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Crib Notes

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Introduction

Human culture reflects our natural world. Caves in modern day France are richly decorated with 30,000-year-old images of animals and their connection to the artist's beliefs. For 10,000 years, Native Americans organized their societies around natural totems and wove the actions of animals deeply into their religion and art. Today, our art, literature, film, and popular culture are influenced by nature's beauty, power, and wonder.

Cultural artifacts suggest ancient and intimate coevolutionary relationships. Human genes and culture coevolve in response to nature's challenges. Living in northern environments where limited sunlight reduced human ability to produce Vitamin D, for example, may have selected for a culture of dairying that, in turn, selected for genetic evolution of lactose absorption (Durham 1991). Plus, human modification of nature often provides a strong impetus for genetic and cultural evolution (Odling-Smee et al. 2003).

We propose an additional synergy between human culture and the environment—a coevolution of human and other species' cultures. We suggest that when humans interact with other social species, who themselves have the ability to evolve culture, then simple feedbacks from a culturally evolving "environment" can stimulate rapid cultural evolution in humans. We term the reciprocal adjustments in two or more species' cultures "cultural coevolution" (Marzluff and Angell 2005). Cultural coevolution may involve genetic fitness benefits or may depend on migration and the diffusion of ideas, cultural drift, differential modeling and role selection, or societal choice and imposition, all of which are important to cultural evolution (Durham 1991).

We illustrate our theory by detailing cultural coevolution between humans and birds of the genus *Corvus* (corvids; crows and ravens). The influence of corvids on human culture is extensive and long-lasting (Armstrong 1958; Feher-Elston 1991; Marzluff and Angell 2005; Nelson 1983; Sax 2003). The potential for humans to change corvid culture is equally impressive (Marzluff and Angell 2005).

Antecedents and a Preliminary Framework

Humans and many social animals have a dual inheritance system whereby gene frequencies change through time in response to mutation, drift, and natural and cultural selection (genetic inheritance), while meme frequencies change through time in response to innovation, natural and cultural selection, learning, and drift (cultural inheritance)(Figure 1). Culture is composed of memes that reflect genetic, individually learned, and socially transmitted information (boxes in Figure 1)(Durham 1991; Laland et al. 2000). We follow the more mechanistic definition of culture—variation acquired and maintained by indirect and direct social learning (Boyd and Richerson 1985; Castro and Toro 2004; Rendell and Whitehead 2001). Memes are units of information transferred among individuals by social learning (e.g., rules, songs, religions, or even specific behaviors like handshakes or dietary choices)(Blackmore 1999).

Humans are potent agents of natural selection affecting the genetic fitness of organisms and modifying the configuration and functioning of the physical environment. Environmental responses to these effects can force cultural and natural selection on humans, affecting an individual's genetic fitness and the cultural fitness of their memes, as originally postulated by Durham (1991) and Odling-Smee et al. (2003).

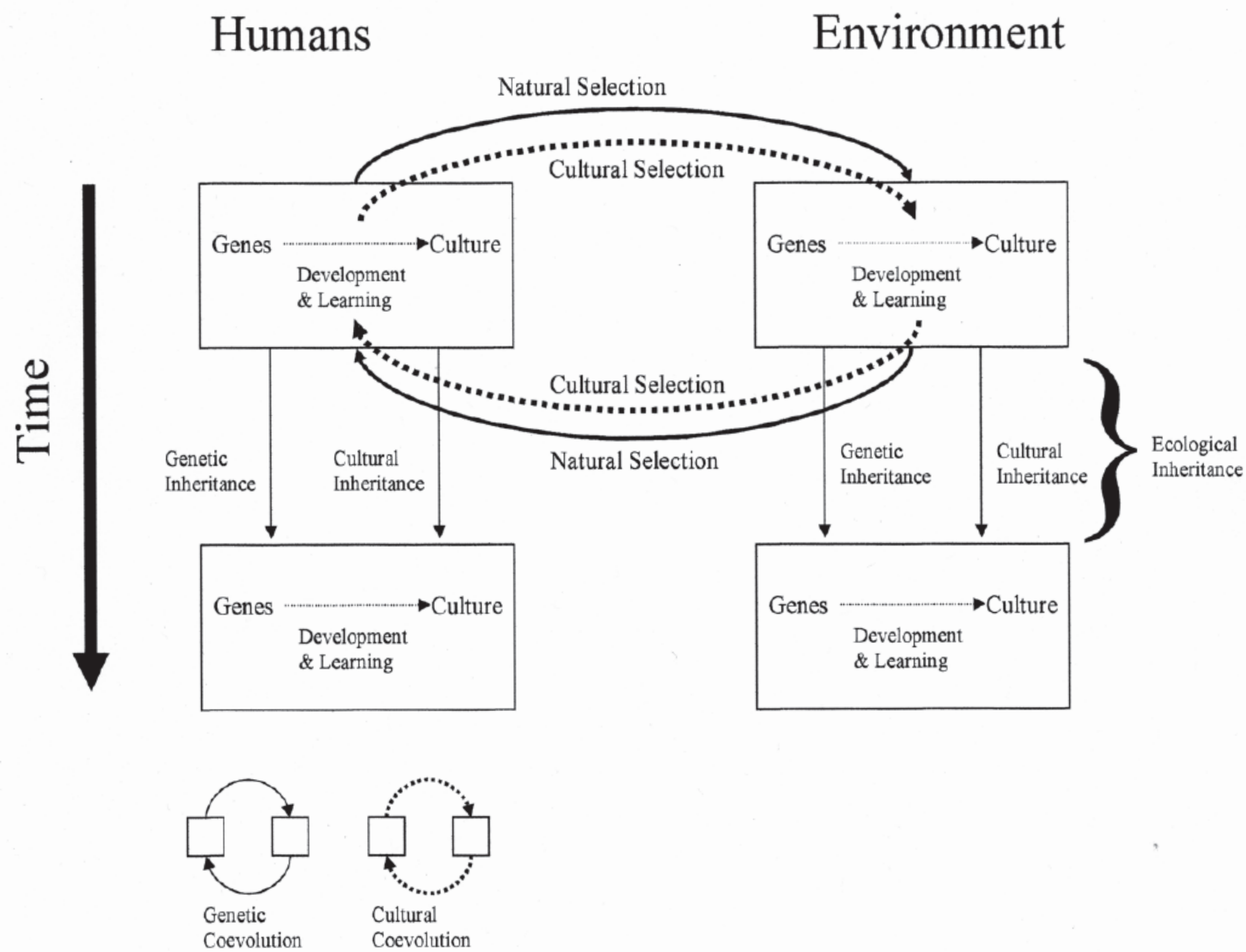

Figure 1. Integration and expansion of gene-culture coevolution and niche construction models to illustrate genetic and cultural coevolution between two interacting species (here humans and another social animal in their environment, after Laland et al. 2000). The collection of phenotypes within a population (□) emerge as a joint product of genetic, individually-aquired, and socially-learned (culture) information. Populations evolve as genetic and learned information is transferred through time by genetic and cultural inheritance. As people interact with their environment they cause changes in other organisms' inclusive fitness (natural selection) or the cultural fitness of their memes (cultural selection). Reciprocal changes in humans caused by organisms in their environment can lead to coevolved genes (—) or cultures (•••).

Niche construction theory represents the environment as an open box (Odling-Smee et al. 2003: Fig. 6.3), but recognizes that the environment changes in response to human natural and cultural selection so that humans "inherit" a change in ecology as well as a change in gene and meme frequency (Laland et al. 2000). We suggest that this 'ecological inheritance' is not only the physical and ecological change wrought by people, but also the cultural change in response to human activity by animals capable of social learning. Many animals acquire information through social learning and develop traditions that meet our definition of culture (Avital and Jablonka 2000; Danchin et al. 2004; Rendell and Whitehead 2001). Where human activity results in differential cultural fitness of another animal's memes (Figure 1; cultural selection from humans to the environment), and the resulting cultural evolution in the animal affects the cultural fitness of human memes (cultural selection from the environment to humans), human and animal memes may become coevolved. This *cultural coevolution* is analogous to traditional genetic coevolution where reciprocal natural selection between organisms drives mutual change in genes (e.g., crossbill bill depth and conifer cone structure) (Benkman 2003).

Recent theoretical insights suggest that cultural evolution should frequently occur where long-lived, intelligent, and social animals live with people. First, Danchin et al. (2004) recognized that observation of public information is adequate to allow social learning and cultural evolution. Second, observation and imitation of others is a simple form of learning that allows culture to develop, even if imitation is not perfect. Rudimentary culture may be refined substantially simply by parents guiding the clumsy or inaccurate imitations of their offspring (Castro and Toro 2004). Third, social learning has been shown to be advantageous where the costs of individual learning are high (Boyd and Richerson 1995; Rogers 1988). Fourth, models of cultural inheritance suggest it is advantageous when environmental change is too fast for genetic change to track but not so fast as to require individual learning (Feldman et al. 1996). Human cultural evolution poses environmental challenges at a pace rapid enough to favor both individual innovations and cultural inheritance.

We expect cultural coevolution where humans interact closely with animals able to learn socially (e.g., non-human primates, cetaceans, social carnivores, rats, parrots, and corvids) (Avital and Jablonka 2000; Emery and Clayton 2004; Rendell and Whitehead 2001). Bottlenose dolphins (*Tursiops truncatus*) have fished with people at Laguna, off the coast of Brazil, since 1847 (Pryor et al. 1990). During this time dolphins developed a culture of driving fish into fishers' nets, signaling to fishers, and feeding on stunned fish. This behavior is cultural because it is learned socially (young imitate or are taught by their mothers), persistent (at Laguna for at least three dolphin generations), and not found in all dolphin populations. The culture of fishers includes an ability to interpret distinctive rolls performed by dolphins, which tell the fishers how many fish the dolphins are herding and where to cast their nets.

Cultural coevolution between fishers and dolphins is geographically restricted. In contrast, cultural coevolution between people and corvids may be widespread. Most humans live in the company of at least one species of crow or raven (Marzluff and Angell 2005). Corvids innovate (Heinrich 1999), and learn from observing their parents and peers (Bugnyar and Kotrschal 2002; Emery and Clayton 2004; Paz-y-Miño et al. 2004). Social learning and cultural inheritance may explain the differentiation of American crow (*Corvus brachyrhynchos*) and common raven (*Corvus corax*) vocal dialects (Brown 1985; Enggist-Dueblin and Pfister 2002), the geographical differences in tool use by New Caledonian crows (*Corvus moneduloides*) (Hunt 2000), and the locale-specific use of automobile traffic to open nuts by carrion crows (*Corvus corone*) (Nihei and Higuchi 2001).

Using the Theory

Cultural coevolutionary theory expands our ability to understand human-animal interactions. Consider maize farming and American crow exploitation of crops. Conventional coevolutionary theory is not applicable—the selective force of corn stealing by crows on people is insufficient to mold our morphology or physiology. We are not stronger or faster because of maize-stealing crows. Niche construction theory is inadequate. It predicts that the maize environment will

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favor genetic and cultural responses by humans, but it does not specify any details of the feedback. A theory of cultural coevolution predicts that the culture of maize-stealing crows evolves in response to the culture of maize-defending farmers, and vice versa.

Defense of maize by people takes the form of many memes that have evolved through time: 1) no defense; 2) defense by children; 3) defense by hanging dead crows on garden fences; 4) defense by shooting; 5) defense by straw-filled scarecrows on sticks; 6) defense by automated, concussive cannons or wild-eyed kites. Curious, exploratory American crows have likely raided American cornfields successfully for a thousand years in part because of their ability to culturally adjust to human defense. Initial chasing of crows by children would have favored increased crow flock size, persistence, and patience. Persistence and patience could represent evolving crow culture as behavioral characteristics initially learned by watching peers or parents foil human children spread through crow populations living in close contact with people. Such fundamental behavioral attributes, arising from simple mimicry (and possible shaping) of public information might later become tightly restricted by genetic biases as consistent responses were favored by life with humans (Lachlan and Feldman 2003).

Human cultural innovations would continue to favor crow cultural evolution. If people responded by shooting or snaring crows, the costs of individual learning and the benefits of imitating public information and peer or parental shaping of poor imitation would be greatly increased. In response, crow memes characterized by selective avoidance and keen recognition would have been favored. A Mimbres bowl from the 11th century suggests selective, but deadly force was used to deter crows. The bowl (itself a cultural response to crows) details how crows were hung from nooses on a fence around a garden to teach other crows to stay away (Brody 1977).

An ability to learn about dangerous situations may have a strong genetic component, but learning to avoid specific places, individual people, or certain circumstances (e.g., people with guns) requires individual experience, and because of the inherent costs of behaving incorrectly, would favor social learning and cultural inheritance. Other humans responded to crows with static scarecrows. A Makah fish-drying rack, photographed 100 years ago, has a scarecrow built into one of its supports (Stein 2000). This human meme would select for habituation and attentiveness by crows and, accordingly, flexibility and innovation by farmers. Learning about changing form, placement, and movement of scarecrows would be facilitated by exploitation of public information (simply flocking to fields where other crows are safely eating) and would drive increasingly complex scarecrow development by people (Shirota 1989). Clearly, the rapid pace of cultural change by people is best matched by reciprocal cultural change by crows, and vice versa.

In more recent times, much of the human cultural response to crows has moved beyond the adaptive responses of farmers trying to protect their crop. Increasingly, fitness-neutral memes characterize human responses to the corn-stealing abilities of crows. Few people are involved in actual crop guarding, but crows grace logos, stimulate hunters, poets, and artists, enrich our language and place names, and take lead roles in print and film. Scarecrows are now used as harvest celebration decorations, characters in movies, and inspiration for art and song. It appears that our perceptions of crows affect culture today, just as our experience with crows affected culture in the past.

Crows in the City

Testing our ideas about cultural coevolution in the past requires deduction and induction, but our basic tenets can also be investigated in modern cities, often with a hypothetico-deductive approach. Human settlements bring corvids and humans together. carrion crow, common raven, and human remains are commingled in ancient (4,000–10,500 years ago) settlements of Syria, Poland, Troy, Mesopotamia, and western Canada (Cavallo 2000; Dobney et al. 1999; Driver 1999; Krönneck 1995; Wyrost 1993). In the modern city, cultural coevolution of demeanor, diet, and food acquisition could be studied to better understand fundamental processes including: 1) the relative roles of genetic, individually-acquired, and socially-learned information to human and crow behavior; 2) the influence of memes on genetic fitness; 3) modes (horizontal, vertical, oblique) of acquiring social knowledge; 4) individual innovation; and 5) occurrence of parental shaping of social learning. We know, for example, that city crows and ravens are more aggressive around their nests than country birds, in part because hazing and shooting birds is rare in the city relative to the country (Knight 1984; Knight et al. 1987). The cultural basis of persecution could be studied in humans and related to corvid demeanor by documenting the acquisition, geographical distribution, and covariation of human attitudes and corvid nest defense behavior.

Urban subsidies also offer experimental opportunities to test cultural coevolutionary theory. Innovative adoption and subsequent spread of unique nest materials (e.g., clothes hangers) (Kubota 2004) could be related to human behavior. The nature of apparent positive feedbacks between some people and the crows they actively feed could be quantified, and the degree to which feeding and foraging are socially-transmitted could be investigated. Exploitation of new foods can be linked to human culture. For example, garbage use by corvids affects their diet and scrounging behavior, and also causes rapid evolution of human waste disposal culture (Connell 2003; Shida 2001), may reinforce language ("to eat crow"), and can affect culinary practices (few modern societies actually eat crow). Our propensity to import fruits, pave ground, and drive cars may be spawning unique corvid foraging, and human driving, cultures. Carrion crows in Sendai, Japan, harvest English walnuts each autumn and carefully place them in front of cars stopped at traffic signals. When the cars move, the nuts are crushed, and the birds fly down to eat the nutritious nutmeat (Nihei and Higuchi 2001). This behavior is spreading slowly from the place it was first observed 20 years ago, which is consistent with social learning. In accordance with cultural evolution, other populations of carrion crows do not use cars to crack nuts, but they do drop nuts to crack them. Further investigation of nutcracking and driving memes (that include purposefully running over nuts) (Higuchi, personal communication) is warranted.

Taken as a whole, the human cultures of scavenging, hunting, farming, and urbanization may have produced a complex set of closely linked human and corvid memes that begin to sum up to what early anthropologists like Tylor (1871) referred to as 'culture'—in humans and crows. The diversity, longevity, and pervasiveness of such interactions show us that the behavior of animals, even those as common as crows, may profoundly stimulate human culture. This leads us to suggest that cultural coevolution is an 'ethological service' that nature provides people. But as we become an increasingly urban and technological species, how can we sustain the services animal behavior provides?

An ecologist might suggest building natural features into cities and encouraging humans and nature to intermingle. This is certainly part of the answer, but we suggest a more thorough understanding of how human culture is stimulated by the sight, sound, and even culture of nature is needed. Studying the processes of cultural coevolution can improve this understanding. We should determine if all interactions with nature are equally stimulating to human culture. In our investigation, competitive interactions often characterize human-corvid coevolution. Do mutually beneficial interactions spawn more or different culture than competitive interactions? How does human culture respond to direct versus indirect natural stimulation? As we have pointed out, and as Durham (1991) anticipated, much of the current cultural stimulation provided by crows is accomplished indirectly as myths, legends, and others' experiences stimulate popular culture. Certainly the range of influence expands with indirect stimulation, but is the process fundamentally different as well? Addressing these questions may be a productive arena for anthropologists, ecologists, urban planners, managers, policy makers, and the urban public to collaborate for scientific advancement and societal benefit. Shared knowledge could inform the design of urban natural areas to facilitate interactions between people and social animals for mutual cultural stimulation. Interpretation could educate city dwellers about the free cultural services nature provides. Restoration might focus on cultural, in addition to ecological, function. At the very least, it will be culturally stimulating.

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