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The evolutionary ecology of despotism

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Abstract

In this paper, I investigate the relevance of recent work in reproductive skew theory to explanations of the evolution of social stratification in human societies. I briefly review human social evolution and corresponding increases in stratification, as well as recent developments in skew theory. I then attempt to integrate basic factors that have been a focus of interest by skew theorists to previous work on human social stratification from an evolutionary ecological perspective. I also discuss factors peculiar to human social systems that could profitably be incorporated into future models of reproductive skew.
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1. Introduction

The word "despotism" refers to extreme bias in the control that some individuals exert over limited resources or other individuals. Biologists discussing despotism focus on reproductive skew, or the degree to which reproduction is monopolized within a society. In traditional human societies, these two aspects of despotism are highly correlated (Betzig, 1986): Individuals with despotic power use it to further their reproduction and that of their relatives. This paper will focus on despotism as an extreme in the spectrum of social stratification, with the assumption that it has been closely associated with reproductive skew during human history.

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Humans lived as hunter–gatherers, in small groups, until about 10,000 years ago (Price & Gebauer, 1995). Studies of hunter–gatherer societies indicate a relatively egalitarian distribution of resources and reproduction (Knauft, 1994). Such societies are not completely egalitarian, but differential reproduction is not pronounced. This suggests that ancient hunter–gatherers also lived in relatively egalitarian societies (Boehm, 1999).

Around 10,000 years ago, increasingly complex social entities such as villages, tribes, and chiefdoms began to appear, followed by kingdoms, empires, and states (Johnson & Earle, 2000). The evolution of these societies was associated with increasing despotism, in terms of control of resources and differential reproduction (Betzig, 1986, 1993). The archaeological record reveals pronounced disparities in wealth with increasing social complexity (Johnson & Earle, 2000). Written records from ancient societies document social disparities in resource distribution and reproduction (Betzig, 1993; Boone, 1986). Comparative and ethnographic studies of recent societies reveal dramatic examples of despotism and differential reproduction (Betzig, 1986; Casimir & Rao, 1995). However, despotism appears to have declined during recent history (Betzig, 1986).

This paper examines the rise of despotism from the perspective of evolutionary ecology. I will first introduce reproductive skew theory (a body of theory focused on differential reproduction within groups) and then briefly review the rise of despotism in humans. I will then summarize more recent developments in skew theory and attempt to integrate factors considered critical in this field with previous research on social stratification in humans. I will also suggest factors that should be incorporated into skew theory to address the peculiarities of human social systems.

Models of reproductive skew (the uneven distribution of reproduction within societies) were developed by Vehrencamp (1979, 1983). Emlen (1982) independently developed similar arguments. These models were inspired (Vehrencamp, 1984) by previous arguments concerning the relationship between subordinates' options for dispersal and the ability of dominants to monopolize reproduction (Alexander, 1974). Vehrencamp (1983)incorporated a variety of assumptions into her models of reproductive skew: (1) there is a single dominant; (2) the mean per capita fitness depends on group size; (3) there is no cost of dominating to the dominant; (4) the total number of offspring produced is independent of who is the dominant; (5) a subordinate can only avoid exploitation by leaving the group and breeding alone; and (6) the cost of dispersing is a function of the travel costs and the availability of breeding sites (slots), relative to the number of individuals competing for them.

The main objective of the models was to determine the allocation of resources or fitness to dominants and subordinates that maximizes the inclusive fitness of the dominant. Vehrencamp (1983) focused on the case of a single dominant partitioning reproduction with a single subordinate, or with a group of identical subordinates. A number of important results came out of these models: Skew was predicted to increase with increasing relatedness between the dominant and subordinate and with increasing ecological constraints (a measure of the expected success of a subordinate that attempts to disperse and reproduce).

The development of skew theory has entailed considerable debate concerning the applicability of specific models to particular social systems (e.g., Johnstone, 2000; Kokko, 2004; Reeve, Emlen, & Keller, 1998). Nevertheless, the theory provides a useful theoretical

framework through which one can interpret variation in despotism and reproductive skew. To understand how this theoretical framework might apply to humans, it will be worthwhile to review the nature of early human social systems and the rise of despotism in human societies.

2. Cooperation in early human societies

Despotism occurs in the context of cooperative social groups, and humans demonstrate substantial propensities to cooperate. Nepotism, direct and indirect reciprocity, suppression of competition, punishment, display, and mutualism are all viable elements of an explanation for much, if not, all human cooperation (Alexander, 1979; Frank, 1995; Gurven, Allen-Arave, Hill, & Hurtado, 2000; Nowak & Sigmund, 1998; Sigmund, Hauert, & Nowak, 2001; Smith & Bliege-Bird, 2000; Trivers, 1971). Whatever form of selection produced these propensities, they were probably in place in early human hunter–gatherers (Winterhalder, 2001). Human propensities to engage in both cooperative and selfish behaviors interacted with the changing environment over the last 10,000 years to affect the trajectory of human despotism, as indicated by historical and comparative analysis. It is not necessary to assume that selection over the last 10,000 years changed gene frequencies to create new propensities for despotic behavior in humans. It is likely that propensities acquired over the previous millennia lead to the expression of tactics in the changing physical, ecological, social, and technological environments, which resulted in high levels of despotism in some societies.

Modern hunter–gatherers typically have a relatively egalitarian system of resource distribution (Knauft, 1994; Winterhalder, 2001). Previous explanations for egalitarianism in hunter–gatherers include demographic instability, nomadic restraints on material accumulation, an absence of economic specialization, and decentralized redistribution systems for meat (Winterhalder, 2001). For example, a number of anthropologists have argued that limits on material acquisition in nomadic hunter–gatherers impose egalitarianism because resources cannot be accumulated (e.g., Cashdan, 1980; Hayden, 1995). However, even when there are temporary surpluses, they are typically divided relatively evenly. A number of researchers have observed that meat is shared in an egalitarian manner in hunter–gatherer societies and that there are specific mechanisms that ensure a relatively equal distribution (Kelly, 1995; Wiessner, 1996). Alexander (1990) argued that intergroup competition might have favored reproductive equality very early on in hominid evolution (see below).

Fried (1967) emphasized the importance of social leveling mechanisms in maintaining egalitarianism in human societies. There are two main components of social control: the presence of a "moral community" enforcing social conformity and the use of social sanctioning to ensure equality among adult males (Alexander, 1979; Durkheim, 1933; Fried, 1967). Following in this tradition, Boehm (1999) proposes that hunter–gatherers create "antihierarchies" that maintain an egalitarian social structure. Group members take control to suppress competition and domination. A survey of the ethnographic literature on Australia, North America, Africa, and Asia (Boehm, 1993) revealed that such sanctioning is ubiquitous across hunter–gatherer societies and takes many forms, including criticism, ridicule, desertion, disobedience, overthrow, expulsion, and execution.

Although hunter–gatherer societies vary in their degree of egalitarianism (Diehl, 2000; Kuhn & Stiner, 2001; Winterhalder, 2001), there is a general consensus that early hunter–gatherers were relatively egalitarian compared with many of the human societies that arose over the past 10,000 years (Betzig, 1986; 1993). Boehm (1999) argues that evolution towards egalitarianism (relative to a chimpanzee-like ancestor) began in the hominid line at least 100,000 years ago and that several hominid traits predisposed humans to develop egalitarian societies: the invention of hunting weapons, the advent of large-game hunting, and the evolution of large brains and linguistic, cultural, and cognitive capabilities. He proposes that the development of effective hunting weapons allowed for much more efficient and rapid killing of conspecifics and made dominants more vulnerable to relatively low-risk attacks by subordinates, particularly groups of subordinates. Bingham (1999) also emphasized the effect of innovations in weaponry on the development of cooperation and egalitarianism in hunter–gatherer societies. He views cooperation among early humans as a form of enforced mutualism, in which defection is prevented by the threat of punishment. Punishment is generally costly to the punisher, but the cost of punishment was dramatically reduced by the invention of effective weapons, particularly projectile weapons (Bingham, 1999). The advent of projectile weapons allowed many more individuals to simultaneously attack a single individual, increasing the firepower brought to bear on the transgressor, distributing the risk of retaliation among more punishers, and reducing the time taken to subdue the transgressor (Bingham, 1999). This greatly reduced the cost of punishing cheats. Bingham argues that this caused coalitional enforcement to become a stable mutualism, in which the benefit of low-cost punishment is shared by all cooperating members of a coalition (the "Coalition Enforcement Hypothesis").

In summary, historical and ethnographic evidence suggest that early hunter–gatherers were relatively egalitarian, in terms of both resource control and reproduction. The available evidence suggests that humans, throughout their history, are likely to have regarded attempts to usurp control of both material and reproductive resources with violent disapproval and with a firm willingness to punish such transgressions, both as individuals and as members of a collective.

3. The rise of despotism in human societies

The rise of despotism in human societies has sometimes been treated as some sort of inevitable consequence of population growth or group size. For example, Bingham (1999) argues that despotism will inevitably increase in large groups, without providing a defense of that claim. My view is that the rise of despotism is a difficult phenomenon to explain and has probably been influenced by a number of different factors. Around 10,000 years ago, the first evidence for larger, more complex societies, comprising increasingly complex social entities such as villages, tribes, chiefdoms, and states, appears in the archeological record (Johnson & Earle, 2000). Human social evolution repeats this pattern across geographic regions, in terms of similar forms of subsistence intensification, political integration, and social stratification (Johnson & Earle, 2000). The emergence of complex societies is associated with increasing

levels of despotism, in terms of both control of resources and differential reproduction (Betzig, 1986, 1993). Convergent change from small bands of hunter–gatherers to large, permanent villages, with evidence of social stratification, occurred in many areas (Sanderson, 1995). Stratification developed without the transition to agriculture in some cases ("complex hunter–gatherers," associated with abundant resources; Sanderson, 1995). However, social stratification was highly correlated with the transition to agriculture and truly institutionalized social stratification characterized by steep social hierarchies, and hereditary inequality was largely restricted to societies based on sedentary agriculture (Price, 1995).

Earle (2002) discusses three main sources of social power that have led to stratification in complex societies: economic, military, and ideological. Most currently debated anthropological theories of the development of social stratification emphasize control of the economy by elites (Earle, 2002). Control derives from differential access to resources, wealth, and labor (Friedman & Rowlands, 1977), although the exact nature of economic control continues to be debated by anthropologists (Earle, 2002). Individuals and families have used various strategies to control wealth, inflict debts, and hence, wield economic power (Hayden, 1995). Why subordinates tolerate such inequalities has been the subject of considerable debate within anthropology.

Fried (1967), following the Marxist tradition, viewed hierarchies as inherently repressive, with elites taking advantage of the productive capacity of the entire population for selfish gain, using force to repress the population when necessary. In contrast, Service (1962) viewed hierarchies as constructs of the populace that coincided with their own best interests. This view has been a prominent part of the functionalist perspective in anthropology, known as the "General Managerial Model" (Diehl, 2000). Some recent analyses have approached the issue from the perspective of the Handicap Hypothesis originally developed by Amotz Zahavi (see Boone, 1998, for an overview and an example of this approach). Individuals can provide benefits to the populace at large through visionary leadership and efficient management. However, this is unlikely to explain the institutionalization of social stratification via hereditary inequality, as seen in many despotic societies (Gilman, 1995).

Evolutionary biologists and anthropologists (e.g., Alexander, 1979; Betzig, 1986; Boone, 1992) have argued that individuals within societies face inherent tradeoffs between the cost of repression within society and the benefits obtained by all members of the society (e.g., enhanced success in intergroup competition). On this view, the average level of exploitation experienced by the members of a society will vary depending on factors such as the frequency and intensity of intergroup competition. In general, however, evolutionary biologists have viewed the development of large, complex societies as being associated with despotism via repression.

Betzig (1986, 1993), in particular, provides compelling evidence that extreme despotism, in the form of complete control of the fate of resources and individuals lower in the hierarchy, strongly characterizes large, preindustrial, and traditional societies with multilevel hierarchies. In a cross-cultural analysis, she found that, as social hierarchies become more complex (contain more tiers) in larger societies, elites become more able to kill commoners with impunity and more able to impose taxes and fines (Betzig, 1986). Research on a variety of ancient states supports the contention that they were generally despotic and reveals strong

correlations between agricultural intensification, social complexity, stratification, and despotism (Betzig, 1993; Price, 1995; Sanderson, 1995). Sexual differentiation was very strong in such societies: Resources were under male control, and the elite males achieved high reproductive success by monopolizing the reproductive output of multiple women (Betzig, 1986, 1993, 1995, 1997).

Social scientists have proposed many hypotheses to explain the development of social stratification in human societies. Increasing group size itself imposes some problems of scale that require political centralization and hierarchical organization (reviewed in Diamond, 1997), although this would not necessarily require social stratification (Mabry, 2000). Some anthropologists have noted an association between military leadership and social control, but this has typically been viewed as an insufficient explanation (Earle, 1997). Other explanations include the following:

(1) Population pressure: Johnson and Earle (2000) and others have argued that the growth of population leads to diminishing returns for labor, resulting in the reorganization of society toward agricultural intensification, putting a premium on the control of arable, fertile land, and leading to social stratification.
(2) Agricultural surplus: As many researchers have emphasized, exploitation requires a surplus to be exploited (Wesson, 1999). This typically consists of both an agricultural and a labor surplus (Allen, 1997).
(3) Food storage: Food surpluses are unlikely to be useful to despots unless they can be effectively stored, and hence, the invention of effective food storage may have been critical for the development of despotic societies (Allen, 1997).
(4) Sedentism: Rich environments may promote a sedentary lifestyle, which, in turn, allows the development of more complex social systems, with consequent increases in hierarchical structure (Plog, 1990).
(5) Control of the means of production: When a subgroup within a society is able to control the means of production, this leads to class formation and the development of steep social hierarchies [Engels, 1972 (1884); Marx, 1967 (1867)].
(6) Control of material wealth: A variety of theories of the emergence of stratification focus on the control, by an elite minority, of material wealth, including commodities (Renfrew, 1972), land (Randsborg, 1982), and capital (Gilman, 1987).
(7) Technological innovation: In a similar vein, the development of technologies that dramatically enhance food acquisition, trade, and communication, and that are owned by a small proportion of society, can promote the development of social complexity and hierarchy (Arnold, 1995).
(8) Large-scale projects: Wittfogel (1957) argued that the state arose to construct and manage large-scale irrigation systems and that despotism was strongly associated with the development of large-scale irrigation agriculture.
(9) Labor control: If some members of society are able to monopolize control of labor, this can allow for the development of stratification and an elite class. Webster (1990) argued that this process may have been an important influence on the development of social stratification in prehistoric Europe.

(10) Ideological control: Rulers may invoke divine law and order (frequently during the practice of religious ritual) to justify and reinforce existing social hierarchies (Earle, 1997).

This list is not exhaustive, but it represents some common themes in the literature on social stratification. Most of these hypotheses do not focus on reproductive inequality within societies. Reproductive skew theory can help identify elements that were critical to the initial evolution of skew in human societies. This does not mean that economic or ideological theories are irrelevant, but that they require more basic elements to be in place before their effects will be stable. Hence, one purpose of this paper is to argue that reproductive skew theory may have something to offer the study of human despotism (and vice versa).

Surprisingly, the evolution of reproductive skew in human societies has not received much attention from evolutionary ecologists. One of the first to address this issue was Alexander (1974), who emphasized the effect of ecological constraints on the ability of subordinates to avoid suppression, leading to social stratification. A few traditional anthropologists have also developed theories that closely parallel developments in skew theory. For example, the Circumscription Theory of Carneiro (1970) emphasizes the role of ecological constraints (in the form of geographic barriers to dispersal) on the development of social stratification, particularly in the context of warfare and conquest. Warfare has also been the focus of attention by evolutionary ecologists and anthropologists (e.g., Alexander & Tinkle, 1968) and can cause social stratification (see below). Boone (1992) and other evolutionary anthropologists have emphasized that asymmetries in resource-holding potential interact with resource structure to cause social stratification.

As noted above, most discussions of despotism in the literature focus on control of resources or other individuals (Hayden, 1995). Does such control typically translate into reproductive skew? Betzig (1986) used cross-cultural analysis of ethnographic research and historical records to demonstrate a significant correlation between despotism and differential reproduction: Rulers typically use their power to enhance their own reproductive success and that of their relatives. Across the ancient civilizations, the political and military hierarchy was paralleled by a reproductive hierarchy. Emperors had access to thousands of women, noblemen (typically kinsmen of the ruler) had access to hundreds of women, and so on (Betzig, 1993). These societies had large numbers of poor, outcast males at the bottom, and many had (and, in some cases, still have) extreme forms of imprisonment and incapacitation of women as mate-guarding mechanisms (Dickemann, 1981).

4. Recent developments in reproductive skew theory

Recent developments in skew theory highlight factors relevant to the development of despotism in some human societies. Evolutionary anthropologists have made use of ideas that comprise part of skew theory for many years (e.g., Turke, 1988). Nevertheless, over the last 10 years, there have been a number of developments in skew theory that have not been incorporated into our understanding of reproductive skew in human societies.

As reviewed by Keller and Reeve (1994), later work revised and expanded the earlier models of Vehrencamp. In general, reproductive skew is affected by four parameters: (1) ecological constraints, (2) group productivity as a function of group size, (3) the genetic relatedness of group members, and (4) the probability that a subordinate would win a lethal fight with a dominant without being severely injured (relative fighting ability). These factors affect the "staying incentive" (reproduction conceded to subordinates to prevent their departure) and the "peace incentive" (reproduction conceded to subordinates to prevent them from fighting for supremacy with the dominant).

The expanded theory made four main predictions: (1) the staying and peace incentives should become smaller as group productivity increases; (2) the staying incentive should decrease with increasing ecological constraints on independent reproduction; (3) the peace incentive should increase with increasing relative fighting ability of the subordinate; and (4) the magnitudes of the staying and peace incentives should decrease as relatedness between dominants and subordinates increases.

Johnstone (2000) reviewed recent developments in skew theory. Most theoretical analyses assume that the dominant has complete control over breeding, but Johnstone (2000) points out that this is not necessarily the case. Dominants may be unable to control subordinate reproduction in some cases, and this can profoundly affect the level of reproductive skew (Clutton-Brock, 1998). This consideration has led to the development of "incomplete control" models of skew (e.g., Johnstone & Cant, 1999a) and to models that incorporate the possibility of eviction by the dominant (Johnstone & Cant, 1999b).

Most models of reproductive skew fall in to two categories: Transactional models focus on group stability under dominant hegemony, whereas compromise models focus on the division of reproduction as function of a struggle among individuals with limited abilities to enforce their own optima. Johnstone (2000) suggests a synthetic perspective that incorporates both the transactional and the compromise approaches.

A key consideration with regard to reproductive skew in transactional models concerns the level of control exerted by the dominant. If the dominant has full control ("concession" models), then subordinates will receive the minimum share of reproduction consistent with group stability (Reeve & Ratnieks, 1993; Vehrencamp, 1983). However, if subordinates can claim unsanctioned reproduction up to the point at which the dominant profits by eviction, then the subordinates will receive the maximum share of reproduction consistent with group stability ("restraint" models: Johnstone & Cant, 1999b). In both concession and restraint models, the level of reproductive skew depends critically on the reproductive benefits of being in a group, the restrictions on independent breeding (ecological constraints), and the relatedness between the dominant and subordinate (Johnstone, 2000). Unfortunately, the concession and restraint models make opposite predictions with regard to these factors. This occurs because the same factors that make the association profitable for the dominant (high benefits to grouping, strict ecological constraints, and high relatedness) also make the association profitable for the subordinate. Hence, the level of skew is determined by the relative control exerted by dominants and subordinates. Under the concession models, the dominant has complete control, whereas under the restraint models, the dominant only has partial control (via eviction).

Models of skew that ignore group stability requirements have also been developed, and instead estimate reproductive skew as a compromise between the conflicting interests of dominants and subordinates, and their ability to enforce them (Cant, 1998; Reeve et al., 1998). One such model is the "tug-of-war" model (Reeve et al., 1998), in which relatedness has a smaller influence on the partitioning of reproduction than in transactional models. Instead, the relative competitive ability of the subordinate is the main determinant of reproductive skew. Other compromise models with different assumptions have been developed and make differing predictions with regard to the effect of relatedness (Cant, 1998; Johnstone & Cant, 1999a). Johnstone (2000) developed a general model that combines considerations of group stability characteristic of the transactional models with the struggle for the control of reproduction characteristic of the compromise models. Not surprisingly, this model yields predictions consistent with the transactional models under some circumstances and consistent with the compromise models under others. Johnstone argues that the extent of dominant control over breeding and the importance of threats of departure by subordinates and eviction by dominants are critical factors that will strongly influence which model of skew is appropriate to a particular species.

My purpose here is not to examine this plethora of models in detail, but rather to pick out a few specific factors that have been the focus of previous modeling efforts that are also likely to be of key importance in the rise of reproductive skew in human societies. I will focus on factors that are likely to be closely related to the balance of power between dominants and subordinates (Beekman, Komdeur, & Ratnieks, 2003). Factors such as resource inheritance, relative fighting ability, and punishment have not yet been formally incorporated into analyses of human despotism. Conversely, although there are a multitude of models of the factors affecting levels of reproductive skew, these models have not been designed to capture features that are unique to human societies. Yet, there are a variety of such features that are likely to affect reproductive skew.

5. Ecological constraints

Ecological constraint constitutes a major factor in many models of reproductive skew (Reeve & Ratnieks, 1993; Vehrencamp, 1983). In the broader literature on cooperative breeding, the importance of ecological constraints has been contrasted to the benefits of philopatry, although in many ways, these are two sides of the same coin (Emlen, 1994). Recent theoretical and empirical work focused on nonhumans indicates that ecological constraints are not required to explain delayed dispersal and associated reproductive skew, although they can be important (Kokko & Ekman, 2002). Ethnographic work has been done on the influence of ecological constraints on systems of cooperative breeding in human societies. For example, Turke (1988) investigated cooperative breeding within families on the Micronesian island of Ifaluk, which may have resulted from constraints on dispersal. More recently, Strassmann and Clarke (1998) demonstrated that ecological constraints influenced cooperative breeding and reproductive skew in the Irish during recent history. Betzig (1986, 1993, 1995, 1997) emphasized the influence of ecological constraints on the ability of dominants to act despotically.

In parallel to the emphasis on ecological constraints in skew theory, a number of anthropologists have emphasized the importance of resource structure on the development of social stratification in human societies (e.g., Boone, 1992). Many of the most despotic preindustrial societies developed in the Middle East and Central and Eastern Asia (Betzig, 1986). The distribution of resources in the regions where highly stratified societies developed was typically extremely patchy, with dramatic differences in productivity and inhabitability between good and bad areas (Boone, 1992). For example, Allen (1997) argued that strong ecological constraints imposed by the harsh environments surrounding the Nile Valley (combined with the storable nature of agricultural crops) were the critical factors allowing the development of extreme despotism in ancient Egypt. He also argued that ecological constraints were critical in generating states with high levels of social stratification in other parts of the Near East. The limiting resource in this region was, often, water for irrigation (e.g., Wittfogel, 1957), which was used to produce defendable resources such as herds of livestock. The patchy nature of the resource structure in these regions, combined with the economically defendable nature of the resources produced, combined to make despotism a more viable strategy for dominants (James Boone, personal communication). This argument closely parallels the ecological constraints argument cited above. When the good patches are saturated, then there will be ecological constraints on the ability of subordinates to disperse and establish their own families. The available evidence indicates that ecological constraints profoundly affect social stratification in humans.

6. Kinship, dominance hierarchies, and skew

Kinship has been a central focus of evolutionary ecology following the seminal work of Hamilton (1964). There is extensive evidence for nepotism in human societies. Genetically related individuals are more likely to offer aid in confrontations (Chagnon & Bugos, 1979) and more willing to share labor (Essock-Vitale & McGuire, 1980; Hames, 1979) and resources (Silk, 1980). All traditional societies operate as kinship systems, where kin are distinguished on the basis of the degree of relatedness and relative dependency (Alexander, 1979).

Kinship is a major factor in most skew models (Reeve et al., 1998), and skew increases with relatedness under most models (Reeve et al., 1998; Vehrencamp, 1983). Kinship and kin recognition have also been proposed as key factors mediating the evolution of sociality and group size in cooperative breeders (Emlen, 1997; Lehmann & Perrin, 2002). Anthropologists have long been interested in the formation of kinship-based lineages and on competition among lineages (e.g., Friedman & Rowlands, 1977). Ethnographic and historical research on human societies suggests that kinship is likely to have influenced reproductive skew in important ways (Shaw & Wong, 1989).

Most models of reproductive skew predict that levels of skew will tend to be higher within kin groups than within groups of similar size and complexity made up of nonrelatives (Keller & Reeve, 1994). I have not found any comparative tests of this hypothesis within or between human societies. In testing the hypothesis with ethnographic or historical data, it

will be important to control for factors such as group size, ecological constraint, and relative fighting ability.

Large human groups (of kin or nonkin) tend to be hierarchical (Johnson & Earle, 2000). Human dominance hierarchies can be complex and take many forms. The simplest is a linear hierarchy, with a single "ladder" of status in which dominance is transitive but hierarchies are often more complex, involving multiple subordinates of similar status at different levels within the hierarchy and multiple hierarchies within a society (Earle, 2002).

Most skew models have considered interactions between only a single dominant and subordinate individual. A few models have considered multiparty interactions (Johnstone, Woodruffe, Cant, & Wright, 1999), but none have specifically considered the influence of dominance hierarchies on levels of reproductive skew. Without formal models, it is difficult to make accurate predictions concerning the effect of dominance hierarchies on skew. Nevertheless, it is likely that dominance hierarchies will (at least under some circumstances) have an amplifying effect on reproductive skew. Hierarchies of reproductive skew with multiple subordinates per dominant can support higher maximum levels of skew than will simple dominant–subordinate interactions, if the excess reproduction obtained by a large number of lower and midlevel dominants feeds back to a smaller number of higher level dominants (culminating in a single top level dominant; Betzig, 1993).

Kinship has fundamental effects on the formation of hierarchies in human societies. Anthropologists have emphasized the relationship between kinship support networks and leadership (e.g., Mair, 1962; Thomas, 1982). When there is no lawful authority, combined strength determines the result of conflicts of interest. Combined strength is typically a function of an individual's strength and prowess, and that represented by the individual's kinship and alliance network (Betzig, 1986). A strong correlation between property, family, and authority is present in the ethnographic literature, with multiple examples of large, powerful within-group factions biasing decisions in their own favor (Betzig, 1986). For example, in the Yanomamo, men with large kinship networks are most likely to be polygynous and are more successful in achieving high status (Chagnon, 1982).

Human hierarchies are often nested, such as conical clans (ancestor-based hierarchies), which, in turn, are structured into a hierarchy of clans (Boone, 1986, 1992). In complex societies, these hierarchies of clans are, in turn, dominant to a population of subordinates (commoners) that may have its own internal hierarchy (Kautsky, 1982).

Chiefdoms were typically kinship systems, in that social status and political position were strongly influenced by relatedness to other members of the hierarchy (Earle, 1997). Rank was typically measured by genealogical distance from the main patrilineal ancestor (Earle, 1997). For example, in Hawaii, chiefs had genealogical specialists, who determined the kinship of individuals applying for political offices, which, in turn, determined their suitability for the position (Earle, 1997). In prehistoric Europe, kinship status had a crucial influence on the ability to achieve political power (Friedman & Rowlands, 1977). Rulers in the ancient chiefdoms of the Andes were supported by a warrior elite consisting of kinsmen (Earle, 1997). Similar systems occurred throughout the world (Betzig, 1993).

Hughes (1986) argued that leaders in traditional societies are typically individuals who have close genetic ties with many other group members. He developed several mathema-

tical methods for investigating patterns of relatedness in kin matrices (matrices of relatedness among individuals), which specify individuals who are foci of genetic relatedness, identify concentrations of relatedness within groups (highly related subgroups), and identify the subgroup relatedness to focal individuals, such as focal offspring. Hughes (1988) discussed several cases that support his contention. For example, in the Nuer, individuals use kin support to achieve high positions in the social hierarchy. Nuer chiefs tend to be the foci of relatedness within large kinship networks. Recent developments in skew theory parallel the approach of Hughes (1986, 1988). For example, Reeve and Jeanne (2003) utilize linear programming to investigate the evolution of reproductive skew in large groups in which the power of each individual is trivial compared with that of the collective. They find that a "virtual dominant" will arise that achieves a measure of reproductive success equivalent to that predicted by classical skew models. In the model, the virtual dominant is the individual that is the focus of group relatedness.

Kinship also has a profound influence on the success of subgroups within societies. For example, in patrilineal societies, related males and their offspring live together, forming a "fraternal interest group" (Otterbein & Otterbein, 1965). When polygyny is common, a large number of cohabiting half-brothers are produced, enhancing the size of these kin coalitions. The anthropological literature is replete with examples of male kinship groups as a basis for organization to defend common interests (e.g., Otterbein, 1968; Otterbein & Otterbein, 1965; Thoden van Velzen & van Wetering, 1960).

Concentrations of relatedness within kin groups are critical to the development of social stratification. Hughes (1988) developed models of kin coalition formation in competition over resources among kin. These models predict that closely related individuals will form coalitions to exclude less closely related individuals from resources. He argued that "feuding societies" are characterized by concentrations of relatedness. The feudal chiefs derive their position from their own competitive abilities and from armies of retainers that are typically constructed from their kin network. Hughes cited examples from Africa (Mair, 1962) and Europe (Davies, 1982).

Jones (2000) notes that kinship has generally been considered to be irrelevant to interactions between distant kin, even though ties between distant kin are frequently emphasized both by ethnographers and their subjects in traditional societies. He develops a theory of "group nepotism" and argues that the scope of kin selection is much larger if we consider the effect of groups of kin providing assistance to other kin.

First, Jones (2000) develops a model of an interaction between nepotism and reciprocal altruism ("conditional nepotism"). In conditional nepotism, individuals who take turns assisting another relative(s) receive higher inclusive fitness payoffs than do individuals acting alone. He demonstrates that conditional nepotists invest more in kin than predicted by the Hamiltonian model of inclusive fitness and that conditional nepotists will invade a population of Hamiltonian nepotists under certain conditions. The model demonstrates that when more than a single relative can potentially aid one or more other relatives, then altruism toward kin becomes a common good and that the effective coefficient of relatedness is higher if kin work together to aid other kin. Jones also developed models of coerced altruism in groups of kin. In large kin groups, every individual is greatly outnumbered by the

rest of the group, and it can be relatively cheap for group members to impose agreed-upon social norms on all individuals in the group (assuming that the group has the resources to monitor and sanction conformity to the rules). Jones demonstrates that, if group members in kin groups can impose social norms such that all individuals from the kin group accept the cost and provide a benefit to another group of relatives, the degree of relatedness favoring altruism is lower than the coefficient of relatedness required for altruism under the classic Hamiltonian model.

Human kin groups can number in the hundreds or more. Jones (2000) argues that relatedness in such large groups is frequently too low to favor individual nepotism but high enough that group nepotism may be important. He provides estimates of coefficients of relatedness from a survey of tribal societies that support his contention. He also reviews examples from the ethnographic literature that illustrate the common belief that even distant kin are treated altruistically and that such treatment is often enforced by social norms (in the jural domain of kinship). Hence, there seems to be a general human proclivity to maintain and enforce an ethic of altruism toward kin.

Jones (2000) argues that ethnocentrism may be an evolved product of group nepotism, resulting in strong in- versus out-group biases (frequently demonstrated in the psychological literature), a view of the social world as being divided up into kin groups of various sizes and a proclivity to join fellow kin group members and participate in enforcing within-group solidarity and between-group enmity.

Kinship has been and remains a potent influence on human behavior: Human kin groups can remain cohesive even when they reach large sizes, and it is likely that patterns of reproductive skew in human societies have developed in the context of large kin groups. In general, kin-structured groups should exhibit enhanced levels of skew relative to groups of nonrelatives. Kinship had a critical influence on the formation of dominance hierarchies in human societies. Competition between kin-based lineages is also likely to have contributed substantially to the development of skew in human societies (see below), both within lineages (Boone, 1986) and in society as a whole (Friedman & Rowlands, 1977).

7. Agriculture and resource inheritance

The transition to agriculture had a profound effect on social stratification and the degree of despotism in human societies (Johnson & Earle, 2000; Price, 1995). This transition was associated with a transition from communal sharing to familial accumulation. Evidence for social stratification appears at the individual, household, and lineage levels, in the archaeological record, with the advent of agriculture (particularly sedentary agriculture). Hence, the transition to agriculture was associated with an increase in hereditary inequality in human society (Price, 1995; Price & Gebauer, 1995).

Why the transition to agriculture was associated with social stratification remains a subject of debate. The transition was associated with increased productivity in most cases (Price & Gebauer, 1995). Increasing group productivity is expected to correlate with higher levels of skew in optimal skew theory (Reeve & Ratnieks, 1993), and this fits well with a

long tradition relating productivity to social stratification in anthropology (Schurr & Schoeninger, 1995). Recent research also provides evidence in support of an association between agricultural productivity and social stratification (Schurr & Schoeninger, 1995). Agriculture also created a resource base that was more economically defensible (*sensu* Hudson-Dyson & Smith, 1978), enhancing resource patchiness, which, in turn, allowed steeper hierarchies to develop (Boone, 1992). Other explanations of the influence of the transition to agriculture on the rise of despotism have focused on the control of agricultural surpluses to retain power over subordinates (e.g., Wesson, 1999). I do not deny the importance of these considerations, but I think they provide an incomplete explanation of the effect of agriculture on social stratification.

A key consideration in the contribution of agriculture to social stratification is that it created a highly heritable resource, a stationary resource that could be economically defended and passed from generation to generation (Shennan, 2002). Models of the interaction between inheritance and long-term fitness demonstrate that the inheritance of wealth can drastically increase the value of resource accumulation to dominants (Rogers, 1995). Recently, skew models have been developed that take into account the possibility that subordinates may stand to inherit dominant status in their group (Kokko & Johnstone, 1999; Ragsdale, 1999). The models indicate that inheritance of dominant status can profoundly affect reproductive skew. Status inheritance can allow for stable groups to form in which the dominant concedes no reproduction to subordinates, even among nonrelatives (Kokko & Johnstone, 1999). Inheritance of dominant status is an obvious feature of most human social groups (Betzig, 1993). The importance of the inheritance of status will depend on associated reproductive benefits. In hunter–gatherer societies, these benefits were modest at best. With the transition to agriculture, inheritance of resources (productive land) made inheritance of high status much more important. The dramatic increase in the importance of heritable wealth that coincided with the development of agriculture and food storage should have produced corresponding increases in social stratification within and among groups.

8. Lineage competition, primogeniture, policing, and punishment

Large kin groups could maintain and defend the agricultural lands necessary to produce the resources to train and equip an effective military and police force (Boone, 1986). Shaw and Wong (1989) viewed the production of warriors as a resource that kin groups (clans or lineages) were prepared to lose in policing or warfare. The development of agriculture (and the associated heritable resource base) had profound effects on social stratification in the context of competition between kin-based lineages, by allowing lineages that controlled agricultural land to produce offspring that had exceptional fighting ability (see below) and by restricting the number of available slots in the lineage hierarchy.

Historically, rulers in hierarchical societies married monogamously (while simultaneously maintaining large harems of concubines) to produce a single heir who could inherit the title and land controlled by the ruler (Betzig, 1993; 1995). Primogeniture and patriliny increased the

inheritance provided to heirs and reduced the number of heirs (Betzig, 1993). Across cultures, nobles maintained control of their heritable properties by marrying among themselves. They also prevented commoners from doing the same (Betzig, 1993).

Boone (1986) has argued that the advent of agriculture led to intense competition among kinship lineages over limited agricultural lands and estates. He argued that these competing lineages favor patriliny and primogeniture when there is a stable source of wealth (agricultural lands), wealth is unequally distributed, and the inheritance of wealth determines rank and power. In this situation, patriliny and primogeniture allow kin groups to maintain control of limited resources in the face of severe competition from other lineages. He provided evidence in favor of this hypothesis from historical records from Medieval Portugal (Boone, 1986). Betzig (1993) argued that the value of an intact empire exceeds the sum of its parts, and breaking up an empire may put the separate parts at high risk of absorption by rival factions, hence favoring primogeniture. Bergstrom (1994) came to a similar conclusion after developing a model of reproductive success in a simple stratified society and comparing it with data from the British Aristocracy in the 17th and 18th centuries. Under primogeniture, successful dominants produce a superabundance of successors. In Medieval Europe, there was an overproduction of males in the queue for dominant status at every level of a complex hierarchy (Boone, 1986). This, in turn, led to expansionism, in which excess noble sons were sent to fight in wars of foreign conquest. It also led to excess sons and daughters being sent to join the church, which probably contributed to the animosity between church and the state in Medieval Europe (Betzig, 1995).

How are stable dominance hierarchies maintained despite the limitation on advancement under systems of primogeniture? As discussed above, it is likely that dominants are the foci of relatedness within kin groups. Although each individual might prefer to be the dominant, the collective interests of the kin group will be best served by supporting an individual who represents such a focal point of kinship. One factor that may contribute to the maintenance of stability is "policing." In the hymenoptera, policing of worker reproduction is carried out by workers who are typically more closely related to the queens' offspring than to their fellow workers' offspring (Ratnieks & Visscher, 1989). In human kin-groups, collective policing may keep individuals who are the foci of relatedness in power (Hughes, 1988). In human dominance hierarchies, individuals may police the activities of other individuals who are close to their position in the hierarchy. As discussed above, the inheritance of rank can stabilize relationships between dominants and subordinates when the potential payoff for queuing exceeds that of fighting to replace the dominant (Kokko & Johnstone, 1999). Excess noble sons may have an incentive to overthrow the dominant (because they have a low probability of inheritance), but older siblings should thwart the attempts of younger siblings to overthrow the hierarchy because they stand to benefit from the stability of the hierarchy through inheritance. First-born sons should keep latterborns from rebelling, if possible, because they stand to inherit the highest rank. However, there may also be a hierarchy of positions achievable by each younger sibling. Hence, older (non first born) sons may have opportunities to serve closer to home in the military and to achieve positions of substantial rank (Boone, 1986). In addition, older siblings will always be higher in the queue for the highest heritable rank than their younger siblings. Hence, each sibling should have some

interest in policing younger siblings, even if they are tempted to disrupt the system in their own interests.

The practice of spying and policing has been central to human society throughout recorded history and probably well before. Some cultures (e.g., Ancient China, India, and Medieval Venice) developed truly impressive networks of surveillance and policing (Andreski, 1968). Archaic states and chiefdoms did not have dedicated police forces. Instead, the aristocracy (which comprised the upper echelons of the military) was the police force, and individuals at each level in the hierarchy ensured the compliance of those further down (Kautsky, 1982; Reyna, 1994).

Lineages in traditional societies focused on ancestry as the basis for rank and inheritance (Earle, 1997). Ancestor-based patterns of inheritance reflected the intense competition among kin groups, making it necessary to maintain united control of property via primogeniture (Boone, 1986). These systems were characterized by intense competition among kin to achieve positions of prominence within the hereditary hierarchy and steep stratification (Betzig, 1995). The connections between specific individuals and the position(s) of their ancestors in the hierarchy were critical in regulating the inheritance of rank and property within the hierarchy (Boone, 1986; Earle, 1997). Hence, in these systems, we might expect an ancestor-based focus of affiliation to be advocated by those in power.

The changing focus of the family unit from preindustrial societies with a focus on ancestor-based lineages to modern families with a focus on common offspring may be involved in the decline of stratification and skew in modern times. Hughes (1988) argued that relatedness to sets of offspring is likely to be crucial to the establishment of group membership, given that such offspring are likely to be the focus of investment by the residential group. He presents an example focusing on residential patterns in modern families in Eastern Tennessee (USA) and shows that residential patterns are better explained by links to common offspring than to common ancestry. This analysis highlights an interesting contrast. The transition between preindustrial hierarchical societies, with generally patriarchal control and patrilineal inheritance of resources (especially agriculturally useful land), property, profession, and title, to the modern nation state, with its emphasis on moving for work (due to trade, specialization, and requisite education), may have changed kinship systems from ancestor based to nuclear family based (i.e., from connections to common ancestors to connections to common offspring). This transition is associated with the disappearance of the large, dominant kin-groups characterized by high skew and social queuing for position.

Although kin-based lineages competed intensely with each other for control of limiting resources (agricultural lands), they also formed coalitions and alliances in the interest of suppressing large populations of subordinates (agrarian peasants). This allowed the effective breakup of kin groups in subordinate populations, which further enhanced the relative power of dominant lineages. A number of researchers have pointed out that elites controlled the kinship ties of peasants in their own interests (Betzig, 1993; Johnson & Earle, 2000; Kautsky, 1982).

Lineages also formed coalitions in the interest of competing with other elite lineages (Boone, 1986). For elite lineages to remain dominant, they did not have to control the entire

society. They needed only to dominate other lineages large enough to threaten their hegemony. Hence, it may pay particular lineages to form strategic alliances with smaller lineages, or even with commoners, to prevent other large lineages from successfully usurping their lands and power. The literature on aristocratic empires contains examples of this kind of strategic alliance formation (e.g., Andreski, 1968; Kautsky, 1982). The effect of coalitions on the degree of skew has not yet been rigorously modeled, although it has been a subject of discussion in the biological and anthropological literature for many years. If dominants can form coalitions among themselves to enforce skew on subordinates, this should increase the amount of skew the dominants can successfully impose. However, to the degree that dominants must rely on support from subordinates to maintain superiority over other dominants, they may be forced to yield significant opportunities to subordinates.

Kautsky (1982) has emphasized that, during the height of power of the aristocracy in Europe, rebellion was virtually unknown. It is likely that the relative fighting abilities of dominants and subordinates had become so distinct that rebellion was not a viable option for subordinates. In this situation, the threat of punishment is likely to have had a strong influence on the high levels of reproductive skew. There has been considerable research on the influence of punishment on animal behavior (Clutton-Brock & Parker, 1995). Crespi and Ragsdale (2000) bring the potential for punishment by the dominant into models of reproductive skew. They based their model on previous ideas concerning parental manipulation of offspring (Alexander, 1974). Their model suggests that if dominants can prevent subordinates from leaving by punishing them, then the conditions for stable skew to emerge are dramatically enhanced. The relevance of punishment to skew in human societies is likely to be high but would not have become an important factor until large differences in relative fighting ability and resource holding potential between dominants and subordinates had developed for other reasons. Temporal shifts in the importance of punishment in human social systems parallel the contrast between the "transactional" and "restraint" models of reproductive skew. As the power of elites grew relative to that of commoners, the dynamics of their interaction became more subject to complete control and manipulation by dominants, making the assumptions of the transactional models (and their predictions of higher levels of skew) more appropriate.

9. Weaponry and relative fighting ability

The importance of the relative fighting abilities of dominants and subordinates is basic to reproductive skew theory (Reeve & Ratnieks, 1993). Relative fighting ability, as determined by advantages provided by the equipment of one polity's warriors over that of another (e.g., bronze over stone, steel over bronze, cavalry over foot soldiers, guns over swords, etc.) is generally acknowledged as a key factor affecting the result of wars of conquest over the course of human history (reviewed in Diamond, 1997). The conquests of the Aztec and Inca empires by small groups of Spaniards are the most famous examples, but many other cases are known (e.g., McNeill, 1982). However, the relative fighting ability of individuals within a society has received little attention as a factor explaining endogenous social stratification.

Here, I will explore the hypothesis that changes in arms and armor, in conjunction with the rise of kin group control of agricultural resources (see above), profoundly influenced the development of social stratification within societies.

The aristocracy dominated the highest military offices in chiefdoms and archaic states (Betzig, 1993; Earle, 1997; Kautsky, 1982). Elite males were trained intensively in the martial arts from an early age and participated actively in military ventures, giving them superior martial skills (Kautsky, 1982; O'Connell, 1989; Reyna, 1994). The development of agriculture provided a heritable resource that could be used by dominant individuals to produce a warrior class, for the purposes of both military conquest and internal policing. The surplus of food provided by agricultural systems and its storable (and hence defendable) nature meant that dominants could train and equip their male offspring in the martial arts more intensively and effectively. As military technology progressed, the cost of equipment and the importance of long-term training increased, and the disparity in fighting ability between those who had excellent equipment and training and those who did not became larger. Hence, there was an interaction between the development of agriculture, the development of military technology, and the relative fighting ability of elites compared with the general populace.

A key prediction of this hypothesis is that levels of despotism correlated with the expense of arms and armor and the training required to use them effectively. The hypothesis does not predict a linear increase in social stratification with technological improvements. Instead, it predicts that social stratification will increase with the rarity and expense of the required raw materials, the difficulty of manufacture of arms and armor (these factors will correlate with the ability of elites to monopolize weaponry), the importance of long-term training to effective use of arms and armor, and the relative fighting ability of well-equipped, well-trained warrior relative to the general populace. These factors will vary depending on many subsidiary factors (see below). Hence, levels of social stratification should respond to changes in weapon technology in a dynamic fashion, increasing or decreasing as a function of the consequent relative fighting ability of elites and commoners.

A brief history of weaponry reveals striking relationships between factors relevant to relative fighting ability and social stratification. Copper metallurgy was developed independently at several (probably six) locations in the Old World starting around 7000 BC (Muhly, 1988). Copper weapons appeared approximately 5000 BC. There was a gradual progression from copper to bronze, passing through a variety of technical stages and associated alloys (Muhly, 1988). Transitions to the use of metals were associated with increasing costs of production for weapons and armor (O'Connell, 1989). Early on in the development of metallurgy, elites in many societies exerted control over the acquisition and development of both metal production and weapon manufacture (Andreski, 1968). There is archaeological and historical evidence for increasing social stratification in association with changes in the materials critical for the manufacture of effective arms and armor, particularly transitions to metal working, and among different kinds of metallurgy, particularly bronze, for example, China, Southeast Asia (Higham, 1988), Egypt (Aldred, 1967), Crete (Hood, 1967), Cyprus (Knapp, 1993), Scandinavia (Earle, 1997), Iberia (Garcia San Juan, 1999), central Europe, Anatolia, and Mesopotamia (Muhly, 1988).

The effectiveness of metal weapons increased over time with technical changes in alloy composition, heating regimes, and metalworking. These changes resulted in greater strength and edge retention (Reid, 1976). The perfection of bronze metallurgy allowed for the production of effective swords and armor, making close combat extremely effective and essentially making bronze armed and armored warriors immune to attacks by untrained individuals without bronze arms and armor (O'Connell, 2002). Archaeological and historical evidence indicates that weapon production during early Bronze Age Europe and Asia was difficult and specialized, and specialists were controlled by the elites (Earle, 2002; O'Connell, 2002). During this period, battles were typically decided by a relatively small group of military elites with the best armor and weaponry. Common soldiers had little chance of success against elites (O'Connell, 2002).

In various parts of Europe, archaeological traces of hierarchical social structure (in burials and dwellings) appear in concert with the development of elaborate arms and armor (Earle, 2002). The high cost of bronze arms and armor strengthened the position of chiefs in early Bronze Age Europe, and members of the nobility monopolized possession of swords, shields, and armor (Oakeshott, 1960). For example, the rise of steeply hierarchical chiefdoms in Bronze Age Denmark was associated with the production and monopolization of bronze arms and armor (Earle, 2002). Chiefs controlled the procurement of the raw materials through trade networks, and they controlled the manufacture of bronze weapons through the patronage of specialists. The chiefs retained exclusive access to bronze arms and armor and promulgated an ideology of warrior domination and control (Earle, 2002).

The rarity and expense of arms and armor (and the materials to make them) were critical. For example, an increased supply of bronze and increasingly widespread knowledge of bronze-making technology may have led to a collapse in social stratification in late Bronze Age Denmark (Earle, 2002). In China, extreme hierarchies developed in the Shang Dynasty, coincident with the sudden blossoming of bronze metallurgy after its importation from western Asia (Watson, 1967). During this period, towns came under the control of a ruling class that monopolized control of bronze weaponry and armor. Peasants did not have access to metal tools; instead, they had to use stone tools for agricultural work (Watson, 1967). In the early Chinese Iron Age (475–221 BC), the government had a monopoly on iron production, and there was an edict preventing export of iron weapons or tools. High-quality iron weapons were likely restricted to the noble elites of the military (Taylor & Shell, 1988), and stratification remained high (Andreski, 1968).

The transition to iron arms and armor was associated with decreases in stratification in some cases (Andreski, 1968; Earle, 2002). The ore necessary to produce iron was more widely distributed and readily available compared with the materials necessary to produce bronze. With the development of effective smelting and tempering techniques, iron became a cheap and abundant source of highly effective arms and armor. In Europe, this led to a reduction in social stratification, as the relative fighting ability of elites and commoners became more similar (Andreski, 1968; Earle, 2002). Ancient Greek society was relatively stratified during the Bronze Age, with a warrior elite differentiated from the populace by the possession of bronze arms and armor, and horses and chariots (Childe, 1942). However, the development of relatively cheap but highly effective iron arms and armor had a strong leveling effect on

Ancient Greek society (Andreski, 1968). Late in the Chinese Iron Age, more widespread availability of iron weapons and armor (in association with warfare) led to a decline in stratification (see below).

In Medieval Europe, technological developments in arms and armor dramatically increased the cost of equipment and the importance of training. The adoption of the stirrup led to the dominance of heavily armed and armored cavalry as warriors. The right to possess arms and armor was restricted to the aristocracy, who made up an elite warrior class. Membership was typically hereditary, and the nobility was trained in the martial arts from an early age. Individual fighting ability was of paramount importance to nobles, and even during warfare, the focus was on individual confrontations rather than group tactics (O'Connell, 2002). The armaments and mobility of the warrior elite in Medieval Europe made them virtually invincible with respect to commoners (O'Connell, 2002), and this dramatically increased social stratification (Andreski, 1968). The power and importance of knights as a component of the noble class developed in conjunction with the rise of powerful kin groups, feudalism (based on control of land), and technological changes in arms and armor (Gies, 1984).

The development of weaponry that could penetrate armor from a distance and required less strength and training (relative to armored combat) reduced the relative fighting ability of elites and associated levels of social stratification. The incorporation of a longbow effective against armor into the English armory (adopted during the wars with the Welsh) was associated with a decline in despotism: English peasants enjoyed more rights than their continental counterparts (Andreski, 1968). However, the effectiveness of the longbow declined with developments in armor hardening techniques (Jones, 1992). As a result, the status of armored knights increased in England, along with general levels of social stratification. During the Chou Era in China, the widespread use of the composite (reflex) bow, which was capable of piercing the best armor of the time, also led to a reduction in the status of the warrior elite (Andreski, 1968).

During the 14th century, the status of armored knights declined precipitously. This was associated with the development of effective firearms and artillery (Gies, 1984), which rendered knights vulnerable. Nevertheless, elites were able maintain high levels of despotism in some parts of Europe between 1500 and 1650 AD, by maintaining exclusive access to firearms (Petengill, 1979). Later improvements in the manufacture of firearms (and increases in the intensity and frequency of warfare—see below) led to mass armament. The cost of acquiring arms declined substantially relative to the Medieval period, and acquiring fighting skills became significantly easier. Shooting a rifle accurately requires much less training and expertise than close combat with steel arms and armor does (Andreski, 1968).

Of course, extreme social stratification arose in some societies that did not develop metal arms and armor. Yet, most of these societies were not exceptions to the general rule that the importance of advanced arms and armor (and the associated importance of extensive military training) correlated with social stratification. An excellent example in this regard was the Aztec Empire.

Aztec society was multitiered, with a steep hierarchy. Rulers were military, as well as political leaders, and fought in battles alongside the noble warriors. Although it was possible

for commoners of extraordinary military prowess to rise in status, hereditary social class strongly influenced the probability of achieving high status (Hassig, 1988). The Aztecs had a variety of specialized weaponry. They developed extremely sharp and deadly swords (Macuahuitl) made of a long hardwood paddle with obsidian blades glued into grooves along the edges. Aztec defensive armor was restricted to the nobility and included shields, helmets, and various types of body armor. Specialized artisans were employed by the king and nobility to make them. The importance of training to effectively utilize these arms and armor in combat was critical. Commoners and elites could train for military service, but nobles received much better equipment and training (Hassig, 1988).

Changes in the nature of weaponry may have contributed to the decline in despotism during modern times. As noted above, the initial control of guns by elites in Europe led to more effective exploitation by dominants (Petengill, 1979). However, with the rise of industrialization, guns gradually became cheaper to produce, easier for unskilled users to employ effectively, and more readily available. This trend, in concert with the requirement to train and arm a large proportion of the populace for action in large scale warfare (see below), dramatically reduced the relative fighting ability of elites relative to commoners.

The effects of cultural, historical, and environmental factors on the relative fighting abilities of elites and commoners have not been examined in detail in many cultures. Such investigations will be useful in allowing cross-cultural comparisons and tests of the hypothesis that relative fighting ability and social stratification are closely correlated. However, some comparative analyses of factors likely to be associated with disparities in relative fighting ability have been carried out in general comparative analyses. For example, Otterbein (1970) compared 50 primitive societies and found that political centralization (and associated social stratification) correlated with military professionalism, military sophistication, and the use of body armor and shock weapons. These results are consistent with the general argument that changes in relative fighting ability have caused correlated changes in social stratification.

10. Warfare and intergroup competition

In simple form, warfare is probably an ancestral trait in humans, shared with our closest relatives, the chimpanzees (Alexander, 1989). It is hard to overemphasize the importance of warfare in human history (Turney-High, 1949; van der Dennen, 1995). It has likely been responsible for a substantial proportion of human demographic change (population growth, extinction, and replacement, as well as dispersal and migration) over the past 10,000 years (Carneiro, 1994). Hunter–gatherers engaged in intergroup aggression very frequently (Ember, 1978), and warfare accounts for a high proportion of deaths in many tribal societies (Chagnon, 1988). Ethnographic records indicate that warfare is an ubiquitous feature of human societies (Wrangham & Peterson, 1996). Coalitionary bonds among males, male domination over expandable territories, and variable party size favored the evolution of warfare in chimpanzees and humans (Wrangham, 1999).

Darwin (1871) proposed that intergroup warfare was the basis for the unique levels of human cooperation, arguing that groups with stronger within-group cooperation were better able to win in warfare. Spencer (1896) proposed that social structures evolved through the aggregation of polities, and that warfare promotes internal political integration and harmony. Alexander and Tinkle (1968) proposed that humans achieved unprecedented ecological dominance, making human groups the primary hostile force of nature, and leading to strong selection for within-group cooperation.

The effects of warfare on social stratification and despotism are complex. A number of researchers have argued that intergroup aggression enhances and stabilizes hierarchies within societies (e.g., Leeds, 1963). Warfare has this effect for several reasons: It restricts the opportunities for individuals to transfer between groups (McEachron & Baer, 1982), and it causes individuals to accept hierarchies in the interest of maintaining effective defense (Strate, 1985). Military effectiveness requires central, hierarchical authority, particularly in large groups (Andreski, 1968). Positive correlations between the frequency of warfare and levels of social stratification have been found in several cross-cultural analyses of warfare (e.g., Textor, 1967; Wright, 1942). Negative correlations between warfare and democratic power sharing have also been found (e.g., Ember, Ember, & Russet, 1992). Psychological experiments indicate that in-groups tend to become more hierarchical, with increasing acceptance of centralized authority, as the threat of between-group competition increases (Robbie, 1982).

Ultimately, however, frequent and intense warfare can produce trends toward egalitarianism (Alexander & Tinkle, 1968; Andreski, 1968). According to the Balance of Power Hypothesis (Alexander, 1979, 1987, 1989, 1990; Alexander & Tinkle, 1968), a high frequency and intensity of warfare eventually required elites to grant reproductive rights to subordinates, to gain their full cooperation in warfare. This trend was associated with the development of rules and institutions that served as reproductive leveling mechanisms, including laws, morals, and ethics that promoted and enforced monogamy and the reproductive rights of all individuals within societies. The trend was autocatalytic, in the sense that societies that did not adopt the policy were likely to be conquered by societies that did (Alexander, 1990). In turn, the institution of monogamy had profound effects on the kinship structure of human societies. The pattern of bilateral inheritance associated with monogamy produced a more diffuse "kindred," which prevented the formation of clans strongly differentiated from other clans by kinship ties (Alexander, 1979). This produced trends toward increasing individual autonomy and reduced levels of despotism. Andreski (1968) developed arguments very similar to the Balance of Power Hypothesis. He proposed that the "Military Participation Ratio" is critical: the proportion of the populace that actively participates in the military as warriors. He argued that when warfare becomes sufficiently frequent and intense, rulers must arm and train a larger proportion of the populace (enhancing their fighting ability relative to elites), and they must concede power and resources to those lower in the hierarchy to entice them to fight more fiercely for the entire polity. The effect of warfare on social stratification was dynamic, just as the effect of technical developments in weaponry was. Warfare could lead to increases or decreases in social stratification, depending on environmental, historical, and technological circumstances (Andreski, 1968).

Warfare and intergroup competition have not yet been framed in the context of skew theory. Recent models of the effect of group augmentation on cooperation (Kokko, Johnstone, & Clutton-Brock, 2001) are a step in this direction, but they do not explicitly consider intergroup competition. This is certainly a promising area for the development of theory, particularly because previous arguments suggest that the effect of intergroup competition on skew may vary.

11. Exchange, specialization, currency, and skew

Reciprocal exchange of goods is a central feature of all human societies and has likely characterized the hominid lineage for millennia (Ofek, 2001; Trivers, 1971). The evolution of complex societies was structured in many ways by the development of complex economies involving extreme specialization and elaborate systems of exchange (Seabright, 2004). At first, trends toward specialization were likely to enhance social stratification (Andreski, 1968). The reason is that when some members of a society specialize in martial arts and warfare (typically elites), whereas other members must specialize in tasks such as farming or building, the relative fighting ability of the warriors relative to specialists in other areas increases. Ultimately, however, in an environment of increasing economic and technological complexity, specialization may reduce despotism. As the complexity and difficulty of specialized tasks increase, the cost of producing or acquiring qualified specialists increases. To the degree that such specialists provide essential economic or military advantages in intergroup competition, dominants may be required to concede more to specialized subordinates (Betzig, 1986). The development of currency may also have increased stratification at first. Currencies are generally based on durable materials that maintain their value (Seabright, 2004). This property enhances the ability of dominants to accumulate and hoard resources within societies, increasing their degree of resource control relative to commoners (Shennan, 2002). However, the portability of currencies in international monetary systems may ultimately have restricted the ability of dominants to control subordinates within societies (by allowing them to flee with their wealth). How specialization, exchange, and other components of classical economics interact with social stratification and reproductive skew has not been investigated by skew theorists, although a few preliminary attempts have been made to connect reproductive skew theory to the theory of reciprocal altruism (e.g., Emlen & Reeve, 2002). This is a promising area for future research.

12. Conclusions

Recent developments in reproductive skew theory highlight factors that likely affected the development of social stratification in human societies but have not been emphasized previously. Reciprocally, some aspects of stratification in human societies (as elaborated by evolutionary ecologists and anthropologists, such as Richard D. Alexander,

Laura Betzig, and James Boone) suggest potentially productive avenues for further work in skew theory.

Early on in our divergence from the chimpanzee lineage, there was likely a decline in despotism and reproductive skew associated with moralistic aggression towards would-be dominants (Boehm, 1999). This kind of suppression of dominant behavior was greatly facilitated by the development of effective weapons, particularly projectile weapons, which lessened the importance of individual strength and ability relative to the importance of the number of attackers (Bingham, 1999).

As humans came to dominate other species through their effective use of hunting weapons and environmental manipulation, a variety of factors converged to promote the development of social stratification and reproductive skew. Ecological or social constraints on migration were necessarily important in preventing subordinates from simply moving away from would-be dominants (Allen, 1997; Betzig, 1986; Carneiro, 1970). The development of agriculture and associated technologies for the preservation and storage of surplus food were critical in providing a surplus that dominants could expropriate and redistribute (Allen, 1997). The development of agriculture also created a highly heritable resource that was worth competing for on a long-term (multigenerational) basis (Shennan, 2002).

Effective competition required cohesive groups with coincident interests, which were likely to be kin groups (Betzig, 1986; Friedman & Rowlands, 1977). Kin-group size had a critical influence on success in competition for agricultural lands (Boone, 1986; Otterbein & Otterbein, 1965). Control of land as a heritable resource crucial for lineage survival should have increased the levels of reproductive skew tolerated within kin groups. The development of agriculture also produced high levels of stratification between lineages that controlled agricultural lands and those that did not.

Successful kin groups that controlled agricultural lands could produce males with exceptional fighting ability, by providing them with weapons, armor, and long-term training. This became crucial with changes in military technology, which increased the importance of equipment and training to relative fighting ability (e.g., changes associated with transitions in metallurgy).

Limitations on the availability of arable land, intense competition among lineages for agricultural lands, and the production of excess offspring by elites favored intergroup aggression (Boone, 1986; Carneiro, 1994). Warfare enhanced the potential for social stratification in several ways: (1) through the subjugation, repression, and enslavement of conquered peoples; (2) through the development of more efficient military organizations capable of more effective internal policing; (3) through increased tolerance of the status hierarchy in the interest of maintaining group solidarity in the face of intergroup competition; and (4) through increased social constraints on dispersal and independent reproduction. Warfare was also likely to interact with the relative fighting ability of dominants. As dominants were the most actively involved in warfare (Kautsky, 1982), martial skills (of the victorious survivors) were enhanced by warfare relative to the agrarian peasantry. Ultimately, however, increases in the frequency and intensity of warfare required rulers to train and arm commoners and to concede a larger share of resources within societies, resulting in reductions in social stratification (Alexander, 1979).

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