrums in young children) that could be devoted to higher survival and reproduction of all individuals concerned; such conflicts indeed occur in some circumstances only because, on average, they generate a net inclusive fitness advantage to one party (the relative 'winner') at a cost to others.

But the expression, intensity, and outcome of such conflicts depends on who is in control of cognition and behavior, and in this regard it is the mother who, especially in humans, has profound advantages. The mother is thus physically dominant over her young children and can physically repress competition between them; but more importantly, she is culturally dominant, being the primary source of social learning and enculturation. Human children have indeed evolved to 'overlearn'—to accept cultural information more or less uncritically because its assimilation, rapid and copious, is crucially important to becoming a successful adult (van Schaik & Burkart, 2011). What this means is that as soon as children are old enough to understand, the mother can, and should, imbue children with any culturally-based motivations for 'proper' behavior (behavior in the interests of the mother, her kin group, and their social group more generally) that she can.

The best motivations for good, 'moral' behavior would instill a fear of retribution, generate strong and vivid memories, and work even when the mother was not present. These properties are met most directly by supernatural, 'religious' agents, imagined or believed-in by the mother, that reside within her mind and the social/cultural ethos. In its simplest expressed form, such agents inhabit short narratives invented by the mother, her ancestors, or other group members. Such narratives are exemplified by the story from a Mayan boy of six or seven years who urinated in the local river, and was told by his mother words he has 'never forgotten': 'whoever does this, when he dies, he will not be able to go directly to heaven. The soul
will be sent to the ocean in search of the urine … and must remove it from the ocean in order to be accepted into heaven' (Montejo, 2001, p. 189).

This is religion, the supernatural plus morality, at its most basic. The mother tells an imagined story (that she was told as a girl—by her mother, in this case) with supernatural content, to instill 'good' behavior in a relative. The origin of such stories only requires the ability to imagine some powerful agent (that need not exist), and the sense to invoke such an agent to motivate one's young children, thereby increasing one's inclusive fitness. Such stories can teach lessons in any relevant context: to reduce competition among siblings; to foster cooperation among kin or in one's group more generally; to learn and remember the ('sacred') the importance and properties of certain game animals, crops, or water supplies; or to honor one's ancestors (and thereby help serve their interests, and those of the family and group more broadly). The tendencies of children to 'naturally' believe in divine agents from early ages (Bloom, 2007; Richert et al., 2005) suggests that they have evolved to be sensitive to religious enculturation, perhaps due to the benefits thereby accrued.

Within a group of siblings, supernatural proscriptions or other means of cognitive manipulation by the mother benefit her by reducing wasteful, competitive interference between copies of her genes in her offspring (Coe et al., 2010; Palmer et al., 2008); the process can also be beneficial to the offspring themselves to the extent that it motivates behavior that helps kin and one's larger circle of (kin-dense) social significance, and thus teaches children how to maximize their inclusive fitness subject to the contingencies of kin-network and group-level social/cultural cooperation as embodied in moral codes and ecological views of the world. This hypothesis is supported most directly by strong positive associations of parent religiosity with the prosocial behavior of their children, with clear benefits of religious enculturation for their cognitive, emotional, and behavioral development (Bartkowski et al., 2008).
The process whereby the moral joins with the supernatural, to reduce competition between kin and increase cooperation between them, can be generalized and extended across generations, because older-generation individuals will always benefit from reduced competition among their descendants (Coe et al., 2010; Coe & Palmer, 2008, 2013). This cultural mechanism should also work for psychological kin and non-relatives in one's group, in the frameworks of mutualism and repression of competition by religious agents, though the strength of such effects should vary depending upon the strength of among-group (compared to within-group) ecological and social selective pressures (Lahti & Weinstein, 2005). This logic leads to the following question: Why are supernatural and sacred claims, stories, guides, and admonitions so effective at changing behavior when they cannot be objectively verified, and many individuals, especially adults, may secretly question their reality? Why is proper behavior, especially among adults, not sustained predominantly by other, non-religious means such as forms of secular policing?

Powers of the supernatural

Supernatural power and agency exhibit a number of properties that make them ideally suited for motivating human cooperation, compared to other mechanisms. First, supernatural authority, unlike human authority, cannot be questioned without casting aspersions upon the foundations of the cultural identity of one's group, one's ancestors back to stories of creation, and the suite of traits that represent one's 'cultural survival vehicle' (Calhoun, 1980; Pagel, 2012). In historical times, such aspersions have been routinely punishable by death as 'heresy'. In this context, religious and magical power and claims can be sustained as unconscious metaphors for their secular human equivalents, which are accepted as true
because all or most individuals, or individuals in power (in hierarchical societies), usually gain from doing so (Palmer et al., 2010).

Second, supernatural power is complete power; its agents are, or can be, omnipresent, omnipotent, and omniscient, such that in principle one can never 'get away' with transgressions, even within one's thoughts (Rossano, 2007). These properties make supernatural policing socially 'cheap' as well as effective; agents rewarding good behavior and punishing bad behavior are continually present, and indeed should become internalized into one's moral 'conscience' (e.g., Atkinson & Bourrat, 2011). By contrast, direct policing by humans is costly in requiring time and energy that could be devoted directly to the production of goods, services, and offspring; it is also potentially disruptive in that secular power can be abused in the service of nepotistic and personal self-interest. Humans do, of course, engage in actual social and physical punishments of transgressions, but normally, in small-scale groups, they do so in the context of acting, more or less through consensus, on the agreed behalf of supernatural agents (e.g., Wadley, 1999), and often through shamans who mediate between the worldly and divine (Steadman & Palmer, 1994). Supernatural agents though, at their most effective, supremely-motivate self-policing, the most effective way to suppress deviations from proper, moral behavior (Gintis, 2003).

Third, supernatural agents are memorable and engaging (especially for children), and naturally generate cultural narratives that themselves serve as models for teaching and modeling proper behavior in the framework of one's culture. It is these stories, most often oral cultural narratives, which embody, sustain, and transmit core cultural knowledge essential to a group's survival and to maintaining its unique identity (e.g., Rink, 1875, pp. 86-87; Sugiyama, 2001; Coe et al., 2006; Anthony, 2013). Stories with supernatural content are constrained in content only by human imagination, and even today, in the broader contexts of narrative formation in literature, media, and the arts, they revolve around human social conflicts and confluences of interest with the near-universal triumph of good over evil. Humans learn
social skills from such stories, and from the alternative scenario-building—as safe 'play' in the mind—that they inspire (Alexander, 1989).

Finally, supernatural agents are flexible and can take immaterial, human, animal, or landscape forms. They can 'explain', 'a-rationalize', be responsible for, or be thanked for, any events that may transpire in human experience. They also motivate 'worship', considered here as social displays indicative of one's own moral thought and behavior, which serve as mechanisms to instill and sustain optimism, confidence, unity of purpose, and cultural identity. Worship and prayer indeed appear to represent, at least in part, social placebos that are commonly effective (as are medicinal placebos, due to their optimizing effects on neuro-immune functioning; Humphrey & Skoyles, 2012) in leading to favorable social consequences, as are nocebos (belief in negative consequences; Hahn, 1997), when supernatural agents are disobeyed and displeased. Indeed, religious belief can exert a range of positive psychological and physical effects, including the enhanced health effects of religiosity reported across many studies (e.g., Koenig et al., 2012).

Supernatural agents are, of course, not always punishing or rewarding to humans; they may also be capricious, or indifferent, or exhibit other human-like traits. In keeping with our behavioral/ecological, functionalist perspective on religious phenotypes as adaptations, such personality variation should reflect the nature of selective pressures to which different cultures are subjected, and how controllable such pressures are by collective human actions. Thus, more-punishing agents are expected where groups are selected in the context of avoiding collective misfortunes by cooperation, more-rewarding agents are expected when cooperation promotes more-beneficial events such as good harvests, and more-capricious, or disinterested, agents are expected when humans live under ecological and social conditions where collective, cooperative actions can have smaller impacts on fitness-related outcomes. Such considerations lead to clear cross-cultural, comparative predictions, as discussed in more detail below.
Synergism of the supernatural with moral

The previous section discussed a scenario for how morality may have initially merged with supernatural agency and sacred content. How might these two phenotypes coevolve together? Major transitions in ecology and evolution are often driven by positive feedbacks, whereby a suite of changes occurs because two sets of causes or selective agents mutually reinforce one another as change proceeds (Crespi, 2004). In the early evolution of religion, the initial strengthening of moral systems by incorporating supernatural content would be expected, all else equal, to result in a social/economic surplus: As societies became more cooperative under the effects of this new, religious, adaptation, they would have become more prosocial, and collectively-productive. However, as in the evolution of social cooperation among other animals, the generation of new or increased social resources generates stronger selection pressures for gaining benefits through exploitation, and self-serving behavior, by some parties (Lahti, 2009). What this means is that higher, more broad-based levels of moral behavior should themselves select for enhanced and increased means of policing to prevent and reduce exploitation, which in turn should enhance and increase the role of the supernatural and sacred in punishing immoral behavior and rewarding the good.

By this synergism hypothesis, morality and the supernatural may coevolve under positive feedback, at least during periods of disequilibrium when social/behavioral/ecological conditions are subject to culturally-driven change. In principle, after the initial joint evolution of these two sets of phenotypes, periods of synergism could be prompted by changes in either one; for example, increased morality-based cooperation could evolve culturally due to greater external threats, or increased supernatural cultural content could evolve due to an influx of efficacious god-concepts from neighboring groups. This hypothesis, though conjectural, could be evaluated in phylogenetic frameworks and by testing its assumptions, such as economic benefits from more-effective moral systems.
The origins of gods

"The ancestor cult is the transposition to the religious plane of the relationship of parents and children"

Fortes, 1959, page 30

"The people of Nyansongoven view their religion as a set of demands made on them by the ancestor spirits" - Tatje & Hsu, 1969

The supernatural and sacred can be applied to places, plants, animals, humans, and abstract or imagined entities. A more or less universal feature of these applications in small-scale societies is so-called 'animism', the belief or world-view that living creatures in nature, and particular places, are imbued with souls or spirits (e.g., Bird-David, 1999). Although it represents a facet of religiosity, animism remains somewhat separate from morality because it is not directly concerned with relations among humans; instead, its focus is bonds and connections between humans and non-human phenomena in the world that exhibit sacred or spiritual properties. Again, there are no Western distinctions here between 'supernatural', 'natural', and 'not natural'; humans are simply an integral part of the world and, to humans, creatures and places are recognized as 'sacred' to lesser or greater degrees.

A simple behavioral/ecological explanation for animism is that it spiritually 'tags' animals, plants, and places that are especially important, with regard to ecological considerations, for the long-term well-being of one's cultural group (e.g., Anthony, 2013; Rose et al., 2003) (see Table 1). These may be prey animals, medicinal plants, agricultural plants, water holes, streams, defensive positions, shelters, and any other aspects of the world that interact with any of these in functional or indicative ways. Such species and places, and the landscapes and ecological networks within which they are embedded, represent key
sources of sustenance and survival; selection should strongly favor cultural means of teaching and learning about them via rituals, remembering their properties, protecting them via taboos and offerings, and fostering kinship-like emotional bonds with them as a mechanism to sustain the motivation to protect, conserve, and sustain. Indeed, in animism people can be said to 'envision their connection to the animated agencies or 'nature' as bonds of sharing between relatives' (Campbell, 2015). Such psychological/ ecological adaptations will be especially vital for a species that is fully capable, even as small-scale societies, of inflicting severe environmental degradation through tree-cutting, burning, over-harvesting, and disrupting sources of water (e.g., Diamond, 2005). Moral considerations come into play for avoiding tragedies of the commons, although here the indirect reciprocity is more indirect than for human social interactions themselves.

The Australian aboriginal 'dreamtime' ethos represents an especially clear example of the ecological bases of these forms of religious cognition and behavior, in that ecological conditions in the Australian deserts are among the harshest on earth, strengthening selection for cultural/moral/ supernatural mechanisms fostering survival. Indeed, as described by Rose et al. (2003, p. 3), totemism among aboriginals in New South Wales 'articulates a system of kinship with the natural world', with relationships 'based on enduring solidarity, responsibility and care', where individuals forbear to hunt, or burn, due to the sacredness of ecologically-crucial sites. These ideas trace back directly to Radcliffe-Brown (1945, 1952), one of the first anthropologists to consider religious and kinship systems as inter-related, functional, and adaptive components of culture, from social and ecological perspectives. They may also help us in understanding current human emotional bonds with 'nature', and motivations to protect and conserve the natural world based on spirituality, beauty, and human well-being.

A sacred water-hole, or the spirit of goannas, may be supernatural, but we would not necessarily consider them as 'godlike'. 'God' has developed as a concept that is more or less closely attached to
humankind-forms, and its origin appears to stem from another near-universal feature of religiosity in small-scale societies: the worship of ancestors (e.g., Tatje & Hsu, 1969; Shiels, 1975; Steadman et al., 1996). As such, ancestor worship represents a key nexus in the evolution of religion, which for the first time directly combines kinship with socially-interactive morality and the supernatural or sacred.

The 'ancestor' in ancestor worship can have any of several meanings, beyond its generic one as genetic fore-bearer. First, an ancestor can be a deceased relative who, even if no longer living, may not be considered as 'dead' until everyone who knew and loved them has died (Stegeborn, 1999, p. 271). Second, an ancestor may be a deceased relative, or a cultural group member, who has earned this designation as a sign of honor, through having contributed especially highly in some way to one's cultural group or circle of kin (e.g., Plath, 1964, p. 303). Third, an ancestor may be an ultimate, distant progenitor of one's cultural group who was instrumental in its foundation. Across all of these contexts, 'worship' of ancestors refers to obedience, acceptance as a moral conscience, subservience, emotional bonding, supplication, provision of sacrifice, and the performance of rituals; all of these forms of worship display to living kin, and others in one's group, moral character and a willingness to follow the traditional rules of cooperative behavior, as well as reinforcing one's own cognition of kinship ties, service, and emotional support (e.g., Plath, 1964; Wadley, 1999; Coe & Palmer, 2008; Steadman & Palmer, 2008). As noted by Radcliffe-Brown (1945):

Rites can therefore be shown to have a specific social function when, and to the extent that, they have for their effect to regulate, maintain and transmit from one generation to another sentiments on which the constitution of the society depends. (p. 35)

Ancestors are similar in some ways to the spiritual agents who would punish our Mayan boy for defiling his local river, but they differ in functionally important ways. Thus, ancestors do not just represent
supernatural, unquestionable moral authorities and arbiters; they also, literally as well as figuratively, created the living and their culture, and they carry the bonds of kinship and the power of the extended, cooperative family circle of kin into the realm of the sacred (Alexander, 2006, 2013; Crespi & Summers, 2014; Lahti, 2009). They can also do so at multiple levels, given the hierarchical structure of pedigrees and phylogenies: For example, among native peoples of the Late Intermediate Period (1000–1400 A.D.) of the central Andes, one finds archaeological evidence of local kin-group (i.e., household) ancestor worship, ancestor worship at higher levels whose descendants encompass a broader group, and sacred 'founding' ancestors at the highest level (Mantha, 2009). In principle, each of these levels of ancestors would hold sway, through human intermediaries, over a larger and larger set of more and more distant kin, whose collective, cooperative actions may be selected for—invoked by the relevant ancestors—in functionally-salient contexts: at the highest level, defense of the entire group; at intermediate levels, building large structures or time-limited agricultural work; and at the lowest levels, local tasks and day-to-day problem solving. At each level, cultural/psychological kinship, as well as biological kinship, structure and motivate the cooperative activities; failure to obey the ancestors is expected to bring disaster from supernatural sanctions or wrath, and may well bring it through non-supernatural effects of non-cooperation.

More generally, religious rituals focused on ancestors strengthen kinship links (Steadman et al., 1996; Rossano, 2010, p. 148) and foster cooperation broadly (Fischer et al., 2013) through demonstrating social solidarity and awareness of shared pasts and fates. Other central facets of many traditional religions, such as totemism, which involves the assignment of animal or plant 'tags' to individuals within networks of kinship-associated lineages, also generate and maintain links to common ancestors, as well as generate a new form of psychological kinship whose bonds connect humans both with each other and with important features of their local ecology and landscapes (their totems). Totemism can thus serve as
'cultural mechanisms aimed at building and sustaining social relationships between close and distant kin', by encouraging 'family-like cooperation between distant kin' (Palmer et al., 2008, p. 724) (see Table 1).

The concept of God

'Certain types of psychological security found in a relationship to a personal God in the West are found only in relation to the actual family in Japan'  DeVos 1958, page 402

We all have some concept of God, be it an all-powerful white-robed figure above the clouds or a mysterious agent who created the heavens, earth, and underworld. How and in what social context, though, would the original concept of God most likely have arisen? I suggest here, following Alexander (2006, 2013) and Crespi and Summers (2014) that the concept of God arose as a metaphor for one's circle of kin and social significance— one's kinship and cultural network, if you will, including ancestors. Under inclusive fitness theory, the 'meaning' or 'goal' of life is service towards this circle of kin, and our culturally-bonded non-relatives, where 'service' means altruism, cooperation, and mutualism that maximize one's inclusive fitness within the constraints and selective contingencies of one's larger social and cultural context. Under religious moral codes and obligations, the 'meaning' or 'goal' of life is, similarly, service to God (or gods), who represent core concepts and figures within one's social and cultural ethos. The concept of God can thus be seen, fundamentally, as a metaphor for our circle of biological and psychological kin and family, extended across pedigrees and affines, and into the past to powerful, inspiring ancestors. As described by Alexander (2006):
To the extent that the concept of God actually arose as a metaphor for the kindred, or circle of kin, then – perhaps surprisingly, at first – the evolutionary version of the meaning of life becomes synonymous with the religious version of the meaning of life. In both cases the meaning of life is to serve God.

By this line of reasoning, the first human-styled gods derived from ancestors, who, as described above, motivated cooperation among their descendants, thereby reducing competition between them, and thus generating, and sustaining, a suite of traits that enhanced cultural survival and spread (Coe et al., 2010). These first gods, often likely as founding ancestors, 'created' their followers both genetically and culturally, and then, under our functionalist perspective, evolved culturally, in their effects, to foster ecological and social benefits to survival and reproduction. Such benefits accrue through such features as rituals, animism, forms of ancestor worship, and totemism, which are more or less well-matched, adaptively, to local ecological and social conditions (see Table 1)—until, of course, such conditions change.

Ecological revolution and the explosion of kinship

'Most religions teach that God is the power that watches over and guides their particular group. Gods apparently began as tribal gods (which we can consider as “kin circle” gods), and it is obvious but unfortunate that they have never ceased being such, even if particular religions (in effect, large and sometimes fragmented tribes) have become huge and widely distributed (that is, God was, and still is, a way of winning by promoting a particular kind of collective good feeling that makes a group a more formidable force against threatening or competitive human groups). ' Alexander, 2006
The human agricultural transitions, which took place in parallel at various sites across the globe, revolutionized human ecological and social structures within an evolutionary blink of an eye (Gowdy & Krall, 2015). Thus, these revolutions all led to much larger group sizes, economies based on territory and property, and social hierarchies founded on wealth and power (e.g., Lahti, 2009). These political and economic transformations led, in turn, to systems of human cooperation (and competition) based more on repression and coercion, and less on mutualism and genetically-based kinship, although the agents of repression were commonly based around kinship through leadership by a ruling family and lineage. Local kinship, and local ancestor-based gods, certainly still exerted effects, but became more or less subservient to the power of emerging states, which often involved a merging of religious with political/economic power (even if leaders did not also become declared hereditary gods, as described below). The transition from hunter-gatherer to agriculture-based social and religious systems was thus profound in scope, but 'intermediate' religious systems, centered on 'superior ancestral' gods who were uniquely able to serve and protect both ruling families and all others within the group, have been described that neatly bridge the transition (Shiels, 1980).

A key consequence of the agricultural transition is that the emergence of leaders, coincident with states, creates conditions where specific living humans, and their ancestors and descendants, can become self-appointed and culture-appointed gods or godlike figures, thereby consolidating and retaining power through the manipulative co-option of god concepts coupled with political instruments of repression. Such leadership becomes increasingly important as groups become larger, which results in greater potential for within-group conflicts (strengthening selection for repressive leadership) as well as greater potential for coming into conflict with other groups that have different, incompatible gods and leaders. A
leader's subjects may also, however, benefit from leadership in a mutualistic way (relative to less effective central control) if their leaders are effective in retaining and acquiring land and other resources.

What are the expected roles of kinship in religiosity, as these changes proceed? As groups increase in size, bondedness, identity, and kinship at the level of the functional political groups (incipient or actual states) should become more and more psychological and cultural, and less and less based on genetic relatedness, although long-term ancestral (actual or supposed) genealogical links, such as those linking each of the twelve tribes of Israel, or those linking Mormons with the 'lost' tribes of Israel (Dziobel, 2007, p. 53) may gain importance and define group identities. Importantly, such developments coincide with the emergence of monotheism, whereby one all-powerful god excludes all others, along with the emergence of inclusiveness and universality, whereby individuals can freely join a religion, at least for some faiths in this period such as Islam and Christianity (see Figure 1 and Table 1). Both of these historical processes reinforce the emerging primacy of psychological kinship over genealogical kinship, although cultural 'markers' of long-term ancestry, such as skin color and language, may also mediate whether psychological kinship is effective in unifying particular groups.

In the context of psychological reactions to such factors as skin color and language, and more generally, it is important to recognize that with the advent of agriculture and cities, changes to manifestations of culture and religion began to happen sufficiently rapidly that they should represent much more cultural than genetic evolution. The selective pressures that drive changes in religion thus primarily involve cultural group selection, whereby groups with particular means of agricultural production and transport, methods of warfare, and patterns of inheritance and marriage—and their inter-related forms of religiosity that support cultural and demographic success, especially in group-versus-group conflicts—gain advantages over others. Monotheism can thus be considered as a cultural/religious adaptation to especially strong conflicts between groups, where single, strong leaders, both supernatural and secular,
and effective systems of motivation and punishment from both levels of authority, provide adaptive cultural advantages (Johnson, 2005; Lahti, 2009). Given an increasing prevalence and severity of conflicts among groups, the inclusiveness of religions may also provide benefits in that conquered people can be culturally, religiously assimilated, and others can also be motivated to join through perceived advantages to doing so. Both mechanisms thereby increase the power of groups with such religious systems and facilitate their spread.

Monotheistic, inclusive religions may support unique forms of psychological kinship, in that all worshipers become equally-related (indeed, ideally, related by unity) 'siblings' in a huge family with a shared moral code supported by a single, all-powerful, and unquestionable God. Such structures generate systems of potential universal fairness (Lahti, 2009), and to the extent that they also support nuclear and extended family structures (which indeed most do), they are ideally suited for the individual maximization of inclusive fitness through behavioral effects at both the local and cultural group levels. Larger, more-cooperative families make for larger, stronger, more-cooperative and successful religions, as well as states. That said, larger more culturally-diverse religions may also be more prone to 'cultural speciation' by splintering and splitting along ideological grounds, or indeed along kinship and leadership inheritance-based lines, as between Shia and Sunni.

An important final consideration regarding the recent evolution of religiosity and religious institutions is that it is often difficult or problematic to conceptualize 'adaptation' in these circumstances, because (1) human social-cultural environments have changed so rapidly that maladaptations are expected, such that the cognitive architectures of religion, expressed in novel environments, can give rise to behaviors that are non-optimal for some or all parties; and (2) cultural group selection can be considered 'adaptive' in the framework of groups with particular cultural traits increasing in size (and these traits increasing in frequency) more than less-successful groups and traits, but such changes need not result in
any increases to individual well-being, especially when they happen too fast for genetically-based ecological and social adaptation to keep pace. Indeed, there is no question that some or many cognitive and affective aspects of psychological kinship, as embedded and expressed in religions of recent societies, evolved under nuclear-family, extended-family, small-group, and tribal social conditions, which are different in some ways from the situations that people have faced for the past few hundred to several thousand years. These differences need not be profound, because humans have always lived among mixtures of close and distant kin as well as non-kin. However, humans are faced now with one clearly daunting evolutionary/religious novelty: huge, highly armed, religious nation-states driven by parochial moralities and supported by irreconcilable supernatural beings. Evolutionary theory can, I think, be useful here in emphasizing, in a humanistic if not necessarily a scientific way, the core commonalities of religions, especially their shared bases in service to one's circle of kin and service to God, their roles in helping humans to fit harmoniously into their environments, and their ability to motivate forms of altruistic and mutualistic helping that need not be driven by fear of shared enemies or the dehumanization of people harboring other faiths. It is perhaps the teaching to children of such ideas, in conjunction with their enculturation into cultures of their own groups, which provides the most realistic hopes for a future in which the costs of religious and cultural conflicts do not overwhelm their benefits from cooperation.

Conclusions and prospects

Like all other cultural phenotypes, human religion and religiosity have evolved, subject to the facts that human psychological phenotypes and human cultures vary, and that some variants are perpetuated more readily than others. I have described a theory that considers religion as one core facet of human “cultural survival vehicles”, which originated and evolve predominantly in the contexts of human kinship. Indeed, under this theory, religiosity fundamentally represents and embodies forms of genetic, psychological, and
cultural kinship, whereby individuals become bonded together in prosocial relationships that are family-like and mutualistic, but can be even more effective than families at fostering cooperation. In this framework, forms of religiosity should vary among cultural groups in direct relation to the ecological and social selective pressures to which they have been subjected, and in direct relation to the nature of kinship systems themselves. This general prediction makes for straightforward cross-cultural tests (e.g., see Tatje & Hsu, 1969; Shiels, 1975, for non-phylogenetic analyses; Botero Gardner, et al., 2014; Watts et al., Greenhill, 2015 for phylogenetic tests), which are likely to be most effective among hunter-gatherer and other small-scale groups, and early-agricultural groups, for which recent evolutionary novelties and mismatches should not confound results. Other forms of tests for these ideas can most usefully center on the endocrinological, neurological, and genetic bases for religiosity and kinship-related cognition and affect, which should be broadly overlapping (Crespi & Summers, 2014). Most notably, the hormone oxytocin, which mediates bonding between humans in various contexts (Crespi, 2015), is associated with religiosity, spirituality, empathy, and morality, as well as perception of kinship (Grigorenko, 2011; Walter et al., 2012; Zak, 2012; Fischer-Shofty et al., 2013; Crespi & Summers, 2014; De Dreu & Kret, 2015; Holbrook et al., 2015; Sasaki et al., 2015); it should thus represent a proximate nexus for the joint expression and evolution of kinship and religion. For all such analyses, it will be essential to consider genetic, hormonal, and neurological factors in their environmental contexts, since what evolves genetically is culturally-dependent capacities for religious phenotypes, rather than any sort of deterministic effects.

The main conclusion of this chapter is that religion represents a set of culture-specific behavioral-ecological adaptations founded on expansions in conceptualization of kinship. As such, kinship, and its genetic, endocrine, and neurological underpinnings, become crucial to understanding how religious beliefs, behavior and institutions have evolved. These ideas generate strong consilience of evolutionary
theory with religiosity, and provide a foundation for advancing our understanding of religious cooperation, conflict, and personal belief that is based in scientific inquiry but encompasses the diversity and meanings of spiritual experience.
Table 1. Roles of kinship in major features of religion and its components

<table>
<thead>
<tr>
<th>PHENOMENON</th>
<th>ROLE OF KINSHIP</th>
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<tbody>
<tr>
<td>Morality (indirect reciprocity)</td>
<td>Morality evolved from kin-based mutualism and altruism</td>
</tr>
<tr>
<td>Maternal enculturation of moral behavior in offspring, using supernatural</td>
<td>Mothers and offspring are genetically related by one-half; mother reduces conflict among offspring via religious enculturation, reducing interference among copies of her genes</td>
</tr>
<tr>
<td>Animism</td>
<td>Animism involves kinship-like emotional bonds from humans to animals, plants, places and landscapes that are important to survival and reproduction</td>
</tr>
<tr>
<td>Totemism</td>
<td>Totemism represents a cultural tradition that generates and maintains high levels of psychological-kinship bonding between distant relatives and non-kin, through sharing of a supernatural entity</td>
</tr>
<tr>
<td>Ancestor worship</td>
<td>Ancestors, who created a group of people biologically as well as culturally, represent a supernatural moral conscience for proper behavior and perpetuation of traditions</td>
</tr>
<tr>
<td>Concept of God</td>
<td>God represents a metaphor for one’s circle of biological and psychological kin, including ancestors. Serving God equates with serving one’s circle of kin, and maximizing inclusive fitness in one’s social context</td>
</tr>
<tr>
<td>Monotheism</td>
<td>Religious systems with a single God are favored in situations with larger groups and stronger cultural group selection via direct competition. Monotheism unites the group around a single spiritual and secular leader, generating a single large tribe with lineal-ancestor-like family structure</td>
</tr>
<tr>
<td>Universal religions</td>
<td>Universal inclusiveness favors larger, more-powerful religious groups via recruitment, with family-like structures and terminologies maintained, and inclusive fitness benefits to individuals (especially parents, and other adults in control of religious incultation) through religious beliefs, practices and institutions</td>
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Figure 1. Four major manifestations of kinship, which are associated with the origins and evolution of religion. The 'Genetic kinship' pedigree shows genetic relatedness of one individual (filled square) to others for autosomes, as the proportion of the shape that is filled. 'Cultural kinship' refers to psychological kinship that is culture-specific. 'Lineal kinship' may be patrilineal, matrilineal or both. 'Universal religious kinship' involves monotheism and religions that are highly inclusive (can be readily joined), and include people from many cultures (with four shown here).
References


