Chapter 5 Dominance, Power, and Politics in Nonhuman and Human Primates

David P. Watts

As long as politics is the shadow cast on society by big business, attenuation of the shadow will not change the substance ... Power today resides in control of the means of production exchange, publicity, transportation, and communication. Whoever owns them rules the life of the country. The machinery of power ... is business for private profit ... reinforced by command of the ... means of publicity and propaganda.

(John Dewey, quoted in Westbrook 1991: 440, 442)

Abstract Dominance is a common, although not universal, characteristic of social relationships in nonhuman primates. One individual is dominant to another when it consistently wins the agonistic interactions between them. Attainment of high dominance rank can bring reproductive payoffs, mostly because it confers priority of access to monopolizable food sources (for females) or to mating opportunities (for males). For females in particular, a wide variation exists in the frequency of intense aggression, the directionality of aggression within dyads, the tolerance of high-ranking individuals, and other aspects of "dominance style." This variation reflects variation in ecology and is also influenced by phylogenetic history. Variation also exists in male dominance style, although it has not received as much attention. Dominance is one component of power, which also encompasses other sources of asymmetry in relationships that affect the relative ability of individuals to carry out their goals against the interests of others. Leverage is an important source of power in many nonhuman primates; an animal has leverage over another when it controls a resource or service that cannot be appropriated by force, such as agonistic support. Individuals behave politically when they try to increase or maintain their power relative to that of others by manipulating social relationships, both their own and those of others. The concept of power applies universally to gregarious primates, although asymmetries do not occur between adults of all

D.P. Watts

Department of Anthropology, Yale University, New Haven, CT, USA e-mail: david.watts@yale.edu

species, but we should only ascribe politics to species in which the actors have knowledge about the relationships between others in their groups. Some parts of the literatures in political science and political anthropology not only provide useful frameworks for a comparative investigation of power and politics in nonhuman primates, but also highlight qualitative differences between humans and other primates, especially regarding the importance of ideologies and political rhetoric.

5.1 Introduction

Dewey's remarks seem incongruous in a chapter about dominance, power, and politics in nonhuman primates. The influential philosopher of pragmatism was writing about humans in the context of twentieth century industrial capitalism; his ideas about politics, power, and the proper social role of "the means of publicity" were grounded in - and contentious in - that context. They do not describe human universals, and "politics" and "power" have many definitions in political anthropology, a subdiscipline that includes multiple, often contrasting and sometimes complementary, explanatory paradigms that cover the entire range of current and historically known human social arrangements (reviewed in Kurtz 2001, and Lewellen 2003, among others). However, Dewey makes an implicit point about nonhuman primates: without the capacity for language and for symbolically mediated systems of meaning, they cannot engage in "publicity and propaganda" or seek profit, nor can they invent, pursue, or argue about ideologies, whether capitalism or any other: these are qualitative differences from humans. Can we then justifiably ascribe politics and power dynamics to them and seek commonalities with humans?

Any answer starts with the fact that individuals of most primate species maintain long-term social relationships with conspecifics. These often have affiliative dimensions, but they also involve competition over food, mates, and other resources, the outcome of which can have major effects on fitness. Competition may or may not involve social interaction and may or may not lead to dominance relationships. Competitive interactions, or contests, are crucial to the concept of dominance, which becomes part of a social relationship when one individual can monopolize resources at the other's expense or usurp them from the others by using force or threatening to do so, even though not all aggression concerns immediate access to resources or contests over status, and some contests are decided by unprovoked, unilateral submission rather than by aggression.

However, not all resources accessible via social interaction can be appropriated by force, and dominance can be subsumed within a broader category of power (Lewis 2002). Variation in power among individuals potentially allows for social maneuvering that sometimes warrants the label of "politics." Alliance formation strategies illustrate these points well. Most contests are dyadic, but many primate species stand out when compared with most mammals because of the frequency with which they form coalitions, in which two or more individuals collaboratively direct aggression at joint targets (Harcourt 1992). Alliances develop when particular dyads repeatedly and consistently form coalitions; they feature prominently in the competitive strategies of macaques, chimpanzees, and many other species. One effect of coalitions is to help individuals to win contests they would otherwise lose. Male baboons can sometimes forcibly take over consortships with estrous females from higher-ranking males, for example, but require coalition partners to do so. Not all potential partners are equally effective, and males may compete for access to the best partners (Seyfarth 1977; Noë 1990, 1992). Males cannot coerce others to join them; the ability to grant or withhold support gives potential partners power over their would-be allies, and males whose value is higher than that of their partners are likely to take disproportionate shares of the benefits of successful coalition formation (Noë 1990, 1992). Strategic pursuit of alliances and negotiation over the distribution of their costs and benefits easily bring to mind human political maneuvering, as de Waal (1982) argued, for the ways in which male chimpanzees (Pan troglodytes) use coalitions in their complex strategies of competition for status. Other nonhuman primates that also engage in complex social maneuvering for status by using alliances, exchanging social services like grooming, and testing the strength of social bonds arguably also have politics (e.g., white-faced capuchins, Cebus capucinus: Perry and Manson 2008).

However, we should be wary of using "politics" too loosely (e.g., Boehm 1997) and of anthropomorphizing chimpanzees, baboons, capuchins and other nonhumans in the service of superficial and misleading extrapolations to humans (e.g., Fukuyama 1998). In the following section, I define dominance and briefly review concepts of power. Differentials in power among individuals are nearly universal in primates; dominance relationships and dominance hierarchies are not, although they exist in the majority of taxa. I review competing explanations for variation in dominance "style" and briefly summarize evidence concerning the relationship of dominance rank to reproductive success. I also consider the aspects of social relationships in nonhuman primates that involve politics; I argue that politics is far from universal and only characterizes species capable of triadic awareness (i.e., knowledge about the social relationships between others in one's social group). Chimpanzees necessarily figure in large measure in my discussion of politics, because they have been the main subject of relevant research and speculation. Finally, I offer some comparisons between human and nonhuman primates.

5.2 What is Dominance?

Following Hinde (1976; cf. Dunbar 1988), I regard dominance as a property of social relationships, not a characteristic of individuals, who are "dominant" or "subordinate" only in the context of social relationships. This perspective differs from the one common in social psychology, in which dominance is seen as a human personality trait that varies quantitatively among individuals (e.g., Maner et al. 2008). By convention, we can determine whether dominance is part of a social

relationship by quantifying the direction and outcomes of agonistic interactions, i.e., those that involve aggressive and/or submissive acts and/or signals. For example, supplants are agonistic acts in which a stationary individual moves away at the approach of another, who takes its place, while "pant grunts" are formal vocal signals of subordinate status in chimpanzees (Marler 1976) and "silent bared teeth faces" are formal visual signals of subordinate status in and some (but not all) macaque species (Thierry 2000). If one of two members of a dyad consistently wins the agonistic interactions between them, it is dominant to the consistent loser, which in turn is subordinate to the consistent winner. Since the same individual can be dominant to some members of his or her social group and subordinate to others, terms like "dominant individuals" or "dominance interactions," while convenient shorthand, are best avoided because they risk reifying dominance as an inherent aspect of individual phenotypes.

Linear dominance hierarchies, of varying degrees of stability, form when most or all group members or all members of one class of individuals (e.g., adult females) have dominance relationships. These occur in many, but not all, group-living primate species. For example, both macaques (*Macaca* spp.) and mountain gorillas (*Gorilla beringei beringei*) live in multifemale groups; macaque females typically form stable, linear dominance hierarchies (de Waal 1986, 1989; de Waal and Luttrell 1988; Chapais 1992; Thierry et al. 2000; Thierry 2007), but mountain gorilla females do not necessarily do so and many female dyads lack decided agonistic relationships (Watts 1994).

5.3 Functions of Dominance

Group-living primates have many means to manage the tensions that arise from conflicts of interest among individual group members (de Waal 1986, 1989, 2000). The argument that establishing decided dyadic dominance relationships and (when these occur) linear dominance hierarchies limits aggression, and thus mitigates such tensions and reduces the costs of aggression – notably injury risk – has a long history (e.g., Bernstein 1976; Chapais 1991). De Waal (1986) argued that formal signals of subordinate status and "conditional reassurance" from higher to lower-ranking individuals limit the use of force to express competitive tendencies, and stated (*ibid*.: 475) "a well recognized hierarchy promotes social bonds and reduces violence," as evidenced by data from macaques, chimpanzees, and other species.

But this begs the question of why status striving should so often be all that prominent. The standard answer is that high rank, by conferring priority of access to resources, can lead to high reproductive success. A sex difference in the key resource over which individuals compete exists, with females competing mostly for food (although safety can also be important; van Schaik and van Noordwijk 1986) and males mostly for mating opportunities. The literature on the association between rank and reproductive success is too vast to summarize here. In brief, the weight of the evidence generally supports the hypothesis that rank is positively

correlated with reproductive success for both sexes. Data on some species show the expected positive relationship for females (e.g., yellow baboons, Papio cynocephalus: Altmann and Alberts 2005; long-tailed macaques, Macaca fascicularis: van Noordwijk and van Schaik 1999). Exceptions exist (e.g., chacma baboons, Papio hamadryas ursinus: Cheney and Seyfarth 2007), and the strength of social bonds can influence female reproductive success independently of rank (Silk et al. 2003), but rank effects may only become discernable during times of prolonged food shortfalls and thus only become evident in very long-term studies (Cheney and Seyfarth 2007). Harcourt (1987) noted that no cases were known in which female reproductive success was inversely related to rank; this is still true. Accumulating genetic evidence also supports the "priority of access" model for males in many species (reviewed in Di Fiore 2003), including yellow baboons (Alberts et al. 2006), long-tailed macaques (van Noordwijk and van Schaik 2004; Engelhardt et al. 2006), mandrills (Mandrillus sphinx: Setchell et al. 2005), and chimpanzees (Boesch et al. 2006), although the number of males per group and the degree of estrus synchrony among females also influence reproductive skew among males. Behavioral variation linked to differences in personality (or "behavioral syndromes") also can influence male reproductive success independently of dominance rank (Bergman et al. 2008).

5.4 Sources of Variation in Female Dominance Style: Ecology, Phylogeny, and Self-Structuring

Relationships between females vary widely among primate species that form multifemale groups, as do those between males and females and, in multimale groups, those between males. Females in some species may not form dominance hierarchies (e.g., mountain gorillas: Watts 1994; blue monkeys, Cercopithecus mitis: Cords 2000). Aggression directionality and intensity varies among other species (e.g., aggression goes unidirectionally down the hierarchy in rhesus macaques, Macaca *mulatta*, but is common up the hierarchy in stump-tailed macaques, *M. arctoides*: de Waal 1986, 1989; de Waal and Luttrell 1988). Dyadic agonistic asymmetries can vary, sometimes consistently, across contexts, and in some species, they are susceptible to the influence of third parties. Kawai (1958) used the term "dependent rank" to refer to the attainment of dominance by young female Japanese macaques (Macaca fuscata) over larger adolescent and adult females subordinate to their mothers, with the help of coalitionary support from kin and, sometimes, nonkin. White (1996) described bonobos (Pan paniscus) as having female "feeding priority," because females usually win contests with males over food, and males sometimes avoid patches where females are feeding, but males are not necessarily submissive to females in other contexts. Similar variation occurs in tolerance of higher-ranking individuals for their subordinates, dynamics of conflict management and resolution, and other behavior related to preserving social bonds in the face of potentially

serious competition. De Waal (1986, 1989; cf. de Waal and Luttrell 1988) introduced the concepts of "formal dominance" (based on the directionality of formal signals of relative status) and "real dominance" (based on the actual outcomes of agonistic interactions) to clarify understanding of this variation and referred to particular patterns of variation as the "dominance style" of a species or group of species.

Feeding efficiency can crucially influence female reproductive success; thus, variation in the relative strength and intensity of scramble and contest feeding competition may lead to predictable variation in female dominance styles (van Schaik 1989). The socioecological model (Sterck et al. 1997; cf. Koenig 2002) accounts well for much of this variation by considering the effects of competitive regimes; by incorporating sexual conflict, it accounts for much variation in malefemale relationships and helps to explain why in almost all species that form stable social groups, males associate permanently with those females. Briefly, this model holds that when within-group scramble competition predominates and contest competition is inconsequential, females in multifemale groups should either form weak and unstable dominance hierarchies or not form them at all, and females can transfer between groups to minimize scramble competition and/or to choose mates. In contrast, when feeding on clumped resources monopolizable by single individuals or by coalitions that include only some group members is important - i.e., when contest competition for food is important - and monopolization confers nutritional advantages, linear dominance hierarchies occur. Given associated female philopatry, nepotism is the main basis for coalition formation, and related females help each other to acquire and maintain ranks. High within-group contest competition should result in strong ("despotic") hierarchies, stabilized by nepotism. When between-group contest competition also strongly influences female fitness, however, high-ranking females - those able to win within-group contests against most or all others - should be tolerant of lower-ranking females, and hence hierarchies should be weaker, so that high-ranking females can retain their subordinates' support in contests with other groups. Finally, high between-group contest competition combined with low within-group contest competition should lead to egalitarian relationships (no dominance hierarchies or weak ones) combined with female philopatry.

Much evidence supports the model, although accounting for intertaxon diversity in female social relationships minimally also requires other consideration of overall food abundance and variation in food nutritional quality (Isbell 1991; Pruetz 2009). For example, within-group contest competition is relatively weak, female agonistic relationships are egalitarian, and female transfer is common in Thomas langurs (*Presbytis thomasi*), and within-group contest competition is relatively high in "despotic" long-tailed macaques (Sterck and Steenbeek 1997). Likewise, variation in the strength of within-group contest competition accords with variation in the strength of dominance hierarchies among populations of hanuman langurs (*Semnopithecus entellus*: Koenig et al. 1998) and among three species of squirrel monkeys (*Saimiri* spp.: Boinski et al. 2002; cf. Mitchell et al. 1991). Blue monkeys at Kakamega face high between-group contest competition, but within-group contest competition is weak; correspondingly, females are philopatric, but do not form linear dominance hierarchies (Cords 2000). Such egalitarianism in species with high between-group contest competition (e.g., some guenons) may be a general solution to a collective action problem that female superior competitors face, but whether this is actually so depends on how much they could gain by winning within-group contests. If potential gains rarely outweigh the costs of aggression perhaps because most food patches can accommodate all group members (but not more than one group), egalitarianism or tolerance requires some other explanation. Lions provide a valuable comparative example of female egalitarianism: females in the same pride cooperatively defend carcasses against females of neighboring prides and defend cubs against infanticidal males, and they engage in communal care of cubs; they do not form dominance hierarchies despite high potential for within-pride contests over food (Packer et al. 1990; Heinsohn and Packer 1995).

Despite the considerable success of the socioecological model, its generality and functional logic have been strongly challenged, notably with respect to variation in female dominance style among macaque species. Macaques fall into semi-discrete grades along a spectrum in which the directionality of aggression, the relative frequency of high-intensity aggression, the extent of kin biases in social behavior, conciliatory tendencies, and tolerance co-vary (Thierry 2007). This co-variation seems to have a strong phylogenetic signal (*ibid.*; Thierry et al. 2000). In despotic species like rhesus and Japanese macaques, rigid hierarchies co-occur with relatively high rates of intense aggression, unidirectional aggression down the hierarchy, strong nepotism and consistent operation of the "youngest ascendancy rule" in rank acquisition (maturing females assume ranks immediately below those of their mothers and above any older sisters), and low conciliatory tendencies. At the other end of the spectrum, high tolerance is associated with weaker nepotism and less kin-bias in social relationships, low rates of intense aggression, less consistent operation of the youngest ascendancy rule, and high conciliatory tendencies. The extreme despots belong to the fascicularis lineage; the most tolerant species belong to the *silenus-sylvanus* lineage; and other members of these lineages and species in the *sinica-arctoides* lineage occupy various intermediate positions (Thierry 2007), although not all variation sorts neatly by phylogeny (e.g., Tibetan macaques (M. thibetana) belong to the relatively "tolerant" sinica-arctoides lineage, but have despotic female dominance; Berman et al. 2004). Moreover, limited field data indicate that variation in hierarchy strength may not correspond to variation in the strength of within-group contest competition and that high between-group contest competition does not obviously characterize the more tolerant species (Cheney 1992; Berman et al. 2004; Ménard 2004; Thierry 2007).

Thierry (2007; cf. Matsumara 1999; Matsumara and Kobayashi 1998) has proposed that these grades are different evolutionarily stable outcomes of selection on a collection of traits that are linked because all are mediated by the same underlying neurobiological and hormonal mechanisms (e.g., the effects of serotonin on anxiety and aggression intensity). Contrary to the "collective action" explanation for tolerance among female macaques, high-ranking females are not forced to restrain their competitive tendencies to induce cooperation from low-ranking females, because their competitive tendencies are already low. Shallower dominance gradients in tolerant species than in more despotic ones also could mean that for a female of a tolerant species, proportionately more of the other females in her group are potentially valuable allies, although alliances would have less importance for her if the co-evolved system involves low competitive tendencies. Alternatively, Preuschoft and van Schaik (2000) proposed that low asymmetries in fighting ability and less consistent or predictable agonistic support in tolerant than in despotic species means that females of tolerant species need to probe others repeatedly to assess their current willingness to act as allies. This leads to high tolerance for spatial proximity regardless of rank difference, relatively infrequent retaliation against females that direct mild aggression at higher-ranking partners, more need for reconciliation, and more frequent grooming between nonkin. In their view, tolerance is really "calculated generosity."

Problems with the sociological model are not restricted to macaques. For example, female hanuman langurs at Ramnagar engage in high within-group contest competition for food and, as expected, form despotic dominance hierarchies, but are not tolerant despite also facing high between-group feeding competition (Lu et al. 2008). Between-group contest competition seems to be generally a poor predictor of female dominance style.

Hemelrijk has used a series of agent-based simulation models to argue that selfstructuring could account for much of the observed variation in dominance styles (e.g., Hemelrijk 1996, 1999a,b, 2000a,b, 2002; Hemelrijk et al. 2003). Model entities are assigned initial "dominance" values for which the gradients vary across simulations. They then follow one of various alternative sets of rules that determine how they move and how they behave on encounters with others moving in the same space. They may estimate their capacity to win agonistic interactions with others based on their past histories of interaction; alternatively, they may assess the risk of conflicts by directly evaluating their own fighting ability relative to that of the entities they have encountered. Group cohesion also varies, along with the probability that more than two entities meet simultaneously and "coalitions" form. Entities are sometimes divided into species in which aggression intensity is typically high and others in which it is low, and sex differences in attack intensity can vary. Crucially, contest outcomes are probabilistically determined, and both winning and losing are self-reinforcing (winning reinforces an agent's dominance value, whereas losing decreases it), with effects of winning greater for the subordinate of two interactors and the losing effect stronger on the dominant. The selfstructuring effects of these simulations produce dominance hierarchies that vary along the axes of "despotism-egalitarianism" and "tolerance-intolerance", in the degree of nepotism, and in the extent to which male and female dominance hierarchies overlap. Inclusion of variation in food clumping and in sexual attraction between males and females also influences variation in male-female hierarchy overlap (Hemelrijk et al. 2003).

Hemelrijk states that these models are "caricatures" that do not reflect the complete behavior of real monkeys and apes. For example, dyads with established social relationships almost certainly use memory-based assessment (Silk 2002),

coalition formation is nonrandom, and triadic awareness, which depends on learning and memory, leads to strategic decisions about intervening in conflicts and soliciting coalition partners. As Preuschoft and van Schaik (2000) state, nonhuman primates often have accurate information about relationships in their groups. Clear evidence that monkeys classify others on the basis of kinship (e.g., Bergman et al. 2003) argues against the possibility that apparent nepotism is simply a byproduct of variation in the intensity of aggression (Hemelrijk 1999b).

It remains an open question whether we should jettison the socioecological model in favor of game theoretic analyses of alternative equilibria that result from selection on linked traits (Thierry 2007) or can improve it by incorporating data on other aspects of food distribution and quality (Pruetz 2009), better data on the extent to which low-ranking females participate in contests between groups, and consideration of other potential sources of leverage for low-ranking females (e.g., willingness to engage in cooperative defense of infants against infanticidal males; Lu et al. 2008). Ultimately, alternative social equilibria can only be stable within bounds set by species' ecology, and we need much better quantitative data on feeding competition in many species, notably macaques. However, in looking for bivariate associations between competitive regimes and categorical distinctions like despotic versus egalitarian or tolerant versus intolerant, the model's advocates fail to acknowledge that these probably are parts of coevolving complexes that cannot be atomized (Thierry 2007; cf. Thierry 2000; Thierry et al. 2000). Hemelrijk's nonadaptationist models can help to provide proximate explanations for dominance style variation. Superficially, their outcomes strongly resemble the spectrum of dominance styles evident in macaques and some other nonhuman primates. However, they may reproduce the surface structure of dominance styles precisely because in the real world, the variables that lead to self-structuring – winning and losing effects, aggression intensity, group cohesion, sex differences in agonistic power - help to determine developmental outcomes within ranges of possible phenotypic space set by varying histories of evolutionary response to competitive regimes, and whatever explanatory power they have is not independent of phylogeny and ecology.

Occasional references to winner and loser effects in the real world occur; for example, Preuschoft and van Schaik (2000) note that individuals that repeatedly lose contests to various opponents can become "trained losers," who defer to most or all opponents, whereas those that repeatedly win may show the opposite pattern. Any such effects could be hormonally mediated, perhaps by testosterone. An extensive literature on humans (reviewed in Archer 2006) indicates that the relationship between testosterone and competition in both sexes is complex. One apparent generalization based on a meta-analysis of relevant studies (*ibid.*) is that male testosterone levels rise slightly in anticipation of sports competition; they also increase from before to after the competition, with the increase greater in winners than in losers, although variation in personality, in attribution of causality for the outcome, and other factors can influence the magnitude of change. Additionally, losing sometimes decreases testosterone, although this effect may occur only in individuals that attribute their losses to intrinsic factors (e.g., Mehta and Josephs

2006), and drops in testosterone in association with high social anxiety can make losers less willing to compete again (Maner et al. 2008). Differential effects of winning and losing like these, if persistent, could help to produce the kind of self-reinforcement that Hemelrijk envisions.

Attempts to monitor short-term fluctuations in testosterone induced by competitive interactions in wild nonhuman primates face formidable logistical hurdles, but longer-term increases or decreases in testosterone respectively associated with winning or losing contests for alpha male status in mandrills (Setchell et al. 2008) and for control of one-male units in geladas (Beehner and Bergman 2009) suggest that such effects occur. Further circumstantial support comes from the evidence that testosterone influences decisions by male chacma baboons in Botswana (Beehner et al. 2006; Bergman et al. 2006) whether to engage in contests. Testosterone was highest in males rising in rank, and current levels predicted male rank and mating success over the subsequent eleven and seven months, respectively (Beehner et al. 2006). Males avoided others with high testosterone more often than those with low testosterone; relative rank had little effect, and adjacently ranked males (probably each other's most serious current competitors) with high combined testosterone were most likely to avoid each other.

5.5 Variation in Male Dominance Style

Sex differences in dominance style are common, as expected given that variation in female fitness depends mostly on the outcome of competition for food, whereas variation in male reproductive success depends mostly on the outcome of mating competition, and given that dispersal is often male-biased. For example, in some chimpanzee communities, many female dyads lack dominance relationships (e.g., Ngogo: Wakefield 2008), and females usually do not form linear hierarchies. Instead, they reduce feeding competition by adjusting gregariousness to food availability. In contrast, males typically form steep linear hierarchies (e.g., Ngogo: Watts and de Vries 2009), although male-male social relationships are also highly affiliative. Male dominance ranks in nonhuman primates usually depend on individual fighting ability and show an inverse-U shaped relationship to age, even in cercopithecine species in which females form stable hierarchies in which ranks depend on predictable nepotistic and mutualistic support, not on fighting ability (Chapais 2001). Nepotistic effects on male ranks prior to dispersal are more likely in those cercopithecines in which adult size dimorphism is relatively low than in those in which adult males are much larger than females (Pereira 1988). Postdispersal nepotistic effects are unlikely, and nepotism may not be consistently important even in species with male philopatry. For example, while some maternal brothers form alliances in chimpanzees, most allies are not maternally related (Langergraber et al. 2007). Bonobos (P. paniscus) may be exceptional, in that high-ranking females may form alliances with their sons that enable the sons also to attain high rank (Kano 1992), although how pervasive such effects are is unknown.

In general, the extent of intersexual overlap in dominance ranks varies inversely with sexual dimorphism in body size in cercopithecines, presumably because the risk of female aggression to males increases as dimorphism in body size and canine size increases (Packer and Pusey 1979; Thierry et al. 2000); these relationships help to explain the inverse relationship between the sex difference in initial "dominance" (i.e., fighting ability) and male-female rank overlap in Hemelrijk et al.'s (2003) self-structuring model. But in macaques, rank overlap among males and females seems to depend on the extent of kin-biases in female behavior and the strength of female alliances against males; thus, it varies along phylogenetic lines rather like variation in female dominance style and is somewhat independent of variation in sexual dimorphism (Thierry et al. 2000). Variation in male dominance style in macaques also partly mirrors that among females. For example, tolerance between males is lower, serious aggression is more common, and the directional consistency of aggression higher in rhesus macaques than in more tolerant species (Thierry 2007). However, the influence of male rank on mating tactics and reproductive success depends on variation in female mating synchrony in a manner independent of female dominance style variation (reviewed in Thierry 2007). Rank strongly affects reproductive success in nonseasonally breeding species, including highly tolerant ones (e.g., Tonkean macaques, Macaca tonkeana), in which low-ranking males must win aggressive challenges against high-ranking males to have good prospects for siring offspring (cf. van Noordwijk and van Schaik 1985). In contrast, reproductive skew is low in seasonally breeding species, including despotic ones (e.g., rhesus macaques); severe aggression is correspondingly uncommon except in small groups, and rank tends to increase with age and length of group residence.

Variation in population density and demography can strongly influence the costs and benefits of dispersal and of alternative mating tactics for males (e.g., yellow baboons: Alberts and Altmann 1995; macaques: Soltis 2004). Such variation may not fundamentally affect male dominance style; for example, male yellow baboons in low-density populations may delay dispersal, but their ranks, and thus to important extents, their reproductive success, still depend on their fighting ability (Alberts and Altmann 1995). Nevertheless, the potential for such effects bears further investigation, as does variation in the steepness of male hierarchies.

5.6 Power and Politics

Variation in dominance style reflects variation in power and raises questions about political maneuvering. The term "power" is used widely, but often without explicit definition. For example, Datta (1983a,b) implied that power in rhesus macaques (*M. mulatta*) comprises individual fighting ability plus any competitive advantages gained from coalitionary support. Likewise, "politics" is often not explicitly

defined. De Waal (1982) characterized the tactics of alliance formation (including competition for partners and disruption of potential alliances between rivals), strategic and sometimes conditional use of reconciliation, and other ways in which chimpanzees manipulate their social partners and manipulate relationships between other individuals, as political. Subsequently, de Waal (1989) specified that the need for allies in within-community competition for status and the need for all males in a community to cooperate in aggression against neighboring communities are "internal and external 'political reasons" why male chimpanzees require effective mechanisms to cope with within-community competition. In describing challenges for the alpha position among male chimpanzees at Mahale, Nishida and Hosaka (1996) also stressed the complexity and flexibility of alliance formation strategies and the varied ways in which males use social resources like grooming and meat sharing to maintain alliances and referred to such behavior as political (cf. Mitani and Watts 2001; Watts 2002; Mitani 2006). Duffy et al. (2007) characterized the Kanyawara alpha male's selective tolerance of his allies mating behavior in exchange for coalitionary support as a political tactic from which all parties benefited, despite potential tradeoffs (less than maximum mating monopolization vs. prolonged tenure as alpha; additional current mating opportunities vs. foregone attempt to challenge for the alpha position).

A review of the many ways in which political anthropologists have characterized power is beyond the scope of this chapter, but brief attention to some of this literature provides a useful context for considering power and politics in nonhumans. Some explanatory paradigms (e.g., postmodernist ones) provide little or no basis for comparative analysis (sometimes deliberately), but others, such as "processualism," are more amenable. Processualists see politics as the processes involved in determining and implementing public goals and the differential use of power by group members concerned with those goals (Swartz et al. 1966; Adams 1977; Kurtz 2001; Lewellen 2003; Swartz et al. 1966; Box 5.1). Power has many dimensions, not all political; for example, it is embedded in healing rituals (Kurtz 2001). Weber's (1965 [1947]) definition of power as the relative ability of one actor to carry out his or her own will despite resistance underlies the relevant notion of political power, and many anthropologists extend politics to the pursuit of individual goals as well as group goals. For example, Kurtz (2001: 21) writes:

"Politics is all about power: about how political agents create, compete for, and use power to attain public goals that, at least on the surface, are perceived to be for the common good of the political community. Yet just as open and more covertly, political power is used to attain private goals for the good of the individuals involved."

Processualists divide power into several broad categories (Box 5.1). Independent power is based on individual capabilities. Dependent power is granted, delegated, or allocated to others by someone who has independent power, but that individual in turn is subject to consensual power (i.e., the assent of the people).

Anything that contributes to or maintains power counts as support; two basic supports are coercion and legitimacy (Box 5.1).

Box 5.1. Selected examples of how "power" and "politics" have been conceptualized in the literature on political anthropology.

- **Politics**: "The processes involved and determining public goals . . . and the differential use of power by the members of the group concerned with those goals." (Swartz et al. 1966: 7)
- **Power:** "... a quality ascribed to people, and often also to things, that concerns their relative abilities to cope with the real world or their potential effects on it ... [power cannot exist alone,] but must be recognized by others and by the individual possessing it." (Adams 1977: 389)

"... the probability that one actor in a social relationship can carry out his will despite resistance." (Weber 1965 [1947])

An ability to control the behavior of others and/or to gain controlling influence over others; the ability of one individual to bend another to his or her will. (Lewellen 2003)

Components of Power in the "Processualist Paradigm" (Adams 1977; Lewellen 2003):

- Independent power: "A relation of dominance based on the direct capabilities of an individual, such as knowledge, skills, or personal charisma." (Lewellen 2003: 231).
- **Dependent power**: Power that is granted, allocated, or delegated, either by someone who has independent power over its recipient or to a more powerful individual by his or her supporters.
- Granted power: Decision-making rights that one individual gives to another.
- Allocated power: Power given by a group of people to a certain individual (e.g., a "Big Man," a shaman).
- **Delegated power**: Decision-making rights given to a number of different people by a single individual who has a concentration of individual power.
- **Consensual power**: Leadership that arises from the assent of the people (based on tradition, faith in the personal qualities of the leader, etc.) rather than from force alone.
- **Support**: A broad concept that includes virtually anything that contributes to or maintains political power. Two basic supports are coercion and legitimacy.
- **Legitimacy**: A primary basis for power that derives from the people's expectations about the nature of power and how it should be attained (e.g., by election, by holding redistributive feasts) and used.

Box 5.1. continued Power resources (Kurtz 2001):

- Material resources:
 - 1. **Tangible resources**: Culturally defined goods (e.g., money) that individuals compete for and use to attain their goals.
 - 2. **Human resources**: allies and supporters that any political agent requires to be a leader.
- Ideational resources:
 - 1. **Symbolic resources**: material objects, mental projections, actions, ideas, or words that humans infuse with ambiguous, multiple, and disparate meanings; political symbols may be anything in the social or physical environment that leaders can use to convince people to support them; fluid, changeable, respond to shifting social, cultural, and political conditions.
 - 2. **Ideological resources**: a political ideology is "a system of hypotheses, principles, and postulates that justify the exercise of authority and power, asserts social values and moral and ethical principles, sets forth the causal connections between leaders and the people they govern, and furnish guides for action...around a set of beliefs and ideas." (Kurtz 2001: 35).
 - 3. **Informational resources**: Information both includes and produces knowledge; to the extent that leaders can produce and harness the flow of information, it becomes a source of political power.

Kurtz (2001) presents a rather different perspective, in which political power depends on the ability of agents to acquire and maintain control over resources; this resonates with the emphasis on resource competition in the primatological literature, but redistribution of resources often accompanies control in humans. In political struggles, those who control more resources tend to win against those who control less, but agents who control less can win if they use resources more wisely and skillfully. Some resources are material; these include tangible objects and goods as well as human supporters (Box 5.1). Other crucial resources are ideational. These include ideological, symbolic, and informational resources (Box 5.1). Political rhetoric - the deliberate exploitation of eloquence in public speaking or writing by leaders to persuade others - is the most common source of information as political power and is a pervasive and extremely important alternative to coercion. Independent power thus depends on the ability to control culturally constructed ideational resources as well as material resources; a leader must be good at using ideational resources to attract supporters, but maintaining their support ultimately depends on providing them with sufficient tangible resources.

Chapais (1991) and Lewis (2002) explicitly have characterized power in nonhuman primates by drawing on literature in political science. This literature mostly concerns modern nation states and lacks the comparative ethnographic focus of political anthropology, but shares certain themes with it. Chapais (1991) adapted an explanatory framework developed by Bacharach and Lawler (1980). Echoing Weber, power in this framework is defined as the capacity of an actor to carry out its own will despite resistance. It can be "aggression-based" - that is, based on aggression or threat and thus coercive, although this category also includes power based on control of resources, services, or knowledge - or "dependence-based," with the power of actors derived from support that others give them. Acquisition and maintenance of dominance rank in nonhuman primates provide good examples of both categories (Chapais 1991). It generally involves aggression-based power, but sometimes depends largely on agonistic support from third parties (notably among females in macaques, baboons, and vervets; Chapais 1992) and is thus dependence-based. Dependence-based power in this sense is in keeping with Kawai's (1958) "dependent rank." It contrasts with the processualists' dependentpower subcategories of granted and delegated power (Adams 1977; Box 5.1), in which the arrow of dependency points in the opposite direction and those who have granted or delegated power to others can withdraw it; it is closer to allocated power, although without the collectively agreed conferral of status that this term implies. But dependence by leaders is a major theme in political anthropology, and recurring emphasis on the need to attract and retain supporters ("the single biggest problem that any leader confronts"; Kurtz 2001: 34) indicates that dependency is bidirectional in humans. When one individual, human or nonhuman, has dependencebased power over another and has some ability to manipulate outcomes for it, their relationship can take on a political dimension. Chapais (1991) noted that many of the sources of power (whatever allows one to control its basis) that Bacharach and Lawler (1980) identified in humans do not apply to nonhuman primates. For example, "normative power," a form of dependence-based power in which one individual or group can bestow symbolic rewards on another, is exclusively human, as is most, and perhaps all, power based on possession of knowledge that cannot be acquired simply by observational learning. Control of information beneficial to others is an important source of power in humans (Bacharach and Lawler 1980; Chapais 1991) and a potential source in nonhuman primates, but nonhuman primates do not appear to bargain over information (Chapais 1991), and manipulating others by withholding information is uncommon and may be limited to a few taxa (e.g., chimpanzees: Hare et al. 2006). More generally, nonhuman primates make little, if any, use of ideational resources.

Lewis (2002) applied "power" to asymmetries in social relationships that can originate in individual differences in resource holding potential (i.e., fighting ability) or in differences in the strength of alliances, but also in the possession by some individuals of inalienable resources, broadly defined, that can influence the fitness of others. Thus, it comprises both dominance and leverage. Dominance is the agonistic component of power; it is based on force or threat of force. "Intrinsic" dominance depends solely on interindividual differences in fighting ability and is thus roughly equivalent to Chapais' (1991) "aggression-based power." "Derived" dominance (cf. Datta 1983a, b) depends also, or largely, on the relative strength of

coalitionary support and resembles Chapais' (1991) "dependence-based power." When individuals could benefit from resources that others control or services that they could provide, but cannot take these by force, the resource holders and service providers have leverage; implicitly, this idea is also included in dependence-based power.

If politics is all about creation of, competition over, and use of power, it necessarily involves social maneuvering, and not all potential sources of leverage are necessarily available for political use. For example, Lewis (2002) considers possession of fertilizable eggs as a source of leverage that can allow estrous females to gain temporary social advantages (e.g., increased receipt of grooming from males) without changes in dominance, but females may gain such advantages simply because others respond to signals of fertility or receptivity or to proceptive behavior, not because they use these signals to manipulate others socially. In contrast, when individuals have alternative options for distributing allogrooming or coalitionary support, strategic deployment of these options may qualify as political, especially given variation in partner quality. One individual has leverage over another when the second depends on it in some way, and such dependence can be mutual; their interactions can become political when one or both partners can manipulate socially determined outcomes that the other values (Chapais 1991).

Leverage can either increase or decrease power asymmetries, as illustrated by classic examples of male alliances in baboons and chimpanzees. Noë (1990) documented the formation of coalitions by two or three mid-ranking male yellow baboons against higher-ranking males in several contexts, notably in attempts to separate high-ranking males from estrous females with whom those males were consorting. In Lewis' (2002) terms, coalitions temporarily increased the allies' power relative to that of their opponents without changing their dominance ranks (they still behaved submissively to their opponents in dyadic encounters; Noë 1990), but the highest-ranking of the three allies had leverage over the other two (and thus increased his relative power over them) because they had little chance of succeeding without his participation. This presumably explained why he took over the consorts in all observed cases in which the coalitions succeeded. Noë characterized coalition formation by these males as a "veto game" with the highest-ranking ally acting as the "veto player," and pointed out that variation in the value of potential partners should lead to shopping for, and bargaining over, their services (cf. Noë 1992; Noë and Hammerstein 1994). Variation in partner value means that dependence, while bidirectional, is not always symmetrical, but bargaining can also occur in established alliances, and asymmetries can be constrained, when weaker partners have enough leverage (Noë 1990, 1992). Baboon males obliged to negotiate with weaker allies bear some resemblance to "weak leaders" among humans, who "have allies whose commitments to them are transactional...based on what they can get for their support, which therefore is tenuous" (Kurtz 2001: 45).

Derived power is important in status competition among male chimpanzees, and alpha males usually depend on allies to attain and maintain their positions. The third-ranking of three males involved in a status struggle in the Arnhem Zoo community mated more often than expected, based on his rank, while another male depended on his support to consolidate his newly attained status as alpha (de Waal 1982). However, his mating frequency declined when the new alpha's position was secure. Nishida (1983) described a similar case in a wild community that had only three adult males. Duffy et al. (2007) found broader leverage effects in a larger chimpanzee community at Kanyawara, in which mating success for males other than the alpha was positively correlated with the frequency with which they gave the alpha coalitionary support, independently of their own dominance ranks. The alpha male exerted some control over others' mating success by disrupting many copulation attempts; the frequency with which he disrupted those of individual males was inversely related to the amount of support they gave him.

Lewis (2002; see Chapais 1991, for a somewhat different categorization) defined four proximate characteristics of power: its base, or source (e.g., fighting ability); its means, or the way in which individuals negotiate it in relationships (e.g., by using force); its amount, which can vary with context and can be expressed as a probability of winning contests; and its scope, or the range of behavior that an individuals can invoke in others by using dominance or leverage. This framework can help to resolve several longstanding debates and to clarify some terminological confusion. Lewis (*ibid.*) gave de Waal's (1986) "formal" and "real" dominance as one example: formal dominance involves the use of formalized status signals that are consistent across contexts; thus, its scope differs from that of real dominance, which can vary contextually and which also involves derived dominance and leverage.

The issue of "female dominance" in lemurs also benefits from reframing as a question about power. Male-female asymmetries are pronounced in some lemur species; notably, female ring-tailed lemurs (Lemur catta) win all contests against males and evoke formalized submissive signals from them, and aggression is unidirectional from females to males (Pereira et al. 1990; Pereira and Kappeler 1997). However, females are less powerful in other species, and the scope of power differs; for example, aggression is bidirectional in brown lemurs (Eulemur fulvus), males win many contests, and formal dominance does not exist (*ibid*.). Researchers have sometimes used "co-dominance" to refer to species in which neither sex consistently wins contests against the other (e.g., gibbons: Leighton 1987) or "female feeding priority" to refer to those in which females typically win contests over food, but not always in other contexts and in which aggression is bidirectional and formal dominance between males and females absent (e.g., bonobos, P. paniscus: White 1996). Specifying whether sex differences in the amount of power exist would be more productive than arguing about whether a given species has "female dominance" or just "female feeding priority" and about whether these are different phenomena. As Lewis (2002: 154) notes, "female dominance to males occurs only when female fighting ability is superior to that of males in intersexual dyadic interactions." Likewise, if no such dyadic asymmetry exists between males and females, no dominance exists, even if a leverage asymmetry means that the sexes differ in relative power; "co-dominance" is a meaningless term in this context.

Flack and de Waal (2004) have made the most elaborate attempt to define power in nonhuman primates and to link it to politics, on the one hand, and to dominance style, on the other. In their scheme, dominance style operates on the level of social relationships and refers strictly to the discrepancy between the inherent agonistic asymmetry between individuals (roughly, fighting ability) and the degree to which they express this asymmetry, as indicated by the directional consistency of aggression, the typical intensity of aggression, and the types of signals used to indicate dominance or subordination. When inherent asymmetries are high and are routinely expressed in social interactions, for example, dominance relationships are despotic; when they are high to moderate, but only weakly expressed, relationships are tolerant. They did not explicitly distinguish intrinsic from derived dominance, but included alliance formation as a "contextually and temporally stable factor" (p. 169) that makes agonistic outcomes more predictable and thus influences agonistic relationships.

Flack and de Waal (*ibid.*) linked dominance style to politics via "social power," which they defined (p. 167) as "the degree of implicit agreement among group members that an individual is capable of using force in polyadic social situations." In turn, force "leads to the reduction or elimination of the choices of others" (p. 168). They restricted social power to species that use formal signals of dominance or subordination (e.g., macaques, chimpanzees), arguing that "implicit agreement" can only occur if individuals consistently acknowledge status differentiation in nonaggressive contexts. They proposed that we can operationalize social power by comparing, for each individual, the number of others from whom it receives and to whom it gives signals of subordinance or dominance, the frequency of these signals, and the way in which they are distributed among other group members. Such operationalization provides a basis for interspecific comparison, but, as Flack and de Waal acknowledge, their concept of social power is far narrower than those of Chapais and Lewis, and it would exclude many species (e.g., ring-tailed lemurs and gorillas have social power, but brown lemurs and chimpanzees do not). When social power in their sense exists, groups have power structures, which lead to "political systems" at the societal level that reflect "the interplay between the power structure and conflict management" (p. 157). They classified political systems (Table 5.1) based on four main factors: how much social power is concentrated in single individuals versus distributed among all group members, who intervenes in conflicts and what intervention strategies they follow, the extent to which interventions in conflicts reinforce or reduce social power differentials, and how equally resources are distributed.

5.7 Politics and Cognition

The claim that some nonhuman animals engage in politics has been criticized. For example, Schubert (1991) argued that nonhuman primate "politics" is mostly a metaphor and particularly criticized Hrdy (1977) for referring to "regimes" and "usurpation of power" by extra-group males that lead to "regime changes" in hanuman langurs. Boehm (1997) was more sympathetic when comparing power

Dominance style	Distribution of social power	Political system
Despotic	Uniform; increases as <i>social power rank</i> (SPR) increases	<i>Hierarchy</i> : resource allocation determined mostly by SPR; conflict interventions reinforce system
Tolerant	Concentrated in a few individuals and distributed uniformly among others so as to increase with SPR	<i>Informal oligarchy</i> : some resource allocation by SPR; powerful 3rd parties intervene in conflicts impartially or to favor least powerful participants, others intervene to reinforce hierarchy
	Concentrated in a few individuals; others have approximately equal power	<i>Constrained</i> : Leveling coalitions, policing by powerful individuals, and mediation maintain system
Relaxed	Temporally stable, but small, differences in social power	<i>Equal outcome system:</i> maintained by coalitions against individuals intolerant of subordinates and mediation by powerful individuals; policing can lead to equal resource distribution; may be institutional roles
Egalitarian	No temporally stable differences in social power, but some individuals may temporarily be more powerful than others	<i>Equal opportunity system</i> : maintained by punishment of norm breakers and of nonpunishers; can lead to division of labor among arbiters and impartial policing to mediate conflicts between coalitions

Table 5.1 Dominance style, social power, and political systems (after Flack and de Waal 2004)

asymmetries in chimpanzees and human hunter-gatherers. He defined "political intelligence" as "the decision making capacity that enables social animals to further their self-interests in situations that involve rivalry and quests for power and leadership." He ascribed political intelligence to chimpanzees and other nonhumans, but both too broadly and too narrowly, regarding all forms of agonistic behavior involved in such decisions (e.g., bluffing, appeasement, aggression, deference) as its manifestations. By implication, leverage that involves social manipulation also represents political intelligence. This perspective risks conflating politics with power. Attempts to manipulate relationships between others (e.g., separating interventions by male chimpanzees; de Waal 1982) may well be political, but invoking political intelligence adds little to the understanding of, for example, how opponents assess each others' fighting abilities or why targets of aggression might sometimes appease their attackers by directing nonaggressive acts or signals to them that reduce the probability of further attack. Conversely, restricting political intelligence to decisions about "whether to try to dominate or submit to" others (Boehm 1997: 354) neglects how coalition formation can influence power dynamics by reinforcing dominance relationships, by providing successful partners with temporary advantages (e.g., takeovers of consorts with estrous females by male baboons), or by conferring derived dominance in some relationships (e.g., alliances

that allow male chimpanzees to attain and maintain alpha status). Correspondingly, it omits the importance of leverage and of market effects in competition for allies (Noë 1990, 1992; Noë and Hammerstein 1994).

Boehm (1997) argued that political decisions do not necessarily require complex cognition. However, we should turn this around to argue that decisions that enable individuals "to further their self-interests in situations of rivalry and quests for power" are only political if they involve cognitively complex social manipulation. This begs the question of what qualifies as complex cognition, but at least any species capable of triadic awareness can behave politically in this sense. Individuals who can acquire knowledge about the social relationships between others in their groups can use this knowledge in calculated, sometimes opportunistic, ways to gain extrinsic dominance and to exert leverage over allies and potential supporters (Preuschoft and van Schaik 2000) and to avoid or mitigate the costs of conflicts. Flack and de Waal (2004) seem to imply that "political systems" require such knowledge. It is unclear whether their restriction of social power to "polyadic situations" means that it operates only in polyadic interactions; I take it to mean that it can only operate in groups of three or more individuals, in which two or more can "agree" that another can use force against them. But they state that conflict mediation by socially powerful individuals, which occurs in "constrained" and "equal outcome" political systems (Table 5.1), requires cognitive empathy (the ability to take others' perspectives), and list several macaque species and chimpanzees as possible exemplars of these systems. Cognitive empathy would certainly allow for triadic awareness. Additionally, their scheme applies specifically to social variation in macaques, all of which are presumably capable of such awareness.

The list of species in which triadic awareness has been formally demonstrated either experimentally or through statistical modeling is short, but further formal investigation would undoubtedly lengthen it. Chacma baboons show triadic awareness in many ways (reviewed in Cheney and Seyfarth 2007), including avoiding close maternal kin of higher-ranking females from whom they have just received threats and responding more strongly to playbacks that simulate dominance rank reversals between adult females belonging to different matrilines (which are rare and threaten to disrupt the entire female dominance hierarchy) than to those simulating within-matriline rank reversals (also rare, but with much less potential to disrupt other dominance relationships; Bergman et al. 2003). Playback studies also showed triadic awareness in vervets (reviewed in Cheney and Seyfarth 1990). Perry et al. (2004) showed that white-faced capuchins at Lomas Barbudal solicited coalition partners who had better-quality social relationships with themselves than with their opponents more often than expected by chance, and also solicited partners who outranked their opponents more often than expected by chance, although they might have done this simply by preferentially soliciting partners higher-ranking than themselves (cf. Range and Noë 2004, for mangabeys, Cercocebus torquatus). Nonrandom solicitation of potential coalition partners on the basis of relative relationship quality, relative rank, and/or relatedness to opponents has also been demonstrated in bonnet macaques (Macaca radiate: Silk 1999) and Japanese macaques (M. fuscata: Schino et al. 2006). Conflict management and resolution tactics apparently based on the recognition of relatedness between opponents and third parties (e.g., kin-redirected reconciliation and aggression; reviewed in Das 2000 and Watts et al. 2000) provide indirect evidence that triadic awareness is widespread among cercopithecines and perhaps other primates, and use of separating interventions is one of many forms of circumstantial evidence for triadic awareness in chimpanzees.

Triadic awareness combined with comparative knowledge of partner value allows for politics, which is partly a strategic use of such knowledge. A female chacma baboon who opportunistically forms a bridging alliance or a revolutionary alliance (Chapais 1991, 1992) to challenge another female to whom she is subordinate, but who has just lost a challenge to a third individual (Engh et al. 2006; Cheney and Seyfarth 2007) is behaving politically. Likewise, while he was alpha male in the Mahale M group of chimpanzees, Ntologi behaved politically by regularly directing separating interventions at other males, mostly at his main rivals, Nsaba and Kalunde (who nevertheless formed an alliance that allowed Kalunde to defeat Ntologi, although his tenure as alpha was then short; Nishida and Hosaka 1996). Politics also encompasses the strategic use of knowledge about variation in partner value and the corresponding strategic use of leverage, such as the decision by Yeroen, the third ranking male in the Arnhem Zoo chimpanzee colony, to ally himself with Nikkie, then a weak alpha, rather than Luit; Nikkie needed the derived dominance provided by a strong alliance more (de Waal 1982). Several primate species tested in lab settings can solve tasks that require coordinated efforts by two partners (e.g., brown capuchins, Cebus apella: Mendres and de Waal 2000). This suggests that they recognize the necessity of acting jointly and the value of partners and the services they can provide; his would facilitate political exploitation of variation in partner value and political negotiation over services. An alternative explanation is that they simply learn contingencies between their actions and obtaining rewards (ibid.). However, this seems inadequate to explain differential recruitment of partners on the basis of their task-solving skills by chimpanzees (Melis et al. 2006).

Politics may require triadic awareness, but it can occur at the level of dyads. One possible political tactic would be to induce a loser effect in a potential rival by targeting him or her sufficiently to prevent, or at least forestall, any competitive challenge. Unpredictable attacks independent of direct contests over resources might be particularly effective (Silk 2002). Rank changes were common in the baboon group studied by Bergman et al. (2006) and males in that population did not form alliances. Induced loser effects, if they occurred, might thus have often been short lived, but this does not preclude the possibility that they form part of individual competitive strategies. Male chimpanzees are good candidates for such effects because male philopatry means that adolescent males will become rivals of those in older age cohorts, who could benefit by delaying challenges from the adolescents and who could increase the delay by forming coalitions against them. This might help to explain why adult males direct aggression at adolescents at high rates – often higher than those for adult dyads – and sometimes single out particular individuals for persistent attacks (Pusey 1990, Watts unpubl. data). Aggression

sometimes produces direct benefits – e.g., adults sometimes steal meat from adolescents – but much of it may be punishment, in that it has an immediate energetic cost, but changes the target's future behavior in favor of the aggressor (Clutton-Brock and Parker 1995), essentially via negative conditioning. Thinking of punishment as a manifestation of political intelligence in chimpanzees seems reasonable, but the common occurrence of age-related loser effects in ungulates suggests that we should not always assume that political intelligence is involved. Female dominance rank in many ungulates increases with age (reviewed in Côté 2000), and age is the main influence on rank among female mountain goats (*Oreannos americanus*), which form stable hierarchies in which neither the body size nor the horn length influences rank and in which attacks by adult females lead to persistent subordination younger females even after the younger females attain adult size (*ibid.*)

5.8 Politics in Human versus Non-Human Primates

Power and politics in human and nonhuman primate share some similarities and contrast in many ways, only a few of which I will briefly consider. First, politics and power in nonhuman primates revolve around social relationships (or, in Flack and de Waal's (2004) view, politics arises from social relationships via the mediating effects of social power), and political anthropologists sometimes also stress that power is a component of human social relationships (e.g., Adams 1977). Face-toface interactions in which individuals or small coalitions either directly assert their own interests, with at least an implicit threat of force, or use social persuasion to do so form part of human politics and would have characterized most human political behavior during our evolutionary history in small-scale societies (Archer 2006). In some respects, the forms and outcomes of such interaction resemble chimpanzee political interactions and other aspects of power in nonhuman primates (reviewed in Chapais 1991). Humans use visual and vocal threats, engage in physical aggression and contest access to resources as individuals or members of small coalitions, and compete over social partners. However, even at the interpersonal level, humans have sources of power unavailable to other primates. An obvious example is the use of weapons in intraspecific aggression, a uniquely human source of aggressive coercion that distinguishes power relations in our species from those of other nonhuman primates (Gat this volume). But another obvious example, one that highlights human cognitive uniqueness and is probably more important than physical coercion, is the use of political rhetoric (Kurtz 2001).

Aggression-based dominance hierarchies like those in nonhuman primates, whether they result solely from intrinsic dominance or also involve derived dominance, are uncommon in humans, at least among adults (Chapais 1991). Nor should the association of outstanding hunting skill with high reproductive success, common among human foragers, be equated with the positive relationship between dominance rank and male reproductive success in many nonhuman primates.

Hunting skill may provide leverage, but without conferring coercive power or any formal political authority. Thus, Ache men known to be good hunters can get preferential treatment from others in their bands regarding decisions about group movements, but because they can threaten to transfer to other bands and thereby depriving others of their hunting returns, not because they have any formal political power (Hill and Kaplan 1988). Leaders in hunter-gatherer societies and other smallscale human groups are "episodic" or "weak" (Kurtz 2001) and must lead by example and by persuading others (e.g., Tsimane village chiefs: Gurven and Winking 2008). Regardless of the extent to which power ultimately rests on coercive ability, humans have many more sources of dependence-based power than do any nonhuman primates, thus many more ways to control and manipulate the needs of others (Chapais 1991) and many ways to create needs. As Chapais (ibid.: 216) notes, "the most powerful individuals (the ones most able to control the behavior of others) are those with the greatest number of individuals depending on them for the satisfaction of needs." The obverse of manifold sources of dependence-based power is the existence of far more sources of leverage than are available to any nonhumans, such as possession of specialized skills or knowledge and even influence over others' prestige and self-esteem.

Coalitions in nonhuman primates are often conservative or polarizing, in that they accentuate dyadic power asymmetries (Chapais 1992, 2001; Preuschoft and van Schaik 2000). When female macaques follow the "support the high born" rule by forming coalitions with other females whose mothers outrank their opponents, they help the females they support to attain or maintain dominance over the opponents; given that females intervene mostly against targets that they also outrank, such support reinforces the existing dominance hierarchy and is best regarded as mutualism (Chapais 1992, 2001). Likewise, male chimpanzee coalitions at Ngogo mostly include partners who both outrank their targets (Watts and de Vries 2009). But leveling coalitions also occur in some primates. In these, either coalition partners compensate for dyadic power asymmetries by collaborating against higher-ranking opponents, or high-ranking individuals intervene in conflicts on behalf of subordinates against opponents that they outrank and thereby suppress within-group competition, (e.g., Barbary macaques, Macaca sylvana: Preuschoft et al. 1998; Preuschoft and Paul 2000; yellow baboons: Noë 1992; Noë and Hammerstein 1994; chimpanzees: Nishida and Hosaka 1996). At an extreme, individuals can reverse dyadic power asymmetries by forming revolutionary alliances (Chapais 1992); in these, partners collaborate to reverse dominance ranks with targets to which they are subordinate (e.g., male chimpanzees: de Waal 1982; Nishida and Hosaka 1996; female chacma baboons: Engh et al. 2006).

But leveling coalitions in cercopithecines and among male chimpanzees co-occur with linear dominance hierarchies and, although they may limit the ability of high-ranking individuals to monopolize resources (e.g., they may reduce reproductive skew among males), they do not lead to the "egalitarian" politics of human hunter-gatherer societies known from the ethnographic record (Boehm 1997). Recognition of individual merit and accordance of limited authority to certain individuals occurs alongside tracking of people's behavior and linguistic communication about whether this stays within bounds acceptable to culturally variable moral communities. Humans also have broad means to constrain powerful individuals; some of these, like imposition of moral sanctions, are unavailable even to chimpanzees (Boehm 1997; Kurtz 2001). Likewise, a growing body of evidence indicates that people often engage in third-party punishment at some cost to themselves, although considerable cross-cultural variation in willingness to do so exists (Henrich et al. 2006; Gurven and Winking 2008) and people's behavior in economic games may not match that in the real world (Gurven and Winking 2008, Plourde this volume).

In experiments, captive chimpanzees retaliate against others who have stolen food from them (Jensen et al. 2007a) and respond negatively to situations in which they have received unfairly small rewards (Brosnan et al. 2005). De Waal and Luttrell (1988) documented negative reciprocity (or "bidirectionality") in agonistic interventions against others among the Arnhem Zoo chimpanzees - that is, individuals often supported others against third parties who in turn often intervened against them; male chimpanzees at Ngogo show similar bidirectionality (Watts unpubl. data). De Waal and Luttrell (1988) labeled this bidirectionality as a "revenge system," and referred to aggression by food possessors toward others who were trying to obtain food from them in a food sharing experiment, but were reluctant to share when they possessed the food, as "moralistic aggression." De Waal (1989) subsequently argued that revenge and moralistic aggression "introduce powerful sanctions to a social system." However, such behavior appears to be entirely egocentric. Chimpanzees seem to be unconcerned with whether others have been treated fairly (Jensen et al. 2007b), and although retaliation could be considered a form of punishment, currently available evidence indicates that they do not engage in costly third party punishment (Jensen et al. 2007a). Such findings seriously question Flack and de Waal's (2004) categorization of political systems in which, for example, they consider chimpanzees as possible representatives of the "equal outcome" category (Table 5.1), in which policing by powerful individuals leads to an equal distribution of resources; how this could occur when powerful individuals are unconcerned with whether others achieve fair outcomes and are perhaps incapable of such concerns (but see de Waal 2008, for a contrary view), is unclear.

Absent the ability to form moral communities, chimpanzees could also not control the cost and efficiency of punishment by delegating authority to enforce social norms to individuals and institutionalized subgroups at different levels of a hierarchical society: an ability essential for the formation of large scale, hierarchical societies in the first place (Dubreuil 2008). As Boehm (1997) argued, politics among male chimpanzees remain individualistic, even when males try to achieve social goals as members of small coalitions. Although Flack and de Waal (2004) note that "equal opportunity" political systems (Table 5.1) occur only in humans – and, implicitly, only humans construct institutional roles of the sort that can characterize "equal outcome systems" (Table 5.1) – they present their classification of political systems as if it is a continuum, when in fact it incorporates these and other qualitative disjuncture between humans and nonhuman primates. More notably,

not even chimpanzees can engage in symbolically mediated leverage, competition, and manipulation, and their lack of language stringently limits their ability to use information as a source of power. In his comparison of power in humans and nonhuman primates, Chapais (1991) listed many similarities; virtually all of the contrasts involve semiosis or otherwise derive from cognitive differences. Aggressive coercion in nonhuman primates never involves moral justification or attribution of blame to victims, for example, nor does "normative power," based on symbolically based group norms, occur in nonhumans. Primatologists who write about politics in apes and monkeys need to recognize the crucially important semiotic and ideational dimensions of human politics – struggles over meaning and ways in which language, including political rhetoric, mediates these – and to pay attention to corresponding human cognitive uniqueness. We should acknowledge that – to paraphrase Plotkin's (2003) summary comment on calling socially learned behavioral traditions in chimpanzees "culture" – it is not politics as we know it in humans, but it is politics of a kind.

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