



Are agonistic behavior patterns signals or combat tactics – Or does it matter? Targets as organizing principles of fighting



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HIGHLIGHTS

- Fighting involves competition for access to particular body targets.
- Maneuvers during fighting can be interpreted as tactics to access targets.
- Communicative signals can arise by ritualizing combat maneuvers.
- Targets thus provide a framework to discern combat and signaling roles of maneuvers.

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ABSTRACT

During competitive interactions, such as fighting and predation, animals perform various actions, some of which are easy to characterize and label, some of which are reliably repeated. Such 'behavior patterns' are often the measures of choice when comparing across species and experimental contexts. However, as Bob Blanchard and others have pointed out, such measurements can be misleading as in competitive interactions in which the animals compete for some advantage, often the biting or otherwise contacting a particular target on the opponent's body. In this context, the animals' behavior is better analyzed in terms of the tactics of attack and defense deployed by the combatants to gain or avoid contact with those targets. Several examples are shown to reveal that this is an important distinction as simply scoring predefined behavior patterns can obscure the dynamic context in which the actions are performed. This can lead to confounding species and experimental differences and the mislabeling of combat actions as communicatory signals.

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1. Introduction

Studies of fighting in rodents in the 1950s and 1960s were handicapped by poor filming technology, so fights either had to be scored visually in real-time or repeatedly watched on film that ran at normal speed, at relatively low frame rates. This meant that the fighting behavior of rodents, such as rats and mice, had to be inferred, usually from staged laboratory encounters observed or filmed under low light conditions with fast actions being little better than blurry images. Under such circumstances, it is little wonder that the description of what occurred involved fixating on discernible and repeatedly observable behavior patterns: such labels as rearing, boxing, ball fights, lateral displays and supine submission became the mainstay of the field (e.g., [1,2]). By the time there existed the technical capacity, in the early 1970s, to slow down film, or even better, watch filmed fights one frame at the time, especially with images that were in sharp focus,

these categorizations of fighting in rodents had become so entrenched that they remained the standard way of scoring behavior in experimental and comparative studies (e.g., [3–5]) – indeed, this view was so pervasive that some researchers even argued that it was pointless to film such behavior, as it was just as convenient to score it in real time [6].

Perhaps because of their size, the fact that they engaged in interactions in the daylight, and that compared to small rodents, their movements were slower, ungulates provided new insight into the 'behavior patterns' typical of fighting. For example, male deer engage in fights that appear highly ritualized – they size each other up and if they fight, they fight standing face-to-face and then charge one another clashing antlers and perhaps wrestling once the antlers are entangled [7]. When they do clash antlers, observed fights rarely lead to injury or death, further supporting the supposedly ritualized nature of fighting [8]. However, when viewed from the perspective that such fighting is organized around gaining access to a particular body target on the opponent, much of the clashing, wrestling and pushing can be interpreted in a different way. The opponents can be seen to maneuver to gain access to a body target and deny access to that body target [9].

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As noted for deer and for bighorn sheep, where fighting primarily involves clashing antlers and horns, if one animal loses its footing, the opponent may rapidly circle about and deliver a blow to an exposed flank, leading to injury and even death [10]. That is, the flank is the target of attack and defense with the head clashing arising from the combined offensive and defensive maneuvers to catch the strike on the most strongly defended location on the animal's body – in the sheep, the horns and reinforced skull and in the deer, the branching antlers. The rarity of observing such potentially lethal blows is not because the animals refrain from delivering them, but because their opponents effectively maneuver to block such contact [9]. Nonetheless, an inspection of the hides from adult male deer has revealed that 84% had puncture marks on the flanks, consistent with strikes by other deer [11], suggesting that when the defenses are breached, the opportunity is taken to deliver a strike to the flank. Therefore, based on his observations of fighting behavior in a range of North American ungulates, including deer, elk, moose, bighorn sheep and mountain goats (e.g., [10,12–14]), Valerius Geist drew the conclusion that the point of fighting is to attack and defend particular body targets, and in this regard, the so-called 'behavior patterns' are merely snapshots of that dynamic context [9].

2. Back to rodents

By using a variety of approaches to study fighting in rats, Bob and Caroline Blanchard revolutionized our understanding of the fighting of rodents, showing that, like ungulates, rats also engage in a competition to access particular body targets, and that, in this context, the various behavior patterns performed are better understood as tactics of attack and defense [15]. They collected wild rats and examined the body surface for bite wounds and found that, in the adult males, wounds were concentrated in two body areas, the face and the lower dorsum and flanks [16]. Similarly, wounds arising from staged encounters showed the same distribution [17]. By placing an unfamiliar adult male as an intruder into the home cage of an adult male resident (i.e., the resident-intruder paradigm), the Blanchards showed that most of the bites to the lower dorsum and flanks were by the attacking resident and most of the bites to the face were by the defending intruder [18]. This was confirmed by placing an anesthetized intruder into the home cage of a resident – whether placed right side up or upside down, the resident directed its bites to the intruder's lower dorsum and flanks. Quite simply, the attacker directs bites to the lower dorsum and flanks and the defender retaliates by biting at the face of the attacker [17].

This competition for access to body targets creates a dynamic context in which the attacker has to overcome the defensive maneuvers of the defender to gain access to the offensive target – in this case, the lower dorsum and flanks – and do so while avoiding a retaliatory bite to the face. Such coupling of the rump as the offensive target and the face as the defensive target is widespread among mouse-like rodents, but there is variation in the frequency of use of particular 'behavior patterns' associated with fighting [19]. The dynamic context created by competition for access to these targets means that, if behavior patterns associated with fighting are scored, differences in their frequency may be attributable to differences in the tactics adopted by either the defender or attacker, or by subtle differences in targeting. For example, to defend access to their rump when attacked from behind, rats are more likely to rotate to supine than are house mice and this seems to arise because attacking mice are more likely to shift their target of attack from the dorsum to the ventrum [17,20].

Scoring the frequency of behavior patterns in the absence of information on the contextual dynamics of the competition for access to body targets may limit the ability of the numerical scores to identify why species differ or why particular experimental manipulations lead to changes in the frequency of particular actions. The work done by Bob and his colleagues has sensitized students of aggression in general, and those studying rodents, in particular, to record the body areas being targeted (e.g., [21–24]). There is another, less well-integrated lesson to

emerge from the work pioneered by the Blanchards; that is, that many gestures that are seemingly present to signal to the other animal – threat, submission, etc. – are actually combat tactics [25].

3. The problem of characterizing signaling during combat

Discerning whether an action performed during fighting is for its function in combat, in signaling to the opponent or in both, is empirically challenging because many of the signals used in competitive interactions are derived from combat maneuvers [26]. Once recruited as a signal, then, over the course of evolution, these actions can become modified to emphasize the salient features that convey the appropriate information to the opponent [27]. Depending on how far this process of ritualization has progressed, the actions performed can be almost identical to the combat maneuver for recently evolved signals, but very different to ones with a longer evolutionary history [28]. Consider the action of defensive rotation to supine.

As noted above, when a bite to the rump by an attacker approaching from the rear is imminent, the defending rat may rotate to supine, so protecting its rump. Once on its back, the rat can exaggerate some of the salient body gestures that can act as a defensive threat towards the attacker, such as keeping its mouth open with its teeth exposed and oriented towards the attacker's face. If the attacker moves closer, this threat gesturing can be further exaggerated by a lunge that is a feint towards the attacker's head. Of course, if the attacker continues to move closer, the defender can resort to making good on the threat, by lunging and actually biting its opponent's face – producing the wounds on the face such as those discovered by the Blanchards [16]. Indeed, for threats – whether defensive or offensive ones – to be credible, the potential weapons to be deployed, such as the teeth, need to be brought to within striking distance [29]. In this regard, threat signals tend to occur in contexts that are similar to the combat tactics from which they are derived.

Further ritualization of threat signals leads to them being transformed into dominance and submissive signals [28]. Such signals may still have broad outlines of the original combat tactic, but their orientation and correlation to the movements of the opponent are much less similar to how they are used in combat. For example, submissive signals allow a weaker or subordinate animal to remain in close proximity to its opponent, by inhibiting further attack [26]. Typically, submissive signals involve the animal making itself smaller, by crouching or rolling over onto its back and remaining motionless. Other gestures may also be added, such as depressing the ears and lowering the tail [28,30,31]. Critically, when adopting a submissive posture, the animal not only remains motionless but gestures of threat are not expressed. In rats remaining motionless has been shown to inhibit attack in some situations [32]. Therefore, the rotating to supine tactic in rats may serve multiple functions – to defend the rump against an imminent bite, to remain in the supine position as a defensive threat to block further attack, or to remain supine as act of submission to inhibit further attack. For the house mouse, the fact that the attacker is not inhibited in biting its opponent's ventrum [20], limits the use of the supine tactic. It is useful as a defensive tactic for the immediate withdrawal of the rump from an imminent bite, and, to some extent, as a threat signal to block further attack by the opponent momentarily, giving the defender the opportunity to right itself and flee [33]. However, in this case, remaining motionless on its back does not function as a submissive gesture. It should also be noted that, while fleeing may be the act of a submissive animal, it is not, by definition, a signal of submission as such a signal would allow the performer to remain in close proximity to the opponent [28].

The example of rotation to supine during fighting shows how such a maneuver can have multiple functions and also how the degree of ritualization of the maneuver for its potential associated communicatory functions may differ across species. During fighting, maneuvers are deployed to attack or defend particular body targets [9,15], and, in the first instance, a particular maneuver may be best understood as a combat

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