5

Territorial and Nonterritorial Routes to Power: Reconciling Evolutionary Ecological, Social Agency, and Historicist Approaches

Benjamin Chabot-Hanowell
University of Washington
and
Eric Alden Smith
University of Washington

ABSTRACT

We argue that evolutionary and ecological models of territorial behavior are useful to archaeologists holding varied theoretical positions. First, we explain how evolutionary and ecological approaches complement, rather than conflict with, social agency and historicist approaches. Second, we review and expand upon models from evolutionary ecology and their application to the ethnographic and archaeological records. This review reveals that territorial behavior spans a continuum from defense of selected resources, to control of "home ranges" or spheres of influence, to complete defense of a proscribed geographic area. Third, we emphasize that archaeologists and modelers should explicitly define the demographic scale of territorial behavior under consideration, given that resource defense by large groups requires solutions to collective action problems. Finally, we suggest that the economic defensibility logic underlying ecological models of territoriality applies to any resource type, not just territory. Furthermore, social and political power often require successfully defending spatial territory. [evolutionary ecology, economic defensibility, territoriality, human behavioral variation, archaeology]

The chapters in this volume effectively counter the notion that social power can be reduced to control over fixed, discrete, and contiguous territory. In their introduction, VanValkenburgh and Osborne use historical and archaeological examples to argue that social power does not always directly involve control over geographic space. They argue further that the origin and implementation of social power is culturally, historically, and institutionally particular. Together, these arguments seem to imply that models of territoriality developed in evolutionary ecology are not so useful to archaeologists. In our chapter, we maintain that these models of territoriality are useful tools for analyzing the exercise of power over people and places. In fact, we suggest this is the case *because* of particularly human characteristics such as institutions and agency, not despite them.

Our argument is fourfold. First, we explain how social agency, historicist, and ecological approaches to social behavior complement one another. Ecological approaches can and should incorporate the social agency, history, and chance featured in standard social science approaches. Second, we explain the principle of economic defensibility that underlies ecological models of territoriality. Ecological conditions, broadly construed, interact with technological and sociopolitical factors to shape economic defensibility, leading to predictions that anthropologists and archaeologists can and have tested successfully, though much remains to

ARCHEOLOGICAL PAPERS OF THE AMERICAN ANTHROPOLOGICAL ASSOCIATION, Vol. 22, Issue 1, pp. 72–86, ISSN 1551-823X, online ISSN 1551-8248. DOI: 10.1111/apaa.12004.

be done. Third, we show that the economic defensibility of a resource depends in part on the size of the group that is necessary to defend it. For this reason, resources indefensible by individuals or smaller groups may be defensible by larger groups, but only if group members can successfully cooperate in defending them. Defense of territory within larger groups entails solutions to collective action problems, and thus may require multifaceted social strategies and yield complex social dynamics, as other approaches suggest. Finally, we generalize the logic of economic defensibility and show that it can apply to any type of resource, not just territory. In doing so, we bring the argument back to the land, so to speak, showing that social and political power is often a byproduct, however indirect, of successfully defending resources. Yet territorial routes to power are more numerous, complex, and variable than suggested by the standard models contested in this volume. Throughout this chapter, we use examples from the ethnographic and archaeological literature, including ones presented in other chapters in this book, to support our argument.

Evolutionary Ecological Models Are Compatible with Agency, History, and Chance

Evolutionary Ecology and Behavioral Contingency: Room for Agency

"Evolution" has an image problem with many social scientists. Laland and Brown (2011) present a balanced account of the controversies surrounding the use of evolutionary theory to understand human behavior. They note that some researchers think it presumes the existence of rigid, genetically programmed patterns of behavior that have no roles for agency and cultural variation. Others associate it with notions of "stages" of social evolution, from simple to complex. Both images are inaccurate and outdated. Kelly (2013) provides a concise history of how evolutionary thought in anthropology transformed from a unilineal to a multilineal model, beginning with the work of Julian Steward and continuing through the development of human behavioral ecology to the present. Furthermore, recent work showing how humans dramatically alter the adaptive landscape to suit their evolved goals, a process sometimes termed niche construction, makes the theory and methods of evolutionary ecology potentially applicable to all human societies, including postindustrial ones (Broughton et al. 2010; Laland and Brown 2006; Smith and Wishnie 2000).

To demonstrate that evolutionary ecological models are compatible with social agency, we examine the assumption of behavioral rigidity. Many models of evolution by natural selection do assume for simplicity that there are fixed, genetically determined behavioral strategies. Although this approach is sufficient to understand some patterns of human diversity, such as the distribution of blood antigens in response to selection within various disease ecologies, it is insufficient for analyzing complex behavior. Researchers must also consider three other important processes.

First, various *learning mechanisms* allow faster adjustment to selection pressures than do genetic adaptations. While learning itself is not an evolutionary process, the underlying mechanisms that support it are housed in the brain, which like any organ in the human body has been subject to many generations of evolution. The evolution of human cognition may entail variability selection, which is the selection of adaptations suitable to a wide range of environmental conditions, such as the highly variable environments in which early humans evolved (Potts 1998). Second, another adaptation to environmental variability among humans is *social learning*. In humans, social learning involves the imitation of complex tasks, the transmission of large volumes of information using symbolic communication (language), and the imitation of successful or prestigious individuals (Richerson and Boyd 2005). High reliance on social learning creates its own evolutionary dynamic (i.e., cultural evolution) and alters the selective environment for genetic variants (i.e., gene–culture coevolution). Finally, the aforementioned *niche construction* involves the feedback between an organism's effect on its environment and its adaptive fit. In the present volume, Greene and Lindsay (Chapter 4) discuss political transformation in Late Bronze Age Armenia, which included increased investment in built environments. They argue that these built environments mediated transformations in the social order, which may be an example of niche construction.

All three of the processes defined above provide ample room for agency because they depend on people making choices. Choices in turn depend on beliefs and preferences, which may be inherited culturally, partly shaped by evolved learning mechanisms, produced through gene–culture coevolution, and so on. In many cases, we do not need to know which of these processes shaped the behavioral patterns we seek to understand, since the various mechanisms will often produce the same final outcome. Thus, we can simply use evolutionary models (such as the economic defensibility model of territorial behavior discussed below) to derive testable hypotheses about these patterns. No particular degree of determinism, genetic or otherwise, is required for this strategic approach to adaptation. Rather, it assumes that agents inherit or invent *conditional strategies* that respond to varied social and environmental constraints and opportunities with the appropriate (adaptive) tactic. That said, any evolutionary analysis should recognize the constraints on adaptation. In the next section, we discuss these constraints and link them by analogy to key features of historical particularism.

Constraints on Adaptation: Room for History

Phylogenetics is the study of evolutionary relationships between evolutionary lineages, such as species (Felsenstein 2004). Phylogeneticists distinguish between traits shared by common descent on the one hand and those shared through parallel or convergent evolution on the other. Similarly, Boas and other historical particularists focus on how populations influence one another while maintaining characteristic features through time (Perry 2003). The inheritance of cultural traits through imitation is analogous (though not identical) to the inheritance of genetic material (Mesoudi 2007; Mesoudi et al. 2004), and imitation across cultural boundaries (often termed diffusion) is analogous to gene flow between populations. Thus any general model of human behavior must account for historical relationships, else we risk drawing spurious correlations between traits and environments (Gray et al. 2007; Mace and Holden 2005; Mace and Pagel 1994). Increasingly, evolutionary anthropologists have adopted formal phylogenetic methods to resolve the issue of spurious correlations, termed *Galton's problem*.

Historical particularists also emphasize the uniqueness of culture histories. A good evolutionist should not disagree. As evolutionary biologist Ernst Mayr (1983) noted, evolution is opportunistic, acting on whatever variation it encounters. The Sun Dance among Plains Indians provides an example of the importance of history to cultural evolution. Once a signal of the bravery and dedication of prospective warriors, the Sun Dance is now a marker of commitment to ethnic identity (Jorgensen 1972). Another reason history is important is that multiple adaptive solutions exist for the same selection pressure. Which solutions emerge depends in part on phylogenetic constraints, and the adoption of one solution places constraints on future evolution (Mayr 1983).

Related to the historical constraints on evolution is the constraint of genotype cohesion (Mayr 1983). Change in one trait may affect other traits for a variety of reasons, a process called *coevolution*. The relationships between traits are also the product of an organism's evolutionary history. In cultural and historical contexts, the structure of a "cultural recipe" may influence the mode in which it is transmitted and resulting evolutionary outcomes (Mesoudi and O'Brien 2008). Such recipes might include the modular, hierarchical set of skills necessary to construct and use tools (e.g., material selection and procurement, construction, hand–eye coordination). In sum, while evolutionary models do not always account for historical particularity, researchers must and often do extend these models for this purpose when applying the models to real cases. Furthermore, comparative studies drawing on evolutionary theory can strengthen rather than weaken our understanding of how general and particular processes are linked.

Accidents and Stochastic Processes: Room for Chance

In evolution, is there room for surprises or are behavioral and physiological outcomes perfectly determined and predictable? Applied mathematicians and others continue to argue that evolutionary researchers should pay close attention to random processes (Jagers 2010). Meanwhile, historians often question the difference that small changes would make to history (Mason 2009). What if Napoleon had not (apocryphally) suffered from hemorrhoids, which precluded him from surveying the battlefield of Waterloo? What if Churchill had been killed on the Western Front during World War I? If a massive asteroid had hit Earth 1.8 million years ago and annihilated all large-bodied animals including hominids, neither Napoleon nor Churchill would have existed. How does modern evolutionary theory account for such chance events? On the one hand, it is no accident that globally catastrophic events like asteroid impacts would more likely than not lead to the extinction of large-bodied species like hominids (Cardillo et al. 2005). On the other hand, it is also possible that small changes to the experiences of influential figures would make little difference to large-scale historical outcomes because history arises from a multitude of factors, a recognition that dates back in anthropology at least to Kroeber's *Configurations of Cultural Growth* (1944). In such cases, evolutionary reasoning suggests that outcomes commonly attributed to chance or unique events, including those instigated or experienced by influential social agents, may be in some sense determined. Contrastingly, outcomes thought to be caused by specific historical events and figures may be more accurately understood as the product of myriad interacting factors that can, as we shall see, be better understood using evolutionary logic. The rise and fall of empires throughout prehistory and history is a strong example (Turchin 2003). From this perspective, evolutionary theory *must* have "room for surprises" because evolution does not proceed along a single pathway. In order for variants to be selected, they must better fit prevailing conditions than other extant variants. Accidents shape the course of evolution by creating essentially random shifts in selection pressures, such as climatic variation.

Moreover, evolutionary theorists have long recognized the importance of randomness in evolution with two of the four classic forces of evolution, *mutation* and *drift*. The introduction of mutations is in some sense random (though not entirely; see Moxon et al. 1994; Nowak 2006a; Pagel et al. 2007; and Rainey and Moxon 2000 for examples of directional selection on mutation rates). In the cultural domain, "mutations" can result from errors in transmission of cultural information, or from innovations. Importantly, the fact that mutations introduced by innovations may be directed to particular goals (i.e., reflect agency), sometimes even adaptive ones, shifts but does not fundamentally derail the evolutionary dynamics (Boyd and Richerson 1985; Henrich et al. 2008).

As for evolutionary drift (random error in the sampling of traits from generation to generation), when combined with selection, it can lead to different outcomes than predicted by a simple deterministic model (Taylor et al. 2004). A consequence of the balance between drift and selection is that there are no guarantees for the ascendancy of even highly beneficial traits. On the other hand, drift can increase the chance that adaptively superior traits will replace alternatives that are stabilized at lower adaptive peaks on the fitness landscape (Griffiths et al. 2004; Lande 1985; Wade and Goodnight 1991; Wright 1988). For example, Powell et al. (2009) combined models of random copying error and the introduction of innovations to estimate the critical population density sufficient for the emergence of the modern *Homo sapiens* toolkit, demonstrating the importance of population density and size (key determinants of the drift–selection balance) to the proliferation of innovations.

In sum, the evolutionary process is not purely deterministic even if, for simplicity, the models that describe it often are. Accidents and stochasticity play a major role in population dynamics and thus the emergence of behavioral strategies. Combined with the room for agency and history, room for chance in the evolutionary process narrows the gap between evolutionary, social agency, and historicist perspectives. Evolution is not simple, as evolutionary biologists and social scientists well appreciate. However, many evolutionary models strategically treat evolution as simple and deterministic in order to gain insights into evolutionary processes or outcomes. We now turn to one such strategically simple model, the economic defensibility model of territoriality.

Evolutionary Ecological Models of Territoriality

Strategic Territoriality: The Logic of Economic Defensibility

Nearly 50 years ago, the biologist Jerram Brown published a short paper called "The Evolution of Diversity in Avian Territorial Systems" (Brown 1964). Brown's immediate goal, as telegraphed in his title, was to explain why some bird species are strongly territorial, others are not, and some species in fact alternate between territorial and open-access regimes. Further variation exists in the immediate benefits of controlling a resource: for many species, it is local patches of food that are defended, while for others nesting sites or roosts are the object. Brown pointed out that controlling the resources in a territory has benefits, but comes at a cost: time and energy (and potentially risk of injury) spent monitoring an area, advertising one's presence, and deterring intruders. His simple but profound argument was that natural selection would only favor defending territories if the benefits of doing so exceeded these costs—if the net benefits (measured in fitness or its correlates) were positive. This principle has since been called *economic defensibility*. Brown gave this principle empirical meaning by linking it to the spatiotemporal distribution of resources—specifically, their density and their predictability.

Dense resources are more defensible (are more likely to repay the costs of territorial defense) because the area the territory holder must defend to control access to a given resource is smaller, entailing less time and effort in monitoring. Predictable resources are more defensible for two reasons: the area that must be defended to encompass them is easier to locate, and the income (resource consumption) from the area is higher and more reliable. Lest readers think this argument entails environmental determinism, consider that the costs and benefits of both territory defense and resource acquisition are also dependent on the resource user's capabilities (e.g., birds can fly, can advertise territory residence with song, and so on); in the human case, these capabilities include technology and other culturally variable attributes, including social norms and institutions.

Although dated in its particulars, Brown's simple argument has helped biologists explain the diversity of avian territorial systems, just as his title had promised. It harnessed the logic of natural selection (the tradeoffs involved in gaining some benefit at some cost, and their links to fitness) to ecological variation. The economic defensibility model has proved remarkably durable and has been validated in hundreds of studies of spatial behavior in a wide variety of species (Davies and Houston 1984; Dubois and Giraldeau 2005). Dyson-Hudson and Smith (1978) published the first anthropological application of the model. That paper employed qualitative assessments of the economic defensibility model in various ethnographic and ethnohistoric contexts to draw three broad conclusions: (1) territorial behavior (exercise of spatial ownership claims, controlling access to resources) is facultative and varies strategically (i.e., people are at least as clever and flexible as birds); (2) this strategic behavior corresponds to variation in resource density and predictability across space and over time, as predicted by the economic defensibility model; and (3) within the same social system (even the same household), territorial strategies may be applied to some resources but not to others. We now briefly discuss these points, summarizing relevant ethnographic and archaeological data.

Variation in Human Resource Defense

The basic expectations derived from the economic defensibility model are summarized in Table 5.1 (after Dyson-Hudson and Smith 1978; see also Cashdan 1992). Note that these expectations and their predictors are stated in ordinal terms (e.g., low versus high density, intermediate defensibility); rigorous tests would require precise quantitative measures rarely found in the ethnographic and archaeological data on land use (for a recent effort to do so, plus a formalization of the economic defensibility model, see Baker 2003). Nevertheless, the qualitative evidence is quite extensive and (in our view) convincing.

Variation across space

The economic defensibility model predicts that if density and predictability are high enough, territorial systems (property rights in land) will be favored.

There are many cases in which steep gradients in resource density or predictability correlate with marked shifts in land use. For example, over a vast stretch of the Pacific coast of North America (from the Salish of Puget Sound to the Tlingit of what is now Southeast Alaska), dense seasonal runs of salmon fostered permanent villages, territorial claims to salmon streams by corporate kin groups (Donald and Mitchell 1994), and chronic warfare (focused not only on control of resource sites but also on seizing property and slaves). Yet a short distance inland, all along the inland side of the coastal ranges in the Plateau and Subarctic areas, resources were much lower in density and also generally less predictable, and the indigenous societies had traditional land use patterns stressing communal access rights (the exceptions being favored salmon-fishing spots at falls and rapids, which were sometimes owned by kin groups). The contrast between the coast and the interior Pacific Northwest did not match linguistic (and hence presumed cultural historical) divisions: the coastal areas in particular were linguistically diverse, and in some cases language groups spanned the coast–interior divide (e.g., Salishan and Athapaskan languages).

Finer-scale variation in land use within ethnolinguistic areas is perhaps more convincing evidence of economic defensibility in action. The Eskimoan (Yup'ik and Iñupiat) peoples of coastal Alaska strongly defended territorial boundaries (Andrews 1994; Burch 1980). Yet after some Iñupiat spread eastward across the Canadian arctic about one millennium ago (in what archaeologists term the Thule expansion; McGhee 1984), the much lower resource density encountered there led to relaxed boundaries approaching open-access land use. Similar variation in territoriality and related aspects of land use are found in the ethnolinguistically homogenous Great Basin. Most of the Great Basin is very arid, resulting in low resource density and predictability. The indigenous Shoshone and Paiute were highly mobile and had few access rules for land use. Yet in well-watered areas such as the Owens Valley, relatively dense and predictable resources were matched by decreased mobility and forms of land ownership that were clearly territorial (Bettinger 1983; Steward 1938; Thomas 1981). Ambrose and Lorenz (1990), Field (2005), and Kennett and Clifford (2004) present similar archaeological analyses of variation in territorial strategies.

Steep gradients in resource density and predictability can have profound implications for broad aspects of political economy. Many scholars have pointed out that stratified social systems have initially arisen in areas with such gradients, such as fertile floodplain valleys surrounded by arid regions (Carneiro 1970) and rainforests with patchily distributed potable water resources (Lucero 2002). The link to economic defensibility may be quite direct: where kin groups or other coalitions are able to control the resource patches, subordinates have few options, and stable levels of exploitation can increase (Boone 1992; Smith et al. 2010). Again, note that this is not environmental determinism: resource density and predictability are in part functions of social and technological variables (e.g., agricultural techniques, labor division, social stratification), and social agency (in seeking or resisting political and economic domination) is central to the process.

Table 5.1. Resource Density, Predictability, Defensibility, and Resultant Land Use

Resource density	Resource predictability	Economic defensibility	Predicted land use
Low	Low	Low	High mobility, dispersed population
Low	High	Intermediate	Home range system
High	Low	Intermediate	Mobility, information sharing
High	High	High	Geographically stable territoriality

Note: Modified from Dyson-Hudson and Smith 1978.

Variation over time

A theory of spatial behavior that did not allow rapid change over time would be incompatible with human history. In fact, the economic defensibility principle leads us to expect it, and specifies it will occur whenever there is sufficient change in resource density or predictability. This change can arise from exogenous factors, such as environmental shifts that alter these parameters for key resources, or it can be generated by endogenous shifts in resource utilization due to technological, demographic, economic, or political factors.

Examples of both exogenously and endogenously driven shifts in defensibility parameters are evident at various temporal scales. Ethnohistorical data on Algonkian peoples in the North American eastern subarctic document a shift from mobile hunting focused on caribou to semisedentary settlement patterns focused on trapping of furbearers and foraging for moose, hare, and fish (Bishop 1986; Leacock 1954). The former pattern was characterized by high mobility, extreme flux in group composition, and open access to resources, the most adaptive configuration for harvesting caribou with indigenous technology, as these prey clump together and move rapidly and unpredictably across the landscape. In contrast, fish, hare, furbearers, and even moose are dispersed and relatively sedentary prey, most efficiently harvested by foragers in small family-based groups who can economically defend hunting territories and coterminous trap-lines. The shift from the caribou-hunting economy to the fish/hare/moose/trapping economy was a complex process driven by economic factors (particularly the fur trade) as well as technological (steel traps, guns, etc.) and environmental (caribou depletion) ones.

On intermediate time scales, the intensification of agriculture is generally associated with reduced mobility (thus increased resource density) and shortened fallow (thus increased resource predictability), implying greater resource density and predictability. Furthermore, it can be argued that Holocene climate stability (thus greater resource predictability), coupled with suitable local ecological and social conditions, was necessary for agriculture to develop and spread over the last five to ten percent of the time *Homo sapiens* has existed (Feynman and Ruzmaikin 2007; Richerson et al. 2001). Agricultural land also appears to be more heritable than many other forms of wealth, implying that it is subject to intergenerational territorial claims (Shenk et al. 2010). Thus agricultural subsistence appears to have favored more territorial behavior.

Differential defense across resources

There are many cases in which actors (individuals, households, or larger groups) exhibit territorial behavior with some resources but not others. This is fully consistent with the economic defensibility model: if resource X is dense and predictable enough to be economically defensible, but resource Y is not, the simplest expectation is territorial defense of X but not Y. An example is the pattern of land use and property rights found among many East African cattle herders, where garden plots and livestock are claimed as property by individuals or households, but grazing land is communally owned by the "tribe" (ethnic group). This is clearly expected from defensibility logic, as good grazing areas are dependent on patchy and highly unpredictable rainfall distribution, whereas gardens are dense and predictable resources due to direct management. Livestock are even denser, and predictable to the extent that people control their movements (Dyson-Hudson and Smith 1978). Extension of this argument to pastoralists in other areas has found broad support for economic defensibility predictions (Casimir 1992).

Group-Level Territoriality and Collective Action Problems: Room for Complexity

In the previous section, we discussed how the spatiotemporal scale of a resource is critical to its defensibility. This logic applies to the demographic scale as well. Suppose a resource is indefensible at the individual level because monitoring and defense costs are too high relative to the benefits of resource control. The resource may become defensible if individuals cooperate in monitoring and defense, and the economy of scale lowers per capita costs sufficiently. For example, Karimojong households did not defend grazing land against other Karimojong households, but violently defended it against encroachment by other groups (Dyson-Hudson and Smith 1978). Dyson-Hudson and Smith admitted their model does not explicitly treat intergroup conflict of this kind. This limitation does not constitute a failure of defensibility logic. It simply reflects that the authors analyzed the adaptive fit of Karimojong territory defense at the levels of household and individual. The question then is how to secure the cooperation necessary to defend sorghum plots at the household level and grazing land at the ethnic group level. More generally, how and under what circumstances do individuals solve the problem of cooperative resource defense?

A *collective action problem* (CAP) arises when members of a collective (e.g., a household, village, voluntary association, etc.) must pay costs to produce a collective good (Olson 1965). Some theorists define CAPs more stringently as any case in which increasing the number of cooperators in a group increases the average group payoff but any given member of the group is always better off defecting no matter the actions of other members (McElreath and Boyd 2007). The structure of the payoffs to collective action matters. For example, if group members benefit from cooperating whatever their social partners do, there is no problem to solve (Clutton-Brock 2002). If group members can share the benefits or costs of cooperation and the benefit to cost ratio is high enough, a stable mixture of cooperators and defectors (or a stable mixed strategy employing both cooperation and defection) is expected to emerge (Doebeli et al. 2004; Maynard Smith 1982). Even if cooperation is mutually beneficial to all, complications may remain if group members must coordinate their cooperative investments (Alvard and Nolin 2002; Skyrms 2004). The linguistic capabilities of humans may facilitate complex coordination and communication of social norms (Smith 2003, 2010). Coordination problems likely exist in the context of territory defense because group members must coordinate monitoring duties and defensive strategies, especially when matched against cunning adversaries.

In sum, at least two types of CAPs may occur in territory defense: when it is impossible for a group member to defend the territory alone, and when the loss of territory is not costly enough to a single group member to deter a positive fraction of group members from shirking (Boone 1992). Such CAPs are onerous. Even in fairly small groups, the mechanisms that potentially ensure cooperation in dyads such as reciprocity (André 2010; Axelrod and Hamilton 1981; Trivers 1971) and kinship (Foster et al. 2006; Grafen 1984; Hamilton 1964) are insufficient (Boyd and Richerson 1988). If enforcement (punishment of free riders) is also costly to group members, a second-order collective action problem ("Who watches the watchmen?") must be solved (Panchanathan and Boyd 2004; Smith 2003). How then do people solve such CAPs?

One class of solutions emphasizes private (individual) gains linked to collective action. Models of indirect reciprocity posit that individual reputations for cooperation become known through observation or gossip, and then cooperators can avoid helping defectors even if they will not have the repeated interactions required for direct "tit-for-tat" reciprocity (Johnstone and Bshary 2004; Leimar and Hammerstein 2001; Nowak 2006b; Nowak and Sigmund 1998; Panchanathan and Boyd 2003, 2004). Linking this to collective action requires that reputations be determined by contributions to collective action, and then subsequent dyadic interactions allow cooperators to withhold aid from defectors (Panchanathan and Boyd 2004); for example, if B knows A avoids contributing to territory defense, B can then withhold aid from A when A is sick or hungry, or wants to arrange a marriage for his son. In an ethnographic example, Peoples (1982) suggested that, among the Maring, the risk of ostracism by accusation of witchcraft could have motivated individuals to participate in costly military service (Boone 1992). If witches were given less aid during hard times (as evidenced by their higher mortality) then the Maring case is consistent with the link between collective action and mutual aid.

Similarly, contributions to collective action can constitute a signal of individual qualities (such as health, fighting ability, social network size and quality, etc.) that are difficult to observe directly, and observers can use the signal to make mutually beneficial "side deals" with above-average signalers by allying with or deferring to them in other contexts (Gintis et al. 2001). In the Maring example, Peoples argued, military service could also be a signal of an individual's quality as a social partner. In another example, Plourde (2008) and Plourde and Stanish (2006) argue that prestige goods evolved in the Lake Titicaca Basin as honest signals of a putative leader's skills and knowledge. An agent-based simulation of intergroup conflict in the Titicaca Basin shares some characteristics with a prestige model, and simulated patterns of group-defended territory formation match those inferred from archaeological evidence (Griffin and Stanish 2007).

Another class of CAP solutions involves inter-demic group selection, which involves selection among partially isolated and competing groups in a population. Under this model, selection occurs both within and among groups. Within-group evolution selects against altruism because altruism is by definition costly to a given group member (e.g., those who vigorously monitor and defend group boundaries may suffer increased mortality risk). Selection among groups favors altruistic participation in group resource defense (collective action) because this increases the average payoff, thus the rate at which the group proliferates at the expense of other groups. Because within-group variation is usually much greater than variation among groups, selection must be weaker within groups than between them for group selection to work (Boyd and Richerson 2007). Inter-demic group selection may be more likely in cultural species like humans because cultural transmission occurs on one-to-many and many-to-one bases, which, coupled with conformist bias within groups ("When in Rome, do as the Romans"), will decrease variation within groups and increase variation between them (Henrich 2004; Henrich and Boyd 2001), paving the way for group-beneficial traits to proliferate at the expense of individuals. There is some empirical support for group selection involving territorial defense. Soltis et al. (1995) found that cultural group selection among warring territorial groups in New Guinea could have favored group-beneficial traits through the extinction of groups by assimilation, though at a quite slow rate. Mathew and Boyd (2011) analyze ethnographic data on Turkana cattle raids as reflecting the effects of cultural group selection. Bowles (2009) compiled cross-cultural ethnographic and archaeological data on violent deaths and estimates of within- and between-group genetic variation from several small-scale societies. He used a mathematical model of inter-demic group selection to calculate the cost to benefit ratios (for both individuals and groups) of altruistic participation in supposedly group-beneficial warfare. His results demonstrate the possibility that warlike propensities in individuals could have arisen through inter-demic, genetic group selection even in the absence of cultural transmission.

The lesson we draw from this brief review is that territoriality occurring in larger groups requires cooperation among the smaller social units that make up the group. The cooperation requirement introduces possible CAPs. Solutions to CAPs might involve complex conditional strategies, interactions between genetic and cultural inheritance, selection occurring at multiple levels, or a combination of these. Regardless of mechanisms, as long as groups do find a way to cooperatively defend territories, the basic predictions of economic defensibility models apply. Accordingly, researchers should always specify the level(s) of selection (individual, household, ethnic group) in their analyses and critiques of territoriality models.

Generalizing Economic Defensibility: Beyond Territoriality and Back Again

Resource Defensibility and Nonterritorial Political Power

Parker (this volume) describes gradients of neutral buffer zones, vassals, and islands of isolated territory that tied the ancient Assyrian Empire into a complex, multilevel political network. Sugandhi (this volume) describes interacting social, political, economic, and ideational networks through which the Mauryas exerted influence on one another. These cases demonstrate how poorly a model of discrete territorial boundaries fits archaeological reality. Because evolutionary ecologists often apply their territoriality models to areal defense, one might conclude these models do not apply to the cases above. In this and the following section, we explain why we disagree.

First, recall the underlying logic of economic defensibility: put simply, the benefits of defending a resource must exceed the costs. The classic territoriality models envision resources situated within geographic space, which is why spatial and temporal variance and density are critical determinants of defensibility. The alternatives to territorial power discussed by other contributors to this book involve control over social networks. These networks exist within topologies defined by network nodes and the ties between them (Bondy and Murty 2008; Wasserman and Faust 1994). Does the principle of economic defensibility apply to networks? We believe the answer is yes. Any resource that an agent (individual or group) can profitably defend can be characterized as having user benefits that exceed defense costs, regardless of the topology in which it exists. Agents compete for access to valuable nodes and cliques of nodes within networks. Competition within patron–client networks (Smith and Choi 2007; Stein 1984) might be over access to skilled and powerful individuals, valuable subordinates, or both (Boone 1992; Henrich and Gil-White 2001). In political and trade networks, agents compete over access to valuable allies and the political and trade goods they can provide.

Formal analysis of networks is well advanced (Bondy and Murty 2008; Wasserman and Faust 1994). Evolutionary ecologists have a fresh interest in network analysis (Sih et al. 2009), and rigorous mathematical models exist that describe how evolutionary processes occur in populations arranged in networks (Lieberman et al. 2005). Others model the evolution of network structure (e.g., Jackson and Watts 2002). Some archaeologists use formal network models (e.g., Isaksen 2008; Johansen et al. 2004; Knappett et al. 2008; Sindbaek 2007), but the method is not yet widespread and to our knowledge has never been used to analyze the defensibility of network access. Although the formal synthesis of economic defensibility and network models has not yet occurred, we offer the following thoughts.

To defend network access, agents must monitor the behavior of defended nodes (the resource) and competitor nodes, and it seems likely that social networks in which the ties between nodes are less predictable at any given time are thus more costly to monitor. It follows that valuable nodes or cliques are more defensible against competitors if the dynamics of network ties and the current positions of agents within the social network are more predictable. This argument extends to economic defensibility in hierarchical societies, in which the social network connecting different classes is treelike. More to the point of this volume, social, political, and trade networks are defined by multiple types of relationships among nodes and properties of the nodes themselves. One relationship between nodes is geographic distance. One potentially important property of nodes in a social network is the spatially distributed resources they control, which leads us back to territoriality.

Economic Defensibility Always Has a Geographic, Thus Territorial, Dimension

The geographic dimension of economic defensibility is ever-present for two reasons. First and as suggested in the previous section, people and their social relationships necessarily exist on a physical landscape. Even in the present era of telecommunication and the Internet, geographic location is important (Leamer and Storper 2001). Archaeologists usually study populations that lacked means of rapid long-distance communication and travel, for which the importance of geographic distance to social relationships should be strong. The effect of distance on network structures has changed over time due to innovations in transportation technology. For example, Knappett et al. (2008) constructed a statistical model of Aegean trade networks based in part on the geographic distance between nodes. In the discussion, they argue that a more complete model would substitute travel times for distance. Such a model would also account for intermediate ties resulting from stopovers at locations en route to more distant nodes. As transportation technology became more sophisticated, fewer stopovers may have been necessary, leading to fewer intermediate links between nodes.

In the Assyrian political network that Parker (this volume) describes, the distance between islands of territorial control affected their defensibility, as did characteristics of the landscape between territorial nodes. In networks defined by relationships among individuals, the geographic distribution of human resources is more complicated because people are mobile, and mobility of a resource influences its defensibility. In classic ecological models of territoriality, agents defend a geographically fixed area, the size of which depends on the geographic range (e.g., home ranges of caribou versus rabbits in the Subarctic) or temporal predictability (e.g., the seasonality of salmon runs in the Pacific Northwest) of a mobile resource. It may be impossible to proscribe a territory covering the range of a human resource, just as it is impossible to cover the entire range of salmon. Nevertheless, the average geographic distance from a human resource influences one's ability to monitor and control access.

Second, the ability to attract valuable social partners may be a function of territorial control over resources that could be used as cooperation incentives (Boone 1992; Smith and Choi 2007). Positive feedback between territorial control over geographically placed resources and access to valuable social partners is still consistent with the predictions of ecological territoriality models. The "peppered" sovereignty (Ramírez 1985) of elites in 16th-century Peru appears to fit this second point. Curacas held authority over land and canals, which aided them in leveraging control over a dispersed labor force. The economic defensibility of this labor force may have depended on factors discussed in the previous section. The emergence of polities in the southern Maya lowlands, where the social capital of elites was a function of territorial control of water resources (*cenotes*), is another example (Lucero 2002, 2003, 2006). Although the Maya kingdoms that eventually emerged in the lowlands are best described as political networks with shifting urban centers, territorial control over cenotes by the earliest settlers to the region likely provided the initial catalyst for the patron–client relationships that helped generate these complex polities. Once those polities were established, access to dense and predictable water resources still appears to be correlated with polity size, suggesting that territorial control over these resources likely continued to play an important role (Lucero 2002, 2006).

In sum, we believe the principle of economic defensibility can be applied to any resource type, regardless of topology. The topology of most (if not all) resources—including social and trade networks, labor pools, and centers of symbolic significance—have some geographic dimension. Archaeologists studying the dynamics of power will benefit by applying this more nuanced evolutionary and ecological approach to territoriality. In the meantime, evolutionary modelers should construct formal models of economic defensibility in generalized topologies, and in particular models of economic defensibility applicable to the "social" territoriality we describe.

Conclusion

In this chapter, we explicated the use of evolutionary ecological models of human territorial diversity. We argued that they are complementary to other approaches that rightly emphasize social agency, history, and chance as important elements of cultural evolutionary processes. We reviewed the economic defensibility model of territoriality, demonstrating its robust support in nonhuman, ethnographic, and archaeological research. Our review of territoriality models highlighted the importance of assessing model validity relative to the appropriate spatiotemporal as well as social and demographic scales. We argued that the economic defensibility principle of territoriality models applies to a broad range of resource types, including social networks. We further argued that many if not all resources, including social power, have a geographic component.

We draw three conclusions. First, ecological approaches to territoriality as we describe them are useful to archaeologists with interests as diverse as social agency, historical particularity, and long-term cultural evolution. Second, territoriality is a complex set of practices that varies within and across human cultures, and thus requires nuanced understanding and application of evolutionary ecological models. Third, social power is inevitably tied to geographically positioned resources and agents, and thus subject to the effects of variation in resource density and predictability specified in the economic defensibility model.

References

Alvard, Michael S., and David A. Nolin
2002 Rousseau's Whale Hunt? Coordination among Big-Game Hunters. Current Anthropology 43:533–559.

Ambrose, Stanley H., and Kari G. Lorenz
1990 Social and Ecological Models for the Middle Stone Age in Southern Africa. *In* The Emergence of Modern Humans: An Archaeological Perspective. Paul Mellars, ed. Pp. 3–33. Edinburgh: Edinburgh University Press.

André, Jean-Baptiste
2010 The Evolution of Reciprocity: Social Types or Social Incentives? American Naturalist 175:197–210.

Andrews, Elizabeth F.
1994 Territoriality and Land Use among the Akulmiut of Western Alaska. *In* Key Issues in Hunter-Gatherer Research. Ernest S. Burch, Jr., and Linda J. Ellanna, eds. Pp. 65–94. Oxford: Berg.

Axelrod, Robert, and William D. Hamilton
1981 The Evolution of Cooperation. Science 211(4489):1390–1396.

Baker, Matthew J.
2003 An Equilibrium Conflict Model of Land Tenure in Hunter-Gatherer Societies. Journal of Political Economy 111:124–173.

Bettinger, Robert L.
1983 Aboriginal Sociopolitical Organization in Owens Valley: Beyond the Family Band. *In* The Development of Political Organization in Native North America. E. Tooker, ed. Pp. 45–58. Washington, DC: American Ethnological Society.

Bishop, Charles A.
1986 Territoriality among Northeastern Algonquians. Anthropologica 28:37–63.

Bondy, J. Adrian, and U. S. R. Murty
2008 Graph Theory. New York: Springer.

Boone, James L.
1992 Competition, Conflict, and the Development of Social Hierarchies. *In* Evolutionary Ecology and Human Behavior. Eric Alden Smith and Bruce Winterhalder, eds. Pp. 301–337. Hawthorne, NY: Aldine de Gruyter.

Bowles, Samuel
2009 Did Warfare among Ancestral Hunter-Gatherers Affect the Evolution of Human Social Behaviors? Science 324(5932):1293–1298.

Boyd, Robert, and Peter J. Richerson
1985 Culture and the Evolutionary Process. Chicago: University of Chicago Press.
1988 The Evolution of Reciprocity in Sizeable Groups. Journal of Theoretical Biology 132: 337–356.
2007 Group Selection: A Tale of Two Controversies. *In* The Evolution of Mind: Fundamental Questions and Controversies. Steven W. Gangestad and Jeffry A. Simpson, eds. Pp. 221–225. New York: Guilford.

Broughton, Jack M., Michael D. Cannon, and Eric J. Bartelink
2010 Evolutionary Ecology, Resource Depression, and Niche Construction Theory: Applications to Central California Hunter-Gatherers and Mimbres-Mogollon Agriculturalists. Journal of Archaeological Method and Theory 17: 371–421.

Brown, Jerram L.
1964 The Evolution of Diversity in Avian Territorial Systems. The Wilson Bulletin 76(2):160–169.

Burch, Ernest S., Jr.
1980 Traditional Eskimo Societies in Northwest Alaska. *In* Alaska Native Culture and History. Kotani Yoshinobu and William B. Workman, eds. Pp. 253–304. Osaka: National Museum of Ethnology.

Cardillo, Marcel, Georgina M. Mace, Kate E. Jones, Jon Bielby, Olaf R. P. Bininda-Edmonds, Wes Sechrest, C. David L. Orme, and Andy Purvis
2005 Multiple Causes of High Extinction Risk in Large Mammal Species. Science 309(5738):1239–1241.

Carneiro, Robert L.
1970 A Theory of the Origin of the State. Science 169(3947):733–738.

Cashdan, Elizabeth
1992 Spatial Organization and Habitat Use. *In* Evolutionary Ecology and Human Behavior. Eric Alden Smith and Bruce Winterhalder, eds. Pp. 237–266. Hawthorne, NY: Aldine de Gruyter.

Casimir, Michael J.
1992 The Determinants of Rights to Pasture: Territorial Organization and Ecological Constraints. *In* Mobility and Territoriality: Social and Spatial Boundaries among Foragers, Fishers, Pastoralists and Peripatetics. Michael J. Casimir and Aparna Rao, eds. Pp. 153–204. New York: Berg.

Clutton-Brock, Tim
2002 Breeding Together: Kin Selection and Mutualism in Cooperative Vertebrates. Science 296(5565): 69–72.

Davies, Nicholas B., and Alasdair I. Houston
1984 Territory Economics. *In* Behavioural Ecology: An Evolutionary Approach. John R. Krebs and Nicholas B. Davies, eds. Pp. 148–169. Oxford: Blackwell.

Doebeli, Michael, Christoph Hauert, and Timothy Killingback
2004 The Evolutionary Origin of Cooperators and Defectors. Science 306(5697):859–862.

Donald, Leland, and Donald H. Mitchell
1994 Nature and Culture on the Northwest Coast of North America: The Case of the Wakashan Salmon Resources. *In* Key Issues in Hunter-Gatherer Research. Ernest S. Burch, Jr., and Linda J. Ellanna, eds. Pp. 95–117. Oxford: Berg.

Dubois, Frédérique, and Luc-Alain Giraldeau
2005 Fighting for Resources: The Economics of Defense and Appropriation. Ecology 86(1):3–11.

Dyson-Hudson, Rada, and Eric Alden Smith
1978 Human Territoriality: An Ecological Reassessment. American Anthropologist 80:21–41.

Felsenstein, Joseph
2004 Inferring Phylogenies. Sunderland, MA: Sinauer Associates.

Feynman, Joan, and Alexander Ruzmaikin
2007 Climate Stability and the Development of Agricultural Societies. Climatic Change 84(3):295–311.

Field, Julie S.
2005 Land Tenure, Competition and Ecology in Fijian Prehistory. Antiquity 79:586–600.

Foster, Kevin R., Tom Wenseleers, and Francis L. W. Ratnieks
2006 Kin Selection is the Key to Altruism. Trends in Ecology & Evolution 21(2):57–60.

Gintis, Herbert, Eric Alden Smith, and Samuel Bowles
2001 Cooperation and Costly Signaling. Journal of Theoretical Biology 213:103–119.

Grafen, Alan
1984 Natural Selection, Kin Selection, and Group Selection. *In* Behavioural Ecology: An Evolutionary Approach. John R. Krebs and Nicholas B. Davies, eds. Pp. 62–84. Oxford: Blackwell.

Gray, Russell D., Simon J. Greenhill, and Robert M. Ross
2007 The Pleasures and Perils of Darwinizing Culture (with Phylogenies). Biological Theory 2(4):360–375.

Griffin, Arthur F., and Charles Stanish
2007 An Agent-Based Model of Prehistoric Settlement Patterns and Political Consolidation in the Lake Titicaca Basin of Peru and Bolivia. Structure

and Dynamics: eJournal of Anthropological and Related Sciences 2(2):1–47.

Griffiths, Anthony J. F., Susan R. Wessler, Richard C. Lewontin, William M. Gelbart, David T. Suzuki, and Jeffrey H. Miller
2004 An Introduction to Genetic Analysis. New York: W. H. Freeman.

Hamilton, William D.
1964 The Genetical Evolution of Social Behaviour I and II. Journal of Theoretical Biology 7:1–16, 17–52.

Henrich, Joseph
2004 Cultural Group Selection, Coevolutionary Processes and Large-Scale Cooperation. Journal of Economic Behavior and Organization 53(1):3–35.

Henrich, Joseph, and Robert Boyd
2001 Why People Punish Defectors: Weak Conformist Transmission Can Stabilize Costly Enforcement of Between-Group Differences. Journal of Theoretical Biology 208:79–89.

Henrich, Joseph, Robert Boyd, and Peter J. Richerson
2008 Five Misunderstandings about Cultural Evolution. Human Nature 19:119–137.

Henrich, Joseph, and Francisco J. Gil-White
2001 The Evolution of Prestige: Freely Conferred Deference as a Mechanism for Enhancing the Benefits of Cultural Transmission. Evolution and Human Behavior 22(3):165–196.

Isaksen, Leif
2008 The Application of Network Analysis to Ancient Transport Geography: A Case Study of Roman Baetica. Digital Medievalist 4.

Jackson, Matthew O., and Alison Watts
2002 The Evolution of Social and Economic Networks. Journal of Economic Theory 106(2):265–295.

Jagers, Peter
2010 A Plea for Stochastic Population Dynamics. Journal of Mathematical Biology 60(5):761–764.

Johansen, Kasper Lambert, Steffen Terp Laursen, and Mads Kähler Holst
2004 Spatial Patterns of Social Organization in the Early Bronze Age of South Scandinavia. Journal of Anthropological Archaeology 23:33–55.

Johnstone, Rufus A., and Redouan Bshary
2004 Evolution of Spite through Indirect Reciprocity. Proceedings of the Royal Society of London B 271(1551):1917–1922.

Jorgensen, Joseph G.
1972 The Sun Dance Religion. Chicago: University of Chicago Press.

Kelly, Robert L.
2013 The Lifeways of Hunter-Gatherers: The Foraging Spectrum. Cambridge: Cambridge University Press.

Kennett, Douglas J., and Robert A. Clifford
2004 Flexible Strategies for Resource Defense on the Northern Channel Islands of California: An Agent-Based Model. *In* Voyages of Discovery: The Archaeology of Islands. Scott M. Fitzpatrick, ed. Pp. 21–50. Westport, CT: Praeger.

Knappett, Carl, Tim Evans, and Ray Rivers
2008 Modeling Maritime Interaction in the Aegean Bronze Age. Antiquity 82:1009–1024.

Kroeber, Alfred L.
1944 Configurations of Cultural Growth. Berkeley: University of California Press.

Laland, Kevin N., and Gillian R. Brown
2006 Niche Construction, Human Behavior, and the Adaptive-Lag Hypothesis. Evolutionary Anthropology 15(3):95–104.
2011 Sense and Nonsense: Evolutionary Perspectives on Human Behaviour. 2nd edition. Oxford: Oxford University Press.

Lande, Russell
1985 Expected Time for Random Genetic Drift of a Population between Stable Phenotypic States. Proceedings of the National Academy of Sciences of the United States of America 82(22):7641–7645.

Leacock, Eleanor B.
1954 The Montagnais "Hunting Territory" and the Fur Trade. American Anthropological Association Memoir 78. American Anthropologist 56(5, pt 2).

Leamer, Edward E., and Michael Storper
2001 The Economic Geography of the Internet Age. Journal of International Business Studies 32(4):641–665.

Leimar, Olof, and Peter Hammerstein
2001 Evolution of Cooperation through Indirect Reciprocity. Proceedings of the Royal Society of London B 268:745–753.

Lieberman, Erez, Christoph Hauert, and Martin A. Nowak
2005 Evolutionary Dynamics on Graphs. Nature 433(7023):312–316.

Lucero, Lisa J.
2002 The Collapse of the Classic Maya: A Case for the Role of Water Control. American Anthropologist 104:814–826.
2003 The Politics of Ritual: The Emergence of Classic Maya Rulers. Current Anthropology 44:523–558.
2006 Water and Ritual: The Rise and Fall of Classic Maya Rulers. Austin: University of Texas Press.

Mace, Ruth, and Clare J. Holden
2005 A Phylogenetic Approach to Cultural Evolution. Trends in Ecology & Evolution 20(3):116–121.

Mace, Ruth, and Mark Pagel
1994 The Comparative Method in Anthropology. Current Anthropology 35:549–564.

Mason, Phil
2009 Napoleon's Hemorrhoids and Other Small Events That Changed History. New York: Skyhorse.

Mathew, Sarah, and Robert Boyd
2011 Punishment Sustains Large-Scale Cooperation in Pre-State Warfare. Proceedings of the National Academy of Sciences 108(28):11375–11380.

Maynard Smith, John
1982 Evolution and the Theory of Games. Cambridge: Cambridge University Press.

Mayr, Ernst
1983 How to Carry Out the Adaptationist Program? The American Naturalist 121(3):324–334.

McElreath, R., and R. Boyd
2007 Mathematical Models of Social Evolution: A Guide for the Perplexed. Chicago: University of Chicago Press.

McGhee, Robert
1984 Thule Prehistory of Canada. *In* Handbook of North American Indians, Vol. 5: Arctic. David Damas, ed. Pp. 368–372. Washington, DC: Smithsonian Institution Press.

Mesoudi, Alex
2007 Biological and Cultural Evolution: Similar but Different. Biological Theory 2(2):119–123.

Mesoudi, Alex, and Michael J. O'Brien
2008 The Learning and Transmission of Hierarchical Cultural Recipes. Biological Theory 3(1):63–72.

Mesoudi, Alex, Andrew Whiten, and Kevin N. Laland
2004 Perspective: Is Human Cultural Evolution Darwinian? Evidence Reviewed from the Perspective of "The Origin of Species." Evolution 58(1):1–11.

Moxon, E. Richard, Paul B. Rainey, Martin A. Nowak, and Richard E. Lenski
1994 Adaptive Evolution of Highly Mutable Loci in Pathogenic Bacteria. Current Biology 4(1):24–33.

Nowak, Martin A.
2006a Evolutionary Dynamics: Exploring the Equations of Life. Cambridge, MA: Belknap Press of Harvard University Press.
2006b Five Rules for the Evolution of Cooperation. Science 314(5805):1560–1563.

Nowak, Martin A., and Karl Sigmund
1998 The Dynamics of Indirect Reciprocity. Journal of Theoretical Biology 194(4):561–574.

Olson, Mancur
1965 The Logic of Collective Action: Public Goods and the Theory of Groups. Cambridge, MA: Harvard University Press.

Pagel, Mark, Quentin D. Atkinson, and Andrew Meade
2007 Frequency of Word-Use Predicts Rates of Lexical Evolution throughout Indo-European History. Nature 449:717–721.

Panchanathan, Karthik, and Robert Boyd
2003 A Tale of Two Defectors: The Importance of

Standing for Evolution of Indirect Reciprocity. Journal of Theoretical Biology 224(1):115–126.
2004 Indirect Reciprocity Can Stabilize Cooperation without the Second-Order Free Rider Problem. Nature 432(7016):499–502.

Peoples, James G.
1982 Individual or Group Advantage? A Reinterpretation of the Maring Ritual Cycle. Current Anthropology 23:291–310.

Perry, Richard J.
2003 Five Key Concepts in Anthropological Thinking. Upper Saddle River, NJ: Prentice Hall.

Plourde, Aimée
2008 The Origins of Prestige Goods as Honest Signals of Skill and Knowledge. Human Nature 19(4):374–388.

Plourde, Aimée, and Charles Stanish
2006 The Emergence of Complex Society in the Titicaca Basin: The View from the North. *In* Andean Archaeology III: North and South. William H. Isbell and Helaine Silverman, eds. Pp. 237–257. New York: Springer.

Potts, Richard
1998 Variability Selection in Hominid Evolution. Evolutionary Anthropology 7(3):81–96.

Powell, Adam, Stephen Shennan, and Mark G. Thomas
2009 Late Pleistocene Demography and the Appearance of Modern Human Behavior. Science 324(5932):1298–1301.

Rainey, Paul B., and E. Richard Moxon
2000 When Being Hyper Keeps You Fit. Science 288(5469):1186–1187.

Richerson, Peter J., and Robert Boyd
2005 Not By Genes Alone: How Culture Transformed Human Evolution. Chicago: University of Chicago Press.

Ramírez, Susan E.
1985 Social Frontiers and the Territorial Base of Curacazgos: An Interdisciplinary Perspective on Andean Ecological Complementarity. *In* Andean Ecology and Civilization. Shozo Masuda, Izumi Shimada, and Craig Morris, eds. Pp. 423–442. Tokyo: University of Tokyo Press.

Richerson, Peter J., Robert Boyd, and Robert L. Bettinger
2001 Was Agriculture Impossible during the Pleistocene but Mandatory during the Holocene? A Climate Change Hypothesis. American Antiquity 66:387–411.

Shenk, Mary K., Monique Borgerhoff Mulder, Jan Beise, Gregory Clark, William Irons, Donna Leonetti, Bobbi S. Low, Samuel Bowles, Tom Hertz, Adrian Bell, and Patrizio Piraino
2010 Intergenerational Wealth Transmission among Agriculturalists: Foundations of Agrarian Inequality. Current Anthropology 51: 65–83.

Sih, Andrew, Sean Hanser, and Katherine McHugh
2009 Social Network Theory: New Insights and Issues for Behavioral Ecologists. Behavioral Ecology and Sociobiology 63(7):975–988.

Sindbaek, Søren Michael
2007 The Small World of the Vikings: Networks in Early Medieval Communication and Exchange. Norwegian Archaeological Review 40(1): 59–74.

Skyrms, Brian
2004 The Stag Hunt and the Evolution of Social Structure. Cambridge: Cambridge University Press.

Smith, Eric Alden
2003 Human Cooperation: Perspectives from Behavioral Ecology. *In* Genetic and Cultural Evolution of Cooperation. Peter Hammerstein, ed. Pp. 401–427. Cambridge, MA: MIT Press.
2010 Communication and Collective Action: Language and the Evolution of Human Cooperation. Evolution and Human Behavior 31(4): 231–245.

Smith, Eric Alden, Monique Borgerhoff Mulder, Samuel Bowles, Michael Gurven, Tom Hertz, and Mary K. Shenk
2010 Production Systems, Inheritance, and Inequality in Premodern Societies: Conclusions. Current Anthropology 51:85–94.

Smith, Eric Alden, and Jung-Kyoo Choi
2007 The Emergence of Inequality in Small-Scale Societies: Simple Scenarios and Agent-Based Simulation. *In* The Model-Based Archaeology of Socionatural Systems. Timothy A. Kohler and Sander E. van der Leeuw, eds. Pp. 105–119. Santa Fe: School for Advanced Research Press.

Smith, Eric Alden, and Mark Wishnie
2000 Conservation and Subsistence in Small-Scale Societies. Annual Review of Anthropology 29: 493–524.

Soltis, Joseph, Robert Boyd, and Peter J. Richerson
1995 Can Group-Functional Behaviors Evolve by Cultural Group Selection? An Empirical Test. Current Anthropology 36:473–494.

Stein, Howard F.
1984 A Note on Patron-Client Theory. Ethos 12(1): 30–36.

Steward, Julian H.
1938 Basin-Plateau Aboriginal Sociopolitical Groups. Bureau of American Ethnology, Bulletin 120. Washington, DC: US Government Printing Office.

Taylor, Christine, D. Fudenberg, A. Sasaki, and M. A. Nowak
2004 Evolutionary Game Dynamics in Finite Populations. Bulletin of Mathematical Biology 66(6):1621–1644.

Thomas, David Hurst
1981 Complexity among Great Basin Shoshoneans: The World's Least Affluent Foragers? *In* Affluent Foragers: Pacific Coasts East and West. Shuzo Koyama and David H. Thomas, eds. Pp. 19–52. Senri Ethnological Studies, 9. Osaka: National Museum of Ethnology.

Trivers, Robert L.
1971 The Evolution of Reciprocal Altruism. The Quarterly Review of Biology 46(1):35.

Turchin, Peter
2003 Historical Dynamics: Why States Rise and Fall. Princeton, NJ: Princeton University Press.

Wade, Michael J., and Charles J. Goodnight
1991 Wright's Shifting Balance Theory: An Experimental Study. Science 253(5023):1015–1018.

Wasserman, Stanley, and Katherine Faust
1994 Social Network Analysis: Methods and Applications. Cambridge: Cambridge University Press.

Wright, Sewall
1988 Surfaces of Selective Value Revisited. The American Naturalist 131(1):115–123.