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The behavioral ecology of religion: the benefits and costs of one evolutionary approach

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ABSTRACT Applying evolutionary analyses to the study of religion is fraught with complications and potential misunderstandings. Most notably, the evolutionary sciences do not offer one clear procedure to study religion or any human activity. Here we describe the behavioral ecological approach to religion. We explain the theoretical motivations behind behavioral ecological research and discuss the methodologies employed to conduct this research. We argue that despite its limitations, behavioral ecology can offer important benefits to religious scholarship by providing a coherent and powerful framework for generating, testing and discarding hypotheses about specific aspects of religious behaviors and cultures.

KEY WORDS human behavioral ecology; optimization analyses; religion; ritual

Scholars in the humanities and social sciences find themselves in the midst of a Darwinian Revolution presaged by E.O. Wilson in his monograph *Consilience* (1998). Wilson's vision, that the evolutionary sciences would theoretically underpin and unify the arts, humanities, and social and natural sciences, seems less futuristic than it did merely a decade ago. The reach of evolutionary logic has extended to studies in art (Coe 2003; Dissanayake 2000), history (Turchin 2003; 2006), literature (Barash and Barash 2005; Carroll 2004; Gottschall and Wilson 2005), and of course religion (Bulbulia et al. 2008; Kirkpatrick 2005; Wilson 2002). As with any theoretical advance, growing pains are inevitable and confusion regarding the details of such a grand vision should be expected. And applying evolutionary theory to subject matters traditionally tackled by scholars in the humanities, such as religion, may be particularly susceptible to misunderstanding.

One factor contributing to confusion, ironically, is that the core ideas behind Darwin's theory of natural selection – gradual design from variation, inheritance and selection – are fairly straightforward to grasp. Consequently, the power of the Darwinian perspective to explain the emergence of natural designs is readily apparent and enticing to many. However, although the theory of natural selection is easy to comprehend, the application of Darwin's ideas to the complexities of human thought and culture faces many challenges (Laland and Brown 2002). Indeed, disagreement among evolutionary scholars has led to three distinct, and

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often competing, approaches to the evolutionary study of human behavior: evolutionary psychology, dual inheritance theory, and behavioral ecology.¹

Here we focus on what is probably the least known of the evolutionary approaches to human behavior, behavioral ecology, and explain how the theoretical and methodological tools of behavioral ecology can be applied to the study of religion.² Our discussion will be organized around three main questions: (1) What is the behavioral ecology of religion and how does it differ from other evolutionary approaches to religion?; (2) What questions can the behavioral ecology of religion address?; and (3) How is behavioral ecological research on religion conducted? To address this last question we present an illustrative example of behavioral ecological research from our own research program. We conclude by discussing what behavioral ecological research can offer traditional scholars of religion and the limitations of the behavioral ecological approach to religion.

Defining evolutionary approaches

As mentioned above, there are three primary approaches to the evolutionary study of human behavior: evolutionary psychology; dual inheritance theory; and behavioral ecology. Although the three approaches have often positioned themselves competitively (Daly and Wilson 1999; Smith et al. 2000; 2001), there are compelling arguments for complementarity that we fully endorse. (See Smith [2000]). To better understand behavioral ecology's specific explanatory power, we briefly outline the core tenets of evolutionary psychology and dual inheritance theory. (For classic and more detailed treatments of these subfields see the sources cited below.)

Evolutionary psychologists integrate classical cognitive science with the theory of natural selection to formulate specific hypotheses about human psychological architecture. Classical cognitive science approaches cognition (perception, thinking, and behaving) as the processing of information. Because the transition from input to outputs rapidly yields non-computable problems, cognitive scientists notice that any psychological system must divide problems into manageable sub-units. The resulting picture of the mind is one of many discrete but integrated 'modules' dedicated to specific task-domains. Evolutionary psychologists suggest that for task-domains that have remained constant over time, selection will tend to produce adaptive designs. The fact that we can perceive color, balance while walking and generate richly articulated phonetic strings is because the modular designs of our brains have gradually accumulated designs that enable us to compute and integrate information relevant to these tasks. It is assumed that our minds are designed to solve the recurring problems faced during a time period

¹Laland and Brown (2002) offer two additional evolutionary approaches to the study of human behavior – human sociobiology and memetics – but both of these approaches are in decline and have largely been absorbed into the three main approaches outlined here.

²There are probably multiple reasons why behavioral ecology is less well known than the other evolutionary approaches. One factor is that behavioral ecological research receives less media attention than evolutionary psychological research, probably because their main topics of study (e.g., foraging strategies, food sharing, reproductive decisions, etc.) are less exciting to lay readers than those of evolutionary psychology (e.g., mate choice, sex differences, etc.). Another factor is that evolutionary psychology and dual inheritance theory have been embraced by the two largest and most influential behavioral sciences, psychology, and economics respectively. Anthropology, the parent discipline of most behavioral ecologists, is comparatively small.

evolutionary psychologists refer to as the 'environment of evolutionary adaptedness.' Because human cultural environments have changed rapidly over the past several thousand years, evolutionary psychologists maintain that patterns of cognition that were formally adaptive may now be unnecessary, or even maladaptive. To study psychological adaptations, evolutionary psychologists use informal inferences (rather than explicit mathematical models) to derive hypotheses that are tested against experimental and survey data. (See Barkow et al. [1992]; Cosmides and Tooby [1989]; Tooby and Cosmides [1989]).

Dual inheritance theorists recognize that human cultural environments affect cognitive and behavioral outcomes. Because much evidence suggests that humans inherit cognitive and behavioral phenotypes both genetically and culturally, dual inheritance theorists posit that human reliance on cultural strategies has influenced the evolutionary dynamics that have shaped our species. Specifically, dual inheritance theorists focus on the interrelationship and co-evolution of human genetic and cultural inheritance systems. They maintain that since culture exhibits the three characteristics necessary for natural selection to operate on a trait (variation, heritability and differential fitness), it can be subject to evolutionary modeling and analyses. Dual inheritance theorists have developed sophisticated models of cultural evolution that have mainly emphasized the role of social learning in our evolutionary history. (See Boyd and Richerson [1985]; [2005]; Richerson and Boyd [2005]).

What is behavioral ecology?

Behavioral ecology is the application of the theory of natural selection to the study of behavioral adaptation and design in an ecological setting (Winterhalder and Smith 1992). Human behavioral ecology extends the theoretical perspective and methodological tools of animal behavioral ecology (Krebs and Davies 1993) to the study of human populations. Behavioral ecologists assess the degree to which behavior is adaptively adjusted to environmental conditions, broadly defined to include ecological and social parameters (Smith et al. 2001). They use variation in environmental variables to explain variation in human behavior. Environments are vital to the study of adaptive design because traits are only adaptive in relation to a specific environmental context. Behavioral ecologists describe themselves as biological accountants (Emlen 1997); they measure the costs and benefits of behavior in order to understand the selective pressures that have acted on human decision rules and to assess whether individuals are responding adaptively to current environmental conditions. Behavioral ecologists generate hypotheses from simple mathematical and graphical models, which are tested against empirical evidence. Results are used to evaluate, discard or modify the models.

Critically, human behavioral ecologists place great emphasis on the phenotypic plasticity of behavioral traits. That is, behavioral ecologists assume that selection has designed behavior-producing mechanisms (e.g., human nervous system) to be flexible enough to respond to a range of environmental conditions. The foci of study are typically conditional behavioral strategies, which take the form: if facing condition *A*, do *X*; if facing condition *B*, do *Y*, where *X* and *Y* are assumed to maximize fitness in their respective environments.

Whereas evolutionary psychologists and (to a lesser degree) dual inheritance theorists are concerned with underlying psychological mechanisms that produce adaptive responses, behavioral ecologists are largely agnostic with regard to the mechanisms, both psychological and physiological, that produce adaptive responses. This agnosticism is not a rejection of any particular mechanism, or an assumption that no mechanisms can be discovered. Rather, behavioral ecologists start with the assumption that selection has produced behavior-generating mechanisms that enable organisms to respond optimally, given design constraints and tradeoffs, to environmental conditions.³ Most behavioral ecologists leave hypotheses about mechanisms to evolutionary psychologists and dual inheritance theorists, unless consistent empirical deviations from optimality model predictions suggest that mechanistic design is producing maladaptive responses.

Consider an example of behavioral ecological research on modern fertility patterns. It has long been understood that economic development results in decreases to fertility. This fertility reduction associated with economic development, known as the demographic transition, has forced behavioral ecologists to explore the underlying mechanisms that are producing suboptimal fertility decisions (Borgerhoff Mulder 1998). Selection is assumed to favor proximate mechanisms (e.g., breastfeeding regimes, reproductive cycling, etc.) linked to reproductive decisions that detect diminishing returns on parental investment, which for most of our evolutionary history as foragers was associated with food acquisition and energy consumption (Kaplan et al. 2000). Sensitivity to environmental conditions is expected to produce optimal reproductive decisions when there is a direct relationship between parental investments and net energy balance. However, in contemporary environments, behavioral ecologists have suggested that skill-based competitive labor markets result in high parental investments in which diminishing returns on investments are not detected by these proximate mechanisms, thus resulting in low lifetime reproductive outputs (Kaplan et al. 2002). As we discuss below, behavioral ecological approaches to religion also cannot ignore the proximate mechanisms that are generating religious behaviors and beliefs (Alcorta and Sosis 2005; Bulbulia 2004a; Sosis and Alcorta 2003).

Behavioral ecologists are not only agnostic with regard to psychological and physiological design; they also ignore the underlying genetics of the behavioral strategies they study. They employ what is referred to as the phenotypic gambit (Smith and Winterhalder 1992). The phenotypic gambit focuses research attention on conditional behavioral strategies (e.g., if in context *A*, do *X*) while disregarding the underlying genetics that produce these strategies. Behavioral ecologists explicitly assume that the underlying genotypes that yield the behavioral traits of interest (e.g., mating and foraging strategies) are similar within and across populations. While behavioral ecologists recognize that genetic differences exist within and between populations, they discount these differences as a significant influence on behavioral variation. This approach is largely pragmatic: it might take a lifetime of research to understand the genetics involved in producing a simple behavioral decision, such as whether to pursue a deer or a capybara when they are

³There have been recent efforts within behavioral ecology (e.g., Krebs and Davies 1997) that aim to integrate the study of proximate causation (psychological and physiological mechanisms) and ultimate causation (selective forces); indeed some human behavioral ecologists, especially reproductive ecologists, work on both levels of analyses (Ellison 2001; Strassmann 1996a).

simultaneously encountered on a hunt. And of course, even if we knew the underlying genetics, it is not clear that it would enhance our understanding of the selective pressures that shaped the behavior. It is not necessarily correct to ignore the genotypic influence on behavioral traits, but it is a gambit, a cost that behavioral ecologists believe results in long-term dividends. The evolutionary study of human behavior is often falsely accused of genetic determinism (e.g., Sahlins [1976]). Behavioral ecologists could be accused of a naïve ecological determinism, but their assumption that individuals share an underlying genotype makes behavioral ecology the antithesis of genetic determinism.

Behavioral ecologists typically begin their exploration of any behavioral strategy with simple mathematical or graphical models. Such models can offer precise predictions about behavioral patterns and test assumptions about the selective pressures operating on behavioral strategies. Behavioral ecologists rely on optimality (Parker and Maynard Smith 1990) and evolutionary stable strategy [ESS] (Maynard Smith 1982) modeling to generate testable hypotheses. The former are employed when the payoffs to behaviors are assumed to be frequency independent, such as prey-choice decisions, and the latter are employed when behaviors are assumed to be frequency dependent, such as joining a war party. Optimality and ESS models are useful tools, even though their simplicity suggests they cannot be complete characterizations of the world. Indeed, it is important to emphasize that optimization analysis is not a theory but rather a method used by behavioral ecologists to generate hypotheses about the selective pressures operating on a trait. The method is employed because evolutionary theorists assume that selection is a process that is persistent and cumulative. As Smith and Winterhalder (1992: 53) note: 'Given sufficient genetic variation and consistency of selection pressures, it is plausible that one of its cumulative results will be a trajectory improvement in designs. The result may be a design that can be fairly characterized as optimal with respect to the fitness currency, the design problem, and the relevant constraints.' Optimality models, however, are not used to demonstrate that a behavioral strategy is adaptive (Laland and Brown 2002). Rather, optimality models assume adaptive response patterns and deviations from predictions of the models allow researchers to better understand the constraints facing decision makers.

Let us consider the method in more detail. Optimality models always include a decision maker, a set of alternative strategies that will be examined, constraints that are beyond the decision maker's control and a currency which the decision maker, it is assumed, seeks to maximize. While it is true that behavioral ecologists aim to assess the fitness costs and benefits of a behavioral strategy, they rarely measure fitness directly since fitness is a lifetime variable resulting from the cumulative effects of many phenotypic traits (Smith and Winterhalder 1992). Instead, behavioral ecologists measure tractable currencies that are assumed to be correlated with fitness. The specific currency measured is dependent upon the behavioral strategy being analyzed, and include energy expenditure per unit time, calories captured per unit time foraging, survivorship, reproductive success, money and many others.

Human behavioral ecologists are typically trained in anthropology and biology departments, and their methodological toolkit is drawn from these disciplines (especially ethnography and ethology). Most behavioral ecological studies have been conducted among remote non-Western populations (see Borgerhoff Mulder

[1991]; Winterhalder and Smith [2000]), but recently an increasing number of studies have explored urban environments (Anderson et al. [1999]; Kaplan et al. [1996]). Human behavioral ecologists collect observational and interview data using a variety of systematic techniques (Altmann 1974; Borgerhoff Mulder and Caro 1985; Hames 1992). They have relied less on experimental methods than their counterparts in animal behavioral ecology, but human behavioral ecologists are increasingly employing economic game experiments in collaborations with dual inheritance theorists and behavioral economists (Henrich et al. 2004; Sosis and Ruffle 2003).

Following Smith (2000), we conclude this section by summarizing the salient distinctions between the three main evolutionary approaches to human behavior. The explanandum of the three approaches differ: human behavioral ecologists aim to explain behavioral strategies, evolutionary psychologists study pan-human psychological adaptations, and dual inheritance theorists investigate the effects of social learning and epigenetic adaptations. The three subfields also differ in the temporal scale of adaptive change that they examine. Behavioral ecologists study short-term phenotypic change, evolutionary psychologists study adaptations resulting from long-term genotypic change (that influence psychological design), and dual inheritance theorists examine cultural change that temporally falls between these two extremes. The subfields also differ in how they generate and test hypotheses. Behavioral ecologists derive hypotheses from optimality and ESS models, which are tested with quantitative observational data collected through ethnography or historical accounts. Evolutionary psychologists derive hypotheses from informal inference, employing evolutionary logic, and these hypotheses are tested against experimental and survey data. Dual inheritance theorists derive hypotheses from population-level models and they test these hypotheses using diverse methods, including computer simulations, laboratory and field experiments, and ethnographic observation. The diversity of explanandum, research strategies, and topics of interest strongly suggests that the subfields are best viewed as complementary approaches that provide a more complete understanding of how natural selection has shaped the human condition than any one subfield could offer alone (Borgerhoff Mulder et al. 1997; Laland and Brown 2002; Sherman and Reeve 1997; Smith 2000).

The behavioral ecology of religion

Why have behavioral ecologists avoided the study of religion?

The behavioral ecology of religion is in its infancy, and it has progressed more slowly than the other evolutionary approaches to religion. Before exploring what behavioral ecology can offer the academic study of religion, it is instructive to examine why behavioral ecologists, with a few exceptions, have avoided the study of religion despite considerable interest in religion among evolutionary psychologists (e.g., Bering [2006]; Kirkpatrick [2005]; Rossano [2010]) and dual inheritance theorists (e.g., Henrich [2009]; McElreath [2004]; Richerson and Boyd [2005]). One explanation may lie in the small number of academics who pursue human behavioral ecological research. Human behavioral ecology arose in the mid-70s, but it was not until the 90s that several hundred publications had accrued in the field (Winterhalder and Smith 2000). It is possible that with so few researchers the study of religion has simply been passed by, while attention has been focused on

more critical issues in human evolution such as food sharing, foraging and parental-investment decisions. Benign neglect, however, is not an entirely satisfactory explanation for this failure of interest, because behavioral ecologists have studied a wide range of social behaviors. Moreover, anthropologists widely agree that religion has been an important, and even essential, feature of human social life for at least the past 30 000 years (Deacon 1997; Rappaport 1999; Rodseth et al. 1991).

A more likely explanation for why behavioral ecologists have avoided religion as an area of research seems to lie in *how* behavioral ecologists study humanity. Behavioral ecologists study behavioral strategies assuming that selective pressures have shaped psychological and physiological mechanisms to produce nearly optimal behavioral phenotypes in appropriate environmental contexts. Behavioral ecologists' theoretical and methodological focus on phenotypic design poses a difficulty for the study of religion, since religion's most salient, and many would say defining, characteristic is belief in supernatural agents (e.g., Frazer [1922]; James [1961]; Norbeck [1961]; Spiro [1966]; Tylor [1871]). Behavioral ecologists, however, only study beliefs as they affect behavioral patterns. The limited focus on subjects' attitudes and values is theoretically motivated; natural selection can only operate on beliefs as they impact behavior. Behavioral ecologists assume that selection will produce thoughts that justify or motivate optimal behavioral responses to environmental conditions, but the thoughts themselves are rarely the object of study.

Unfortunately, the study of religious behavior is not straightforward for human behavioral ecologists. Ignoring for the sake of discussion of how best to define 'religious behavior', it is likely that the methodological tools of behavioral ecology have limited the ability of behavioral ecologists to study religion. Human behavioral ecologists not only draw theoretical inspiration from animal behavioral ecology, but the observational tools human behavioral ecologists employ are also derived from animal studies. For example, to assess patterns of behavioral activity, human behavioral ecologists have undertaken time-allocation studies that aim to describe the range of activities engaged in by a population and the amount of time invested by individuals in each of these activities. To systematically collect these data, human behavioral ecologists rely on observational techniques such as spot observations and focal follows developed by those who study animal behavior (Altmann 1974; Hames 1992). Behavioral ecologists have collected detailed accounts of the time and energy investments in foraging (Hill et al. 1985; 1987), parental care (Hames 1988; Hewlett 1988; Kramer 2005), and a host of other activities. Remarkably, however, there are no published time-allocation studies on religious or ritual behavior by behavioral ecologists. When the lead author and one of his graduate students (Paul Swartwout) recently contacted leading behavioral ecologists working with foragers about time-allocation data on ritual activity, not one researcher had sufficient data for analysis. This was not negligence on their part. As many of them explained, for pragmatic reasons time-allocation data are only collected during daylight hours, and most ritual activity among hunter-gatherers, such as dancing, occurs in the evening.

The failure of behavioral ecologists to study religion is symptomatic of a larger gap in the behavioral ecological literature; the absence of a fully developed theoretical model of the evolution of norms. Religious customs and taboos are a subset of a large array of social norms. To advance, the behavioral ecology of religion will require a comprehensive model of the emergence and stability of norms. Ultimately, behavioral ecologists are likely to turn to cultural evolution models (e.g.,

Durham [1991]; Henrich [2009]; Richerson and Boyd [2005]). At the moment the two approaches remain distinct (Smith 2000), but recent publications by luminaries in the field suggest that change may be underway (Hill et al. 2009; Smith 2011).

Behavioral ecologists may have avoided the study of religion because of these limitations, yet the study of religious *behavior* remains an area of significant potential for behavioral ecological research. Only by understanding inter-group and intra-group variance in religious behavior will scholars be able to explain why religion is a pervasive and persistent feature of human social life. We now turn to the types of questions the behavioral ecology of religion can address.

An evolutionary koan: is religion adaptive?

Because we work on the evolution of religion we are regularly asked by students, colleagues, and journalists: ‘Is religion adaptive?’ This is an unfortunate question, and indeed impossible to answer without further context. What constitutes religion is unclear, and as readers of this journal are well aware, considerable ink has been spilled on this topic. (See Bulbulia [2005]; Sosis [2009]). Moreover, the term ‘adaptive’ can also lead to confusion.

A trait is adaptive when it confers fitness benefits on its bearers. Adaptive is often assumed to be synonymous with adaptation, but they are distinct concepts. Adaptation is a notoriously slippery concept (Reeve and Sherman 1993). Mayr perceptively observes: ‘The difficulty of the concept adaptation is best documented by the incessant efforts of authors to analyze it, describe it, and define it’ (1983: 324). Adaptation refers to both a process of phenotypic modification by natural selection, as well as the products of that process. Natural selection is the gradual process that adapts organisms to their environments. The effects of this process are phenotypic traits – adaptations – that solve particular ecological problems organisms face in acquiring energy for growth and reproduction. More specifically, adaptations foster survival and reproduction of the substrates that express these phenotypic traits (typically gene-sequences) (Andrews et al. 2002; Gould and Vrba 1982). Demonstrating that a trait confers a net fitness benefit upon its bearer, in other words, that a trait is ‘adaptive,’ does not establish that the trait is an adaptation (Laland and Brown 2002). Buying a winning lotto ticket may be adaptive, but the behavior should not be considered an adaptation. Craving sugar and salt may adaptations, even if they are not adaptive.

When evolutionary psychologists, or cognitive scientists of religion, ask whether a trait is adaptive, they are asking about whether there exists a universal psychological mechanism that selection has favored to produce a particular behavioral pattern. They are asking about psychological adaptations. Confusion arises because when behavioral ecologists ask about whether a trait is adaptive they are asking a very different question concerning whether a particular behavioral pattern results in net fitness benefits for its performers. Importantly, traits are only adaptive in relation to particular environments. Thus, ‘Is X adaptive?’ for a behavioral ecologist is really shorthand for: ‘Does the trait result in the highest fitness gains, in a specific environment, relative to other alternative available strategies?’ This difference in interpretation also highlights the behavioral ecological emphasis on context. In behavioral ecological analyses, behaviors are rarely assumed to be

adaptive in all contexts. A religious behavior, such as a prayer recitation that provides comfort, may bestow fitness benefits upon its performers in one community, but the same behavior may also result in excommunication or death in another.

What questions might the behavioral ecology of religion address?

As noted above, the question 'Is religion adaptive?' requires clarification. Notice, however, that even with clarification the question does not address evolutionary origins. If we wish to ask about the evolutionary origins of religion we should ask: did the set of phenotypic traits we refer to as 'religion' evolve because those individuals or groups who exhibited these traits had higher fitness than those who did not? Answering this question is beyond the reach of traditional behavioral ecological methodologies, but behavioral ecology can offer some insight into the origins of religion. For example, if religion is shown to be beneficial in situations that resemble ancestral settings, then these observations may be relevant for understanding why selection favored religious strategies in our evolutionary history. To understand the historical origins of religion however, evolutionary researchers will most likely require collaborations with archaeologists and paleoanthropologists.⁴ Measuring the fitness costs and benefits of traits in modern environments, the modus operandi of behavioral ecology, does not inform us about the origins of a trait; it informs about the selective pressures currently operating on a trait (Laland and Brown 2002).

Questions about origins of religion would be a poor place for behavioral ecologists to begin their study of religion. We currently have few data in any currency that measure the costs and benefits involved in the human investment in religious behavior. Establishing empirical knowledge about the costs and benefits associated with religious behavioral patterns should be pursued before the more challenging questions about origins and phylogeny are examined. Here are several types of questions that behavioral ecologists are currently equipped to answer:

- Is religious behavior *X* currently adaptive in environment *A*?
- What are the ecological determinants that can explain the variation in religious behavior *X* within a population? What are the ecological determinants that can explain the variation in religious behavior *X* across populations?
- How does religious behavior *X* relate, if at all, to fitness maximizing goals?

Such questions about the effects of specific behaviors in specific environments are not likely to excite reporters, or admittedly, fellow colleagues. These questions lack the grandeur and emotion of speculation about evolutionary origins. But all of these questions are essential for a comprehensive evolutionary understanding of religion. Moreover, each is answerable using contemporary behavioral ecological methodologies, including observational and interview techniques. And importantly, answers to these questions can form a platform for successive inquiry, resulting in a progressive knowledge.

⁴Fortunately, behavioral ecological models play a significant role in many archaeological and paleoanthropological analyses (e.g., Adler and Bar-Oz 2009; Kennett and Winterhalder 2006).

How human behavioral ecologists study religion

The costs and benefits of religious behavior

Let us consider the first question raised above: Is religious behavior X currently adaptive in environment A ? Specifically, do the fitness benefits of a particular religious practice in a population outweigh the costs? Examples abound of religious practices, most notably celibacy and martyrdom, in which fitness costs appear to significantly outweigh any benefits. A cursory review of the ethnographic and historical literatures reveals many rituals that carry extraordinarily high costs, including genital mutilations, scarifications, ingestion of toxic substances and many other dangerous and bizarre practices. Even the seemingly tame pursuits of religious singing, dancing, and prayer exact a toll in time, energy, and opportunities lost. One task of behavioral ecology is to understand whether the fitness benefits gained from these behaviors outweigh the costs entailed. For any given case, the behavioral ecology of religion must answer two interrelated questions: (1) What are the determinants of variance in ritual costs within and across communities?; and (2) Are the costs of religious practice outweighed by corresponding fitness gains?

Evolutionary scholars have primarily focused on four types of benefits of religious behaviors. Two types likely involve manipulation and thus may result in fitness benefits only for those with power advantages: reproductive control (Boster et al. 1998; Strassmann 1992; 1996b) and political control (Bulbulia 2009; Cronk 1994). And two types of benefits may be more widely distributed among communities: health (Alcorta 2006; Bulbulia 2006; Sosis and Handwerker 2011) and intra-group cooperation (Atran and Norenzayan 2004; Bulbulia 2004a; 2008; Irons 2001; Norenzayan and Shariff 2008; Shariff and Norenzayan 2007; Sosis 2003). Here we focus on a research program that has specifically examined the last of these benefits. Our aim is to provide an example of how behavioral ecologists pursue their trade, but also to highlight the strengths and weaknesses of the behavioral ecological approach to religion.

An example: costly signaling theory and religious prosociality

Winterhalder and Smith (1992) describe the research strategy of human behavioral ecology as hypothetico-deductive. Specifically, the hypothetico-deductive method is a cyclical process that involves generating abstract models that are tested against empirical data. Models are then revised accordingly and tested against new data. Models are ultimately rejected if their assumptions are shown to poorly represent the behavioral decisions they were developed to characterize. In contrast to the holistic research strategy endorsed by most anthropologists, human behavioral ecologists advocate a piece-meal approach in which cultural patterns are understood by analyzing one set of behavioral decisions at a time (Winterhalder and Smith 2000). Research in human behavioral ecology is diverse, but we can describe the typical research strategy as a nine-step process. We illustrate this process with a set of studies that examined the survivorship rates of 19th century US communes (Sosis 2000; Sosis and Bressler 2003).

1. Research question

All behavioral ecological studies begin with a broad question, known as the research question, about a behavioral pattern that motivates the research. Research questions are too general to be answered directly, but more specific study questions that identify the context (e.g., time and place) of the behavior are derived from the research question, and these questions can be answered through systematic investigation.

Example: the research questions that motivated the research described below were 'Why do humans engage in costly religious behavior?' and 'How could natural selection favor behavioral patterns that are so costly?'

2. General model

As noted above, behavioral ecologists typically begin their exploration of any behavioral pattern with simple mathematical or graphical models.

Example: in trying to understand why selection would favor costly religious behaviors, behavioral ecologists drew upon two main insights from cultural anthropology. First, anthropologists have often approached religion as a form of communication (Rappaport 1979; 1999), and second, they have long maintained that religion promotes group solidarity (e.g., Durkheim 1995/[1912]; Turner [1969]). Appreciating religious behavior as form of communication, behavioral ecologists turned to evolutionary signaling theory to understand how selection could have favored ostensibly costly religious behavior (Cronk 1994; Irons 2001). Costly signaling models show that communication between individuals with conflicting interests can be reliable when there is a link between the quality of a signaler and the signal produced. Under these conditions, selection can favor signals whose qualities enable audiences to reliably discriminate between honest and dishonest signalers. One means for such discrimination is to exact demands that are more costly to low quality signalers than they are to high-quality signalers (Grafen 1990; Zahavi and Zahavi 1997). In other words, signals expressing phenotypic condition can be honest if the costs to lower quality individuals of imitating the signals of higher quality individuals outweigh the benefits that can be achieved (Figure 1). Irons (2001) argued that that the costliness of religious behaviors enables them to serve as honest signals of commitment to the group because only those who are committed to the group's beliefs and goals will be willing to incur the time, energetic, and opportunity costs of such actions. Such commitment displays are important because the solidarity created within religious communities enables them to offer social, insurance, and material benefits to community members. These benefits, however, can sometimes be exploited by freeriders who are not committed to the community. Those individuals who pay the costs of religious performance thereby demonstrate their commitment and loyalty to the group and can thus achieve a net benefit from the social and material resources the group offers.⁵

⁵For a more detailed account of the application of costly signaling theory to religion see Bulbulia (2004a; 2004b; 2010) and Sosis (2003; 2005; 2006).

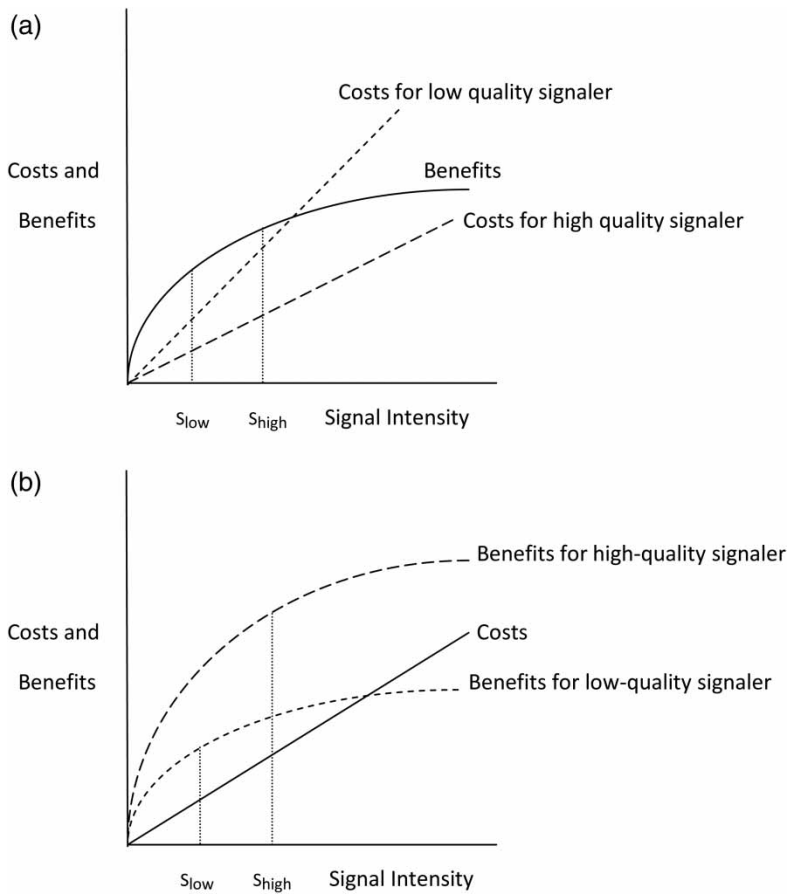


Figure 1. Graphical illustration of how differential costs or benefits can maintain signal reliability. Optimal signal intensity is higher for high-quality signalers than low-quality signalers under conditions in both graphs.

Notes: (a) All signalers gain the same benefits but low-quality signalers pay higher costs than high-quality signalers; (b) All signalers pay the same costs but high-quality signalers gain higher benefits than low-quality signalers.

Source: Adapted from Johnstone (1997: 168).

3. Predictions

Behavioral ecologists use simple models to generate predictions.

Example: the costly signaling model offers a number of predictions about religious behavior. Here we consider only two, which are examined in the studies discussed below.⁶

- The costliness of religious obligations will be correlated with cooperative behavior.

⁶For additional predictions derived from the costly signaling model and associated tests see Boster et al. (2003), Bulbulia and Mahoney (2008), Fincher and Thornhill (2008), Ginges et al. (2009), Ruffle and Sosis (2007), Soler (2008), Sosis and Ruffle (2004) and Sosis et al. (2007).

- Religious groups with costly obligations will maintain high levels of intra-group trust and commitment because non-committed members will be unwilling to pay the costs of membership.

4. *Ethnographic context*

Behavioral ecologists typically assess model predictions using behavioral data obtained in natural settings. Such a research strategy has the advantage of investigating ecologically valid behavior but it lacks the experimental control that laboratory studies offer. Experimental control is important for evaluating causal determinants of behavior. As discussed above, most behavioral ecologists collect their data through ethnographic fieldwork, but some research has exploited already-existing databases and historical records (Boone 1988; Dunbar et al. 1994; Low 1991; Volland 1990; Volland and Dunbar 1995).

Example: before investing in ethnographic fieldwork, Sosis used historical data collected from 19th century US communal societies to assess the merits of the costly signaling model. Communes provide a fertile environment for evaluating the costs and benefits of religious behaviors. First, communes generally share their productive output equally irrespective of individual labor investments. Communal societies, therefore, face significant free-rider problems (Taylor 1982). Second, communes are associated with diverse secular and religious ideologies, thus enabling comparisons between religious and secular groups. Third, there are good records for the growth and decline of individual communes over a fairly long historical period. Fourth, the investments required for participation in communal living can be accurately estimated from historical sources. Because the success of communes is strongly correlated with how well they solve the free-rider problem, it is possible to assess the extent to which religious ideologies and costly religious practices are associated with solutions to the free-rider problem. While there may be multiple determinants of success and failure in any given case (including unpredictable events, wars, famines, disease and others) the investigation of many communes over a long time period reduces the effects of randomness.

5. *Hypotheses*

Hypotheses are simply statements about the world that can be evaluated. Once the cultural context of the behaviors to be investigated has been established, the behavioral ecologist will develop specific testable hypotheses.

Example: the studies on 19th century communes evaluated a variety of hypotheses. We offer two here by way of example.

- If religious beliefs foster commitment and loyalty among individuals who share those beliefs, communes that were formed out of religious conviction should have greater longevity than communes that were motivated by secular ideologies such as socialism.
- Communes that impose greater costly requirements on their members will have higher survivorship rates than communes that impose requirements that are less costly.

Notice that hypotheses establish the currency that will be measured: in this example, commune survivorship. All communes share the goal of survival, and thus longevity is a valid measure of a commune's ability to overcome problems

of collective action. It is also worth noting that the hypotheses examined here are group-level comparisons. While behavioral ecologists are often interested in explaining intra-group behavioral variation, they also study how social and ecological factors generate group differences (e.g., Blurton Jones et al. [1994]; Hurtado et al. [1992]).

6. Data collection

Data collection strategies in behavioral ecological research are dependent upon the environment in which data are collected and the hypotheses to be tested.

Example: in the appendix of his book *Two Hundred Years of American Communes*, historian Yaacov Oved (1988) included a list of 277 communes founded between 1663 and 1937. Oved's list includes the years of existence, location by state, and a classification of each commune according to ideology (e.g., socialist, anarchist, religious). The dataset Sosis (2000) used to assess the survivorship rates of religious and secular communes (first hypothesis above) consisted of 200 of the original 277 communes.

To evaluate the second hypothesis presented above, that religious costs support solutions to free-rider problems, Sosis and Bressler (2003) developed a questionnaire aimed at collecting behavioral data on these communes. The survey consisted of more than 50 questions covering 14 main topics: consumption, material possessions, membership, dress, communication, communal activities, rituals and taboos, marriage and sexual relationships, family, work, social control, finances, communal knowledge, and cause of dissolution. The surveys were completed by trained undergraduate students using 37 books, primarily secondary sources; standard coding procedures were used. Sufficient data for analyses were found for 83 (30 religious, 53 secular) of the 200 communes in the original dataset.

7. Test hypotheses

Behavioral ecologists use quantitative behavioral data to statistically evaluate the hypotheses they posit.

Example: all communes inherently face collective problems that must be overcome if the community is to survive. Sosis (2000) argued that if religious practices foster commitment and loyalty among individuals who share those practices, then communes that were formed out of religious conviction should survive longer than communes that were motivated by secular ideologies, such as socialism. Using a dataset of 200 19th century US communal societies, Sosis found a highly significant difference in the longevity of religious and secular communes. Logistic regression analyses showed that religious communes were about four times more likely to survive in every year of their life course than their secular counterparts.

These results bring some preliminary evidence to bear on the costly signaling model, revealing a strong relationship between a group's religiosity and its ability to overcome the problems of collective action. However, the analysis left many questions unresolved. Most important, the analyses did not examine the impact of costly ritual requirements on this relationship, which was ultimately addressed in later research by Sosis and Bressler (2003). They predicted that those 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. The authors found that religious communes imposed more than twice as many costly requirements on their members as secular communes. Overall, the number of costly requirements was positively correlated with commune longevity, after controlling for population size and revenue. However, further analyses showed that this effect only existed among religious communes; religious communes with more costly requirements survived longer than those that had fewer requirements, whereas there was no relationship between costly requirements and secular commune longevity.

8. Revise model

As discussed above, systematic hypothesis testing allows behavioral ecologists to assess the limitations of their models. Any of the parameters of the model (currency, strategy set, constraints, etc.) may need to be adjusted. Since models are always imperfect characterizations of the world, even when hypotheses are supported, models can generally be improved. Following analyses and a report of the findings, models are revised accordingly.

Example: whereas religious communes that demanded more of their members survived longer, this was not true for secular communes, where there was no relationship between the requirements imposed and commune longevity. This finding was not predicted by the costly signaling model and was surprising since secular groups such as militaries and fraternities appear to successfully employ costly rites to maintain cooperation. The results of the commune studies indicate that costliness is not the only feature of religious obligations that enable them to promote solidarity. The costly signaling model offered some predictive accuracy but it also failed to capture some critical elements of religious belief that distinguish it from belief in a secular ideology. Subsequent signaling models of religious behavior have revised the classical signaling model specifically to accommodate religious belief (Bulbulia 2004a; 2010; Henrich 2009; Sosis 2003). These models demonstrate that supernatural convictions can alter the payoff dynamics of the signaling model by increasing perceived benefits or lowering perceived costs, suggesting why under certain conditions selection might favor such commitments over secular alternatives.

9. Return to step two

The hypothetico-deductive method employed by behavioral ecologists is cyclical. Once models are revised to accommodate new empirical findings, new data must be collected to test the updated model.

Example: the mixed results of the 19 century studies motivated considerable additional research. First, Sosis sought to test predictions from the costly signaling model on extant communes, thus he pursued a series of experimental studies on Israeli secular and religious kibbutzim (Ruffle and Sosis 2007; Sosis and Ruffle 2003; 2004). Second, the signaling model suggests that religious signals may promote cooperation in multiple domains. All of the commune studies focused on the free-rider dilemmas surrounding cooperative resource acquisition and consumption, but throughout our evolutionary history, individuals have faced an array of other collective-action problems, most notably warfare and defense. To explore the substantial

free-rider problem posed by warfare and defense, Sosis et al. (2007) conducted a cross-cultural analysis of the relationship between ritual costs and warfare. Third, the absence of a correlation between ritual costs and secular commune longevity motivated experimental studies with collegiate Greek fraternities on the relationship between initiation rites and trust (Sosis, Ruffle and Divietro unpublished data).

Benefits of the human behavioral ecology approach

The behavioral ecology of religion is young and underdeveloped, but it draws its theoretical and methodological foundation from a thriving and well-respected field. A fully developed behavioral ecological approach to the study of religion will benefit religious studies scholars and human behavioral ecologists alike. Behavioral ecology offers a coherent theoretical approach to the study of religion that can generate and systematically evaluate hypotheses concerning the variability of religious practices within and across cultures. Behavioral ecologists can also contribute methodological rigor to the study of religion and collect data that are currently lacking from contemporary studies. For example, scholars of religion have produced an abundance of descriptive material on religious behavioral practices, but few studies in the humanities or social sciences have collected observational data on how people allocate their time and energy in the religious arena. These are precisely the types of data that behavioral ecologists regularly gather for other behavioral domains, and will eventually gather for religious behaviors as well. Behavioral data are particularly important for the study of religion because many experimental studies have shown significant differences between online and offline religious cognition (Barrett and Keil 1996), suggesting that responses to surveys and interviews may not accurately reflect the religious beliefs and practices of respondents.

Because of their diverse ethnographic field sites and use of systematic data collection techniques, behavioral ecologists have been at the forefront of intercultural comparative analyses. Recent studies, for example, examined wealth inheritance across hunter-gather, agricultural, pastoral and industrial societies (Borgerhoff Mulder et al. 2009). Similar studies are lacking for religion. Yet comparative analyses of religious systems in societies with different subsistence economies would be invaluable for understanding the evolutionary trajectory of religious beliefs and behaviors. We have little understanding of how religious systems have changed as humanity has moved through significant subsistence transitions, such as from foraging to agriculture. Behavioral ecologists could make significant progress in this area of research.

Limitations of the human behavioral ecology approach to religion

Despite the merits of the behavioral ecological approach to religion, there are also notable limitations. Religion is an extremely complex set of phenomena and although behavioral ecology has something to offer to the academic study of religion, behavioral ecologists can neither expect, nor be expected, to study many of the most fascinating aspects of religion. As discussed above, behavioral ecologists are generally not concerned with beliefs, and for a subject such as religion, that is indeed a severe limitation. Behavioral ecologists who study religion have in fact examined the effects of supernatural beliefs on their models' predictions, but behavioral ecology is not psychology, and it does not provide the rich and

subtle understanding of human psychology that cognitive and evolutionary psychological research offers. But belief is not the only challenge for behavioral ecologists. Behavioral ecology will have little to contribute to discussions on a variety of topics of interest to religious scholars, such as the symbolic meanings of ritual behaviors, the structure of myth, or how religious ceremonies represent the social structure of a community. Put simply, behavioral ecology does not offer a comprehensive approach to the study of religion. But this apparent weakness might also be seen as a virtue. The sheer complexity of human societies and minds should make us suspicious of any theory that pretends to offer a comprehensive explanation. We believe the limitations of the behavioral ecological study of religion argue for complementarity with other evolutionary and other scholarly approaches, including those firmly grounded in the humanities. We hope the future brings collaborations in which behavioral ecologists of religion join ranks with other scholars of religion, employing rigorous scientific methods that are complemented by vital and rich ethnographic descriptions and insights that can only be gathered by living, sharing, and experiencing with the people one works with.

Conclusion

Here we have offered an introduction to the behavioral ecology of religion. It is a field with great potential but its position in the intellectual marketplace of approaches to the study of religion remains uncertain. There is admittedly a gulf between religious studies scholarship and evolutionary analyses of religion, but we are optimistic that this bridge can be crossed (e.g., Wilson and Green [2007]). Most scientists appreciate the depth and quality of research conducted in the humanities and evolutionary researchers understand that religious studies scholarship is essential for any comprehensive understanding of religious life. We also believe that all three evolutionary approaches – evolutionary psychology, dual inheritance theory, and behavioral ecology – have theoretical and methodological contributions to the study of religion that have not been fully recognized. This may partially be a function of distractions arising from attacks on religion from evolutionary quarters, but it is also due to the lack of a clear and unified evolutionary approach to the study of religion that religious studies scholars can embrace. While interdisciplinary collaborations are becoming commonplace, a unified evolutionary approach will not be forthcoming anytime soon, and we suspect that the diverse approaches to the study of humanity that have emerged from the evolutionary sciences are a positive outcome for the advancement of knowledge. Appreciation of the complementary roles that each subfield can play – evolutionary psychology for the study of religious cognition, dual inheritance theory for the study of religious cultural evolution, and behavioral ecology for the study of religious behavior – will only enhance our understanding of religion. We believe the benefits of this perspective clearly outweigh the costs.

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