

Signaling, Solidarity, and the Sacred: The Evolution of Religious Behavior

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Anthropologists have repeatedly noted that there has been little theoretical progress in the anthropology of religion over the past fifty years.^{1–7} By the 1960s, Geertz² had pronounced the field dead. Recently, however, evolutionary researchers have turned their attention toward understanding the selective pressures that have shaped the human capacity for religious thoughts and behaviors, and appear to be resurrecting this long-dormant but important area of research.^{8–19} This work, which focuses on ultimate evolutionary explanations, is being complemented by advances in neuropsychology and a growing interest among neuroscientists in how ritual, trance, meditation, and other altered states affect brain functioning and development.^{20–26} This latter research is providing critical insights into the evolution of the proximate mechanisms responsible for religious behavior. Here we review these literatures and examine both the proximate mechanisms and ultimate evolutionary processes essential for developing a comprehensive evolutionary explanation of religion.

Many challenges confront evolutionary scholars of religion. The origins and adaptive value of religion

and the conditions that selected for its evolution are difficult to discern. Patterns of religious behavior, like other areas of human social behavior, have undergone significant change over our evolutionary history. Evans-Pritchard¹ argued that dramatic historical changes in religious behavior render it impossible to generalize across categories of religions such as tribal, chiefdom, and contemporary world religions. Evolutionary theories of religion, however, necessarily assume that the relevant behaviors can be generalized across time and space. Moreover, the multiple roles and complex functions of religion render it difficult to capture within a single theoretical approach. Indeed, examining the origins of religion, the development of religious institutions, the ecological determinants of religious behavior, and whether religion is currently adaptive constitute separate areas of inquiry requiring different methodological tools. Even when analyses are restricted to a specific time and place, there is an extensive range of phenomena that fall under the rubric of religion, including myth,

ritual, taboo, symbolism, morality, altered states of consciousness, and belief in noncorporeal beings. Concomitantly, there is enormous cross-cultural variability within any one of these phenomena.

Religious behaviors often entail significant proximate costs, such as time, energetic, and material costs, as well as physical and psychological pain, that appear to be greater than any derived benefits. Consequently, religious behavior poses a genuine challenge for those who employ optimization, rational choice, or other egoistic-based models to explain human behavioral variation. Researchers have sought to unravel this dilemma by positing somatic, reproductive, and psychological benefits conferred by religious behaviors on their practitioners that could outweigh these costs. Realized benefits include improved health, survivorship, economic opportunities, sense of community, psychological well-being, assistance during crises, mating opportunities, and fertility (see Reynolds and Tanner²⁷ for a review). Various scholars have independently concluded that religious communities are able to offer many of these benefits because religions solve significant communication problems inherent in human life.^{28–31} Although our understanding of how religion solves such problems is still incomplete, recent theoretical and empirical findings offer intriguing clues to religion's evolution and efficacy.

WHAT IS RELIGION?

While there are countless definitions of religion in the anthropological literature,^{6,32,33} belief in the supernatural (that is, noncorporeal beings)

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is probably the most commonly offered definition.^{33–40} Although this definition captures the ineffable and unknowable aspects of religion that separate it from ordinary perceptual experience, it does not distinguish supernatural beliefs associated with ritual practices from unverifiable paranormal beliefs that do not elicit such behaviors. Nearly a century ago, Durkheim⁴¹ offered a definition of religion that may serve as a valuable bridge between anthropological and neurobiological approaches to the evolution of religion. He proposed that religion is “a unified system of beliefs and practices relative to sacred things . . . that unite into one single moral community . . . all those who adhere to them.” All societies possess certain holy or sacred ideas and objects that evoke shared responses, conscious and voluntary, unconscious and autonomic, among adherents. These sacred things incorporate powerful emotional charging that renders them impervious to time and logic. As Boyer⁸ noted, attribution of the sacred is frequently counterintuitive in relation to the actual object involved (for example, undrinkable holy water, inedible totemic animals, and crying wooden statues). Because sacred things are defined by their emotional charging rather than by their intrinsic properties, their existence depends on the shared creation and evocation of emotionally valenced symbols. While specific beliefs and rites exhibit enormous cross-cultural variation, it is the enduring framework of religious ritual that actualizes these symbols and defines the sacred within a community.^{31,41–47} Durkheim’s definition thus emphasizes religion’s behavioral and social components of interest to anthropologists while incorporating the emotional aspects of religion that are critical to neuroscientists examining the neurological and physiological substrates of the religious experience.

THE ORIGINS OF RITUAL

To understand the origins of human religious ritual, many researchers have looked to nonhuman ethological studies for comparative data.^{16,28,48} Some have argued that mammalian ritual provided the seeds for the development of more elaborate human rit-

uals and have drawn a link between mammalian and human ritual as the phylogenetic origin of religion.^{48,49} Anthropologists^{31,50–52} and ethologists^{53–55} have independently reached several common conclusions about ritualized behavior, most notably that it is a form of communication. The recurrent components of ritual, including exaggerated formality, sequencing, invariability, and repetition, have been selected to facilitate communication by eliciting arousal, directing attention, enhancing memory, and improving associations.^{56,57}

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While these features of ritual improve message reception, retention, and understanding, the encoded informational components of ritual, which vary widely across species, elicit specific response behaviors in the receiver.

Early ethologists argued that ritualized signals develop out of common behaviors when there are benefits to be gained through coordination of the signaler and receiver.^{58,59} Like Darwin,⁶⁰ these researchers^{53–55} viewed

ritualized signals as essentially mutualistic and designed to communicate honest information about a signaler’s emotions and motivational state. Ritual signals, by allowing clear communication of intent, were seen as promoting coordination and reducing the costs of agonistic encounters, thus laying the foundation for the development and stability of social groups.⁴⁹

SOCIAL SOLIDARITY THEORIES

Many anthropologists reached a similar conclusion about human rituals, although they focused their attention on the collective nature of human ritual ceremonies, in contrast to the dyadic ritualized signals of primary interest to ethologists. These authors maintained that one of the primary functions of religion is the promotion of group solidarity.^{43,41,62,63} They argued that collective rituals enable the expression and reaffirmation of shared beliefs, norms, and values, and are thus essential for maintaining communal stability and group harmony. Durkheim⁴¹ claimed that the “effervescent” state of ritual performance minimizes individual distinctions and emphasizes the unity of the group. Turner⁶³ also viewed this effervescent state as central to ritual’s efficacy. He observed that the temporary removal of adolescents from society during rites of passage increases a sense of *communitas*, which he characterized as a strengthening of social bonds and heightened solidarity among ritual performers.

These early social-solidarity theorists focused on the mutualistic function of religious ritual in creating and maintaining intragroup solidarity and perpetuating the social order. With the emergence of an ecological perspective in the 1960s and 1970s, this homeostatic function of religious ritual was extended to encompass ecological parameters as well.^{64–67} Researchers viewed religion as the medium through which communities interact with their environment and examined how religious practices maintain stable ecologies.^{66,68} Religious beliefs and practices were viewed as “‘positive-functioned’ and probably ‘adaptive’ processes of the ecological system of which they are a part.”⁶⁵ Harris’s^{65,66} writings on food

taboos, Harner's⁶⁴ research on cannibalism, and Rappaport's⁶⁸ analysis of Maring *kaiko* ceremonies as resource regulators all sought to identify the ecological utility of the seemingly "irrational, noneconomic and exotic aspects" of religion.⁶⁵ These researchers did not negate the importance of religion in creating and maintaining social solidarity, but rather expanded its role to encompass ecological parameters as well. In so doing, they situated social groups within a larger ecological and evolutionary context.

In later ecological work, Hayden⁶⁹ proposed that religious behaviors have been favored by selection because of their ability to promote interband alliances. Arguing that intermittent resource shortages throughout human evolution have selected for mechanisms capable of creating and maintaining intergroup alliances, he suggested that such mechanisms are provided by religious ecstasy because "religious emotions served to cement bonds between groups."⁶⁹ Hayden further claimed that ecstatic states lead directly to the development of transcendental concepts such as deities and spirits. Using data from a sample of societies coded in the HRAF database, he demonstrated that celestial deities are most common in societies facing resource stress. Subsequent HRAF work by Snarey⁷⁰ further showed that societies facing severe water scarcity are much more likely than societies with an abundance of water to believe in supreme deities concerned with human morality. Snarey argued that moralizing supreme deities promote prosocial use of scarce resources, thus enhancing societal survival. Roes and Raymond,⁷¹ also employing HRAF data, have recently shown that larger societies are more likely to control valuable resources, engage in high levels of external conflict, and possess moralizing deities. All of these researchers provide empirical support for a relationship among ecological parameters, social dynamics, and religious beliefs.

While the scope of inquiry for social-solidarity theorists has shifted over the past century, these theorists share a view of religion as a mechanism that enhances a group's longev-

ity. Whether positing that the function of religion is to foster social cohesion, preserve the social order, or maintain population-resource homeostasis, all of these researchers have interpreted religion from a group perspective. The most recent proponent of this view, David Sloan Wilson,¹⁹ also argues that religion enhances social solidarity. In contrast to the implied group selection of previous theorists, Wilson explicitly embeds this solidarity function of religion within an evolutionary framework in which groups operate as adaptive units. Noting that many resources can be acquired only through the coordinated action of several individuals, he argues that human groups form to acquire these resources. He contends that such groups are able to function as adaptive units because they have moral systems, expressed through religious imagery and symbolism, that regulate behavior. Adaptive features of religion are posited to have evolved through an ongoing process of cultural group selection: Some religious experiments and ideas survive, others do not. Wilson convincingly argues that religious teachings are aimed at encouraging adherents to behave for the benefit of the group. Wilson, like Alexander,⁷² maintains that because religion enhances cooperation within groups, it provides a selective advantage in competition between groups. Wilson views such intergroup competition as the driving force for the evolution of religion.

RITUAL AS DECEPTION

Behavioral ecologists have sharply challenged both the mutualistic view of ritualized behaviors implicit in the work of the social-solidarity researchers and the group-selection theories with which they are associated.^{73,74} They have argued that evolution is a competitive process in which selection occurs at the individual rather than the group level. As a result, this process should not favor organisms that signal their honest intentions if greater gains can be achieved through deception. Selective pressures will favor deceptive strategies when individuals can exploit other group members for individual advantage. Thus, interactions between signalers and receivers

should escalate in an evolutionary arms race in which signalers attempt to influence the behaviors of receivers to their own advantage, while receivers attempt to recognize deception and resist manipulation that is not in their best interests. The result of such escalation would be increasingly complex ritual behaviors as senders attempt to deceive receivers and receivers seek to determine the truthfulness of the sender's signal.

Cronk⁹ applied this reasoning to explore human moral systems cross-culturally. In contrast to previous work such as that by Alexander,⁷² which emphasized how moral systems enhance cooperation within groups, Cronk observed that despite the benefits of mutualism there are still conflicts of interest within groups. As a result of these conflicts, moral statements can be used to manipulate others to benefit signalers at a cost to receivers. Cronk argued that religion can be used by elites to maintain social control. He rightly noted that this claim is supported by Swanson's⁷⁵ classic cross-cultural study, which found inegalitarian societies to be more likely than egalitarian societies to believe in moralizing and punishing gods. Cronk followed Krebs and Dawkins,⁷⁴ who claimed that cooperative signals should be simple, whereas manipulative signals should be more elaborate, with greater repetition. Thus, he expects religious communities concerned with conquest, control, and conversion to have more elaborate and repetitive displays than do communities with little interest in "convincing any nongroup members of their correctness."⁹

WHY THE SACRED IS A SACRIFICE: THE COSTLY SIGNALING THEORY OF RITUAL

Some researchers have observed that the hypothesized "arms race" between deceivers and receivers does not always occur. For example, when a direct link between signal and underlying condition exists, as between physical size and vocal-signal frequency, deception is precluded.⁷⁶ Zahavi⁷⁷ further proposed that even in the absence of such direct physical linkage, it is possible to ensure signal

reliability if signals are differentially costly to produce. In other words, signals expressing phenotypic condition can be honest if, for lower-quality organisms, the costs of imitating the signals of higher-quality organisms outweigh the benefits that can be achieved.⁷⁸ This may result from the different costs or benefits faced by high- and low-quality signalers and may, itself, generate an “arms race” among signalers. For example, Zahavi and Zahavi⁷⁹ have argued that stotting, the jumping behavior observed among springboks and Thompson gazelles, is an honest signal to predators of physical condition, and hence their ability to evade capture. Springboks and gazelles that are in poor condition cannot imitate the behavior. Stotting thus is an energetically costly signal based on escalating competition among signalers of varying quality, which simultaneously communicates reliable information to the receiver.

Various researchers have proposed the application of costly signaling theory to religious ritual.^{9–12,18,30,80,81} Like the social-solidarity theorists, these researchers view religion’s ability to promote solidarity as its primary function. They recognize that social bonding is not an end in itself; by increasing solidarity, religion facilitates intragroup cooperation. Indeed, Irons posits that the primary adaptive benefit of religion is its ability to promote cooperation and overcome problems of collective action that humans have faced throughout their evolutionary history, including cooperative hunting, food sharing, defense, and warfare. When faced with the conditions of collective action, the incentive to claim falsely that one will cooperate is especially high because individuals can achieve their greatest gains by refraining from cooperation when others cooperate. Although everyone may gain if all group members invest in the cooperative goal, attaining such large-scale cooperation is often difficult without social mechanisms limiting the potential for some group members to free-ride on the efforts of others. Therefore, whenever an individual can achieve net benefits from defection, the only credible signals of cooperative intentions are those that are costly to fake. If commitment signals

are not costly to fake, they can easily be imitated by free-riders who do not intend to invest in the cooperative pursuit. The costly signaling theory of ritual posits that religious behaviors or rituals are costly-to-fake signals that advertise an individual’s level of commitment to a religious group. Preferred signalers are those who are highly committed to the goals and ideals of the group, which typically include in-group altruism (see, for example, Alexander⁷²). Cooperation is facilitated because those who are uncommitted can be avoided as partners in collective action because they will

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find it too expensive to pay the costs of religious behavior.

Observers of religion have long noted the costliness of religious obligations. For example, many populations require males and females to undergo initiation rites that include beatings, genital mutilations, exposure to extreme temperatures, tattooing, isolation, food and water deprivation, consumption of toxic substances, and death threats.^{82–85} In literate societies, religious legal codes such as the Laws of Manu and the Talmud outlining appropriate behavior tend not only to be formalized and to

regulate a wide range of activities, including food consumption, work, charitable commitments, and dress, but also to define the frequency and structure of ritual ceremony and prayer. Stigmatizing religious markers and taboos often prevent adherents from achieving social and economic gains with nongroup members.^{29,86} Although there may be physical or mental health benefits associated with some ritual practices,^{27,87} the significant time, energy, and material costs involved in imitating such behavior may deter anyone who does not accept the teachings of a particular religion. Therefore, religions often maintain intragroup solidarity by requiring costly behavioral patterns of group members. The performance of these costly behaviors signals commitment and loyalty to the group and the beliefs of its members. Thus, trust is enhanced among group members, which enables them to minimize costly monitoring mechanisms that are otherwise necessary to overcome the free-rider problems that typically plague collective pursuits.

The performance of religious obligations may be differentially costly for performers if they have varying opportunity costs, such as potential economic gains that would be limited if they were stigmatized by religious requirements. Sosis⁸⁰ has argued that even when the performance of rituals is not differentially costly, believers are likely to perceive the costs of ritual performance as being less than non-believers do, or to perceive the benefits as being greater, for example, by ensuring a pleasant afterlife. Only believers perceive the net gains of ritual performance and are therefore willing to pay the short-term costs in order to achieve the long-term benefits offered by religious communities. Ritual performance reinforces the cognitive and emotional substrates of individual commitment to group ideals and values. Thus, the willingness to perform costly religious behaviors is a reliable signal of beliefs and commitment to the group.

By way of example, consider Ensminger’s⁸⁸ argument that the spread of Islam throughout Africa resulted from the economic advantages of religious conversion. Ensminger⁸⁸ claims that “Islam was a powerful ideology

with built-in sanctions which contributed to considerable self-enforcement of contracts. True believers had a non-material interest in holding to the terms of contracts even if the opportunity presented itself to shirk." In other words, by accepting supernatural sanctions such as eternal hell, the short-term gains that could be achieved from defecting on a trade agreement were outweighed by the perceived costs. Consequently, believers were considered trustworthy trading partners, thus enabling Muslims to overcome the collective-action problems of long-distance commerce. Conversion to Islam increased trust among traders, which reduced transaction costs and made trade more profitable. In addition, high levels of trust among Muslim coreligionists allowed greater credit to be extended, facilitating further trade expansion. Ensminger contends that the steep initiation costs of entry into Islam, such as daily prayer, abstaining from alcohol, fasting during Ramadan, and the pilgrimage to Mecca, served as the means for establishing a reputation among traders for trustworthiness. These rituals and taboos functioned as costly signals of commitment that prevented free-riders from achieving the benefits of more efficient trade.

Costly signaling theory may offer valuable insights into the distribution of costly ritual practices across varying ecological conditions. We expect costly in-group requirements to be more prevalent in communities characterized by high potential gains from collective action, low genetic relatedness, and high intergroup mobility. When residents have few constraints limiting their ability to transfer to another group, the threat of punishment and social ostracism are less effective free-rider deterrents. Under these conditions, costly religious requirements are likely to provide a valuable means of facilitating intragroup cooperation.

While these hypotheses await evaluation, over the past few years Sosis and colleagues have conducted various studies on religious and secular communes in order to empirically test the costly signaling theory of ritual. Because the economic success, and thus the survival of communal societies, depends on solving the collective-

action problem posed by cooperative labor, such societies offer an opportunity for direct assessment of religion's influence on intragroup cooperation. The results of this research have largely supported the costly signaling theory of ritual (Boxes 1 and 2), although some findings suggest the need for additional theoretical development. As shown in Box 1, costly constraints have a positive impact on the longevity of religious communes, suggesting that increases in the level of sacrifice imposed on members enhances group commitment. However, it is equally apparent that costly sig-

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naling has no effect on the longevity of secular communes.

Yet common experience suggests that costly secular rituals can promote cooperation and intragroup commitment. Pledges undergoing a fraternity hell week and recruits in a military boot camp offer two clear examples. Moreover, numerous animal species engage in nonreligious ritual behaviors that appear to enhance trust and cooperation. For example, Watanabe and Smuts⁸⁹ recently argued that greetings among male olive baboons

are a ritual that signals trust and commitment among former rivals. If baboons and fraternity pledges are able to establish trust through fairly simple ritualized interactions, why is it necessary for human religious rituals to be so mysterious, elaborate, and infused with supernatural elements?

WHY SACRIFICES ARE SACRED

Imbuing rituals with sanctity seems to be critical for their success in promoting long-term solidarity. As Rappaport⁹⁰ noted, "to invest social conventions with sanctity is to hide their arbitrariness in a cloak of seeming necessity." Although secular rituals can generate a sense of community and obligation toward group members, the bonds forged through secular ritual do not appear to create the long-term trust and commitment achieved by religious ritual. In explaining the reasons for this difference, Rappaport argued that because religious rituals sanctify unfalsifiable postulates that are beyond the vicissitudes of examination they provide more stable referents than do secular rituals. Steadman and Palmer,⁶ and Steadman,⁹¹ also maintain that performing religious rituals is *de facto* accepting a claim that cannot be verified, namely the untestable cosmological justification for the structure and necessity of performing the ritual itself. Rappaport⁹⁰ claimed that since religious beliefs and behaviors cannot be verified logically, adherents verify them "emotionally" through the "religious experience"^{35,45}; the truth of which "seems to the communicant to be sufficiently demonstrated by its mere occurrence."⁹⁰ The ability of religious ritual to evoke such an experience differentiates it from both animal and secular ritual and lies at the heart of its efficacy in promoting and maintaining long-term group cooperation and commitment.⁸¹

Rappaport's³¹ observation that religious ritual requires performance ensures that participants directly experience the somatic affects induced by the elements of ritual. The elicitation of these physiological states through religious ritual provides a means whereby specific stimuli can be emotionally valenced.^{92,93} Association of these emotions with sanctified sym-

Box 1. Costly Requirements and Commune Survival

All communes inherently face collective problems that must be overcome if they are to survive. Sosis¹⁸ argued that if religious practices foster commitment and loyalty among individuals who share those practices, then communes formed out of religious conviction should survive longer than communes motivated by secular ideologies such as socialism. Using a dataset of two hundred nineteenth-century communal societies in the United States, Sosis found (Fig. 1) a highly significant difference in the longevity of religious and secular communes (log rank T statistic = 40.14; *df* = 1; *p* < 0.00001). Logistic regression analyses showed that religious communes, in every year of their life course, were about four times more likely to survive than were their secular counterparts (odds ratio = 0.255; *p* < 0.0001). Although these results suggested a strong relationship between a group's religiosity and its ability to overcome the problems of collective action inherent in communal life, the analyses did not examine the impact of costly ritual requirements on this relationship.

Sosis and Bressler⁸¹ predicted that communes that required a higher number of costly rituals and taboos would more effectively deter free-riders and promote cooperation, and therefore would survive longer than communes that had less demanding requirements. Using 37 secondary sources on nineteenth-century communal life, they collected information on the number of constraints that 83 communes (30 religious, 53 secular) imposed on their members. All data were collected using blind coding. The costly requirements and restrictions used in their analyses are listed in Table

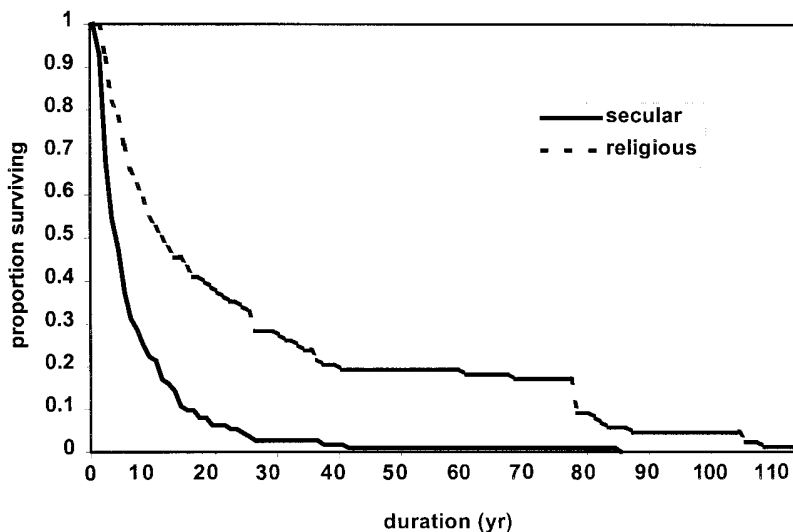


TABLE 1. Commune Costly Requirements

Requirement or Constraint on:	
1 Coffee	12 Communication with outside
2 Alcohol	13 Marriage
3 Tobacco	14 Sex (celibacy)
4 Meat	15 Family structure
5 Other foods or beverages	16 Child ownership
6 Owning photographs	17 Gambling
7 Use and ownership of certain technology	18 Trial period for membership
8 Use and ownership of other material items	19 Surrender of material belongings for membership
9 Clothing	20 Fasts
10 Hairstyle	21 Mutual criticism
11 Jewelry	22 Knowledge

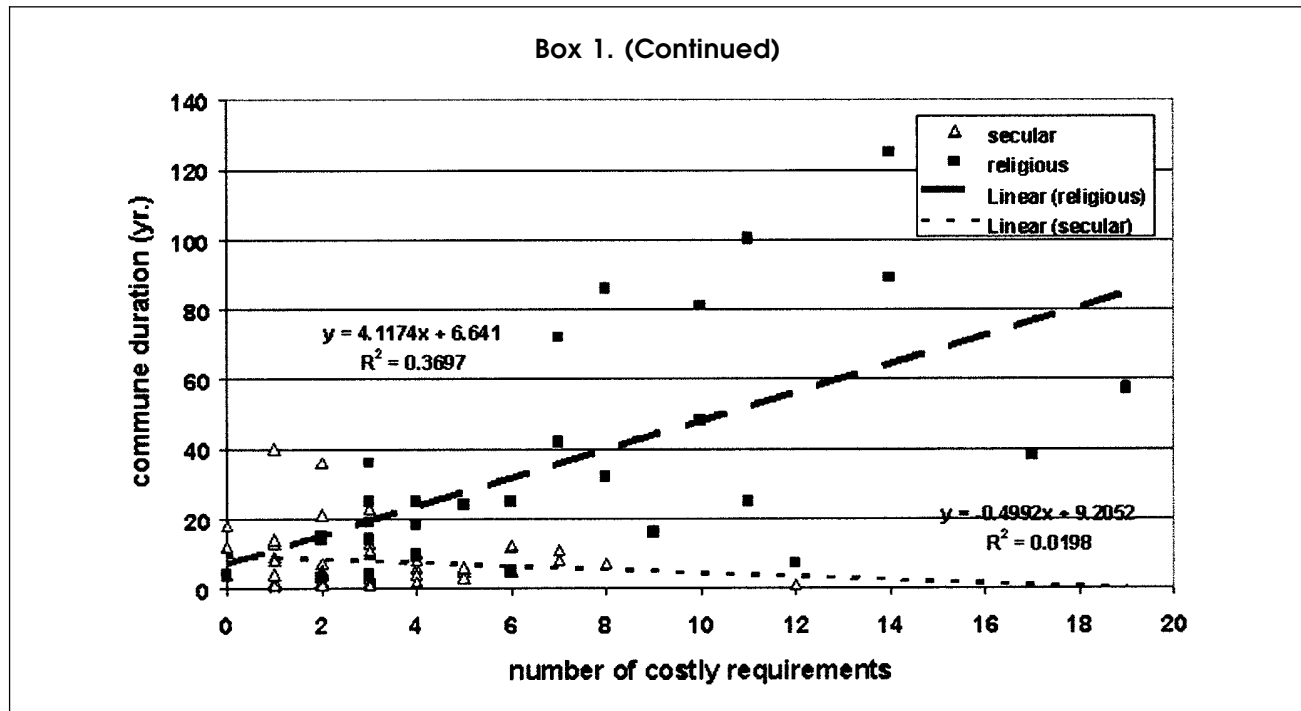
1. They found that religious communes imposed more than twice as many costly requirements on their members as did secular communes (religious mean = 7.0, *n* = 30; secular mean = 3.0, *n* = 53, *t* = 1.69, *df* = 36, *p* < 0.0001). Overall, the number of costly requirements was positively correlated with commune longevity after controlling for population size and revenue (*F* = 48.84, *n* = 83, *p* <

0.0001). However, further analyses showed that this effect existed only among religious communes (Fig. 2). Religious communes with more costly requirements survived longer than did those that had fewer requirements (*F* = 16.42, *n* = 30, *p* < 0.001), whereas there was no relationship between costly requirements and secular commune longevity (*F* = 1.03, *n* = 53, *p* = 0.31).

bolistic stimuli, such as talismans or totems, may provide a catalyst for emotionally anchored social solidarity. In addition, because emotions are manifested in autonomic nervous system responses and are thus beyond voluntary control, they provide honest sig-

nals of a sender's physiological and motivational state. The ability of emotions to "rapidly organize the responses of different biological systems including facial expression, muscular tones, voice, autonomic nervous system activity, and endocrine

activity"⁹⁴ ensures that emotionally motivated signals are both visible and reliable. As many researchers have noted, facial expressions and body language generated by emotion differ from those under voluntary control.^{60,92,95,96} Moreover, both con-



scious and unconscious processing of these signals in judgments of trustworthiness involves neural structures specifically activated by the extraordinary aspects of religious ritual.⁹⁷⁻¹⁰⁰ The ability of religious ritual to elicit emotions makes it difficult for nonbelievers to imitate and renders it a powerful tool for social appraisal. As a result, ritual practices promote trust and commitment among adherents, thereby providing a foundation for cooperative group enterprises.

RITUAL HEALING THEORY

Religious rituals, like related symbolic systems of music, art, and language, are unique to humans. Although such rituals clearly share functional and evolutionary relationships with animal and secular rituals, they differ in a critically significant way. While animal and religious rituals evoke specific responses in the autonomic nervous system, only religious rituals intensify, entrain, and conditionally associate these responses with abstract stimuli. The ability of religious ritual to entrain participants (that is, to

elicit congruent autonomic states) ensures equivalent emotional valencing of stimuli associated with such states. This creation of "secondary emotions"^{92,93} and their conditioned association with abstract stimuli shifts triggering mechanisms from the indexical to the symbolic level. Various authors have noted the importance of this shift for the evolution of other symbolic systems, such as language.^{28,31} What remains unclear, however, is how such symbolic entrainment could initially have benefited its practitioners.

McClenon^{15,16} offers an intriguing theory of the evolution of religion that directly relates to this question. He notes that ancestral primates undoubtedly used rudimentary rituals to alleviate social stress. Social grooming among nonhuman primates, the ritualized hand gestures of hominoids,¹⁰¹ and the chimpanzee "rain dance" described by Goodall¹⁰² all constitute such rituals. McClenon argues that hominins developed more complex rituals that produced therapeutic altered states of consciousness. He claims, citing Winkelman, that shamanic healing "was present in all regions of the world at some time in their hunting

and gathering past."¹⁰³ According to McClenon, those who were most suggestible in our evolutionary past would have benefited most from shamanic healing ceremonies, resulting in lower morbidity and mortality rates. Accepting the efficacy of shamanistic healing would have been particularly valuable to birthing mothers, and thus would have directly contributed to reproductive success. McClenon concludes that suggestibility and susceptibility to hypnosis confer adaptive advantages on those who possess these traits.

McClenon's theory integrates several critical features of religion and suggests a linkage between proximate neurophysiological mechanisms of religious ritual and evolutionary causation. First, it addresses what most believe to be the earliest form of religion, shamanism.^{26,103-106} Although Irons¹⁰⁷ has shown how Yanomamo shamanistic religion and beliefs can be understood as costly signals of commitment, the costly signaling theory of religion does not explain why shamanistic religion should focus on healing. Indeed, the second important contribution of the ritual-healing theory is that

Box 2. Ritual and Cooperation on Israeli Kibbutzim

Costly signaling theory predicts that ritual performance will be designed to assure honest signals of commitment to the community and thereby enhance intragroup cooperation. However, for signals to be useful they must be observable by the intended audience. One way to ensure this is for rituals to be performed collectively. In contrast, privately performed rituals are not expected to affect intragroup cooperation because they appear to be a form of communication with oneself.^{31,80}

To evaluate whether collective ritual has an impact on prosocial behavior, Sosis and Ruffle¹³³ conducted experiments on Israeli kibbutzim that were aimed at measuring individual cooperative decision making. The kibbutz offers natural conditions to evaluate how variation in collective ritual performance affects cooperative behavior because kibbutz members vary in their frequency of collective ritual performance. Members of religious kibbutzim engage in collective ritual much more frequently than do members of secular kibbutzim. Moreover, within religious kibbutzim males engage in collective ritual more frequently than do females. Most notably, thrice-daily communal prayer,

which cumulatively lasts 1.5 to 2 hours, is a religious obligation incumbent only upon males.

Sosis and Ruffle designed an economic game that captured the notion of cooperation relevant to the social conditions of the kibbutz, whose members regularly face common-pool resource dilemmas such as the consumption of communal food, water, electricity, and the use of communal cars. The game involves two members from the same kibbutz who remain anonymous to each other during and after the experiment, and who make their decisions in the game independently of each other. Each player is told that there are 100 shekels (approximately \$25 U.S. when the experiments were conducted) in an envelope to which both members have access. Each participant simultaneously decides how much of the 100 shekels to withdraw from the envelope and keep. If the sum of the requests to keep money exceeds 100 shekels, then neither member receives money and the game is over. If the total requests are less than or equal to 100 shekels, then each player keeps the amount he or she requested. In addition, the amount that remains in the envelope in-

creases by 50%; this amount is divided in half and given to each participant. The amount of money taken out of the envelope provides a measure of a player's cooperativeness. The more one cooperates by exhibiting self-restraint in one's request, the greater the level of total resources available to be divided.

Controlling for significant predictors, Sosis and Ruffle found that religious kibbutz members remove significantly less from the envelope than secular kibbutz members (that is, they exhibited higher levels of cooperation). In addition, religious males removed significantly less than religious females, secular males, and secular females. Synagogue attendance by religious males was negatively correlated with the amount removed from the envelope and, in large measure, accounted for the observed difference between religious and secular kibbutz members. Religious males who did not attend synagogue daily and religious females did not claim significantly different amounts from the envelope. Overall, these results strongly support the thesis that a costly collective ritual such as thrice-daily communal prayer can promote cooperation.

it accounts for the universal association of religion with health and healing practices. There is an extensive literature showing a negative relationship between religious practice and belief and morbidity and mortality rates.^{87,108,109} The ritual-healing theory of religion, and accumulating research on the neurophysiology of altered states, offer possible insights into this relationship. Frecska and Kulcsar¹¹⁰ noted the ability of ritual to elicit endogenous opioid peptides. Pointing out that such peptides decrease pain perception, enhance thermoregulation, affect immunocompetence, and have an impact on symbiotic bonds, these authors proposed both health and social benefits from ritual participation.

Although McClenon¹⁶ rejects social-solidarity theories of religion, it is clear in his writings and those of others¹¹¹⁻¹¹³ that shamans, in addition to their role as healers, actively maintain social cohesion in their communities by solving disputes and easing tensions among conflicting parties. Shamans may actually gain the trust and commitment of community members through various costly practices such as sexual abstinence, accepting food taboos, and consuming dangerous substances. Various ethnographies have described the training and regular responsibilities of shamans as physically demanding and challenging.¹¹⁴⁻¹¹⁶ A shaman's willingness to make sacrifices and put himself at risk of attack may allow him to achieve the status of a fair arbiter unselfishly committed to the communi-

ty.¹¹⁵ Of course, as Cronk⁹ noted concerning all religious leaders, shamans are also likely to manipulate conditions for their own self-interest, so that their activities may diminish social cohesion. In some communities, such as the Washo¹¹⁷ and Jivaro,¹¹⁸ shamans are feared because it is believed that they can use their powers to harm others. In addition, the shamanic contests that occur in various groups such as Athapaskans, Kwakiutl, and Tlingit can be socially disruptive and result in the death of one or more shamans.^{115,117}

COSTLY RITUALS AND INTERSEXUAL RELATIONS

Deacon²⁸ proposed an alternative evolutionary theory of religion that situates the origins of human reli-

gious ritual in our unique social structure. Observing that humans are the only pair-bonded primate with significant paternal investment that lives in large multimale groups, he noted that the inherent difficulty of maintaining pair bonds when females are in close proximity to other potential mates probably accounts for its rarity across species. Deacon further argued that the risk of cuckoldry is compounded by the human foraging ecology: Males cannot continually mate guard during periods of high female fertility because males and females often acquire resources separately. Deacon proposed that symbolic culture arose as a response to this dilemma in order to represent a social contract for which prior indexical communications such as calls and display behaviors were insufficient. He argued that rituals allowed a shift from indexical signs that connect abstractions with objects to signs that connect two abstractions. Religious ritual achieves this by inducing new “gestalts” and binding abstractions through emotions. For example, marriage rituals link the abstraction of future behaviors regarding sexual fidelity to the community and are sanctified through emotional associations. Deacon, like Durkheim,⁴¹ Rappaport,³¹ and Burkert,¹¹⁹ maintains that ritual is the foundation of the human social contract and enables the extensive reciprocal relationships that make human life, as we know it, possible.

Deacon’s hypothesis positing hominin pair bonding as the fundamental impetus for the evolution of religious ritual is necessarily speculative. Understanding how ritual is used as a commitment mechanism in intersexual relations, however, is an area of research that holds much promise. Spousal relationships, as Deacon noted, face significant trust and free-rider problems. It should not be surprising, therefore, that religious rituals have emerged to signal female fidelity and commitment. The costliness of these rituals can range from the extreme pain and health hazards of genital-mutilation ceremonies¹²⁰ to the more benign regular attendance of church, which males in some communities interpret as a signal of fidelity.³⁰

Variations in severity may be explained by variations in both paternal-investment expectations and relatedness among signalers. The few studies that have explored spousal commitment signals have found these signals to be reliable and honest. For example, Boster, Hudson, and Gaulin¹²¹ have shown that Jewish priests (*kohanim*) have the highest levels of paternity certainty recorded, a finding that they attribute to the laws of sexual purity adhered to by Jewish women. Performance of these laws, such as attending a ritual bath (*mikveh*), can be understood as a costly signal of commitment to sexual fidelity.

In one of the only observational studies on ritual behavior conducted by an evolutionary ecologist, Strassmann¹²² argued that menstrual taboos among the Dogon are an anti-cuckoldry strategy that males impose on females. By attending the menstrual hut, females signal their reproductive status to their husbands. Because other women also attend the menstrual huts, including kin of a menstruant’s husband, it is difficult for a woman to falsely signal the timing of her menstruation. Nonetheless, Strassmann¹²² noted that “the threat of supernatural sanctions is crucial for enforcement,” a sentiment shared by Dogon informants. These supernatural sanctions are apparently effective. Using hormonal data collected among 93 Dogon women, Strassmann¹²³ demonstrated that visits to the menstrual huts are reliable signals of a female’s reproductive status: Women attend the menstrual hut only when they are menstruating.

IS RELIGION ADAPTIVE?

Although we have focused on adaptive explanations of religious behavior, various scholars have recently offered nonadaptive explanations for the origins of religion. Some of these authors have argued that while religion may have been adaptive in the environment in which it originally evolved, in novel environments it may be maladaptive.^{17,124} Others maintain that religious beliefs are a byproduct of psychological mechanisms that were shaped by selective pressures to solve ecological problems unrelated to

religion.^{4,8,125–129} One basic point that seems to be lost in all of these discussions, however, is that traits are adaptive only with respect to a particular set of selective pressures.¹³⁰ Adaptationists study traits within specific ecological contexts and evaluate whether or not, given the alternative strategies available, a current trait produces the highest reproductive success. This has yet to be determined for any religious trait. Nor have researchers examined religion’s ability to respond to the selective pressures of diverse ecological contexts, which may explain its universality and endurance. Thus, it is premature to assume that religious behaviors are maladaptive because they are costly. Indeed, costly signaling theory suggests that costliness may be a critical adaptive feature of religious behavior.

DIRECTIONS FOR THE FUTURE

This is an exciting time for the nascent field of evolutionary religious studies. There is much work to be done. Research that addresses the most basic adaptive questions is still desperately needed: What are the fitness benefits of a particular religious practice? How is such behavior related to life-course events? How does this behavior contribute, if at all, to fitness-maximizing goals? What are the ecological determinants that can explain the variation in this behavior within a population? And what are the ecological determinants that can explain the variation in this behavior across societies? At the moment we have little understanding of what costs and benefits are involved in the human investment in religious behavior, although empirical observational studies are beginning to address this gap in our knowledge.

Outside of academia, evolutionary studies of religion will be judged by their relevance to contemporary issues. We will require an understanding of both ultimate and proximate causes of religion if we are to identify the determinants of such phenomena as modern religious fundamentalism and its distribution across varying ecologies, as well as such large-scale religious trends as the stability of religious belief and

practice in the United States¹³¹ and the significant decline of religiosity across Western Europe.¹³² Anthropology must now focus on the short-term goals of data collection and rigorous evaluation of the many competing theories of religion. It is only through such work that we can achieve the long-term goal of a comprehensive theory of religion that is capable of explaining origins, identifying the selective pressures that have shaped the capacity for religion in humans, and interpreting current intra- and intercultural variation in religious practices.

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