

Practice Random Acts of Aggression and Senseless Acts of Intimidation: The Logic of Status Contests in Social Groups

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A group of baboons is scattered across the open plains. Most members of the group are digging up grass corms, while a few rest in the shade of thorny bushes. Several juveniles bounce on the unstable limbs of a dead tree. One female who is resting in the shade looks up as a dominant female approaches. The dominant female stops a few meters away and begins feeding. Suddenly the dominant female lunges at the resting female, who leaps away, screaming and grimacing. The dominant female grunts and resumes feeding.

Events like this occur every day in cercopithecine primate groups. What is striking about these attacks is that they are sudden, unprovoked, and unpredictable. These kinds of interactions reinforce existing dominance relationships, but do not directly affect access to valuable resources. Here, I suggest that randomly timed attacks on randomly selected subordinates are part of an evolved strategy that has been favored by natural selection because it maximizes the negative impact on the victim and minimizes the cost to the aggressor.

THE LOGIC OF CONTESTS

In conventional models of contests, it is assumed that animals fight with

strangers over important resources. In contests over resources, the payoffs derived from escalated contests are a function of the fighting abilities, or resource-holding potential, of the participants and the value of the resource to each party.¹ The payoffs determine how hard each participant is willing to fight to gain access to a particular resource. When fighting is costly, it is profitable for individuals to exchange information about asymmetries in their payoffs. These signals allow each individual to assess its opponent's payoffs and compare them to their own. Thus, Harper² stated that "Contests should escalate gradually in a way that increases the probability that any asymmetry is detected before injury is risked. . . . Gradual escalation is a common feature of animal contests."

In status contests, asymmetries in payoffs are based only on differences in fighting ability, or resource-holding potential. This is because the value of winning contests is likely to be the same for both parties: Dominant animals benefit from remaining dominant and subordinates benefit from becoming dominant. Thus, differences in resource-holding potential will determine the relative payoffs. If the participants perceive differences in resource holding potential, contests may be resolved without fighting. For example, substantial differences in

body size or weight may be detected by both parties, and the less powerful contestant may cede the resource to its opponent. But if differences in resource-holding potential are not certain, then gradual escalation of conflicts is expected to be advantageous to both parties.

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only once or that they are unable to remember the outcome of previous encounters.³ This assumption does not hold for animals like primates, which live in social groups, recognize individuals, and remember past interactions. Prior experience may provide information about relative resource-holding potential because animals

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recognize their opponents and remember the outcomes of previous conflicts. Contests are often used to reinforce dominance relationships among individuals, even in groups with very stable dominance hierarchies and rare challenges to dominant members.

When differences in resource-holding potential are known before a conflict begins and resources are not at stake, then there is no need to exchange information about payoff asymmetries. In these cases, it might be advantageous for aggressors to strike suddenly and without warning. Unpredictable and unprovoked attacks enable aggressors to deliver the maximum damage to their victims at minimum cost to themselves. If aggressors signal their intention to attack, their victims will be able to escape, launch counterattacks, or recruit allies to defend them. Thus, aggressors are not expected to signal their hostile intentions² and victims are not expected to be able to guess when aggressors will attack.

The best way to prevent victims from anticipating when they will be attacked is to launch randomly timed attacks. However, this does not mean that animals will ignore all contextual information. For example, animals might avoid launching attacks on victims who are surrounded by their relatives or sitting near powerful allies. Similarly, they might not interrupt productive foraging bouts or satisfying grooming bouts to attack others. In these cases, the costs of aggression may outweigh the benefits gained from intimidating subordinates. However, for this strategy to be effective, there must be a high degree of unpredictability in the timing and context of aggression and the selection of victims.

An alternative strategy is to launch attacks when potential victims are least able to protect themselves or evade aggression. By "biding their time," aggressors may be able to increase the likelihood of winning and reduce the costs they incur. However, if aggressors bide their time and choose particularly auspicious moments to attack, victims may learn to increase their levels of vigilance and reduce the aggressor's advantage at these times. This would produce an "arms race" as aggressors become

more cunning and potential victims become more wary.

THE LOGIC OF RANDOM AGGRESSION

The logic of random aggression exploits mammalian stress physiology. The stress response is adaptive because it enables animals to mount rapid responses to external threats. However, long-term activation of the stress response is pathogenic.⁴⁻⁶ In social species within which subordination is associated with high rates of stressors and

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low availability of coping responses, subordinates tend to suffer the most stress and are most vulnerable to stress-related diseases that impair health and reduce fertility. In species that show these patterns, subordinates, as compared to dominant animals, have been reported to have higher glucocorticoid levels, higher levels of hypertension, fewer circulating lymphocytes, lower levels of HDL cholesterol, impaired cardiovascular responses, and higher risk of developing atherosclerosis and reduced fertility.⁶

When the source of stress is held constant, animals react most strongly to stressors they cannot predict and cannot control.^{4,6,7-10} If animals can anticipate when they will be stressed, they are able to mount physiological responses that help mitigate the impact of the stressful stimuli. But when animals cannot predict when stressful events will occur, they are unable to prepare for them and therefore react more strongly. In addition, if animals cannot predict how long stressors will continue, they are unable to determine how long they must sustain the response.

Randomly timed attacks on randomly selected targets are effective because the victims of aggression cannot predict when they will be subjected to harassment. If animals cannot predict when or where they will be attacked, then they must maintain physiological responses that prepare them to respond to aggression. If animals cannot anticipate how long attacks will last, they are unable to calibrate the length of their response or predict when it is safe to relax. Long-term activation of these physiological responses carries significant biological costs.⁶

Randomly timed attacks on randomly selected targets are also efficient because the potential for unprovoked, unanticipated violence is sufficient to generate stress in subordinates, while potential aggressors do not regularly incur the costs associated with high levels of escalated aggression. Of course, if threats are never translated into action, potential victims will eventually learn that they have no reason to be fearful. Thus, aggressors must sometimes attack subordinates to legitimate the threat of aggression. But these attacks need not be common to be effective in generating stress in subordinates.

Launching randomly timed attacks on randomly selected targets is an advantageous aggressive tactic because it limits the costs to dominants while increasing costs incurred by subordinates. The random timing and selection of targets provides a means for dominant animals to generate continuous uncertainty in subordinates. Uncertainty about when, where, and to whom attacks will be directed produces long-term, low-level stress in subordinates. Long-term stress has

debilitating effects and is likely to shorten life span and reduce reproductive success. At the same time, dominants need only attack often enough to maintain the plausible threat of aggression. This reduces the costs that they incur when they become involved in escalated aggression.

APPLYING THE LOGIC OF RANDOM AGGRESSION IN CERCOPITHECINE PRIMATE GROUPS

The logic of unprovoked and unpredictable aggression potentially applies to any animals that live in stable groups of familiar individuals, interact repeatedly, remember past interactions, and use dominance to mediate access to valuable resources. In these situations, payoffs in contests will be determined mainly by differences in resource-holding potential or dominance rank. Asymmetries in resource-holding potential will often be evident to group members. Here I explore the logic of random aggression in one group of Old World primates.

The anecdote that begins this paper reflects the general consensus that it is often impossible to identify the immediate reasons why nonhuman primates, particularly cercopithecine females, fight. For example, Walters and Seyfarth¹¹ wrote, "Much of the aggression within primate groups is not directly related to resource competition but instead appears to involve the establishment and maintenance of dominance relationships. . . . Dominant individuals in many species frequently approach subordinates, apparently causing them to withdraw, or they may actively harass subordinates by directing aggression at them without apparent provocation, thus eliciting submissive behavior" (p. 308). Smuts¹² noted that females frequently attack other females without warning, citing work on Sykes monkeys, chimpanzees, savanna baboons, and vervet monkeys.

Cercopithecine females compete over access to resources. In many species, however, resource competition usually takes the form of nonagonistic supplants in which a dominant female approaches a subordinate female and the subordinate female moves away.

The outcome of supplants is tightly linked to relative dominance rank: Dominants supplant subordinates, but not vice versa. Hence, dominance rank mediates access to resources. Rates of escalated aggression are very low, and the majority of aggressive contests among females cannot be linked to specific events or contexts. In contrast, supplants are more common and most often involve access to valued resources such as food, desirable resting spots, or grooming partners.

Among cercopithecine females, asymmetries in resource-holding po-

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tential are generally known to the participants. Females form matrilineal dominance hierarchies that remain stable over years, even decades.¹³ In these species, dominant females invariably defeat subordinates in status contests. Monkeys seem to know whether they rank above or below other monkeys; they also seem to know the relative ranks of other pairs of animals in their groups.¹⁴⁻¹⁶

In female monkeys, uncertainty about the prospect of receiving aggression produces stress. Castles, Whiten, and Aureli¹⁷ found that rates

of self-directed behavior, which are correlated with physiological measures of stress, rose 40% when female baboons were near higher ranking females, even when no overt signs of aggression were given. Similarly, in a small sample of captive rhesus macaque females, Aureli, Preston, and de Waal¹⁸ found that approaches by dominants produced increases in heart rate, while approaches by kin and subordinates had no effect on heart rates. When female macaques are near dominant males, rates of self-directed behaviors also increase.^{19,20} Thus, in situations in which conflict is possible, rates of self-directed behavior tend to rise.²¹⁻²³

Responses to actual aggression are similar to the responses to potential aggression. The elevation of victims' heart rates triggered by aggressive attacks persists for several minutes after fights have ended.^{24,25} Rates of self-directed behaviors also rise after conflicts and remain elevated for several minutes if there is uncertainty about whether the fight has actually ended.^{26,27} When former opponents reconcile after conflicts, thus reducing uncertainty about whether aggression will continue, heart rates and rates of self-directed behaviors decline rapidly to baseline levels.

AN ANTIDOTE TO RANDOM AGGRESSION

The tactic of launching randomly timed attacks on randomly selected subordinates has at least one major drawback: if attacks are effective, then it will be difficult for dominants to interact with subordinates, even when their intentions are peaceful. This may make it hard for dominants to approach subordinates in order to solicit grooming, handle their infants, or huddle together for warmth. This dilemma may have favored the evolution of signals that alleviate uncertainty about actors' subsequent behavior. Baboons and macaques sometimes give quiet calls when they approach other females. These signals reduce the likelihood that subordinate females will be supplanted or show spontaneous signs of submission.^{28,29} Baboons sometimes give these calls to former opponents in the minutes that follow conflicts and almost always before handling infants. Playback exper-

iments indicate that post-conflict grunts reassure former victims of aggression that the agonistic dispute is over and that the caller will behave peacefully.^{28,30} Thus, these signals of benign intent may be an antidote to random aggression.

TESTING THE HYPOTHESIS

This is not an easy hypothesis to test because it is difficult to detect random patterns in nature. While an observer may conclude that an aggressive attack is unprovoked and unanticipated, the animals may perceive subtle signals that observers miss or respond to environmental cues that observers do not detect. However, the hypothesis generates several predictions that could be tested empirically.

The logic of random aggression is not expected to apply when asymmetries in resource holding potential are not well established. For example, in cercopithecine groups ambiguity about females' resource-holding potential regularly arises when young females begin to establish their position in the adult female dominance hierarchy. Female rank acquisition has highly consistent outcomes among baboons and macaques, with young females typically acquiring ranks just below those of their mothers and adjacent to those of their older sisters.³¹ Nonetheless, there is considerable variation in the timing of rank acquisition.³² Females often encounter resistance as they target older, larger, and stronger females for rank reversals.^{32,33} In situations of this kind there is likely to be uncertainty about resource-holding potential. Thus, we would expect that contests in which young females target older females for rank reversals would involve gradual escalation and be more protracted than contests among females whose ranks are firmly established.

Similarly, on the rare occasions when rank relationships among females become unstable, we would expect aggression to involve gradual escalation and assessment. This prediction is consistent with events observed during the reorganization of the adult female hierarchy in a group of savanna baboons at Gilgil. While female baboons at Gilgil normally attacked suddenly and without warning, during the period of rank change fe-

males performed "ritualized threats," including repeated circling, tooth grinding, and yawning. Females also solicited support from other females using elaborate gestures.¹²

In cercopithecine primates, males are expected to use different aggressive tactics than females do because there is greater uncertainty about resource-holding potential and because males more often fight over access to resources, such as receptive females.

The logic of random aggression predicts that the timing and predictability of aggression will be linked to the context in which contests occur. When animals fight over food or females, they are expected to initiate contests soon after they come into proximity with potential opponents. However, when animals fight over status and there is little uncertainty about resource-holding potential, contests are expected to be randomly distributed across time.

Uncertainty about resource-holding potential among males comes from two sources. First, males in these species can be ranked in linear dominance hierarchies, but these hierarchies shift at frequent intervals.¹¹ Second, males are the dispersing sex and therefore confront unfamiliar males when they move to new groups or when males immigrate into their groups. Cercopithecine males are armed with dangerous canines, and males

are sometimes seriously wounded in aggressive contests with other males. Several studies have reported that males are wounded more often than are females.^{12,34,35} In agonistic encounters with other males, male baboons, vervet monkeys, and macaques use ritualized threats such as yawning and tooth grinding.¹² Ritualized threats usually precede agonistic encounters among males. Moreover, when male baboons attempt to take over consortships, they often engage in protracted contests involving elaborate yawning, loud vocalizations, long chases and counterchases, recruitment of allies, and gradual escalation. Of course, this does not entirely eliminate the risk of escalation. Males are sometimes wounded in male-male contests. Rank challenges are also expected to involve sequences of aggression of progressively greater intensity.

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The logic of random aggression also applies to the selection of targets. When differences in resource-holding potential are well known, contests over resources will tend to involve animals of similar rank because animals of very disparate ranks will settle contests without fighting. However, contests over status will not be limited to animals of adjacent rank; aggressors will harass randomly selected subordinates. For example, if female monkeys compete for grooming partners,^{36,37} we would expect aggressive contests over grooming partners to be

most common among females of adjacent rank, while aggressive contests over status would be evenly distributed among females of all rank distances. Although females may derive little benefit from harassing much lower ranking females, who are unlikely to challenge them, there is also a concomitant reduction in cost because much lower ranking females are unlikely to retaliate.

CONCLUSIONS

Conventional models of the evolution of contests focus mainly on the dynamics of contests over resources among unfamiliar individuals. But for animals that live in stable social groups, interact repeatedly with familiar individuals, and remember the outcome of previous contests, these conditions do not represent the norm. In this situation, randomly timed attacks on randomly selected targets creates continuing uncertainty in subordinates about when and if they will be attacked. This uncertainty generates long-term, low-level stress, which has deleterious long-term effects on subordinates. Dominants benefit because they are able to inflict these costs on subordinates but are able to minimize the risks associated with escalated aggression. Thus, randomly timed attacks on randomly selected targets may be favored by natural selection because this strategy is both effective and efficient. Cercopithecine females seem to adopt this strategy, launching unprovoked attacks on unsuspecting subordinate targets.

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