

Power: Insights from Evolutionary Biology, Primates & Other Animals

Authors

Christopher Boehm^{1,2} and Jessica C. Flack³

Affiliations

¹Director, the Jane Goodall Research Center

²Departments of Anthropology and Biological Sciences
University of Southern California

³Santa Fe Institute, Santa Fe, NM

This chapter is the product of an equal co-authorship.

This chapter is in press. PLEASE DO NOT CITE OR CIRCULATE WITHOUT PERMISSION.

Asymmetrical outcomes drive biological and social evolution. At the social level one cause of asymmetrical outcomes is power. Yet what power is and how it is acquired are in dispute. Two aspects of power make it hard to pin down. The first is that as neither a behavior nor material object, power is not directly observable. The second is that power structures vary in complexity. In its weakest form, power is completely coupled to the dynamics of agonistic interactions. Individuals are said to have power if they can force compliance in self-interest (Weber, 1954). In its most complicated form power is institutionalized and to a large extent decoupled from the dynamics of underlying agonistic asymmetries. It is here that a full-blown concept of authority arises. Individuals *granted* authority do not have to resort to the threat of force to influence others. This variation suggests that the search for a unitary concept of power is misguided (Giddens, 1968). What is required is a hierarchical theory of power that can account for the evolution of complex power structures from simple ones. The theory should explain the conditions under which a time scale separation arises between power and its underlying dynamics. And it must identify the dynamical and mechanistic causes of transitions from simple power structures, characterized only by an epiphenomenal pattern of asymmetrical outcomes at the group level, to power structures based on consensus, to the emergence of structural constraints that are decoupled from underlying agonistic interaction dynamics.

The objective of Part One of this paper is to lay the groundwork for a hierarchical theory of power. To do so, we draw on evolutionary biology where research on the emergence of hierarchy – particularly in terms of the evolution of new levels of individuality (e.g. multicellular organisms from unicellular ones)—is relatively well developed (e.g. Buss, 1987; Maynard-Smith & Szathmary, 1995; Michod, 2007; McShea & Changizi, 2003). We introduce power as a concept by stating basic assumptions. We summarize the essential arguments for interest-based (Weber, 1954) and consensus-based (Parsons, 1963) views of power and place these within the context of a similar debate in evolutionary biology. We highlight some fundamental issues using three types of power structures found in animal societies: simple dominance structures in fishes, slow timescale dominance structures in monkeys, and a rudimentary consensus based power structure of some monkeys and apes. We argue that

the emergence of robust dominance structures from simple ones, and consensus-based power structures from robust dominance structures, depends the evolution of specific cognitive and behavioral mechanisms. We also argue that these power structures *vary* in terms of robustness—the ability to withstand perturbations (Jen, 2003), the degree of time scale separation between power and its underlying dynamics, and the extent to which power structure feeds down, constraining individual behavior. Robustness, timescale separation, and feed-down causality are important organizing principles of all hierarchical systems. Consider the human body. By virtue of its immune system it can continue to function even when subject to perturbations caused by invading pathogens. There is a separation of time scales in that the body remains functionally coherent despite the continual turnover of cells. In addition, the functional and structural requirements of the whole system feed down, constraining individual gene expression during the production of diverse cell types (Noble, 2008).

In Part Two, we explore how having a concept of power changes how power can be exercised, particularly in the context of coalition formation and intergroup encounters. Specifically, we show how having a concept of power modulates who gains power within a given system and how conceptions about power can be useful in decision making during agonistic encounters and competitive interactions. We also discuss how having a concept of power gives individuals a degree of control over power structure. To illustrate these points we draw on data from primates, specifically chimpanzees, bonobos, and gorillas. In doing so we gain insights into both the role of feedback mechanisms in the emergence and maintenance of power structures as well as the role played by power dynamics in human evolution.

Part One: Groundwork for a hierarchical theory of power

Basic properties of power

The defining feature of power is the production of causal effects, and in the case of social power, the capacity to bring about consequences in the social world (Scott, 1994). A useful concept of power however requires further specification. Here we enumerate several relatively uncontroversial properties

we take as foundational. Power is a *relational concept* (Simon, 1953; Weber, 1954; Bierstedt, 1960; Parsons, 1963), emerging through a process of a feedback out of observed or (typically) repeated interactions among individuals, and not a property of any single individual (Emerson, 1962). Power is *rooted in the use of coercion / sanctions* (Weber, 1954; Bierstedt, 1960; Parsons, 1963; Lukes, 2005). Power is fundamentally *based on perception* (Bierstedt, 1960; (Parsons, 1963) about the capacity to use force successfully and therefore subject to manipulation and error (Flack & Krakauer, 2006). Power is *normatively indeterminate* (Parsons, 1963; Bowles & Gintis, 2008) in the sense that its exercise can result in undesirable or desirable outcomes. Power is *domain specific* (domains often being referred to as ‘scopes’ in the sociological literature) in that it need not apply or be salient across all contexts (Wrong, 1968). Accordingly, the criteria by which an individual or entity is deemed powerful can vary with context. Power must be *temporally stable*, and must change on a *slower timescale* than the underlying dynamics giving rise to it, if it is to have any significant effect on social organization (Dahl, 1957; Flack & Krakauer, 2006). The ability to exercise power can be undermined by an asymmetry in competitive motivation, transient third-party influences (like coalitions), and leverage (Hand, 1986; Lewis, 2002). Leverage is the temporary possession by subordinates of resources desired by dominants but which are not appropriable by force. Power can result in *unintended effects* (Dahl & Lindblom, 1953; Wrong, 1968) as long as the effects follow from a perception that power is being (or could be) exercised, whether accurate or not. Finally, whereas ‘power’ is relevant in pair-wise interactions as well as higher-order interactions, ‘power structure’ is only relevant in network contexts when at least three individuals are interacting (Parsons, 1937; Flack & Krakauer, 2006).

Parsonian and Weberian views on power

Weber defined power as the probability of individuals realizing their interests through the threat of force despite resistance from others (Weber, 1954). Parsons (Parsons, 1963) argued this definition is not sufficient. To Parsons, power is a (p. 237) “generalized capacity to secure the performance of binding obligations by units in a system of collective organization when the obligations are legitimized with

reference to their bearing on collective goals and where in case of recalcitrance there is a presumption of enforcement by negative situational sanctions—whatever the actual agency of that enforcement.” To illustrate this point Parsons states (p. 237), “Securing possession of an object of utility by bartering another object for it is not a monetary transaction. Similarly, by my definition, securing compliance with a wish, whether it be defined as an obligation of the object or not, simply by the threat of superior force, is not an exercise of power.”

There are four major criticisms of such legitimation-based definitions of power (Giddens, 1968; Lukes, 2005). First, these definitions seem to lose the intuitive sense of power as defined by the ability of individuals to force compliance in self-interest. Secondly legitimation requires at least implicit acceptance of subordination. Yet this is often only transitively the case as the drive for upward mobility is an empirical fact of almost every social system studied. Thirdly legitimation requires consensus—in the sense that how much power any one individual has arises from collective perceptions of group members. Yet no adequate theory exists for how consensus arises¹. Finally, legitimation based definitions seem to presuppose that system objectives take precedence over individual objectives, and that the system is a well-integrated, harmonious entity.

The debate between the ‘Parsonians’ and ‘Weberians’ reflects an ideological divide in which one camp views social construction processes as fundamentally cooperative and the other views them as fundamentally conflictual (Giddens, 1968). Proponents of the conflictual view of power see it as ‘legitimized’ through coercion and ideological manipulation. Proponents of the cooperative view, see power as legitimized through social learning, consensus, and optimization at the organizational level.

Parallels with evolutionary processes

¹ Attempts to study consensus processes include (among many others) French (1956), who developed a digraph model of interpersonal relations in effort to capture the topological conditions required to generate unanimous agreement; Flack & Krakauer (2006) who use an information theoretic metric to measure consensus about power on subordination signaling networks; and Holme & Newman (2006), who model the coevolution of network structure and opinions, along with Boehm (1996) on consensus dynamics in small-scale human societies.

This divide is not unique to political science and sociology. The competition / cooperation bias has been a critical point of contention in evolutionary biology ever since Darwin published *The Origin of Species*. Only recently was it recognized that setting conflict and cooperation at odds is perhaps to poorly pose the problem (Okasha, 2006). Increasingly favored is the question of how (and why) life is hierarchically organized and what role conflict and cooperation have played in the emergence of new organizational levels (e.g. Buss, 1987; Michod, 2007; Maynard Smith & Szathmary, 1995; Gould, 2002). The goal of this research program is to understand the functional and mechanistic causes for the major transitions between levels of organizational complexity in the history of life. Transitions typically include the evolution of solitary replicators to networks of replicators, genes to chromosomes, prokaryotes to eukaryotes, single celled organisms to multicellular ones, solitary organisms to colonies, and aggregates to societies. Most research has focused on the role of selection (e.g. Michod, 2007), the evolution of new mechanisms of inheritance (e.g. Jablonka, 1994; Maynard-Smith & Szathmary, 1995), and information compression (e.g. Krakauer & Zanolto, 2008).

A second, more recent emphasis has been on niche construction, defined here as an organism's attempt to control the selection pressures to which it is subject by building the environment in which it lives (Odling-Smee, Laland, & Feldman, 2003). Organisms build structures, like beaver dams, to construct constant, predictable local environments. Niche construction is about incorporating ecology into phenotype and therefore increasing control over exogenous variables. This aspect of niche construction makes it relevant to both transitions between levels of individuality and the evolution of complex power structures.

Construction of top-down constraints and social objects

Although originally conceived of as an ecological process, niche construction occurs in social settings as well in that individuals through interactions build the social organizations in which they live and are then constrained by them (Flack, Girvan, de Waal, & Krakauer, 2006). The social niche can be operationalized in network terms as the local connections of a node (that is, an individual) to other nodes in multiple,

overlapping social networks. Social organization is comprised of all group members' social niches (Flack et al., 2006). Whereas the ecological niche is composed of resource vectors (availability of food for building dams, prey items, and so on (Hutchinson, 1957; Odling-Smee et al., 2003), the social niche is composed of an individual's vector of behavioral connections in the set of overlapping social networks in which it participates. These behavioral connections provide critical social resources including alliance and coalition partners, which involve power relations, along with opportunity to food sharing and the exchange of goods, and access to important social and ecological information. As with ecological niches, social niches vary in quality and affect one another. If one niche fragments, connectivity, and consequently social resource availability in other niches, is affected. As partners, individuals depend on one another. However, individuals also compete with each other for access to better partners. This means social niche construction results from a complicated interplay of competition and cooperation.

Aggregate level properties of social organizations can be quantitatively described in terms of macrostates. Following Shalizi & Moore (2003) we define a macrostate as a probability distribution defined over an ensemble of microstates. In this case the microstates are the local interactions among individuals as they build their social niches. Macrostates are useful because they can predict the future state of the system without having to specify all the details of individual behavior and are thus called 'sufficient statistics' (see Kullback, 1997; Crutchfield & Shalizi, 1999; Shalizi & Crutchfield, 2001). As Markovian partitions of phase space, macrostates constitute the minimal number of variables required to account for all regularities in a time series². This property of macrostates makes them relatively objective and principled choices for describing systems. Macrostates, however, can be more than just predictors or sufficient statistics. As good predictors, they effectively represent selective contexts against which lower level components must adapt. It is this transition between a macrostate as a sufficient statistic to a macrostate as a selection pressure that is of interest here. Our goal in the next section of the paper is to explore the conditions under which construction processes, to include the interaction of individual traits,

² For detailed explanation see Crutchfield and Shalizi (1999); for further discussion of the utility of this concept in evolutionary biology see Krakauer and Zanutto (2008).

strategies, and interaction patterns, at the local level produce power macrostates that can be interpreted as social objects with causal consequences in the sense of Parsons.

Power: An empirical continuum

We organize this empirical discussion around three power structures of different complexity—simple dominance structures, slow timescale dominance structures, and primitive consensus-based power structures. We discuss these in context of the processes (respectively) generating them—winner and loser effects, and formation of simple dominance relationships and formalized dominance relationships. Space considerations keep us from discussing institutionalized power structures common in human societies.

Aspects of all three of the power structures we discuss can be found in the social systems of humans and some cognitively sophisticated animals, including prosimians, monkeys, apes, wolves, dogs, and hyenas (see Flack & de Waal, 2004). Simple and slow time scale dominance structures are found in gregarious birds (e.g. corvids: Paz-Y-Mino, Bond, Kamil, & Balda, 2004), ungulates (e.g. horses: Rubenstein & Hack, 1992), fishes and insects (Hsu, Early, & Wolf, 2006). Transitions to more sophisticated power structures, we argue, depend on the evolution of cognitive and behavioral mechanisms that support new kinds of social niche construction. Mechanisms discussed include memory, learning, inference (to include attribution), integration, error-buffering, and uncertainty reduction in communication.

It is worth noting that our goal in ‘classifying’ power structures is to simplify the problem so that the dynamical processes and mechanistic factors involved in the evolution of power structures can be more readily identified. Our goal is not to provide a power-structure taxonomy. Many of the mechanisms we discuss as present or absent for a given power structure are continuous traits. Furthermore, we discuss sets of traits as if these traits were linked or at least well correlated by underlying cognitive processes. In actuality, causal relations among these traits are not well understood.

Initial conditions driving the evolution of power structures

Here we discuss the sources of asymmetries in initial conditions that lead to the emergence of power structures.

Competition over resources like food and mates generates contests. Contests can be resolved through fighting, but if fighting is unlikely to produce a favorable outcome for at least one of the two adversaries, it makes sense from evolutionary and developmental perspectives to prevent the conflict from escalating (Maynard Smith & Price, 1973). Fighting can be costly insofar as it requires energy expenditure and can result in injury or death. Consequently, it pays to avoid fighting if the probability of positive payoff is low. Three sets of factors account for asymmetries in the ability to win conflicts. These include:

- Temporally and / or contextually variable factors at the individual level, including competitive motivation, short-term or opportunistic coalitions, and leverage as defined above.
- Socio-ecological factors and structural constraints, including demography, degree of relatedness, availability of alternative living situations, and the existence of normatively and culturally defined class systems.
- Temporally and / or contextually invariant factors at the individual level, including body size and fighting ability, size of alliance network (alliances are long term coalitions), and social experience.

Subsequent discussion focuses only on the role of temporally and / or contextually invariant factors in generating power structures. Structural / socio-ecological factors are *alternatives to power* for producing outcome asymmetries.³ Contextually and temporally variable factors are *modulators* of both power and structural constraints, and thus outside the scope of this paper.

0th order power structures: Simple dominance structures

³ Of course, once power structures become largely decoupled from underlying dynamics they effectively become structural constraints.

Here we discuss the simplest form of power observed in social systems that meets the foundational criteria set down earlier in this paper.

Predictable agonistic interaction outcomes can result from a mechanism as simple as a physiological change induced by one's own past performance during contests. Called winner and loser effects (Frey & Miller, 1972), this is the tendency of individuals to perform in future encounters as they did in past encounters with winning and losing each being reinforcing. Experiments with fish (and other animals, including insects) have shown that when a former loser is paired with an unfamiliar but considerably smaller opponent, the former loser is likely to lose again (Hsu et al., 2006). Winner fish become more aggressive with each contest won. 'Loser' fish become less likely to initiate contests and more likely to yield when challenged. The contextually / temporally stable factor producing these simple outcome asymmetries at the group level is the contestant's internal state. Internal state stability results from the fact that the winner-loser effect is a feed-forward reinforcement learning process.

Winner and loser effects can produce patterns of asymmetric outcomes at the group level, ranging from loose dominance structures characterized by some transitivity to rigid linear dominance hierarchies (Dugatkin & Early, 2003; Hsu et al., 2006). The pattern, however, does not appear to change more slowly than the underlying agonistic interactions dynamics. In fact the data suggest that a single loss or win can change an individual's place in the dominance hierarchy (Alexander, 1961; Nelissen & Andries, 1988).

In summary, a simple power structure can result from purely self-interested strategic interactions of individuals with minimal cooperation and no consensus. Although there is memory at the individual level, there appears to be no timescale separation between the individual and aggregate levels, as 'power dynamics' are identical to agonistic interaction dynamics.

1st order power structures: Slow timescale dominance structures

In this section we discuss the emergence of slow timescale dominance structures from dominance relationships.

In many gregarious animal societies individuals interact often and so have the opportunity for repeated agonistic interactions. When individuals are capable of individual recognition, remember the outcomes of their agonistic encounters and can integrate over that history, they can ‘estimate’ the likelihood of winning future interactions with particular opponents (Pagel & Dawkins, 1997). This estimation, which is subject to error, allows individuals to make decisions about whether the better strategy is to fight or signal an intention to yield before the conflict becomes a full-blown fight. Signaling yielding is called submission. The individual emitting the signal in conflict contexts is considered the submissive individual in the dominance relationship (Rowell, 1974). Submission signals are typically ritualized (i.e. stereotyped and exaggerated) and are often moderately, to highly, unidirectional. This means they are emitted by the same individual in a pair until the relationship reverses (de Waal, 1986). In monkeys and apes, unidirectional, ritualized signals are better indicators of dominance relationships than agonistic interaction outcomes, or the direction of aggression during the interaction, both of which can vary in response to modulating factors, like the presence of third-parties and leverage (de Waal, 1986; Preuschoft & van Schaik, 2000; Lewis, 2002). The signal means the sender perceives the receiver capable of using force successfully and agrees to yield in the present interaction. The evolution of the ritualized unidirectional submissive signal is essentially the first step in decoupling power from the underlying agonistic interaction dynamics in that its usage stabilizes the existence of a learned relation.

In some species individuals can estimate the costs of engaging with an opponent by observing that opponent’s agonistic interactions with others (see Chase, 1980; Shettleworth, 1998). Combining individual recognition, observational learning and the ability to infer, through transitive inference⁴ (McGonigle & Chalmers, 1977; Rapp, Kansky, & Eichenbaum, 1996), the consequences of others’ interactions for oneself is an efficient strategy for updating estimates about the fighting abilities of others when complete information is only possible with complete interaction. Furthermore, utilizing information

⁴ Individuals capable of transitive inference can infer unknown relations from known ones, such that if $A > B$ and $B > C$, then $A > C$. Although linear dominance hierarchies are characterized by this pattern, the existence of the pattern does not necessarily mean that individuals have the capacity for transitive inference.

obtained through observational learning can reduce single source state assessment errors by effectively increasing sample size. These factors are thought to produce dominance structures that more accurately encode the underlying distribution of agonistic asymmetries due to fighting ability, body size and size of alliance network, and are robust against minor fluctuations in contest outcomes (see Flack & Krakauer, 2006).

A potentially important consequence of the emergence of slow timescale dominance structures is facilitation of triadic interactions, like coalition formation. Individuals choose partners as if there was a ‘biological market’ (Noë & Hammerstein, 1995). Choice is based on perceived capacity to provide aid during conflicts with others. In some primates, the degree to which an individual is perceived capable of providing aid is largely thought to be a function of rank (Noë, 1992). Information about rank can be obtained by tracking the entire outcome of agonistic interactions of each pair in the group. Alternatively rank information can be gained by watching who signals to whom. The stability and relatively slow timescale dynamics of signaling interactions presumably enables individuals to reliably choose partners using information from a signaling event that might have occurred several time steps ago. If this is correct, submission signaling increases the possibility and utility of coalition formation. This allows individuals to build local networks, or social niches, that are richer and more diverse in terms of the social resources they provide.

The evolution of submission signaling and individual recognition, combined with observational learning and transitive inference, allow the emergence of a robust, slow time-scale power structure that is based partly on cooperation but also firmly rooted in individual self-interest. Submissive signals are ‘cost-free’ (Maynard Smith & Harper, 1995; Lachmann, Szamado, & Bergstrom, 2007) because both sender and receiver, in knowing the likely conflict outcome, benefit from the signaling interaction. However, over longer time scales it pays for the submissive signaler to invest in reversing the relationship. This means that at the individual level behavior changes on two time scales—a fast time scale capturing the decision to signal and a slow timescale over which submissive individuals chip away at the status of their

dominant partners. Paradoxically slow timescale ‘background dynamics’ at the individual level make possible abrupt changes in what is otherwise a slow time scale dominance structure at the group level.

2nd order power structures: Primitive consensus based power structures

Here we discuss the emergence of a consensus-interest based power structure from formalized dominance relationships.

In some highly gregarious species, including some primates, hyenas, dogs and wolves, submission signals communicating willingness to withdraw in the present interaction have evolved into subordination signals, which communicate general agreement to a pattern of submissive behavior (de Waal, 1986; Preuschoft, 1999; Flack & de Waal, 2004; Flack & Waal, 2007). The key properties of these signals are that they are nearly 100% unidirectional and are used in peaceful contexts like pass-byes and greetings in addition to agonistic contexts (Flack & Waal, 2007). Shifting contextual usage to the peaceful context, where submission is unwarranted, reduces receiver uncertainty that the sender is communicating agreement to a pattern of subordinate behavior. Reducing receiver uncertainty changes the nature of the relationship by decreasing the rate of aggression required to assay status. This, in turn, reduces constraints on positive social interactions between sender and receiver. The invention of formalized subordination signals further establishes the power relation in that the signal is essentially an acknowledgement of acceptance of the subordinate role in the relationship. In this sense signal exchange is like an implicit contract in which the sender agrees to a subordinate pattern of behavior in future interactions and the receiver agrees to tolerate proximity (Flack & Waal, 2007). As with submission signals, these unidirectional subordination signals are cost-free.

At the dyadic level, the subordination signal encodes the sender’s perception that the receiver can successfully use force and that the sender will yield when conflicts arise—in other words the sender is saying, “I know I am subordinate in this relationship.” Encoded in the network of these signaling events is how much agreement, or consensus, there is among group members about who is capable of successfully

using force⁵ (Flack & Krakauer, 2006). Individuals are said to be powerful if they receive many subordination signals from many group members as this means they are widely perceived as capable of using force successfully. Consequently, it pays for individuals to adjust their social niche construction behavior to maximize the number of signals received. In chimpanzees, for example, adult males actively solicit subordination signals from group members through bluffing (de Waal, 1982). The data show consensus is a particularly important aspect of power in systems in which interactions often involve multiple individuals. This is because the ability to influence the outcome of these events depends critically on how the *set* of participants perceives the intervener (Flack, de Waal, & Krakauer, 2005).

The power structures arising from networks of subordination signals are robust—they have built in mechanisms for error correction, highly predictive of the future power structure (and are thus good macrostates), and change slowly relatively to underlying agonistic dynamics (Flack & Krakauer, 2006). Three things account for the slower timescale. First the signals themselves change (in terms of which individual in a pair is the sender) slowly because the sender remains the sender until the relationship reverses. Secondly the power structure arises from N group members integrating over the signaling decisions of $N-1$ potential senders. Thirdly, the network can be rewired in a multitude of ways and still produce the same distribution of power. These temporally stable, slow timescale power structures provide the selective context—largely by modulating cost—against which other behaviors evolve or are learned. In particular they can support special forms of third-party conflict management that are advantageous at the group level in that they facilitate the building of robust and well-integrated social niches (Flack, Krakauer, & de Waal, 2005; Flack et al., 2006). That a consensus-based process gives rise to power structure in no way implies that the resulting structure be of a particular type (e.g. egalitarian—for discussion of variation in monkey societies see Thierry, 2000). The resulting structure will depend on the construction rules individuals use to build their local networks. Consensus does not necessarily require explicit coordination as it can arise when individual decisions are independently made but in

⁵ Consensus has multiple meanings in the literature. Flack and Krakauer (2006) measure how much consensus there is among group members about whether a particular individual is capable of successfully using force. The distribution of scores is effectively the distribution of power.

agreement.

The cognitive and behavioral mechanisms that support communication about roles rather than just immediate behavior in the immediate context are not well understood. One controversial candidate is the ability to attribute mental states to others (see Heyes, 1998). Also not well understood are the heuristics individuals use to estimate how much power they have relative to others. This seems to require two things. First, receivers must be capable of integrating over the population of potential subordination signal senders in order to assay their power. Secondly, receivers must be capable of transitive inference in order to estimate the power others are perceived to have.

Part 1 Conclusion

We have attempted to lay the groundwork for a hierarchical theory of power. The goal of a hierarchical theory of power is to identify the processes by which legitimation based power structures arise from simpler forms, including epiphenomenal patterns of agonistic asymmetry at the group level. To do so we have drawn on work in evolutionary biology on the emergence of hierarchy—particularly the role of niche construction in the evolution of new levels of individuality, including the transition between unicellular and multicellular organisms and aggregates of individuals to societies. We suggested that social organization, and the macrostates (like power) which describe it, arise from individuals building predictable local social environments. To illustrate these concepts, we used examples from animal societies, including primates. An advantage of working with simpler systems like animal social organizations is that fundamental features and relations are easier to identify.

Data from these systems suggest that the roots of power lie in underlying agonistic asymmetries, self-interest and strategizing, but that the stability and utility of power structures are derived from partially decoupling power from these underlying dynamics. The decoupling appears to require a legitimation process based on consensus. Consensus need not be explicit or require coordination. The data also suggest that individual recognition, transitive inference, and the evolution of concerted submission signaling are required for the evolution of slow time scale dominance structure from simple patterns of

asymmetry at the group level. Evolving a rudimentary consensus based power structure from a slow time scale dominance structure appears to require the evolution of unidirectional signals communicating agreement to roles in dominance relationships, as well as the ability of individuals to integrate over the signals, ‘opinions’ or behaviors of many group members.

A final point worth making concerns why understanding the emergence of power structures is a worthwhile enterprise. We mention two reasons here. The first is that power structure has consequences for organizational complexity and integration. Changes in power and simpler analogs, like asymmetries in resource holding potential (e.g. by allowing for the emergence of policing mechanisms that decrease conflict and increase cooperation (Frank, 2003; Flack et al., 2006), have likely played a pivotal role in the occurrence of transitions over evolutionary history by helping to mediate fitness transfers from lower level units to higher level ones. This applies at the social level as well where changes in power structure are thought to have substantial effects on organizational productivity and efficiency (Denison & Mishra, 1995).

A second reason is that the co-evolution of power structure and individual cognition has in primates and possibly other animals produced individuals with a concept of power. The evolution of a concept of power makes possible for the first time active manipulation of power relations and power structure. We discuss this in Part Two.

Part Two: The utility of a concept of power: Case studies of coalitionary behavior in primates

For the sake of simplicity Part One largely ignored the role of feedback mechanisms in the emergence of power structure. Here we show how having a concept of power modulates who gains power within a given system and how conceptions about power can be useful in decision making during agonistic encounters that although potentially involving physical coercion are not necessarily mediated through power dynamics. To do so we draw on data from primates, specifically three of the four great ape species.

We organize the discussion around four contexts in which a concept of power has proven valuable: intragroup competition, territorial aggression, predator defense, and hunting and meat sharing.

The four-species African clade that humans belong to (Diamond, 1992; see also Stanford, 1998b) is a closely-related one (Ruvolo, et al., 1991), and behaviors shared by all of them may be attributed to their Common Ancestor (Wrangham, 1987); thus, any use of power that is unanimous among the four great ape species is extremely likely to have been present—homologously—in the shared African ancestor starting perhaps 7-9 million years ago. A more recent ancestor exists, as well, for there is the mutual ancestor of *Homo* and *Pan* at 5-7 MYA. “Ancestral *Pan*’s” behaviors may be reconstructed using exactly the same methodology (Boehm, 2000). Thus, this analysis of how a concept of power influences how it is exercised in primates and in African great apes in particular should also further understanding of the ethological basis of human coalitionary behavior in general (e.g., Muller and Mitani, 2005), and in the practice of warfare in particular (e.g., Boehm, 1992; Manson and Wrangham, 1991).

Large power coalitions within the community

Wild and captive chimpanzees

The dynamics of power in chimpanzee society are very similar to those described for 2nd order power structures in Part One of this paper, insofar as power is acknowledged through the exchange of subordination signals and power structure arises out of the network of subordination signaling events. Here we discuss how individuals use coalitions and alliances to modulate the power of others and gain power for themselves, ultimately by changing or undermining the signaling dynamics.

For the first three decades of wild chimpanzee research, very large coalitions were not seen to form in the context of within-group politics. Then Goodall (1992) published a unique account of an entire large male foraging party turning against the recently-displaced alpha male when he tried to make a comeback; their attack was so menacing that he left the group for a period of months, and when he did return he acted submissively and fell to a very low rank. Subsequently, similar accounts were published for the Mahale Mountains study group (e.g., Uehara et al., 1994; Nishida, 1996; Nishida et al., 1995),

with both males and females ganging up against aggressive former alphas, and with similar periods of exile following the attacks. Such males surely risk being wounded when they are ousted, or possibly even being killed in the process (see Nishida, 1996), an outcome that has been documented subsequently at two other field sites (Fawcett and Muhumuza, 2000; Watts, 2004). Exile means subsisting in peripheral areas of the home range, which in turn increases the risk of being lethally ambushed by an enemy patrol, thereby compounding the total cost. For high-ranking males the ability to make complex political calculations and decisions is critical to social and physical welfare, both in behaving so as not to arouse such group ire, and in knowing when it is time to submit or retreat.

What about females? There is no account of a resident female's being attacked by her entire group or a large coalition. However, females may join males in attacking ex-alpha males, and even though there is no instance of all-female group attacks on males in the wild, adult wild females do sometimes help each other to resist domination by single adolescent males or in attacking another resident adult female. They also may gather in a large coalition to attack an immigrating stranger female, who will be defended by group males (Goodall, 1986). In captivity, however, with major socioecological differences, collective female attacks on adult males take place and are routine (de Waal, 1996). These captive groups are smaller than wild ones, and tend to have fewer males proportionately. In two different groups, at Arnhem and Atlanta, females regularly formed large coalitions to defend victimized females (and sometimes younger males) from strong aggression by high-ranking males (see de Waal, 1982, 1996), and this routinized coalitionary behavior greatly increased the potential for females to acquire power.

One indication of this is the fact that in the wild, males who are politically frustrated routinely redirect their aggression at females, usually with no adverse consequences for themselves (Goodall, 1986). In captivity, however, the females are able to damp such behavior by collectively threatening or attacking such a male. The alpha male role continues in captivity, nonetheless, probably in part because this involves the alpha's important role in reducing conflicts between females or males (see de Waal, 1982, 1996). Sometimes, when these female coalitions try to play "king-maker," a male is simply too powerful for them to do so. But usually their collective power is such that they can choose their alpha.

Wild and captive bonobos

Wild bonobo females join together to hold their own against physically stronger males in situations of feeding competition (Kano, 1992). It would appear that these coalitions often are dyadic but sometimes approach half a dozen. Female bonobos in captivity routinely do the same thing. In the wild, the only small, within-group coalitions formed by bonobo males are dyadic alliances with their mothers (Ihobe, 1991), who back them against other males as they try to ascend the male hierarchy. However, the males also join large parties, which forage together, and they threaten neighboring groups they meet along their frontiers—at which point the males of a foraging party become a political coalition.

There are reports from Wamba (Kano, 1992) and Lomako (see Parker, 2007) indicating that bonobo females' anti-male coalitions can include as many as five females. Within their groups, bonobos, perhaps even more than chimpanzees, tend to direct their physical attacks at the digits of their adversaries, and in one captive situation five hostile females gnawed at the toes of a male while attacking, whereas in a serious attack by multiple females in the wild group Hohmann was studying, the male, who had menaced a female in the presence of several other females, was never observed again (see Parker, 2007). Thus, both bonobos and chimpanzees may experience serious attacks by sizable female coalitions.

Captive Gorillas

In the wild, female gorillas compete to gain proximity to the silverback harem-leader, and normally it is the first female to join the group who holds first place (Fossey, 1983). For both mountain and lowland gorillas, there is no report of females forming coalitions against other females or against males in the harem. However, because silverbacks so dominantly intervene in female conflicts, the competitive behavior of females is not likely to develop very far (see Watts, 1996).

There is, however, one report in captivity, which involves a zoo situation in which a young lowland blackback male was heading a female harem and a larger silverback was introduced by zoo keepers (de Waal, 1982). The females as a group turned against the newcomer, attacking him and driving

him to one corner of the enclosure, from which he had to be removed. This would suggest that it is partly the harem's social structure, and partly the extreme dominance of silverbacks, which make other manifestations of the gorillas' potential to form coalitions unlikely in a small group with just one or two adult males, and perhaps three adult females.

The critical point of this section on intragroup competition is that by having a concept of power, chimpanzees and other apes are better able to 1) choose appropriate partners in conflicts against others and 2) recognize the need to undermine the attempts of others to gain power. This has enabled apes to more actively manipulate the resultant power structure, both in terms of how powerful the alpha male (in the case of chimpanzees) is, and in terms of the rank order of individuals. This corresponds to the beginnings of a manipulated, legitimation-based power structure, where there is risk both of powerful individuals implementing strategies to maintain the status quo and of weak individuals actively subverting or attempting to overturn the status quo, typically through the use of 'coalitions from below'.

Territorial power

Here we address how having a concept of power influences the ability of individuals to choose suitable partners for defending the community against outsiders. Strictly speaking, the ability of a coalition of individuals from one community to win against a coalition of individuals from another is not based on direct observation of power dynamics as the opportunity for interaction is low and thus the perception about capacity to use force successfully is not well formed. Consequently, balance of power assessments are necessarily inferred and not established. In the case of perceived imbalance of power, chimpanzees' inter-group conflicts are often resolved using severe aggression. In the case of perceived balance of power, bluffing is substituted for fighting. It is because individuals have a concept of power, as we will show, that they are able to make estimates about the utility of group mates during conflicts and the potential strength of adversaries.

Chimpanzee patrolling behavior

Chimpanzees are evolved to live in territorial communities whose males stay put, whereas females typically transfer to neighboring groups at adolescence (e.g., Goodall, 1986). The males regularly patrol the peripheries of their home range wherever other groups are adjacent, and one way to explain the intercommunity political dynamics that take place is through “imbalance of power” theory (see Wrangham, 1999).

A chimpanzee patrol consists of from 5 to 10 or more of a territorial community’s males, and all of them will move very deliberately toward an overlap zone between their own and a neighboring group’s home range, doing so silently so as to take interloping strangers by surprise. At Gombe, if they meet a singleton stranger, male or female, predictably it will be violently attacked—unless this individual happens to be an adolescent female who is trying to transfer, or an older female who is in estrus. Whereas these protracted gang attacks are not necessarily carried to the point of death, usually the severely wounded victim will crawl into the brush afterwards and die, and patrols are known to return the next day and search the immediate area (e.g., Goodall, 1986).

Wrangham’s (1999) theory predicts group attacks which favor situations in which decisively superior force can be applied, and, of course, “overwhelming force” credos are also pervasive in modern military academies. However, the practical outcomes are quite different with chimpanzees and modern humans. When a patrol of five or more adult chimpanzees attacks a lone stranger, killing their adversary poses virtually no risks. Indeed, the victim will make little attempt to fight or escape, because submission in the face of decisively superior force is a strongly innate trait in chimpanzees (e.g., Goodall, 1986). Thus, in effect the victim will “acquiesce” to being beaten, pummeled, thrown violently to the ground, severely bitten, and otherwise brutalized.

Wrangham’s (1999) theory applies also to humans. However, surely in large part because they bear arms and are conditioned by heroic cultural values, members of a numerically outclassed modern human army may stand and fight valiantly, and inflict heavy casualties while losing. The same may be true of nonliterate people like the *Inupiaq* of Northwest Alaska (Burch, 2005), unusual hunter-gatherers who live in tiny, highly territorial “tribes” and attack other tribes genocidally. But more often nonliterate

tribesmen practice not warfare but raiding, with tactical use of surprise, avoidance of power imbalances, and careful, non-heroic avoidance of casualties. This politically “prudent” approach is shared all over the world by tribesmen such as the Yanomamo (Chagnon, 1983)—and also by chimpanzees everywhere in Africa.

What happens when two hostile chimpanzee groups with approximately equal numbers meet at their borders? When a sizable Gombe patrol sees a sizable group of patrolling strangers, the reaction is quite predictable, and uniform on both sides. The two groups will vocalize ferociously at each other, with the males putting on intimidation displays for some time, and then each side will retreat toward the center of its own home range (e.g., Goodall, 1986; see also Wrangham, 1999). By contrast, at one extreme of the human behavioral spectrum we have the trench warfare of World War I, which of course was based on iron discipline from above. This type of *directive* political power is not found in other primates (see Boehm, 1999), among whom power relations basically arise from competitive interactions while the following of leaders is voluntary. Thus, a chimpanzee alpha male can have enormous competitive power, but if he happens to be at the head of a patrol, he has no ‘power’ to command—only the capacity to influence those who are prone to emulate him.

In both species the decision to attack or hold back has a cognitive basis; this is obvious in humans who send out scouts to count the enemy, whereas chimpanzees may reckon how numerous a group of strangers is just from its vocalizations, and will retreat, quietly stay in place, or approach, accordingly. Wilson and Wrangham (2003) have demonstrated this by using playback experiments (see also Wilson et al., 2001). Chimpanzees’ natural behavior while on patrol suggests that reading others’ assessments of enemy coercive potential makes use of body language and other cues (Boehm, 1991).

One of the authors (Boehm) did fieldwork at Gombe National Park in East Central Africa, and patrolling behavior there generally seems to be similar to that reported in Ngogo, in nearby Uganda, and at Mahale, in Tanzania. In contrast, at Tai Forest in West Africa, in a more tropical environment with a flat terrain and much denser vegetation, it appears that because patrols are much less able to see one another a rather different pattern of intergroup agonism prevails. Boesch and Boesch-Achermann (2000)

report that “captures” and ‘relief expeditions” take place as smaller, fragmented groups are ambushed and rescued, and although balance of power theory still explains how a larger group of males may surround a smaller one, and how a relief expedition can effectively come to their rescue, often the “big-picture” calculations inferred at Gombe are not apparent in terms of entire patrols making reasonably accurate mutual assessments about overall discrepancies in coercive potential. It appears that low visibility—combined with strict silence while on patrol—can make “quantitative” calculations about relative coercive potential very difficult. But the behavioral differences between East and West Africa, assuming they are not genetic, underscore the importance of cognitive calculations.

Whereas at Mahale encounters with physical violence have merely been assumed, many have been witnessed at Tai Forest, Gombe, and Kibale. It is clear that at the latter two field sites the protracted attacks, which involve pinning heavily-outnumbered victims to the ground, are lethal in outcome whatever the attackers’ intentions may be. At Tai Forest, with a more “atomized” pattern of intergroup interaction, the victims often carry over a dozen superficial wounds—even though lethalties remain unreported so far.

Although with proper visual or aural cues chimpanzees are able to reckon the numerical strength of an enemy group, other criteria may be operating in their calculations about coercive potential, as well. For instance, at Gombe a very large male-female *expedition* from the large central Kasakela group made a foray deep into the home range of the much smaller Mitumba group, to feed on a fruiting tree; the latter community’s few males, after discovering the much more numerous intruders, were able to aggressively chase away several times their own number of males (Jane Goodall, personal communication). It seems possible that in this instance, because the Mitumba Community was reacting to a major incursion deeper than usual into its home range, this may have increased the competitive motivation to chase away their adversaries in spite of a marked numerical inferiority.

In terms of group dynamics, it is the set of patrolers’ individual imbalance-of-power calculations, plus their silent communication about these (e.g., Boehm, 1991), that keeps same-sized patrols from entering into conflicts that might result in wounding or death.

Bonobo territoriality

Wild bonobos have been studied much less than chimpanzees, but the data suggest that in both species large foraging parties tend to react actively and xenophobically to large foraging parties of neighbors—even though bonobos do not go out on routine patrols with the intention to ambush. Bonobos' communities tend to be larger than those of chimpanzees, as do their foraging parties. In the long-term study at Wamba, such parties are reported to react to sighting or hearing stranger groups with agonistic vocalizations, and sometimes with larger groups chasing smaller ones that retreat into their own home ranges (Idani, 1991; Kano, 1992).

In explaining why bonobo territorial patterns are relatively nonviolent there is likely more than just the genetic natures of the two species at issue, as has been discussed in the literature (e.g., Stanford, 1998). Environments for the two species differ (Wrangham and Peterson, 1996; see also Chapman et al., 1994), and most chimpanzee environments have sufficiently sparse resources that daily foraging parties are not very large, normally, and often females are obliged to forage alone with their offspring with less socially connected mothers riskily using peripheral areas (e.g., Goodall, 1986). Males also use these areas to mate exclusively with a female, or forage there solo because of a problematic political position in the group. This makes it logistically possible for single apes to fall prey to stealthy patrols. In contrast, bonobo environments permit larger sizes for foraging parties with neither females nor males being obliged to forage by themselves, so politically-vulnerable individual bonobos are not so likely to fall prey to stranger groups. Thus, bonobos do experience moderate imbalances of power that result in larger groups chasing and smaller ones avoiding, but the overwhelming power ratio needed logistically for a safe attack is unlikely logistically.

If we set aside the deliberate nature of chimpanzees' patrols, and their sometimes lethal ambushing of individuals, the "territorial politics" of the two species are quite similar. When two *sizable* groups meet at the extremities of their home ranges, they predictably put on displays of hostility but are not likely to engage physically with each other. And it would appear that calculations about power

imbalances are shaping bonobo behavior not only when two opposing parties stand their ground and vocalize in a situation of balanced power, but when larger parties displace smaller ones (e.g., Idani, 1991). This helps to keep home ranges geared to the relative power of groups, purely through bluffing. Thus, when individuals have a concept of power they can use their understanding of the capacities giving rise to power to infer the power potential of others, in the absence of direct or observational experience. We may assume that frequent coalitional power calculations within the group are providing the cognitive wherewithal for making similar calculations between groups.

Mobbing predators

Here we discuss how having a concept of power influences the behavior of great apes in their response to predators.

Large predators like pythons, leopards, and lions pose a direct and lethal threat to African great apes (e.g., Boesch, 1991; D'Amour et al., 2006; Hiraiwa-Hasegawa et al., 1986; Tsukahara, 1993; Zuberbüler and Jenny, 1993), but mobbing of such predators has been reported only for chimpanzees (e.g., Goodall, 1986; see also Goodall, 2001). We must keep in mind, however, that in no field study of African great apes have predators like these been habituated to human observers, so whereas indirect evidence of predation can be readily obtained from a predator's fecal matter, or perhaps when there is other evidence of a kill, the prey's typical political responses are likely to remain unstudied if occasionally reported.

Although predation on bonobos is reported (D'Amour et al., 2006), no instances of mobbing or any other prey response have been witnessed. Given the predator nonhabituation problem, plus the relatively short study time for bonobos, this lack of evidence is not conclusive. Indeed, for chimpanzees there is considerable anecdotal evidence for mobbing (e.g., Byrne and Byrne, 1988; Hiraiwa-Hasegawa, 1986), and it at least suggests that balance of power calculations are operative just as they are in conspecific territorial encounters. Goodall (1986) mentions aggressive acts toward leopards, lions, pythons, and large monitor lizards.

One of the authors (Boehm) has unpublished videotape from Gombe showing about a dozen chimpanzees noisily harassing a sixteen foot python which, unable to hunt by ambush in a highly disturbed forest and probably aware of the field assistant who was videotaping, eventually leaves the scene. At Tai Forest, where in a short time an unusually-numerous series of leopard attacks decimated the study group, it became apparent to observers that although a single ape could be readily eviscerated by one swipe of a big cat's paw (see Boesch, 1991), when two or more chimpanzees were together they seemed to be able to bluff a leopard and avoid attack.

At Mahale National Park in Tanzania, observers were drawn to a noisy scene in which a group of chimpanzees had threatened and basically cornered a leopardess with cubs. One of the males actually invaded her retreat and took one of the cubs, which was subsequently killed (Byrne and Byrne, 1988). This lethal attack carried "mobbing" to a physically-aggressive level which was duplicated at an Ivory Coast site (Boesch 1991), where sticks were thrown or poked at a cornered leopard. There were also two early filmed experiments by Kortlandt (see Goodall, 1986), with both unhabituated and captive chimpanzees, in which a stuffed leopard with a moving head was exposed to these apes to record their reactions. They at first showed a combination of alarm and aggression, but as the object's passive nature became apparent (the body was moved by pulling on a string), their bluffing became aggressive and physical—even though the "leopard" was not seriously attacked—whereas frequent bids for reassurance suggested that the apes were not entirely confident about the imbalance of power they sensed in their favor.

The above descriptions suggest that chimpanzees deal readily in collective bluffing, which sometimes carries the potential of a physical attack, and that their political behavior is flexible enough to adapt their reactions to a different species. Such episodes may involve either conspecific strangers or predators of other species, and they are premised on intuitions about power imbalance, which go far beyond counting numbers or a reckoning of combined fighting power. Rather, predators and prey alike are making calculations about the likelihood that their counterparts will turn aggressive, as opposed to bluffing, submitting or engaging in flight.

Hunting and meat sharing

Here we discuss how having a concept of power influences partner choice in hunting coalitions as well as the mechanics of the coalitions.

Active hunting of small to moderately-sized game goes back to Ancestral *Pan*, but not to the Common Ancestor, for whereas gorillas don't hunt, humans, bonobos, and chimpanzees all take and eat modest-sized animals. All three also share the meat to some degree, and when a single carcass can feed multiple individuals often a competitive situation arises. With such a prized food source, this means that power relations are involved.

The chase, itself, involves coalitionary relations of several types depending on the prey. When chimpanzees go after colobus monkeys the multiple males in a troop are sizable, and in defending their mates and offspring they bite at the testicles of the hunters (Stanford, 1998a). Numerous chimpanzees may hunt simultaneously, but the degree to which their efforts are coordinated depends on the environment and challenges that go with it (see Boesch, 1994b). At Gombe, solo hunting is feasible, but often groups of half a dozen or more apes hunt simultaneously for colobus monkeys.

At the several field sites where wild pigs are hunted this dangerous species defends its young vigorously by making attacks that can be lethal (Boehm, 1999; Goodall, 1972), and chimpanzee hunters seem unlikely to go after pigs without at least one partner to help cause confusion (Goodall, 1986). Thus, calculations involving the application of power enter into these hunting decisions. On the other hand, in the case of small forest antelope the barking mother will try to lead the predator away from her young, who freeze in place and are readily taken by a solo chimpanzee.

Bonobos also hunt actively (see Fruth and Hohmann, 2002; Hohmann and Fruth, 1993, 1996, 2008; Ihobe, 1992; Bermejo et al., 1994; White, 1994), if far less frequently than chimpanzees. Almost always solo, they go after small forest antelope, flying squirrels, and monkeys. Bonobos' overall meat intake is far less than for chimpanzees (see Stanford, 1999), but both chimpanzees and bonobos share their own kills or ones they have taken over with certain individuals of the same community. Because

they do not share this coveted food even-handedly there are asymmetries involved in the control of a food source, which, in both species, generates intense interest and a likelihood of political competition.

The carcass holder in many cases appears to enjoy a “respect” of possession (e.g., Boesch, 1994a,b; Goodall, 1986; Hohmann and Fruth, 1996; Stanford, 1999), in that no other ape will try to take the carcass away. Among chimpanzees this is normally a male (e.g., Mitani and Watts, 2001; see also Watts and Mitani 2002) and among bonobos it is more often a female (Hohmann and Fruth, 1996; see also White, 1994). However, in chimpanzees this special privilege, which affords superior nutrition, benefits the higher-ranking males disproportionately (e.g., Boesch and Boesch-Achermann, 2000; Goodall, 1986).

One must ask why adult males excluded from a chimpanzee meat-sharing session don't quickly form a coalition in order to confiscate the carcass for themselves. The fact that the possessor is likely to fight for such prized resources (see Goodall, 1986) helps explain the political dynamics, but a further hypothesis would be that alliances are involved (e.g., Stanford, 1998a; see also Gilby, 2006). Although Blurton-Jones (1991) believes that meat possessors' sharing amounts to “tolerated theft,” we suggest that by allowing at least a few cronies or kin to share the meat, the meat-holder is, in effect, creating a latent coalition that would provide him with political backing should the excluded individuals try to use coalitionary force to obtain meat. Thus, rather than “tolerating theft,” often the meat-possessor may be using meat to gain just enough allies to be immune to power-based theft by the rest of the group.

Nomadic human hunters have arrived at a very different approach to meat sharing, in that the entire group acts as a coalition to ensure an even distribution within the band (e.g., Erdal and Whiten, 1994; Wiessner, 1996). Competition dynamics involve the kind of moralistic social control that regulates many other aspects of human social life; foragers regularly form coalitions of the whole band, not only to curb cheating and lying, but to keep alpha types from gaining too much ascendancy (Boehm, 1993, 2004a). This fits with van Shaik et al.'s (2004) “coalition of lesser individuals against a dominant” model, and more generally it goes with the egalitarian effects described by Vehrenkamp (1983) even though in

humans it is active coalitions that help to produce these effects through a good understanding of coalitionary power.

Both chimpanzees and bonobos gang up against higher-ups, but they never manage to actually abolish the alpha role as egalitarian human foragers do (see Boehm, 1999). This may explain why higher-ranking individuals firmly control meat in the two *Pan* species, whereas with human hunting bands large carcasses in effect become communal property (Boehm, 2004b), and alpha-types are severely punished—by coalitions formed of entire bands—if they try to abrogate this system.

Part Two Conclusion

Individuals with a concept of power can deploy it to make strategic assessments even in the absence of power dynamics. In other words, even when no power relation has been established through direct or indirect experience with a particular individual, a concept of power can inform the decisions individuals make in their interactions with one another. Examples that we discussed include calculating the coercive potential of a group of male chimpanzees from a neighboring community and calculating how many partners would be required to threaten a predator with minimum risk. Power concepts also appear to play a critical role in intragroup dynamics. Individuals use such concepts to recognize and inhibit the acquisition of power of others—in particular to check the power of alpha males, and to recruit the best available individuals into coalitions against other group members. Individuals also benefit from a concept of power when attempting to manage competitive interactions, like those that follow a successful collective hunt in so far as the carcass holder might share some food with particular others, thereby creating a latent coalition, which could become active if other group members challenged the carcass holder for possession.

The data suggest that once individuals begin to understand what power is, they can manipulate it—thereby offering the possibility to bring even a legitimation-based system into greater alignment with their specific interests. At each level of complexity except the ‘0st order’ power structure described in Part

One of this paper, we see that power structures arise from the interplay of conflict and cooperation, and that both reflect different forms of self-interest.

With respect to 2nd order power structures as described in Part One, chimpanzees, although they lack institutionalization of power, seem to have accurate and rather sophisticated cognitive understandings not only of their personal power in dyadic contests and working in small coalitions, but of the overall power structures they are embedded in. For instance, when an alpha male routinely displays to maintain his dominant status, basically he is targeting his entire community and is expecting submissive signals from all group members in terms of postures, submissive pant-grunts, fearful screams, and fleeing from his presence. There are two effects. One is that he reinforces his dominance over every individual present, and keeps in place a social consensus. The other is that in effect he is testing the group, all at once, and will direct his dominance at any individual prone to challenge his preeminence. This reinforces his “authority” in the roles of competitor and peacemaker, but it does not result in the kind of authority that enables stronger human leaders to literally command their entire group in directions chosen by them, either through charisma or through use of centralized coercive force (e.g., Weber, 1954).

Conclusions

African great apes provide a useful homological model for studying how a concept of power affects power relations in humans. In particular data from ape societies suggests that egalitarian social organizations are derived—the outcome of subordinate individuals recognizing that collectively they have power and can control the acquisition and exercise of power by stronger individuals. However, one respect in which data from primates and other animals is unlikely to be useful is in understanding how consensus based power structures become institutionalized. By “institutionalized” we mean that positions of power (e.g. ‘president’) are collectively established and do not need to be continually occupied to persist. Nothing approximating this complexity seems to exist outside of human societies. However by adopting the process-based approach of Part One it should be possible to develop testable hypotheses

about the organizational features and cognitive / behavioral mechanisms required to generate these institutionalized power structures.

Acknowledgements

JCF thanks David Krakauer for valuable comments. Support for JCF during this project was provided by the Directorate of Intelligence and NIH grant 1 R24 RR024396. CB thanks the University of Southern California for support of the Jane Goodall Research Center and its primatological videotape collection.

References Cited

- Alexander, R. D. (1961). Aggressive territoriality and sexually behavior in field crickets. *Behaviour*, 17, 130-223.
- Bermejo, M., Illera, G., & Sabater Pi, J. (1994). Animals and mushrooms consumed by bonobos (*Pan paniscus*). *International Journal of Primatology*, 15, 879-898.
- Bierstedt, R. (1960). An Analysis of Power. *American Sociological Review*, 15, 730-738.
- Blurton Jones, N. G. (1991). Tolerated theft: Suggestions about the ecology and evolution of sharing, hoarding, and scrounging. In G. Schubert & R. D. Masters (Eds.), *Primate politics* (pp. 170-187). Carbondale: Southern Illinois University Press.
- Boehm, C. (1991). Lower-level teleology in biological evolution: Decision behavior and reproductive success in two species. *Cultural Dynamics*, 4, 115-134.
- Boehm, C. (1992). Segmentary “warfare” and the management of conflict: Comparison of East African chimpanzees and patrilineal-patrilocal humans. In A. Harcourt & F. B. M. de Waal (Eds.), *Us against them: Coalitions and Alliances in Humans and Other Animals* (pp. 137-173). Oxford: Oxford University Press.
- Boehm, C. (1993). Egalitarian society and reverse dominance hierarchy. *Current Anthropology*, 34, 227-254.
- Boehm, C. (1996). Emergency decisions, cultural selection mechanics, and group selection. *Current Anthropology*, 37, 763-793.
- Boehm, C. (1999). *Hierarchy in the forest: The evolution of egalitarian behavior*. Cambridge: Harvard University Press.
- Boehm, C. (2000). Conflict and the evolution of social control. *Journal of Consciousness Studies, Special Issue on Evolutionary Origins of Morality* (L. Katz guest editor), 7, 79-183.
- Boehm, C. (2004a). Large-game hunting and the evolution of human sociality. In R. W. Sussman & A. R. Chapman (Eds.), *Origins and nature of sociality among nonhuman and human primates* (pp. 270-287). New York: Aldine.
- Boehm, C. (2004b). What makes humans economically distinctive? A three-species evolutionary comparison and historical analysis. *Journal of Bioeconomics*, 2, 109-135.
- Boesch, C. (1991). The effects of leopard predation on grouping patterns in forest chimpanzees. *Behaviour*, 117, 220-241.
- Boesch, C. (1994a). Cooperative hunting in wild chimpanzees. *Animal Behaviour*, 48, 653-667.

- Boesch, C. (1994b). Hunting strategies of Gombe and Tai chimpanzees. In R. Wrangham, W. C. McGrew, F. B. M. de Waal & P. Heltne (Eds.), *Chimpanzee cultures* (pp. 77-91). Cambridge: Harvard University Press.
- Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Tai forest: Behavioural ecology and evolution*. New York: Oxford University Press.
- Bowles, S., & Gintis, H. (2008). Power. In *New Palgrave Encyclopedia of Economics*. London: McMillan.
- Burch, E. S., Jr. (2005). *Alliance and conflict: The world system of the Inupiaq Eskimos*. Lincoln: University of Nebraska Press.
- Buss, L. W. (1987). *The evolution of individuality*. Princeton, NJ: Princeton University Press.
- Byrne, R. W., & Byrne, J. M. (1988). Leopard killers of Mahale. *Natural History*, 97, 22-26.
- Chagnon, N. (1983). *Yanomamo: The fierce people*. New York: Holt, Rinehart and Winston.
- Chapman, C. A., White, F. J., & Wrangham, R. (1994). Party size in chimpanzees and bonobos: A reevaluation of theory based on two similarly forested sites. In R. W. Wrangham, W. C. McGrew, F. B. M. de Waal & P. G. Heltne (Eds.), *Chimpanzee cultures* (pp. 41-58). Cambridge: Harvard University Press.
- Chase, I. D. (1980). Social processes and hierarchy formation in small groups: a comparative perspective. *American Sociological Review*, 45, 905-924.
- Crutchfield, J. P., & Shalizi, C. R. (1999). Thermodynamic depth of causal states: Objective complexity via minimal representations. *Phys. Rev. E.*, 59, 275-283.
- D'Amour, D. E., Hohmann, G., & Fruth, B. (2006). Evidence of leopard predation on bonobos (*Pan paniscus*). *Folia Primatologica*, 77, 212-217.
- Dahl, R. A. (1957). The concept of power. *Behavioural Science*, 2, 201-215.
- Dahl, R. A., & Lindblom, C. (1953). *Politics, Economics, and Welfare*. New York: Harpers.
- de Waal, F. B. M. (1982). *Chimpanzee Politics: Power and Sex Among the Apes*. London: Jonathon Cape.
- de Waal, F. B. M. (1986). The integration of dominance and social bonding in primates. *Quarterly Review of Biology*, 61, 459-479.
- de Waal, F. B. M. (1996). *Good natured: The origins of right and wrong in humans and other animals*. Cambridge: Harvard University Press.

- Denison, D. R., & Mishra, A. K. (1995). Toward a theory of organizational culture and effectiveness. *Organization Science*, 6, 204-223.
- Diamond, J. (1992). *The third chimpanzee: The evolution and future of the human animal*. New York: Harper Perennial.
- Dugatkin, L. A., & Early, R. L. (2003). Group fusion: the impact of winner, loser, and bystander effects in hierarchy formation in large groups. *Behavioral Ecology*, 14, 367-373.
- Emerson, R. (1962). Power Dependence Relations. *American Sociological Review*, 27, 31-40.
- Erdal, D., & Whiten, A. (1994). On human egalitarianism: An evolutionary product of Machiavellian status escalation? *Current Anthropology*, 35, 175-184.
- Fawcett, K., & Muhumuza, G. (2000). Death of a wild chimpanzee community member: Possible outcome of intense sexual competition. *American Journal of Primatology*, 51, 243-247.
- Flack, J. C., & de Waal, F. B. M. (2004). Dominance style, social power, and conflict management: A conceptual framework. In B. Thierry, M. Singh & W. Kaumanns (Eds.), *Macaque Societies: A Model for the Study of Social Organization* (pp. 157-181). Cambridge: Cambridge University Press.
- Flack, J. C., & de Waal, F. B. M. (2007). Context modulates signal meaning in primate communication. *Proceedings of the National Academy of Sciences*, 104, 1581-1586.
- Flack, J. C., & Krakauer, D. C. (2006). Encoding power in communication networks. *American Naturalist*, 168, E87-E102.
- Flack, J. C., de Waal, F. B. M., & Krakauer, D. C. (2005). Social structure, robustness, and policing cost in a cognitively sophisticated species. *American Naturalist*, 165, E126-E139.
- Flack, J. C., Girvan, M., de Waal, F. B. M., & Krakauer, D. C. (2006). Policing stabilizes construction of social niches in primates. *Nature*, 439, 426-429.
- Flack, J. C., Krakauer, D. C., & de Waal, F. B. M. (2005). Robustness mechanisms in primate societies: A Perturbation study. *Proceedings of the Royal Society of London, Series B*, 272, 1091-1099.
- Fossey, D. (1983). *Gorillas in the mist*. Boston: Houghton-Mifflin.
- Frank, S. (2003). Repression of competition and the evolution of cooperation. *Evolution*, 57, 693-705.
- French, F. R. (1956). A formal theory of social power. *Psychological Review*, 63, 181-194

Frey, D. F., & Miller, R. J. (1972). The establishment of dominance relationships in the blue gourami. *Behaviour*, *42*, 8-62.

Fruth, B., & Hohmann, G. (2002). How bonobos handle hunts and harvests: Why share food? In C. Boesch, G. Hohmann & L. F. Marchant (Eds.), *Behavioural diversity in chimpanzees and bonobos* (pp. 231-243). Cambridge: Cambridge University Press.

Giddens, A. (1968). 'Power' in the recent writings of Talcott Parsons. *Sociology*, *2*, 257-272.

Gilby, I. C. (2006). Meat sharing among the Gombe chimpanzees: Harassment and reciprocal exchange. *Animal Behaviour*, *71*, 953-963.

Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behavior*. Cambridge: Belknap Press.

Goodall, J. (1988) *In the shadow of man*. New York: Houghton Mifflin.

Goodall, J. (1992) Unusual violence in the overthrow of an alpha male chimpanzee at Gombe. In T. Nishida, W. C. McGrew, P. Marler, M. Pickford, & F. B. M. de Waal (Eds.), *Topics in primatology, Vol. I: Human origins* (pp. 131-142). Tokyo: University of Tokyo Press.

Gould, S. J. (2002). *The Structure of Evolutionary Theory*. Cambridge: Belknap Press.

Hand, J. L. (1986). Resolution of social conflicts: dominance, egalitarianism, spheres of dominance and game theory. *Quarterly Review of Biology*, *61*, 201-220.

Heyes, C. (1998). Theory of mind in nonhuman primates. *Behavioral and Brain Sciences*, *21*, 101-114.

Hiraiwa-Hasegawa, M., Byrne, R. W., Takasaki, H., & Byrne, J. M. E. (1986). Aggression toward large carnivores by wild chimpanzees of Mahale mountains national park, Tanzania. *Folia Primatologica*, *47*, 8-13.

Hohmann, G., & Fruth, B. (1996). Food sharing and status in unprovisioned bonobos. In P. Wiessner & W. Schiefenhövel (Eds.), *Food and the status quest* (pp. 47-67). Providence: Berghahn.

Hohmann, G., & Fruth, B. (2008). New records on prey capture and meat-eating by bonobos at Luikotal, Salonga national park. *Folia Primatologica*, *79*, 103-110.

Holme, P. & Newman, M. E. J. (2006). Coevolution of networks and opinions. *Physical Review E*, *74*, 056108.

Hsu, Y., Early, R. L., & Wolf, L. L. (2006). Modulating aggression through experience. In K. Laland, C. Brown & J. Krause (Eds.), *Fish Cognition and Behavior* (pp. 96-113): Blackwell Publishing.

Hutchinson, G. E. (1957). Concluding remarks. *Quantitative Biology*, 22, 415-427.

Idani, G. (1991). Cases of inter-unit group encounters in pygmy chimpanzees at Wamba, Zaïre. *Primate today: Proceedings of the XIIIth congress of the International Primatological Society, Nagoya and Kyoto*, pp. 18-24.

Ihobe, H. (1991). Male-male relationships among wild bonobos (*Pan paniscus*) at Wamba, Republic of Zaïre. *Primates*, 33, 163-179.

Ihobe, H. (1992). Observations on the meat-eating behavior of wild bonobos (*Pan paniscus*) at Wamba, Republic of Zaïre. *Primates*, 33, 247-250.

Jablonka, E. (1994). Inheritance systems and the evolution of new levels of individuality. *Journal of Theoretical Biology*, 170, 301-309.

Jen, E. (2003). Stable or robust? What's the difference? *Complexity*, 8, 12-18.

Kano, T. (1992). *The last ape: Pygmy chimpanzee behavior and ecology*. Stanford: Stanford University Press.

Krakauer, D. C., & Zanolto, A. P. (2008-to appear). Viral individuality & limitations of the life concept. In *Transitions from Non-living to Living Matter*. Boston: MIT Press.

Kullback, S. (1997). *Information Theory and Sufficient Statistics*. Dover.

Lachmann, M., Szamado, S., & Bergstrom, C. T. (2007). Cost and conflict in animal signals and human language. *Proceedings of the National Academy of Sciences*, 98, 13189-13194.

Lewis, R. (2002). Beyond dominance: The importance of leverage. *Quarterly Review of Biology*, 77, 149-164.

Lukes, S. (2005). *Power: A Radical View* (2nd ed.): Palgrave Macmillan.

Manson, J. H., & Wrangham, R. W. (1991). Intergroup aggression in chimpanzees and humans. *Current Anthropology*, 32, 369-390.

Maynard Smith, J., & Harper, D. G. C. (1995). Animal signals: models and terminology. *Journal of Theoretical Biology*, 177, 305-311.

Maynard Smith, J., & Price, G. R. (1973). The logic of animal conflict. *Nature*, 246, 15-18.

Maynard Smith, J., & Szathmary, E. (1995). *The Major Transitions in Evolution*. Oxford: Oxford University Press.

McGonigle, B. O., & Chalmers, M. (1977). Are monkeys logical? *Nature*, 267, 694-696.

- McShea, D. W., & Changizi, M. A. (2003). Three puzzles in hierarchical evolution. *Integrative Comparative Biology*, 43, 74-81.
- Michod, R. (2007). Evolution of individuality during the transition from unicellular to multicellular life. *Proceedings of the National Academy of Sciences*, 104, 8613-8618.
- Mitani, J. C., & Watts, D. P. (2001). Why do chimpanzees hunt and share meat? *Animal Behaviour*, 2001, 915-924.
- Muller, M. N., & Mitani, J. C. (2005). Conflict and cooperation in wild chimpanzees. *Advances in the Study of Behavior*, 35, 275-331.
- Nelissen, M. H. J., & Andries, S. (1988). Does previous experience affect the ranking of cichlid fish in a dominance hierarchy? *Annals of the Royal Society of Belgium*, 118, 41-50.
- Nishida, T. (1996). The death of Ntologi, the unparalleled leader of M group. *Pan Africa News*, 3, 4.
- Nishida, T., Hosaka, K., Nakamura, M., & Hamai, M. (1995). A within-group gang attack on a young adult male chimp: Ostracism of an Ill-Mannered Member. *Primates*, 36, 207-211.
- Noble, D. (2008). *The Music of Life*. Oxford: Oxford University Press.
- Noë, R. (1992). Alliance formation among male baboons: shopping for profitable partners. In A. H. Harcourt & F. B. M. d. Waal (Eds.), *Coalitions and Alliances in Humans and Other Animals*. Oxford: Oxford University Press.
- Noë, R., & Hammerstein, P. (1995). Biological markets. *Trends in Ecology and Evolution*, 10, 336-339.
- Odling-Smee, J., Laland, K. N., & Feldman, M. W. (2003). *Niche Construction: The Neglected Process in Evolution*. Princeton, NJ: Princeton University Press.
- Okasha, S. (2006). *Evolution and the Levels of Selection*. Oxford: Oxford University Press.
- Pagel, M., & Dawkins, M. S. (1997). Peck orders and group size in laying hens: 'future contracts' for non-aggression. *Behavioural Processes*, 40, 13-25.
- Parker, I. (2007). Swingers: Bonobos are celebrated as peace-loving, matriarchal, and sexually liberated. Are they? *New Yorker Magazine*, July.
- Parsons, T. (1937). *The Structure of Social Action*: McGraw Hill.
- Parsons, T. (1963). On the concept of political power. *Proceedings of the American Philosophical Society*, 107, 232-262.

- Paz-Y-Mino, C. G., Bond, A. B., Kamil, A. C., & Balda, R. P. (2004). Pinyon jays use transitive inference to predict social dominance. *Nature*, *430*, 778-781.
- Preuschoft, S. (1999). Are primates behaviorists? Formal dominance, cognition and free-floating rationales. *Journal of Comparative Psychology*, *113*, 91-95.
- Preuschoft, S., & van Schaik, C. (2000). Dominance and communication. In F. Aureli & Rapp, P. R., Kansky, M. T., & Eichenbaum, H. (1996). Learning and memory for hierarchical relationships in the monkey: Effects of aging. *Behavioral Neuroscience*, *110*, 887-897.
- Rowell, T. (1974). The concept of social dominance. *Behavioral Biology*, *11*, 131-154.
- Rubenstein, D. I., & Hack, M. A. (1992). Horse signals: The sounds and scents of fury. *Evolutionary Ecology*, *6*, 254-260.
- Ruvolo, M., Disotell, T. R., Allard, M. W., Brown, W. M., & Honeycutt, R. L. (1991). Resolution of the African hominoid trichotomy by use of a mitochondrial gene sequence. *Proceedings of the National Academy of Science*, *88*, 1570-1574.
- Scott, J. (Ed.). (1994). *Power: Critical Concepts* (Vol. 1-3). London: Routledge.
- Shalizi, C. R., & Crutchfield, J. P. (2001). Computational mechanics: Pattern, prediction, structure, and simplicity. *Journal of Statistical Physics*, *104*, 817-879.
- Shalizi, C. R., & Moore, C. (2003). What is a macrostate? Subjective observations and objective dynamics. *arXiv:cond-mat/0303625v1 [cond-mat.stat-mech]*.
- Shettleworth, S. J. (1998). *Cognition, Evolution, and Behavior*. Oxford: Oxford University Press.
- Simon, H. (1953). Notes on the observation and measurement of political power. *Journal of Politics*, *15*, 500-516.
- Stanford, C. B. (1998a). *Chimpanzee and red colobus: The ecology of predator and prey*. Cambridge: Harvard University Press.
- Stanford, C. B. (1998b). The social behavior of chimpanzees and bonobos: Empirical evidence and shifting assumptions. *Current Anthropology*, *39*, 399-420.
- Stanford, C. B. (1999). *The hunting apes: Meat eating and the origins of human behavior*. Princeton: Princeton University Press.
- Thierry, B. (2000). Conflict management patterns across macaque species. In F. Aureli & F. B. M. de Waal (Eds.), *Natural Conflict Resolution* (pp. 106-128). Berkeley: University of California Press.

- Tsukahara, T. (1993). Lions eat chimpanzees: The first evidence of predation by lions on wild chimpanzees. *American Journal of Primatology*, *29*, 1-11.
- Uehara, S., Hiraiwa-Hasegawa, M., Hosaka, K., & Hamai, M. (1994). The fate of defeated alpha male chimpanzees in relation to their social networks. *Primates*, *35*, 49-55.
- van Schaik, C. P., Sagar A. Pandit, and Erin R. Vogel (2004). A model for within-group coalitionary aggression among males. *Behavioral Ecology and Sociobiology*, *57*, 101-109.
- Vehrencamp, S. L. (1983). A model for the evolution of despotic versus egalitarian societies. *Animal Behavior*, *31*, 667-682.
- Watts, D. P. & Mitani, J. C. (2002). Hunting and meat sharing by chimpanzees at Ngogo, Kibale national park, Uganda. In C. Boesch, G. Hohmann & L. Marchant (Eds.), *Behavioral diversity in chimpanzees and bonobos* (pp. 244-255). Cambridge: Cambridge University Press.
- Watts, D. P. (2004). Intracommunity coalitionary killing of an adult male chimpanzee at Ngogo, Kibale national park, Uganda. *International Journal of Primatology*, *25*, 507-520.
- Weber, M. (1954). *On Law in Economy and Society*. Boston: Harvard University Press.
- White, F. J. (1994). Food sharing in wild pygmy chimpanzees (bonobo), *pan paniscus*. In J. Roeder, B. Thierry, J. R. Anderson & N. Herrenschmidt (Eds.), *Current primatology volume II: Social development, learning and behavior* (pp. 1-10). Strasbourg: Universite Louis Pasteur.
- Wiessner, P. (1996). Leveling the hunter: Constraints on the status quest in foraging societies. In P. Wiessner & W. Schiefenhövel (Eds.), *Food and the status quest: An interdisciplinary perspective* (pp. 171-191). Oxford: Berghahn Books.
- Wilson, M. L., & Wrangham, R. W. (2003). Intergroup relations in chimpanzees. *Annual Review of Anthropology*, *32*, 363-392.
- Wilson, M. L., Hauser, M. D., & Wrangham, R. W. (2001). Does participation in cooperative intergroup conflict depend on numerical assessment, range location, or rank for wild chimpanzees? *Animal Behavior*, *61*, 1203-1216.
- Wrangham, R. W. (1987). African apes: The significance of African apes for reconstructing social evolution. In W. G. Kinzey (Ed.), *The evolution of human behavior: Primate models* (pp. 51-71). Albany: SUNY Press.
- Wrangham, R. W. (1999). The evolution of coalitionary killing: The imbalance-of-power hypothesis. *Yearbook of Physical Anthropology*, *42*, 1-30.
- Wrangham, R., & Peterson, D. (1996). *Demonic males: Apes and the origins of human violence*. New York: Houghton Mifflin.

Wrong, D. H. (1968). Some problems in defining social power. *American Journal of Sociology*, 73(673-681).

Zuberbüler, K., & Jenny, D. (2002). Leopard predation and primate evolution. *Journal of Human Evolution*, 43, 873-886.