

Aggression- Ritualized fighting

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In most species, individuals occasionally come into conflict over access to resources important for their survival and reproduction. Resources such as food, shelter and territories are sources of competition when they are difficult to obtain. The time and material investments made by either sex in producing and raising offspring also represent important reproductive resources for the opposite sex. The availability of mates to invest or co-invest in offspring often is limited and males very often fight over access to females, and sometimes visa versa.

To resolve conflicts over resources, animals use various aggressive behaviors ranging from brief and subtle threats to dramatic, intensive, potentially injurious fighting. In addition to regular fighting, many species utilize so-called ritualized fighting behaviors to settle conflicts: species-typical display patterns that communicate fighting ability, but that entail less energy use or risk of physical harm than all-out fighting.

The key to understanding the evolution of ritualized fighting is to recognize that all-out-fighting will not be in the best interest of either rival if both contestants can reliably predict which one of them would win a real fight using mutual assessment behaviors that are less costly than all-out-fighting.

The ability to predict the outcome of an all-out fight without actually engaging in one comes from the fact that individuals in conflict over a resource often are not particularly closely matched in ability or motivation. Most animals' sensory systems are so sensitive that they are able to detect which one of them is the underdog. Ritualized fighting behavior has evolved such that during a fight, the underdog will withdraw as soon as his probability of winning a full fight is revealed to be low enough that searching for another opportunity to gain the contested resource elsewhere will increase his lifetime fitness (i.e. number of offspring).

Animals routinely avoid full combat because using ritualized assessments of fighting ability provide a more effective and efficient way to cooperatively estimate each other's *resource-holding power* (RHP) and settle conflicts without suffering injury or death. RHP refers to the ability of an individual to procure, defend, and compete for resources. RHP depends upon suites of individual traits and circumstances that include more than conventional notions of fighting ability. For example, in some species the RHP of an individual may be increased by having more information concerning the quality of the resource and how to make best use of it (e.g., by knowing the content and structure of a territory) and the logistics of fighting there (e.g., the locations in a complex fighting arena, such as a spider web or a talus slope, where one can get the best footholds).

RHP can also be increased if an individual has social allies who will help win the fight. For example, male baboons may form alliances to help one another gain access to females for mating. In lions, females help the current males of her pride fend off other male groups that attempt to take over in order to avoid infanticide

by new pride males. In many territorial species, territory holders who want to avoid the costs of working out boundaries all over again with a new neighbor may help their current neighbor fight off his challengers, the so-called “dear enemy” phenomenon.

Even in species in which RHP is mainly determined by fighting ability *per se*, the fact that body size, quality of weaponry, experience, motivation, and health all influence fighting ability helps assure that perfect matches in RHP between opponents will be rare during animal contests, thus creating the asymmetries in the probability of winning an all-out fight that has caused the evolution of behavior that allows individuals to assess each other in ritualized contests. Ritualized fighting allows opponents to estimate the cost of full combat so it can be weighed against the benefit of obtaining the resource that they are fighting over.

Ritualized behaviors are considered signals, which have evolved for the purpose of communicating information. In the context of fighting, ritualized behaviors are signals that encode information about RHP, the sender’s fighting ability and motivation. The receiver of the signal is the opponent, who must be able to properly assess the signal information and respond accordingly. Through these cooperative behaviors, contestants gain information about each other’s full combat capability and their willingness to escalate the fight. In all species in which there has been an evolutionary history of direct competition within species for some resource, thorough investigation of contest behaviors should reveal some form of ritualized fighting.

Ritualized fighting signals are less costly than all-out fighting, but they must be somewhat costly for them to be honest signals (i.e. signals that are not misleading) that rivals have reason to pay attention to. Their cost to produce should reflect the quality of information needed about the opponent, which may vary greatly with circumstances (see below). In the most demanding circumstances the cost of ritualized fighting may approach that of real fighting, perhaps not in terms of the risk of permanent injury or death, but certainly in how much they tax each contestant’s metabolic, developmental, and neurological competence. Ritualized fighting behavior may also be important for self-assessment; an accurate up-to-date estimate of one’s own fighting ability, which is just as important as assessing one’s rival in obtaining a useful measure of relative RHP.

Ritualized fighting behaviors include everything from subtle or distant signaling via postures, vocalizations, and chemical communication to dramatic behaviors entailing obvious demonstrations of strength, coordination, and determination. Posturing is a commonly used no-contact threat display employed by a variety of animals. Aggressive body posture can visually convey important information about an opponent’s competitive ability, such as size. For example, many animals posture by presenting the side of their body as they strut or stand, called a broadside display, in order to appear as large as possible to their opponent. Additionally, animals may also increase the size of their profile through body markings that give the impression of greater than actual length or by manipulating physical features, such as fluffing feathers and raising fur. Iguanid lizards have a particularly impressive number of behaviors and structures to exaggerate size, including the extension of skin located on the throat (dewlap), crest raising, back arching and lateral body compression.

Birds, amphibians and some mammals exchange loud, repeated vocalizations during contests. Vocal threat displays can provide contestants with information regarding size, condition or age. In cricket frogs, males in conflict over a mate will decide whether to attack or retreat from an opponent based on acoustic frequency of calls. Fundamental frequency production (the lowest frequency in a sound, perceived as pitch) is constrained by body size. Consequently, vocal displays can reliably indicate body size because small animals cannot produce a call as low in pitch as a larger animal. Vocal display bouts may also depend on strength and stamina, providing information about body condition through relative sound intensity or the length of the display. Baboons males use energetically demanding ‘wahoo’ calls during aggressive interactions, high-ranking and older males call at higher rates and are able to call for a longer period of time.

In some mammal species, olfactory cues used during an encounter with an opponent can provide information about dominance status, stress levels, and health by revealing hormone levels, such as testosterone and corticosteroids. Chemicals that are purposely used to communicate such information between members of the same species are referred to as pheromones; if the transmission is accidental but the information is used by the recipient, the chemical is called a kairomone; only pheromones qualify as proper signals, and thus as potential components of ritualized chemical fighting displays. One impressive example of pheromone use is the

ring-tailed lemur ‘stink fight’, which males engage in over access to females. Males rub secretions from a wrist gland onto their boldly marked tails, which they hold high overhead and wave in their opponent’s direction in order to dispense scent and provide an agonistic visual display (Fig. 1).

Ritualized fighting behavior may involve body contact or sparring with specialized structures, such as horns, antlers and tusks. Physical contact during ritualized fighting provides a tactile way to assess relative RHP while limiting potential injury. Many animal contests involve a form of ritualized ‘wrestling’; a cooperative form of fighting that allows opponents to gauge each other’s strength and endurance. In sierra dome spiders (*Neriene litigiosa*), males meet each other on a dome-shaped web and lock pedipalps (mating structures found on the front of the body) in order to grapple while hanging under the web. During the wrestling match, spiders attempt to jam one another up through the dome of the web by pushing forwards and upwards, using the strength of their legs and pedipalps. Sparring contests with weapons like horns or antlers, can be a relatively safe test of strength and stamina. In caribou, full combat with antlers can cause injury or death, however, almost all fights are resolved with a form of ritualized fighting. Caribou begin antler sparring by slowly and carefully adjusting their antlers before they begin to push each other. Some insects have horns, which they use in a similar fashion to caribou antlers, by locking horns and pushing each other until one opponent gives up or gets dislodged from the fighting platform (Fig. 2). Rocky Mountain Bighorn sheep butt heads in incredibly high impact frontal collisions by using their horns in conjunction with injury reducing physical adaptations in the head and neck. Such violent ritualized behaviors can only be understood as less costly than full fighting when one knows the context and style in which full combat would occur – running full speed on very steep rocky slopes trying to inflict blows to the sides of each other’s bodies and mate with fleeing females at the same time!

In addition to various techniques, species also greatly differ in the number of ritualized behaviors used in fighting. House crickets employ an extreme number of displays and diverse tactical maneuvers. Male house crickets display by flaring mandibles and stridulating (chirps produced by rubbing wings together). They use fighting tactics that include head butts, mandible sparring and foreleg punches. They also engage in harder physical contact, such as head charging, kicking and wrestling, although these behaviors rarely result in significant injury (Fig. 3). On the other end of the spectrum, some species only use one threat display. Weakly electric fish use pulses of electricity to communicate aggressive intent to each other, often in territory defense. Unlike most fish that are able to incorporate visual displays into their repertoire, weakly electric fish are nocturnal or live in murky water and are limited to the kind of sensory signal that they can use to communicate fighting ability. Rivals threaten each other by trying to jam the opponent’s signal. They compete by altering their own pulse rate to overlap with their opponent. In response, the loser will either shift its pulse rate to avoid the winner’s pulse rate or cease electric signaling for some time after the fight.

Most animal conflicts begin with the least physically costly and injurious tactics in order to assess RHP. Male sierra dome spiders may escalate sequentially through two ritualized and one unritualized fighting behaviors, in which each successive behavior is clearly more risky than the former, and whose energetic costs, on average, are 3.4, 7.3, and 11.3 times higher than resting metabolic rates, respectively. Male sierra domes who differ more than 20% in weight seldom escalate beyond the least expensive fighting behavior. In many species, opponents who are not closely matched in RHP, may not even get close to one another. Qualities of vocalizations, which in some species carry for many miles (e.g., elephants, whales) or long distance assessments of body size and condition (e.g., via pheromones or antler size) may be possible when there is considerable disparity in relative fighting ability. Where RHP differences are large, very efficient assessment methods are effective at communicating competitive ability; decisions that are likely to improve survival and reproduction can be based on easily gathered comparative information on self versus other.

In many species, ritualized fighting behaviors may escalate quantitatively (e.g. intensity and duration) or in quality (e.g., where entirely different behaviors are employed) if both contestants need better information on their rival’s ability relative to their own in order to win the match. As relative ability becomes similar, contestants are more likely to escalate and contest behaviors become increasingly costly in terms of time, metabolic energy, or injury. Cichlid fish of the species *Nannacara anonala*, for example, proceed through a number of stages depending on how close the contestants are matched in size and strength. Cichlids begin their fights by swimming side-to-side, which is a type of broadside display used to assess size. If both fish are not greatly different in size, they proceed to ‘tail-beat’ each other. Tail-beating behavior causes a stream of water to

push against the rival, which allows the receiver of the water stream to gauge the opponent's strength more accurately. The individual performing the tail-beating display may assess the ability of the receiver to withstand the stream's force. Cichlid fights may subsequently escalate further with frontal confrontation (Fig. 4) and mouth-wrestling, where the contestants push and pull each other by grasping jaws. Finally, if fish are closely matched in RHP and cannot resolve the conflict with ritualized behaviors, mouth-wrestling ceases and full combat ensues; the opponents circle around and bite each other.

The relationship between the effectiveness of a ritualized behavior in demonstrating true ability and the efficiency of performing that behavior (in terms of energy cost and injury risk) is dependent on the degree of difference in RHP between contestants. As the RHP of contestants becomes more similar, more effort is required to effectively and reliably demonstrate superiority. Each contestant will have to perform closer to its maximum potential. In cichlid fish, contestants closely matched in RHP escalate to mouth wrestling, which requires more metabolic energy and physical contact (potentially causing mouth injury) than previous stages of ritualized behavior. Mouth wrestling is less energy efficient than other ritualized fighting behaviors, but provides contestants with better information about maximum strength and stamina and so is more effective at providing contestants with knowledge of relative RHP. A smaller, weaker fish may be able to exaggerate size by spreading its fins and bluff a larger fish into believing that it has similar or better RHP, however if the contest escalates to mouth wrestling, it could not win a wrestling bout against an opponent that has greater true ability. In any contest, it is in each individual's interest both to deceive an opponent by exaggerating RHP and simultaneously to avoid deception by accurately gauging the RHP of a rival relative to itself during a contest; thus more expensive behaviors make cheating more difficult for both contestants while making true RHP assessment accuracy more possible.

In every species with ritualized fighting behaviors, there are situations likely to trigger escalation to all-out fighting. Opponents that find themselves closely matched may resort to full combat if the information gained from ritualized behaviors is insufficient for making a confident prediction about the outcome of an unritualized fight. Conversely, there may be circumstances where opponents who are grossly mismatched will proceed to all-out fighting. If success in all-out fighting depends more on luck than success in a ritualized fight, an obviously inferior opponent may escalate the fight beyond ritualization. This is more likely to happen when the resource is exceptionally valuable or if the underdog has little to lose in terms of expected future reproduction. In sierra dome spiders, unritualized fighting consists of frenzied biting and grappling where the first contestant to deliver a bite to the body or even the foreleg is very likely to win. As the end of the breeding season nears and the window of the future closes on male sierra domes, escalations to this kind of fighting become more frequent.

One might also expect underdogs to escalate to full combat more often if they have only enough energy to effectively fight in a short and intense all-out fight where luck can play a major role in the outcome. Alternatively, a superior fighter also may escalate to all-out fighting during a contest even though he would be almost certain to win using ritualized behaviors. This may happen in cannibalistic species where the RHP dominant gains a major meal by killing his rival, as in sierra dome spiders. Reducing the costs of display may also cause the RHP dominant to escalate, for example, if ritualized displays take a long time, if they are energetically expensive or run the risk of attracting and increasing vulnerability to predators.

The general principle underlying ritualized fighting is illuminated by considering situations, like those above, in which it escalates to all-out fighting: ritualized fights are good for both contestants under circumstances that make low-cost assessments reliable and economic, but not otherwise. Many factors potentially can tip the cost-benefit balance toward dangerous unritualized fighting, and most species are fully capable of it. This is one of many ways that even organisms with incredibly small nervous systems exhibit impressive responsiveness to the environment.

Illustration suggestions

1. Ring-tailed lemur stink-fight

http://www.lastrefuge.co.uk/images/html/lemurs/ringtail/image_html/ringtails158.html

Adrain Warren photo. photos for sale- approximately \$100 for book usage.

OR Lemur book- get from library.

2. Beetles wrestling

In sexual selection (Andersson) Drawing by T. Prentiss copyright by Scientific American

3. Crickets fighting (mandible flaring)

Nice illustration of a Mace Hack photo in Animal Communication (pg 602) drawings by Precision Graphics:

Nancy Haver or Abigail Rorer. Contact info: <http://www.precisiongraphics.com/>

4. Cichlid fish display

<http://www.cichlidae.com/articles/a139.html>

Thorichthys pasionis males displaying for territory. Photo by Juan Miguel Artigas Azas

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