Grunts, Girneys, and Good Intentions:

The Origins of Strategic Commitment in Nonhuman Primates

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Social groups are composed of individuals with very different interests, needs, and abilities. Despite these differences, members of social groups manage to synchronize their activities; negotiate about certain kinds of decisions; anticipate what others will do in certain situations; and broker social transactions that include cooperative and competitive elements. To accomplish these feats, primates must somehow provide information to others about their dispositions and intentions. Detailed observations of the behavior of many species reveal that monkeys and apes use a variety of signals to communicate this information. Some of these signals function as generic commitments, and convey information about what animals will do next (Nesse, Chapter 1). Thus, many primates use vocalizations to indicate their readiness to travel or the direction in which they intend to move (reviewed by Boinski 2000). These kinds of signals are likely to enhance coordination, even when group members have competing interests. Monkeys also use signals to communicate their intention to behave peacefully toward others and to reconcile disputes with former opponents. These signals may function as stragegic commitments, which guarantee that the actor will subsequently behave in ways that are sometimes contrary to its own short-term interests (Nesse, Chapter 1).

Strategic commitments can be enforced by external forces, reputational effects, or internal emotional motives (Nesse, Chapter 1). The latter constitute subjective commitments. We have no evidence that primates experience the kinds of emotions that are thought to influence subjective commitments in humans (Frank, Chapter 4), although some researchers argue for their presence in great apes, particularly chimpanzees (e.g. Killen and de Waal 2000). Some emotions, such as sympathy and empathy, may require the ability to understand the perspectives of other individuals. Present evidence suggests

that monkeys and apes know very little about what goes on in others' minds, and have limited abilities for empathy, perspective-taking, and mind-reading (Tomasello and Call 1997, Povinelli and Eddy 1996). It is possible, however, that internal motivational states influence behavior in primates without being mediated by conscious emotions or moral sentiments. Sexually active male elephants, for example, experience a condition called musth (Poole 1989). Males who are in musth signal heightened aggression and intention to fight with glandular secretions, vocalizations, and urine marking. Musth appears to be a costly, honest signal of males' motivation to behave aggressively.

It is not clear whether internal motivational states or emotions regulate strategic commitments in primate groups. Researchers have not identified any signals in primates that are analogous to musth in elephants. It is possible that the behaviors that accompany aggressive displays, such as pilo-erection in chimpanzees or counter-chasing in baboons, may communicate information about the intention to fight, regardless of the immediate consequences. These might then constitute subjective commitments. However, this issue has not been systematically investigated among nonhuman primates.

There is, however, good reason to believe that strategic commitments in primate groups are enforced by reputational effects. Reputation is likely to be an important factor in shaping signaling strategies in species in which individuals recognize one another, interact repeatedly, and remember their previous encounters. Here, I present empirical evidence that primates make use of strategic commitments that are enforced by reputational effects and consider how evolution has shaped the evolution of these kinds of signals. This body of work is valuable because it demonstrates that subjective

commitments are not the only vehicle for generating behavior that contravenes self-interest.

Listening in on primate groups

Observers of primate groups know that monkeys and apes are rarely silent for long. Infant baboons cry loudly and persistently when their mother will not allow them to nurse (Altmann 1980), juvenile macaques scream to recruit support in conflicts with other group members (Gouzoules et al. 1984), gibbons perform complex duets at the borders of their territories (Mitani 1985), macaques and baboons give loud copulation calls after mating (O'Connell and Cowlishaw 1994; Hauser 1993), and male chimpanzees pant hoot loudly when they meet members of other traveling parties (Goodall 1986). These are the kinds of calls that most studies of primate communication focus upon. This is a bias that reflects the evolutionary design of these signals–they are loud and meant to attract attention. However, most primates also have a repertoire of quieter and less conspicuous vocalizations. A growing body of research suggests that some of these kinds of quiet vocalizations provide reliable information about the actor's intentions and disposition and are effective in facilitating social interactions.

Communicating peaceful intentions

Monkeys and apes tend to be contentious creatures. Macaques and baboons form strict dominance hierarchies, which often remain stable over years or even decades.

High rank confers both short-term and long-term advantages upon individuals. Dominance rank acts as an intervening variable which mediates access to resources, so high ranking individuals gain preferential access to food and mates. As a consequence, high ranking individuals tend to reproduce more successfully than lower ranking group members (Silk 1987).

In primate groups, some conflicts involve contests over food, but in many species the majority of aggressive interactions occur spontaneously (Walters and Seyfarth 1987). The prevalence of unprovoked aggression generates considerable uncertainty for females whenever they are in proximity to higher ranking females because there is always some risk of being threatened, chased, or attacked (Aureli et al. 1989). This may create an obstacle for friendly interactions. A female who is uncertain about whether she is going to be groomed or attacked, may be inclined to take evasive action when she is approached by more dominant female. While this may limit the risk of being attacked, it also restricts opportunities for friendly interactions, such as grooming. A growing body of data suggests that monkeys have devised an effective solution to this problem. They use quiet calls to communicate their intent to behave peacefully. This conjecture is based mainly on work conducted on semi-free-ranging rhesus macaques on the island of Cayo Santiago (Silk et al. in press) and free-ranging chacma baboons in the Moremi Reserve of Botswana (Cheney and Seyfarth 1997; Cheney et al. 1995b; Rendall et al. 1999; Silk et al. 1996).

Rhesus macaques have a repertoire of quiet calls, including two calls that are frequently used in affiliative contexts, grunts and girneys. These calls are both quiet, low frequency vocalizations. Grunts are short, harsh sounds produced through open lips with

a slightly dropped jaw (Hauser et al. 1993). Girneys are soft, low frequency, chewing noises accompanied by rapid lip movement (Green 1975). A careful analysis of the sequence of events that follow grunts and girneys suggests that these calls signal the actor's intention to behave benignly.

For female rhesus macaques, it is often dangerous to be close to higher ranking females. On Cayo Santiago, nearly one-quarter of all approaches by females led to some form of aggression. However, the likelihood that aggression would occur was directly associated with the use of grunts and girneys (Silk et al. 2000). Figure 1 demonstrates that females were much less likely to initiate aggression if they called as they approached other, lower ranking females than if they approached and remain silent. The magnitude of the effect was quite substantial: females were nearly 30 times more likely to act aggressively if they approached and remained silent than if they approached and grunted or girneyed.

These results suggest that grunts and girneys provide recipients with reliable evidence that the caller's subsequent behavior will be peaceful. This conjecture is supported by the fact that females were four times more likely to show spontaneous signs of submission when they were approached by females who did not call as when they were approached by females who called as they came near. Thus, females behaved as if they had some knowledge of what other females would do if they called and what they might do if they remained silent.

Callers really did seem to be motivated to interact affiliatively when they called. Females who called as they approached, subsequently groomed their partners nearly half

the time. On average, females who called as they approached were more than twice as likely to groom their partners as females who remained silent as they approached.

There is some evidence that grunts and girneys may play a similar role in other macaque species. Muroyama (1991) reported that Japanese macaques give girneys during grooming interactions, using one variant when they are attempting to groom others and another variant when they are attempting to solicit grooming from others. Masataka (1989) suggested that monkeys use calls to assess each others' motivation to interact peacefully.

Resolving Conflicts

Grunts seem to have much the same effect among baboons as grunts and girneys have among rhesus monkeys. Analyses of tape-recorded vocalizations indicate that baboon females' grunts carry acoustic information about the identity of the caller (Owren et al. 1997). Playback experiments conducted in the field show that grunts also carry rudimentary information about the context in which the call was given (Rendall et al. 1999). In the Moremi Reserve, grunts facilitate nonaggressive interactions and inhibit supplants among adult females (Cheney et al. 1995b; see also Barton et al. 1996).

In baboons, there is also evidence that grunts play an important role in resolving conflicts (Castles and Whiten 1998; Cheney & Seyfarth 1997; Cheney et al. 1995b; Gore 1994; Silk et al. 1996). In primate groups, former adversaries (or their kin) often interact peacefully with one another soon after conflicts have ended. These interactions are particularly striking because they are so unexpected–one would expect aggression to

drive former opponents further apart, not closer together. Nonetheless, former opponents are far more likely to interact nonaggressively in the minutes that follow conflicts than they are at other times (reviewed by de Waal and Aureli 1996). De Waal and van Roosmalen (1979) labeled these peaceful post-conflict interactions "reconciliation" because they hypothesized that they helped to mend social relationships that were damaged by conflict. Although there is some dispute about the long-term function of these interactions, there is broad consensus about their immediate effects. Peaceful post-conflict interactions relieve former opponents' anxiety that aggression will continue and facilitate affiliative interactions among former opponents (e.g. Aureli et al. 1989; Cheney and Seyfarth 1997; Silk et al. 1996).

In many primate species, it has proven difficult to identify specific behaviors that produce reconciliatory effects. But in baboons, both observational and experimental data confirm that baboons use grunts to signal that conflicts have ended and the callers' intentions are now benign. After conflicts have ended, aggressors sometimes approach and grunt to their former victims (Castles and Whiten 1998; Gore 1994; Silk et al. 1996). In Moremi, females who grunt to their former victims are more likely to interact peacefully with them in the minutes that follow conflicts than females who remain silent. Grunts also reduce the likelihood that aggression will resume (Figure 2). The importance of grunts in facilitating peaceful contact after conflicts is further supported by playback experiments in which reconciliation was simulated by playing the aggressor's tape-recorded grunt to her former victim. After hearing these calls, the victim was more likely to approach and initiate peaceful interactions with her former aggressor (Cheney and Seyfarth 1997).

Grunts may facilitate peaceful interactions among former opponents because they they relieve females' anxiety that the aggressor will continue to harass them. Evidence in support of this hypothesis comes from another playback experiment conducted in Moremi (Cheney et al. 1995b). This experiment took advantage of the fact that females sometimes scream when they are attacked by other group members, and victims of aggression sometimes redirect aggression toward lower ranking individuals. Thus, a female who hears the scream of a higher ranking female may expect to become the target of an attack herself. To determine whether grunting during the post-conflict period reduces females' anxiety about whether former aggressors will redirect aggression toward them, the tape-recorded screams of aggressors were played to their former victims: (a) shortly after they had fought and the aggressor had grunted to her former victim, (b) shortly after they had fought but the aggressor had not grunted to her former victim, and (c) after a period of 45 minutes in which they had not interacted at all. The last condition functions as a control. Females react most strongly to the screams of aggressors who had not grunted to them. Females' responses to aggressors who had subsequently grunted matched their responses when they had not interacted at all. Thus, grunts essentially erased the effects of prior conflicts. This suggests that grunts reassured former opponents that the conflict was over and the aggressor's intentions were peaceful.

Mother, May I?

In most primate species, females are intensely interested in other females' infants. They crowd around new mothers, attempting to sniff, nuzzle, touch, inspect, and tug on

infants who are still too young to stray from their mothers'embrace. Females groom new mothers assiduously, occasionally pausing long enough to touch the infant or peer at its genitals (Altmann 1980). We do not fully understand the adaptive function of "natal attraction", although a growing body of evidence suggests that it is a byproduct of selection for appropriate maternal care (Paul and Kuester 1996; Silk 1999b). But whatever its function, virtually all primate females fall under the thrall of newborn infants.

In macaque and baboon groups, infant handling is generally gentle, although females sometimes try to pull infants away from their mothers, creating a tug-of-war over the infant (Maestripieri 1994). Infants sometimes give distress calls when they are handled, particularly when they are disturbed while they are nursing or pulled vigorously. In macaque and baboon groups, mothers are usually wary when others try to handle their infants. In her classic book on baboon mothers and their infants, Jeanne Altmann wrote, "Mothers 'perceived' the mere approach or presence of certain individuals, and certainly handling and pulling of the infant as a threat or source of distress" (Altmann1980, 109). In Altmann's study, mothers exhibited the highest rates of distress during the months when their infants were the focus of the most intense interest by other females. Mothers' reluctance to allow their infants to be handled is presumably linked to concerns about their infants' welfare (Maestripieri 1994), although risks to infants during infant handling have not been assessed systematically.

In this situation, there is a clear conflict of interest between wary mothers and zealous handlers. Female macaques and baboons effectively resolve this impasse by vocalizing to mothers before they attempt to handle their infants. When female baboons

approach the mother of a newborn infant, they usually grunt softly to the mother before they reach out to touch or inspect her infant (personal observation). Similarly, stumptailed macaque (*Macaca arctoides*) mothers are less likely to respond aggressively to females who give quiet staccato grunts before they attempt to handle their infants than to females who remain silent (Bauers 1993). These soft grunts seem to act as signals of the callers' intention to behave benignly toward infants (Bauers 1993). Maternal tolerance reflects confidence in the reliability of the potential handler's commitment. .

If grunts signal females' benign disposition toward infants, then females who call as they approach mothers of newborns should behave nonaggressively toward their infants. Moreover, these calls should allay mothers' concern about the safety of their infants. As a consequence, calls should facilitate infant handling interactions. Detailed analyses of infant handling interactions among rhesus macaques confirm all three of these predictions (Kaldor 1996; Silk et al 2000).

Females usually handle infants gently, but on some occasions they do treat infants roughly and cause distress. Females who grunt or girney as they approach infants are significantly less likely to handle them roughly and cause distress than females who do not call as they approach. Mothersare less likely to respond aggressively or fearfully if females call before they handle infants than if they remain silent. Finally, females are significantly more likely to handle infants if they call to mothers and their infants than if they remain silent. As you can see in Figure 3, the magnitude of this effect is substantial– females who approached and remained silent handled infants 10% of the time on average, while females who approached and called handled infants 61% of the time on average. Thus, for rhesus macaques, who are otherwise contentious and competitive creatures,

grunts and girneys seem to convey important information about the caller's disposition and subsequent behavior toward infants.

The Evolution of Low Cost Signals of Commitment

Biological signaling theory provides a framework for understanding how signals should be designed and what kind of information they should convey. In order for communication to be effective, signals must convey reliable information, otherwise recipients will stop attending to them. However, honesty is not always the best strategy from a signaler's point of view. That is why you don't show your cards when you are playing poker, and why it would be unwise to believe your opponent if he tells you what cards he holds.

When the advantages of deception undermine the credibility of signals, how can honest communication be preserved? Zahavi (1975) provided the answer to this question. He suggested that the reliability of signals will be maintained by their cost. Signals that are very costly to produce or risky to give cannot be corrupted because it is not profitable for low-quality or poorly motivated individuals to give them. Thus, male red deer roar in the early stages of contests. These roars, which are loud and energetically expensive to produce, provide a reliable index of male's current physical condition (Clutton-Brock et al. 1982).

The same logic implies that when there is no incentive to lie, there is no need for signals to be costly. Suppose that you are engaged in a cooperative venture with a colleague, such as writing a textbook. You would probably decide to divide up the work

according to your expertise and interest. It would make no sense to tell your partner that you are willing to write the chapter on molecular genetics, if you have no intention of doing so. Since you share a common interest in completing the book, you have little reason to deceive your colleague about your intentions. Thus, you can send a brief email outlining your plans; and you don't need to work very hard to convince your partner that your message is credible.

This intuition was confirmed by Maynard Smith (1991, 1994) who explored the dynamics of low -cost signaling when there is no conflict of interest between the participants. The basic rationale underlying of evolutionary game theory is outlined by Dugatkin in Chapter 5. Maynard Smith devised the Philip Sidney game, which takes its name from a famous act of altruism performed by Sir Philip in the battle of Zutphen. Sir Philip, a member of the court of Elizabeth I, was a celebrated poet and diplomat. In the service of the Queen, Sir Philip joined a military campaign that was intended to protect the Netherlands against ongoing attacks by Spain. In 1586, Sir Philip was mortally wounded in the battle of Zutphen, an event that was recorded by his life-long friend, Sir Fulke Greville:

> An unfortunate hand brake the bone of Sir Philip's thigh with a musket shot. The horse he rode upon, was rather furiously choleric than bravely proud, and so forced him to forsake the field, and being thirsty with excess of bleeding, he called for drink, which was presently brought him; but as he was putting the bottle to his mouth, he saw a poor soldier carried along, who had eaten his last at the same Feast, ghastly casting up his eyes at the bottle. When Sir Philip perceiving, took it from his head,

> before he drank, and delivered it to the poor man, with these words, Thy necessity is greater than mine…(Greville 1652: 128).

Sir Philip died from his injuries three weeks after the battle at the age of 32.

In the Philip Sidney game, a potential donor (Sir Philip) is paired with a potential benficiary (the soldier). The donor has a resource (water bottle) that can be given to the beneficiary. The donor suffers some cost if he gives up the water bottle, but the beneficiary gains an advantage from obtaining it, particularly if he is thirsty. If the donor and the recipient have an interest in each other's survival, either because they are kin and share common genes or because they are allies and share a common interest in the outcome of the battle, then evolution can favor the evolution of cost-free signals of the beneficiary's need for the resource (Maynard Smith 1991) and cost-free signals of the donor's willingness to provide the resource (Maynard Smith 1994).

There are other situations in which deception is unprofitable, and signals may consequently be inexpensive. Suppose that you and your partner want to have dinner together after work. It makes no sense to tell your partner you will meet at the Mexican restaurant downtown if you actually intend to go to the Thai restaurant near your office. Since you have no incentive to lie, your partner does not need to worry about your credibility. But Farrel and Rabin (1996) have demonstrated that truthful low-cost signaling does not necessarily depend on both partners having the same preferences. Even if you want to eat at the Thai restaurant and your partner wants to go the Mexican restaurant, you are better off being truthful if you'd rather eat together than alone. Again, since you don't benefit by lying, your partner has little concern about your credibility.

The basic logic of this situation is explored in the Battle of the Sexes game. In the traditional version of the game, both parties choose their destination without communicating their intentions. Then, the only evolutionary stable strategy is for both players to choose their own preferred destination with the same probability. If you follow this strategy to decide which restaurant to go to, you and your partner will often end up at different restaurants. Of course, in this situation, most people do not rely on chance–they talk. Since they want to eat together, they have no reason to lie about where they intend to go and no reason to doubt their partner's credibility. Farrel and Rabin (1996) have shown that low cost signals (cheap talk) can be favored when preferences differ, as long as coordination is sufficiently valued. (This does not necessarily mean that signallers will obtain their most preferred outcome. When preferences differ, individuals may have to negotiate, sometimes at length, or adopt on a conventional asymmetry, such as flipping a coin, to resolve the impasse.

When monkeys grunt after conflicts or girney before they groom, it's plausible that both partners benefit from the exchange of information, and that explains why the signals that they use in these situations are quiet and inconspciuous. But the same kinds of quiet, low-cost calls are used to facilitate infant handling, an interaction that seems to represent a real conflict of interest between females who have no interest in coordination. How can this be?

Most of the work on the evolution of communication in conflict situations assumes that individuals interact only once. But for animals who live in social groups, meet repeatedly, and remember their interactions this is not a realistic assumption. If individuals use their memory of past experiences to evaluate the reliability of

information, then reputation may play an important role in the assessment of signals (Maynard Smith 1982; van Rhijn 1980; van Rhijn and Vodegel 1980). Actors who give false signals may benefit initially from deceiving others, but the benefits of deception will be short-lived if recipients stop believing those who have deceived them in the past (Slater 1983).

The conflict between the short-term benefits of lying and the long-term benefits of telling the truth may be very real for animals living in social groups. The reluctance of mothers to allow their infants to be handled is likely to be based at least partly on the fact that other females sometimes harass and attack infants (Maestripieri 1994). Harassment of infants is generally interpreted as a form of reproductive competition (Silk 1980, Wasser 1983). If females benefit from harassing other females' infants, then they might be able to use grunts to lull mothers of newborns into complacency. A female who grunts as she approaches a mother-infant pair, and then bites the infant, may be able to catch the mother unawares. But if mothers remember acts of deception, such strategies will only work once. Subsequently, the deceptive female will not be able to use this device again and she won't be able to handle the females' infant either.

My colleagues and I have explored the dynamics of signaling when there is a potential conflict of interest, but individuals meet repeatedly, remember their interactions, and condition their behavior on their prior experience (Silk et al. 2000). We imagine a situation in which one individual approaches another individual. The actor's disposition is benign some fraction of the time, but the recipient is initially unaware of the actor's disposition. When the actor approaches the recipient ,she can produce a signal that conveys information about her disposition. At this point, the recipient can decide to stay

and interact or flee. If the actor's disposition is benign and the recipient stays put, then they interact peacefully.

In our model, actors have three strategies. Truthful signalers (TF) call when they intend to behave nicely, and otherwise remain silent. Deceptive signalers always signal (AS) no matter what they intend to do. Nonsignalers (NS) remain silent even when they intend to behave benignly. Recipients also have three possible responses: they may always interact (AI) regardless of the signalers behavior, they may always flee (AF), or they may alter their behavior based on the actor's prior experience. Conditional believers (CB) believe the actor until they are deceived, but once they have been deceived, they always flee. The CB strategy provides a simple way to capture the idea that the recipient's behavior is contingent on the their previous experience with the actor. The decision tree shown in Figure 4 outlines all of the possible combinations of strategies and the behavioral outcomes that result.

The results of this game theory model indicate that if conditional believers are common, truthful signaling is an evolutionarily stable strategy whenever the future benefits of being believed exceed the short-term benefits achieved by lying. Moreover, the more often the actor is disposed to behave benignly, the less advantageous it is to lie in any given interaction. The results confirm that it is not necessary for the participants to rank outcomes in the same order. Thus, low cost signals can evolve even when there is a conflict of interest between participants as long as partners interact repeatedly and condition their behavior on the basis of past experience.

Communicating Commitment

Monkeys who give grunts or girneys typically behave peacefully, while monkeys who do not call in the same contexts are more likely to behave aggressively, cause distress to infants, or resume fighting. Females' responses indicate that they have some awareness of the association between these calls and the kinds of outcomes that typically follow. Monkeys' use of signals of intent does not require any conscious knowledge of the consequences of their behavior, just as males' interest in mating with receptive females does not imply any conscious knowledge of the association between copulation and conception. We have no evidence that female monkeys understand other individuals' intentions or have insight about their internal mental states. The effectiveness of these signals simply implies that they have learned to associate these kinds of calls with benign outcomes (Cheney and Seyfarth 1996).

Nonetheless, signals of intent fit the definition of strategic commitments because they entail an obligation to behave in certain ways and preclude certain alternatives. When females give grunts or girneys, they are effectively guaranteeing that they will behave peacefully. These kinds of calls function as pledges or promises to behave peacefully, even when it might be in their short-term interest to behave aggressively. It is females' confidence in the reliability of the promise that makes them effective. A female who grunts as she approaches the mother of a newborn infant gives up her option to harass the infant, even though there are some circumstances under which this deception might yield short-term benefits.

Unlike costly signals, which are not profitable to use deceptively, low-cost signals of intent could be faked readily. But deceit may be counterproductive in the long term. "In close-knit groups of animals, where individuals recognise one another and interact with each other over extended periods, the long-term penalties which may arise if deceit is discovered may more than outweigh any short-term gain it makes possible" (Slater 1983). In fact, there are very few well-documented examples of tactical deception among monkeys, although apes may be more devious (Whiten and Byrne 1988). This is usually explained as a result of the fact that monkeys do not have the cognitive abilities that are required for deception, such as attribution and perspective-taking. However, it is also possible that deception may be uncommon because it is ultimately an unprofitable tactic for group living animals with long term social bonds.

I have suggested here that strategic commitments are enforced through reputational effects. If this is correct then it might be productive to study how reputation influences the nature of social interactions within animal groups. Primates seem to know a considerable amount about their own relationships to other group members, including kinship, relative dominance rank, and the quality of social bonds (Tomasello and Call 1997). A growing body of evidence indicates that primates also know something about the same aspects of the relationships among other group members (Bachmann and Kummer 1980; Cheney and Seyfarth 1999; Cheney et al. 1995a; Dasser 1988a,b; Silk 1999a). It is not clear whether or how monkeys use this information to assess the behavioral predispositions of others. We are reasonably certain that monkeys make use of information derived from their own interactions with other group members to regulate their social relationships. For example, female baboons selectively groom unrelated

females who groom them in return (Silk et al. 1999), male bonnet macaques are most likely to intervene against the males who are most likely to intervene against them (Silk 1992), and female macaques selectively reconcile with kin and close associates (Cords and Aureli 2000). However, we do not know whether primates' assessments about the behavioral predispositions of their partners are based solely on their own experiences or include information derived from observations of their interactions with others.

It should be possible to design experiments that would address this question empirically. For example, we might artificially manipulate exchanges of valued food resources, and investigate whether observers were attracted to individuals who reciprocated reliably or were indifferent to this information. We might also evaluate the weight animals placed on their own experiences with particular partners versus the experiences of others. It might also be useful to conduct playback experiments to examine the effects of manipulating the honesty of signals. For example, a dominant baboon's grunt could be paired with a subordinate baboon's scream. This is an anomalous sequence if grunts are reliable signals of peaceful intent (Cheney et al. 1995a). If baboons keep track of the reliability of other animals' signals, then those who hear this sequence of calls would be expected to respond more warily when approached by the "unreliable" dominant female than those who have heard a typical sequence of calls. Experiments like these would help us to determine whether primates make use of third party information about the reputations of other group members.

The mechanisms that underly strategic commitments in nonhuman primates are not yet fully understood. Detailed ethological observations and carefully designed experimental studies may help to clarify the role of reputational effects and subjective

commitments in enforcing strategic commitments among monkeys and apes. By documenting the full range of commitment strategies that we see in nature, we may ultimately be able to trace the evolutionary history of the human capacity for subjective commitment.

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Figure Legends

Figure 1. Among rhesus macaques, grunts and girneys inhibit aggression. Here, the proportions of approaches with and without calls that were followed by aggression are plotted. Each pair of open circles linked by a line represents paired values for a single female. The solid circles represent pairs of females who had identical values and the solid diamond represents three females who had identical values. (From Silk et al. 2000).

Figure 2. Females who grunted as they approached former victims were more likely to interact peacefully and less like to supplant or harass their former victims than former aggressors who remained silent as they approached. (From Silk et al. 1996.)

Figure 3. Among rhesus macaques, grunts and girneys facilitate infant handling. Here, the proportions of approaches with and without calls that were followed by infant handling is compared. Open circles represent individual females, solid circles represent pairs of females with identical values, and the solid diamond represents three females who had identical values. (From Silk et al. 2000.)

Figure 4. This decision tree summarizes the sequence of possible moves and associated payoffs for each player. Initially, the actor's disposition is benign or hostile, but this internal state is not known by the recipient. The actor or signal or not signal. The recipient may interact or flee. The behavioral outcomes that result from each sequence of moves are given at the terminal nodes of the tree. The payoffs associated with each sequence are given on the right side of the figure. The actor's payoffs reflect the effects

of interacting peacefully (*I*), supplanting the recipient (*D*), or attacking the recipient (*E*) minus the costs of signaling honestly (*t*) or dishonestly (*k*). The payoffs to the recipient reflect the effects of interacting peacefully (*i)*, being supplanted (*d*), or being attacked (*e*). (From Silk et al. 2000.)