ANIMAL BEHAVIOUR, 2008, **76**, 1453–1454
doi:10.1016/j.anbehav.2008.09.005

Available online at www.sciencedirect.com
ScienceDirect

IN FOCUS

Featured Articles in this Month's *Animal Behaviour*

Up Close and Personal

Which would you find more threatening? Someone waving their fists right in your face and threatening to punch your head in, or someone standing several metres away, brandishing his or her fists, while making the same threat? It's not hard to decide that the first is more threatening, mainly because it seems more likely that you will actually get punched, and it is also clear that your opponent isn't too worried that you might fight back. Standing several metres away while brandishing your fists is much less frightening in comparison, and also conveys a sense that perhaps it is all bravado, and that the individual making all the noise is actually quite frightened too. In this month's issue (pp. 1455–1463) Szabolcs Számadó uses a simple theoretical model to show that this 'proximity risk' is precisely what keeps animal threat displays honest.

Threat displays are a common feature of animal life (Fig. 1). They allow an individual to stake its claim to resources without injuring itself, and they often work extremely well: opponents back down before actual fighting takes place, and resources are gained at lower cost. This, of course, raises an enduring evolutionary puzzle: what ensures that threat displays remain honest? If contests are generally resolved with no actual fighting, what stops weak individuals from coming on strong, displaying a threat of physical force that they cannot follow up on should this prove necessary? Enquist (1985) presented a model to show that threat displays were kept honest by the potential costs of being forced into a fight with a strong individual. He never expanded on the exact nature of these costs, however. In the current paper, Számadó notes that the costs of threatening another take the form of the inherent risk that one's opponent will be willing to fight back. What is more, this will depend on the distance between two opponents at the time the threat is made: proximity, therefore, indicates both the ability to inflict damage and the willingness to do so. Accordingly, the model developed here reveals that the honest use of threat displays is evolutionarily stable only within a certain distance threshold (the 'honest striking distance'). Above this threshold distance, it is possible for there to be a zone where a mixture of honest and cheating displays can be evolutionarily stable (the 'dishonest striking distance'). Beyond this distance, however, threat displays are unreliable, and animals are not expected either to use them or to pay attention to animals that do.

As Számadó notes, the proximity risk of a display will depend both on the kind of weapons a given species possesses, and on the specific fighting technique used. The longer the reach of the weapon, the greater both the honest and dishonest striking distance will be (think of fighting with a sword compared to a fist-fight). Similarly, the more mobile the fighting technique, the greater the honest and dishonest striking distances. Számadó compares giraffe, which fight from a standing pose and exchange blows using their heads, with species that fight by running at and ramming each other: in the former, the honest striking distance is much shorter, as a credible threat can only be made once animals are in a position to make physical contact. This isn't the case for an animal that runs up from a distance as part of the ramming technique, and so the honest striking distance is correspondingly larger.

This explains why weak individuals cannot use threat displays dishonestly to scare away rivals: as the display conveys willingness to fight, and not actual fighting ability, then any threat display in which an animal presents its weapons as 'ready-to-use' within striking distance of an opponent should be treated as honest, because it indicates an ability and willingness to inflict damage. A weak individual that isn't willing to inflict damage simply cannot mount a credible threat display. Reviewing the animal behaviour literature, Számadó presents a number of empirical examples where both the patterning of behaviour, as well as the spatial proximity at which certain behaviours occur, provide support for his model. In doing so, his paper makes the important point that describing the specific postures and behaviours that animals perform can be crucial to understanding what their evolved strategies might be. Theoreticians need to get physical to understand why animals don't.

Louise Barrett
Executive Editor

Calling for Different Purposes

We all know we should, but we rarely do; explicitly test multiple hypotheses, that is. Yet many behavioural questions

0003–3472/08/$34.00/0

Figure 1. 'Proximity risk' keeps threat displays honest. The distance at which an animal displays its weapons to an opponent ensures a threat is credible. Photo: S.P. Henzi.

in fields such as antipredator behaviour have been around for so long that a number of alternative hypotheses have been proposed to explain common phenomena. By focusing on only a single hypothesis we may miss interesting complexity.

Alarm calling is a common antipredator behaviour; upon detecting predators, prey may utter vocalizations referred to as alarm calls. It's a particularly interesting activity because it seems to carry a personal risk; by calling, prey may increase their vulnerability to predators. Solutions to this potential paradox include ways that animals may obtain personal fitness (they increase their probability of surviving), direct fitness (they increase the probability of their descendant kin surviving) and inclusive fitness (they increase the probability of their nondescendant kin surviving).

On pages 1465–1475 of this issue, Brandon Wheeler focuses on tufted capuchin monkeys and, using a multiple-hypothesis testing approach, evaluates eight different hypotheses to explain why capuchins give calls in response to their predators. Broadly, Wheeler was interested in knowing whether calling was a selfish or altruistic act. Importantly, he examined capuchin responses to different predators. Most species have more than one predator and, if having species-specific strategies is beneficial, we should expect selection for predator-specific strategies. Felids, raptors and snakes create different sorts of risks and we might expect capuchins to have different benefits associated with different responses.

Wheeler went to Argentina to study the monkeys with an armament of scary things that included models of ocelots, snakes and hawk-eagles. Sample sizes were necessarily low, and he focused on only three social groups, but these are understandable shortcomings given the difficulty of habitutating the groups and the nature of the experiments. None the less, by looking at the situations in which capuchins called, how the presence of other capuchins influenced the propensity to call, and how capuchins responded to calls, he found that, indeed, capuchins responded differently to these types of predators, and they did so in ways that suggested different functions of alarm calling.

When capuchins called, other capuchins responded by investigating and ultimately mobbing the predator. Predator mobbing helps the caller as well as any kin because the risk of attack is reduced for all members of the group. Snake-elicited calls seemingly functioned to warn kin that there was a snake around, thereby suggesting such calling is maintained by kin selection. Felids rely on stealth, and once detected, their hunting success declines precipitously. Felid-elicited calls were seemingly directed to the predator to discourage attack; personal fitness may therefore maintain these calls.

Overall, this interesting study demonstrates the power of a multiple-hypothesis testing approach, even if there are nonmutually exclusive outcomes. In this case, Wheeler discovered that different functions may maintain alarm calling for different predators.

Daniel T. Blumstein
Editor

Reference

Enquist, M. 1985. Communication during aggressive encounters with particular reference to variation in choice of behaviour. *Animal Behaviour*, **33**, 1152–1161.