

## Agonistic and Affiliative Signals: Resolutions of Conflict

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### Vocal Displays

Most competitive interactions among animals take the form of vocal, visual, or gestural displays: loud calls, threatening postures, or other behaviors that allow rivals to assess each other without escalating the displays into potentially costly attacks. Regardless of the species involved, displays have one essential property: they involve signals of competitive ability that are difficult, if not impossible, to fake. Male red deer, for example, challenge and assess one another by the amplitude and pitch of their roars. These acoustic features are reliable indicators of size and endurance because only large males in excellent condition can produce loud, low-pitched roars. In much the same way, songbirds challenge and assess one another by the size of their song repertoires. Males with large and complex song repertoires are often older, more experienced, or in better condition than others. Repertoire size is therefore a reliable indicator of a male's age and condition, which in turn is correlated with his competitive ability.

Because natural selection favors the skeptical observer and acts against any individuals who allow themselves to be duped by traits that are unrelated to fighting ability, the only displays that persist over time are 'honest' indicators of a male's condition. Displays will always be more common than actual fighting because, regardless of the competitive ability he brings to the table, it invariably pays a male to display first, before the fight escalates and results in injury. Avoiding injury is of paramount importance because the cost of being injured almost always outweighs the benefits to be gained from any single dispute.

Male baboons' competitive displays take the form of violent chases and loud 'wahoo' calls. Wahoos are low-pitched calls that can be produced only by adult males in good condition. They are costly to produce, not just because of their loudness and low pitch, but also because males give them in long bouts, often as they run or jump through trees. A wahoo display is therefore an exhausting demonstration of a male's stamina and coordination. High-ranking males are more likely than low-ranking males to enter wahoo contests. They also give wahoos at the highest rate and produce wahoos with longer and louder *hoo* syllables than the wahoos of other males. As males

age and fall in rank, they are less likely to enter wahoo contests, and the quality of their wahoos deteriorates substantially. The predictable relation between a male's rank and the quality of his wahoos allows competitors to assess each other without actual fighting. Males of very disparate ranks seldom engage in wahoo contests, presumably because subordinate males can assess, through their rival's wahoos and behavior, that they are outmatched. By contrast, wahoo contests involving males of similar rank – whose wahoos sound more alike – occur at high rates. Their contests also involve longer calling bouts, occur for unpredictable reasons, and are more likely to escalate to physical fights and wounding.

### Vocalizations as Aggressive Signals

Wahoos allow male baboons to assess each other without escalating the contest to fighting. Other primate vocalizations also function to mediate and influence aggressive interactions. Female baboons, like females in most Old World monkey species, remain in their natal groups throughout their lives and maintain close bonds with their matrilineal kin. They assume dominance ranks similar to their mothers', with the result that the female dominance hierarchy is a stable hierarchy of matrilineal. During aggressive disputes against lower-ranking opponents, female monkeys often form alliances both with their close relatives and with higher-ranking individuals. In baboons, most alliances do not involve physical intervention but occur in the form of vocal support: a female utters a series of threat grunts as she observes another female threaten another. In a series of playback experiments, subordinate female baboons were played the threat grunts of their opponent's relative within minutes after they had been threatened. As one control, they heard the same individual's threat grunt in the absence of a recent fight. After receiving aggression, subjects responded strongly to the threat grunts of their opponent's relative, and in the next hour they avoided both their opponent and the relative whose threat grunt they had heard. In contrast, if they had not recently been threatened, subjects ignored the threat grunts, and they did not try to avoid the signaler or her relative. In this case, subjects appeared to regard the threat grunts as directed as someone else.

Vocal 'alliances,' therefore, appear to serve the same function as alliances involving chases and threats. Rather than physically intervening, however, female baboons signal their support by communicating their willingness to do so.

### **The Resolution of Ambiguity**

Communicative signals can also resolve the ambiguity surrounding less aggressive interactions. For example, when a high-ranking female baboon approaches a lower-ranking one, there is always some ambiguity about what will happen next. On the one hand, the high-ranking female might be attempting to groom the lower-ranking one. On the other hand, she might be attempting to supplant or threaten the lower-ranking female from a desirable resource. This uncertainty creates a dilemma, both for high-ranking females who want to behave in a friendly manner and for low-ranking females who are reluctant to give up a resource. In the face of such uncertainty, analyses based on game theory predict the evolution of low-cost, reliable signals that provide accurate information about the signaler's disposition and motivation. In baboons and other monkeys, grunts serve this function. They are individually distinctive and highly predictive of friendly behavior, and listeners respond accordingly. If a high-ranking female baboon grunts while approaching a lower-ranking one, the lower-ranking one is likely to remain seated. High-ranking females almost never threaten a lower-ranking female after grunting to her. Conversely, if the approaching female remains silent, the lower-ranking female usually moves away.

Finally, when aggression does occur, communicative signals can mollify its effects. Nonhuman primates are frequently aggressive toward one another, yet they live in relatively stable, cohesive social groups. A number of studies have shown that opponents mitigate the effects of aggressive competition by grooming or interacting in a friendly manner soon after they fight. In baboons, such interactions are usually preceded by a grunt from the dominant aggressor to her subordinate opponent. Dominant female baboons grunt to their subordinate victims following roughly 13% of all fights. These grunts appear to serve a reconciliatory function because subordinate victims are more likely both to approach their former opponent and to tolerate her approaches if her opponent has grunted to her than if she has remained silent.

### **Testing the Reconciliatory Hypothesis**

The hypothesis that grunts alone, in the absence of other corroborating behavior, can serve a reconciliatory function, has been tested in a playback experiment that mimicked vocal reconciliation. Within minutes of being threatened by a higher-ranking female, subjects were played their opponent's grunt.

As controls, subjects heard either no grunt or the grunt of an uninvolved, high-ranking female unrelated to their opponent.

After hearing their opponent's grunt, subjects approached their opponent and tolerated her approaches – by not moving away – at significantly higher rates than they did under baseline conditions, when no aggression had occurred. These results confirmed observational results, which indicated that rates of approaching and grunting increase substantially after conflict. Apparently, a reconciliatory grunt caused subordinate females not just to relax but to seek out their former opponent.

If, however, subjects heard either no grunt or the grunt of a different dominant female, they continued to avoid their opponent and retreated from her approaches. Subjects approached their former opponent after only 2% of the trials involving either no grunt or the control female's grunt. In contrast, they did so in 42% of the trials conducted after playback of their opponent's grunt.

Subjects did not, however, simply change their disposition toward *any* female whose grunt they heard, because hearing the control female's grunt caused no change in their behavior. After playback of the control female's grunt, subjects did not approach that female at higher rates or attempt to interact with her: the change in their behavior was specific to their opponent. They appeared to regard their opponent's grunt as directed at themselves, and they acted as if they regarded the control female's grunt as irrelevant and directed at someone else.

This is not to say, however, that aggression causes baboons to attend only to their opponent's vocalizations and to ignore all other individuals' calls. Although they appear to regard the grunts of unrelated females as irrelevant to the fight, this is not true of the grunts of their opponent's relatives. To test how kinship affects reconciliation, subjects were played the 'reconciliatory' grunt of their opponent's relative soon after being threatened. A grunt from a dominant female from a different matriline served as a control. Once again, subjects responded as if they assumed that the relative's vocalization was directed at themselves and related to the recent fight. Moreover, the calls seemed to serve a reconciliatory function. After hearing the grunt, subjects did not avoid their opponent or her relative; indeed, they often approached both the relative and the opponent. And when they did so, their first interaction with their opponent was less likely to be submissive, and more likely to be friendly, if they had heard a reconciliatory grunt from their opponent's relative than if they had heard a grunt from anyone else.

## The Cognitive Mechanisms Underlying Reconciliation

What are the mechanisms that underlie vocal reconciliation in baboons? In its richest interpretation, 'reconciliation' implies that the dominant female recognizes that her victim is anxious and afraid – emotions that she herself is not experiencing – and grunts to alleviate the subordinate's anxiety. The subordinate, in turn, recognizes the dominant's intent to reconcile. In contrast, an alternative hypothesis based on learned contingencies makes no assumptions about animals' ability to recognize other individuals' mental states. It argues only that dominant females grunt to subordinates in order to influence their behavior. Through experience, dominant females learn that subordinate females are less likely to move away from them when they grunt than when they remain silent. Being sensitive to contingencies, subordinate females learn that grunts are associated with friendly behavior, so they do not move away when their former opponent grunts to them.

The playback experiments just described indicated that subordinate females were more likely to approach their former opponent and to tolerate her approaches if they heard her grunt than if they did not. In contrast, hearing the grunt of a different, unrelated dominant female produced no change in their behavior. They appeared to regard that call as directed at someone else. These results are consistent with the hypothesis that baboons have a rudimentary understanding of other individuals' intentions toward themselves, an ability that constitutes a crucial precursor to the attribution of other individuals' mental states. Alternatively, a recent interaction with a particular individual might simply prime baboons to attend preferentially to that individual's vocalizations. This more parsimonious explanation does not require that baboons make inferences about the directedness of calls.

A playback experiment to examine whether baboons' responses to another female's vocalizations are influenced by the nature of prior interactions with that individual again followed a matched-pair design. In the first condition, a subordinate female was played the threat grunts of a dominant female shortly after that female had threatened her. Because females sometimes threaten their victim again soon after their original fight, listeners might interpret these threat grunts as an indicator of renewed aggression directed at them. In the second condition, the same subordinate female was played the same dominant female's threat grunts shortly after the two had groomed. Because females almost never threaten a recent grooming partner, listeners might interpret the call as directed at someone else.

If baboons' responses to threat grunts are simply the result of priming by a recent interaction, subjects' responses after being threatened should have been the same as their responses after being groomed. If, however, listeners take into account the nature of recent interactions when making inferences about the intended recipient of a call, they should interpret the two threat grunts differently – directed at themselves after aggression, but directed at someone else after grooming. Specifically, subjects might respond more strongly to threat grunts after receiving aggression than after a grooming bout. We also predicted that a subject would be less likely to approach her former opponent and more likely to retreat from her approaches after being threatened by her than after having been threatened by a different dominant female. In contrast, when the subject heard the same female's threat grunts after grooming with her, she should have been just as likely to approach and to tolerate her approaches as she was after having been groomed by a different dominant female.

Subjects responded more strongly to a dominant female's threat grunts after being threatened by her than after grooming with her. After aggression, subjects were quicker both to look toward the speaker and to move away from the area. In the ensuing 15 min, they were also less likely to come near their former opponent than they were after they had been threatened by a different female. In contrast, when subjects heard the same female's threat grunt after a grooming bout, they were just as likely to tolerate her approaches as they were after a grooming bout with a different female. Finally, subjects were significantly more likely to approach and to tolerate the approaches of the dominant female if they heard her threat grunts after grooming than after a threat.

As in the experiments testing reconciliatory grunts, subjects' responses were specific to the calls of their former opponent. Hearing their opponent's threat grunt did not affect the likelihood that subordinate subjects would approach another, uninvolved dominant female or the likelihood that they would be supplanted when approached. Taken together, therefore, these experiments suggest that female baboons make inferences about the intended target of a vocalization, even in the absence of visual cues, and that the nature of prior interactions affects subsequent behavior. After a fight, the subordinate assumes that the dominant has aggressive intentions toward her. After grooming, or after hearing a reconciliatory grunt, she makes the opposite attribution.

It seems likely that baboons make inferences about the intended target of a call whenever they hear any vocalization. For example, when subjects heard the threat grunts of their opponent's relative soon after

being threatened, they treated the grunts as a vocal 'alliance' directed at themselves. In contrast, when they heard the same threat grunts in the absence of aggression, they ignored the call and acted as if they assumed that the call was directed at someone else. Similarly, when subjects heard the 'reconciliatory' grunt of their opponent's relative after a fight, they often approached both their opponent and her relative. They did not do so, however, if they had heard the 'reconciliatory' grunt of another, unrelated dominant female. Here again, subjects behaved as if they assumed that a grunt from an opponent's relative must be directed at themselves, as a consequence of the fight. An unrelated female's grunt was irrelevant.

The ability to distinguish signals that are directed at oneself from those directed at someone else appears to be widespread in animals. For example, studies of 'eavesdropping' in birds indicate that listeners readily distinguish between songs that are directed at a third party and ones that are directed at themselves. To date, however, most of the evidence for this ability has come from studies in which individuals are interacting with only one or a few other animals and when factors such as the location of the signaler and the nature and pattern of the song provide information about the intended recipient. The challenge of inferring both the intended target of a signal and the signaler's probable behavior may be considerably more difficult in large social groups.

When deciding, Who, me? on hearing a vocalization, baboons must take into account the identity of the signaler (Who is it?), the type of call given (Was it friendly or aggressive?), the nature of their prior interactions with the signaler (Were they aggressive, friendly, or neutral?), and the correlation between past interactions and future ones (Does a recent grooming interaction lower or increase the likelihood of aggression?). Learned contingencies doubtless play a role in these assessments. Because listeners' responses depend on simultaneous consideration of all these factors, however, this learning is likely to be both complex and subtle.

Moreover, explanations based solely on learned contingencies seem unable to explain some aspects of baboons' behavior. For example, in the reconciliatory grunt experiments, subjects who heard their opponent's grunt following a fight were even more likely to approach their opponent than they were under baseline conditions, in the absence of a fight. If listeners' responses were guided solely by learned contingencies, they should have associated the call only with a low

probability of aggression. Hearing the call should have returned their behavior to baseline tolerance levels, but it should not have induced them to approach their former opponent. Instead, females acted as if they interpreted their opponent's grunt as targeted specifically at them, as a directed signal of benign intent. They therefore specifically sought out their opponent.

When attending to vocal signals, female baboons appear to take into account, not only the signaler's identity and her probable subsequent behavior, but also the target of her attention. The ability to integrate these social cues simultaneously may represent a first critical step toward the recognition of other individuals' intentions and motives. In children, inferences about other individuals' intention constitute an early precursor to language learning and full mental state attribution. Do monkeys have a rudimentary understanding about other individuals' intentions toward themselves? If they do, this understanding would represent a crucial first step toward a communication system like language, in which speakers and listeners routinely assess each other's motives, beliefs, and knowledge.

*See also:* Animal Communication: Honesty and Deception; Communication Networks and Eavesdropping in Animals; Electrical Perception and Communication; Endocrinology of Animal Communication: Behavioral; Pheromones and other Chemical Communication in Animals; Primate Communication: Evolution; Seismic and Vibrational Signals in Animals; Visual Signaling in Animals.

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