How threat displays work: species-specific fighting techniques, weaponry and proximity risk

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Whether threat displays can reveal information about the strength or condition of the contestants is a long-debated issue. Enquist (1985, Animal Behaviour, 33, 1152–1161) showed that communication of such information is possible by means of choice of action in aggressive encounters. The key assumption of Enquist’s model is that weak individuals signalling that they are strong (i.e. cheaters) cannot get away without fighting even if they want to, if they meet an honest strong individual. However, this assumption was not elaborated further and Enquist’s model is often cited in support of Zahavi’s handicap principle. Here I elaborate this assumption and show in terms of Enquist’s model, by introducing spatial distance between opponents as a continuous variable, that it is the proximity of the opponent, what I call ‘proximity risk’, that maintains the honesty of threat displays. I show that the honest use of threat displays, sensu Enquist, is evolutionarily stable only within a certain distance threshold. Outside this threshold there may or may not be a zone where a mixture of honest and cheating displays can be evolutionarily stable. Outside this second zone threat displays are unreliable and thus expected not to be used and attended to. The model gives specific predictions about weaponry, species-specific fighting techniques and the value of these thresholds. Finally, I show that key predictions of the model, namely the relation between signal intensity, riskiness and proximity has strong support in the literature.

Keywords: dishonest striking distance; honest signalling; honest striking distance; proximity risk; species-specific fighting technique; threat displays; weaponry

The reliability of threat displays has been a long-standing enigma for biologists (Maynard Smith 1974, 1979; Caryl 1979). Threat displays are signals used when there is a conflict of interest over deterring opponents from valuable resources. The catch-22 of threat displays is very simple: if these displays work, then everyone should be using them since it is in the interest of any animal to deter competitors without costly and risky physical fights. However, if everyone is using these displays then there is no point in attending to them as they convey no valuable information to the receiver. For threat displays to be reliable (and useful for the receivers in the long term) only those individuals should be using them who can back up the threat with physical strength if necessary. However, it remains unclear what prevents weaker individuals from using these displays. Early game-theoretical models reinforced this sceptical stance and some concluded that threat displays cannot be honest (Maynard Smith 1974). In turn it was proposed that there should be a constant turnover of devalued displays (Andersson 1980). Finally, Zahavi (1975, 1977) and Zahavi & Zahavi (1997) applied the handicap principle to threat displays and proposed that only those displays that impose an extra cost on the signaller can be reliable (Maynard Smith 1974). In turn it was proposed that there should be a constant turnover of devalued displays (Andersson 1980). Finally, Zahavi (1975, 1977) and Zahavi & Zahavi (1997) applied the handicap principle to threat displays and proposed that only those displays that impose an extra cost on the signaller can be reliable, ensuring that only those individuals in the best condition can afford this cost. In the meantime, ethologists and behavioural ecologists were describing the threat displays of dozens of species which showed a certain pattern (discussed below), yet this pattern was rarely taken into account in theoretical discussions. Grafen’s (1990) model of handicap signalling meant that the handicap principle became widely
accepted (Godfray 1991; Maynard Smith 1991). This general recognition, coupled with Zahavi’s examples, resulted in most biologists accepting the handicap principle as a viable explanation of the reliability of threat displays.

In the meantime, Enquist (1985) was able to show that honest cost-free signalling is possible in competitive situations if certain key conditions are met. Enquist’s model is still frequently cited as a model that supports Zahavi’s prediction. Later, Szamadó (2003) was able to show within the framework of Enquist’s model that handicaps cannot spread in a population using cost-free threat displays, whereas so-called negative handicaps (displays that confer some other advantage) not only spread but once established are also evolutionarily stable against the invasion of both handicaps and cost-free signals. In the context of threat displays, these negative handicaps are signals that prepare the animal for the fight, that is, postures positions related to species-specific fighting techniques, mostly involving getting weaponry in a ready-to-fight position. Empirical observations support this prediction; for example, the first step in the species-specific fighting technique of ungulates is a threat display (Walther 1984), and the ready-to-fight presentation of weapons is a universal threat display among animals (reviewed in Szamadó 2003).

Nevertheless, the fundamental question still remains, namely, what maintains the reliability of these displays? If displaying weaponry is an efficient threat display then what prevents its use by weak individuals? Enquist’s model suggests that it is the potential cost of fighting against a strong individual, and this is the main reason why Enquist’s model is often cited in support of the handicap principle. However, this cost is clearly not a production cost as it crucially depends on the strategies of other individuals in the population (see Szamadó 2003). Also, this cost is not a ‘vulnerability handicap’ as there is nothing in these postures that makes the signaler more vulnerable. To the contrary, as discussed above, they prepare the weapons, and thus the animal, for the fight. So where does this potential cost come from? Szamadó (2003) argued that this cost is inherent in the situation: it is the inherent risk of threatening someone who might be willing to fight back. Here I want to elaborate on this proposition and show, with the help of a simple model, that it is the proximity risk that maintains the reliability of threat displays. Proximity risk means that threat displays are credible only within a certain distance of the opponent, and this threshold distance is strongly related to weaponry and the species-specific fighting technique.

This proximity risk, of course, is strongly related to Enquist’s (1985) model. The basic assumption of his model is that weak individuals pretending to be strong (i.e. cheaters) will not be able to get away without a fight if they meet an honest strong individual, and thus will pay the cost of fighting even if they are not willing to do so. This assumption, however, was not elaborated further. Here, my aim is to show first that without this assumption honest signalling is not an ESS in Enquist’s model. Second, I aim to show that if this assumption is relaxed by allowing the spatial distance between signaler and receiver to be a variable, honest signalling (sensu Enquist 1985) is an ESS only within a certain distance from the opponent, and this distance is strongly related to weaponry and the species-specific fighting technique.

**The Model**

Here I use Enquist’s (1985) model, which can be seen as a modified version of the Hawk–Dove game (Maynard Smith 1982), where each player can be weak or strong and knows its own strength but not that of the opponent. The game has two steps. In the first step each player can choose between two cost-free signals A or B, then in the second round each animal can give up, attack unconditionally or attack if the opponent does not withdraw. Let V denote the value of the contested resource, and CWW and CSS the expected costs of a fight between two weak and two strong individuals, respectively. We assume that the expected utility of a contest between opponents of equal strength is greater than zero, that is, 0.5V − CWW > 0, 0.5V − CSS > 0. We further assume that a strong animal can always beat a weak one with a cost CWW and CSS is the expected cost that a weak animal should suffer on this occasion. The following relation holds between these costs: CW ≥ CWW CSS ≥ CSS. Let us further suppose that there is a cost of attacking a fleeing opponent (F), and there is a cost of waiting (i.e. cost of conditional attack) if the opponent attacks unconditionally (F). It is biologically realistic but not necessary to assume that CSS > F and CSS > F (Hurd 1997). The frequencies of weak and strong individuals are denoted by q and 1−q, respectively. The payoffs for weak and strong contestants can be written as shown in Table 1 (see Szamadó 2000). Enquist (1985) was able to show that the following strategy (S) is evolutionarily stable. Strong individuals should show A in the first round and then attack unconditionally if the opponent shows A or wait until the opponent flees if it has shown B. Weak individuals should signal B at the first step and then attack unconditionally if the opponent shows B or withdraw if the opponent signals A. Strategy S is a pure strategy in which both strong and weak animals signal honestly. The corresponding dishonest pure strategy (Sd) can be defined as follows. Always display A in the first round, regardless of strength; then in the second round, if strong attack unconditionally if the opponent shows A or wait until the opponent flees if it has shown B; if weak withdraw if opponent signals A or wait until opponent flees if it has shown B.

First I show that if we relax the assumption that weak individuals using signal A cannot get away without paying the cost of fighting if the opponent attacks (unconditionally), then honest communication cannot be an ESS. The fitness of honest weak individuals and cheaters, under this assumption, in a population of individuals using strategy S is as follows:

\[
E(S_a, S_b) = q(1) - C_{WW}
\]

\[
E(S_b, S_a) = qV - (1 - q)0
\]

For any S strategy to be an ESS the following condition must be fulfilled (Maynard Smith 1982):
Modified after Hurd (1997). V: value of the contested resource; $C_{SS}$, $C_{WW}$: expected cost of fight between equal opponents; $C_{SW}$: cost for strong individual to beat weak one; $C_{WS}$: cost to weak individual when beaten by strong one; $F_A$: cost of attacking fleeing opponent; $F_C$: cost of waiting if opponent attacks unconditionally.

Let $E(S_1, S_1) > E(S_i, S_j)$ \hspace{1cm} (3)

or if $E(S_1, S_1) = E(S_i, S_j)$ then

$E(S_1, S_1) > E(S_i, S_j)$ \hspace{1cm} (4)

where $E(S_i, S_j)$ denotes the payoff of strategy $S_i$ against strategy $S_j$, and where $S_1$ can be any mutant (pure or mixed) strategy. Thus, for $S_1$ to be an ESS against the invasion of cheaters, the following condition must hold (from equations 1 and 2):

$q \left( \frac{1}{2}V - C_{WW} \right) > qV \hspace{1cm} (5)$

However, the right-hand side is always greater than the left since $C_{WW} > 0$, therefore $S_1$ cannot be an ESS.

Now, allow the distance between the two players to be a continuous variable ($x$). Let $f(x)$ denote the chance of a successful attack, where $f(x)$ can take values between 0 and 1. Let us further assume that $f(x)$ is a monotonically decreasing function of the distance between opponents, that is, the further away the opponent the more difficult it is to reach it with an attack. Then equation 2, will be modified as follows:

$E(S_0, S_0) = qV - (1 - q)f(x)C_{WS} \hspace{1cm} (6)$

Accordingly, the stability condition for $S_0$ to be an ESS will be modified as well:

$q \left( \frac{1}{2}V - C_{WW} \right) > qV - (1 - q)f(x)C_{WS} \hspace{1cm} (7)$

After rearrangement we have:

$f(x) > \frac{q \left( \frac{1}{2}V + C_{WW} \right)}{(1 - q)C_{WS}} \hspace{1cm} (8)$

One can see that $S_0$ can be an ESS only if the value of $f(x)$ is larger than a given threshold specified by the right-hand side of the inequality. That is, the opponent must be closer than the distance corresponding to this threshold. Let us denote this threshold distance as $x_{HSD}$, ‘honest striking distance’, within which the chance of reaching the opponent with a successful attack is high enough for honest communication to be an ESS.

What can be expected outside this distance? Obviously a pure $S_a$ strategy will not be an ESS. However, a mixed strategy ($S_m$) supported by $S_a$ and $S_0$ can be, as shown by Szamádó (2000). The proportion of cheaters at this mixed equilibrium, given Enquist’s original assumption, is as follows (Szamádó 2000):

$p^* = \frac{q \left( \frac{1}{2}V + C_{WW} \right) - (1 - q)C_{WS}}{2qC_{WW}} \hspace{1cm} (9)$

where $p^*$ denotes the equilibrium frequency of the cheaters. Taking into account our $f(x)$ function, equation 9 will change as follows:

$p^* = \frac{q \left( \frac{1}{2}V + C_{WW} \right) - (1 - q)f(x)C_{WS}}{2qC_{WW}} \hspace{1cm} (10)$

One can see that when equation 8 does not hold (i.e. $S_a$ is not an ESS) then $p^*$ is always greater than zero (as expected). An honest strategy will exist at this equilibrium as long as $p^* < 1$, that is:

$f(x) > \frac{q \left( \frac{1}{2}V - C_{WW} \right)}{(1 - q)C_{WS}} \hspace{1cm} (11)$

Equation 11 gives another threshold (let us denote it $x_{HDISD}$, ‘dishonest striking distance’) as once the opponents are further away from each other than this threshold then only cheaters will be present, which implies that no communication should take place (with regard to choice of action) as signals will no longer transfer any relevant information about the signaller’s future choice of action (which in turn means that receivers should pay no attention to these signals). This of course, does not mean that another kind of

| Table 1. The expected payoffs of the strategies in a model of aggressive communication (as in Szamádó 2000) |
|----------------|----------------|
|                | Strong          | Weak            |
| Egostrength    | Attack          | Conditional attack | Flee | Attack          | Conditional attack | Flee |
| Strong         | $0.5V - C_{SS}$ | $0.5V - C_{SS}$  | $V - F_A$ | $V - C_{SW}$  | $V - C_{SW}$  | $V - F_A$ |
| Attack         | $- C_{SS}$     | $0.5V - C_{SS}$  | $V$ | $V - C_{SW}$  | $V - C_{SW}$  | $V$ |
| Flee           | $- C_{SS}$     | $0.5V - C_{SS}$  | $V$ | $- C_{SW}$   | $0.5V - C_{WW}$ | $V - F_A$ |
| Weak           | $- C_{WS}$     | $- C_{WS}$      | $V - F_A$ | $0.5V - C_{WW}$ | $0.5V - C_{WW}$ | $V$ |
| Attack         | $- C_{WS}$     | $- C_{WS}$      | $V$ | $- C_{WW}$   | $0.5V - C_{WW}$ | $V$ |
| Conditional attack | $0$          | $0.5V - C_{WW}$  | $V$ | $- C_{WW}$   | $0.5V - C_{WW}$ | $V$ |
| Flee           | $- C_{WS}$     | $- C_{WS}$      | $V$ | $- C_{WW}$   | $0.5V - C_{WW}$ | $V$ |

Modified after Hurd (1997). $V$: value of the contested resource; $C_{SS}$, $C_{WW}$: expected cost of fight between equal opponents; $C_{SW}$: cost for strong individual to beat weak one; $C_{WS}$: cost to weak individual when beaten by strong one; $F_A$: cost of attacking fleeing opponent; $F_C$: cost of waiting if opponent attacks unconditionally.
communication, such as dominance or territorial displays, cannot take place once the opponents are outside $x_{\text{DSD}}$, only threat displays, that is, displays signalling further choice of action with regard to fighting behaviour, will be utterly unreliable and thus not expected to be attended to.

In summary, honest signalling ($S_a$) is an ESS within $x_{\text{HSD}}$: a mixed strategy supported by honest and cheating signallers is an ESS between $x_{\text{HSD}}$ and $x_{\text{DSD}}$; outside $x_{\text{DSD}}$ threat displays are unreliable and thus will not be used.

Note that the mixed strategy can exist both on the level of the population (i.e. different individuals playing strategies $S_a$ and $S_b$) and on the level of the individuals (i.e. each individual plays strategy $S_a$ or $S_b$ with a probability of $1-p$ and $p$, respectively).

Figure 1 gives a numerical example showing the proportion of cheaters as a function of the value of the resource ($V$) and the distance between the opponents ($x$, measured in arbitrary units), and Fig. 2a shows the corresponding $f(x)$ function. Figure 2b shows the $x_{\text{HSD}}$ and $x_{\text{DSD}}$ thresholds (which are the 0 and 1 isolines of Fig. 1, respectively) as a function of the value of the resource. It is clear from Fig. 2b that as both $x_{\text{HSD}}$ and $x_{\text{DSD}}$ decrease with $V$, first $x_{\text{HSD}}$ then $x_{\text{DSD}}$ will reach zero. That is, with increasing $V$ first the honest region will disappear (as expected, see Számádó 2000), then communication through choice of action will disappear too (again as expected, see Maynard Smith & Harper 1988; Enquist & Leimar 1990). Figure 3 depicts how $x_{\text{HSD}}$ and $x_{\text{DSD}}$ depend on $C_{\text{WW}}$ (Fig. 3a) and $C_{\text{WS}}$ (Fig. 3b). Figure 3a shows that if the assumption of the model $0.5V - C_{\text{WW}} > 0$ does not hold, then the honest region will disappear. It also shows that if $C_{\text{WW}} = 0$, that is, weak individuals can decide their conflict without cost, then the region of the mixed strategy will disappear (this follows from equations 8 and 11). Figure 3b shows that $C_{\text{WS}}$ has to be larger than a given threshold (which was Enquist’s original result, indirectly specified by equation 7) for the honest strategy to be an ESS. It is clear from the figure that with increasing $C_{\text{WS}}$ the values of the $x_{\text{HSD}}$ and $x_{\text{DSD}}$ thresholds increase as well. However, these values (even for very large values of $C_{\text{WS}}$) will not go beyond the range of a potentially successful attack (see Fig. 2a).

**DISCUSSION**

I have shown that it is the proximity risk that maintains the reliability of threat displays. There is a given threshold of distance (honest striking distance, $x_{\text{HSD}}$) within which honest signalling is an ESS; outside this threshold a mixed strategy supported by honest and cheating signallers is an ESS up to another threshold of distance (dishonest striking distance, $x_{\text{DSD}}$), while outside $x_{\text{DSD}}$ threat displays are unreliable and thus will not be used. Depending on the value of the contested resource ($V$), the honest striking distance ($x_{\text{HSD}}$) can be as low as zero (see Fig. 2) which corresponds to the mixed equilibrium supported by honest and dishonest signals (see Számádó 2000).

What determines the shape of the $f(x)$ function? I propose that the weaponry being used and the species-specific fighting technique determine its shape. The longer the reach of the weapon and the more mobile the attacking technique the larger both $x_{\text{HSD}}$ and $x_{\text{DSD}}$ will be. In addition, the more static the animal during the attack the steeper the $f(x)$ function will be. For example, animals fighting from a standing pose exchanging blows with their weapons (e.g. giraffes) have a relatively short $x_{\text{HSD}}$ (compared to the size of the animal) and a steep $f(x)$
At this point we can ask what prevents weak individuals using such threats to scare away rivals. First, threat displays need not be ‘honest’ in the sense that they reveal differences in strength between opponents. The function of threat displays is to convey information about the risk of an impending attack, that is, about the willingness to fight (Walther 1984; Popp 1987; Waas 1991a) and not about differences in resource-holding potential (RHP, sensu Parker 1974). In this sense, any threat display that shows weaponry in a ready-to-use form within striking distance of an opponent should be treated as honest, as it shows the ability and the willingness to inflict damage. However, there are conditions under which threat displays can serve the function suggested by Enquist (1985), that is, when they can convey information about differences in strength. Not surprisingly, these conditions are related to proximity again. Threatening someone who can retaliate, that is, has the weaponry, who is aware of the signaller’s approach and who is within striking distance, is a risky enterprise. This risk, which I called ‘proximity risk’ because proximity (being within striking distance) is a necessary condition for this risk, is what maintains the ‘honesty’ of threat displays. Weak individuals will not accept this risk and will flee before they get within the honest striking distance of the given species.

Note that this risk is not a handicap in any way (as supposed by Zahavi & Zahavi 1997). The signaller does not have to take up a vulnerable position or show a vulnerable spot or anything like that. It has only to do (1) what is in its best interest, that is, prepare its weapons to fight, and (2) what is necessary to dispose of rivals, that is, approach its opponent. In other words, this risk follows from the way threat displays works; it is the proximity of the opponent who can retaliate that maintains honesty and there is no need for any strategic cost (sensu Grafen 1990; which is the definition of handicaps).
What relation is there between the two potential functions of threat displays? What correlation can we expect between strength and willingness to fight? Signals at the honest equilibrium give information not just about the strength of the signaller but also about the expected move (i.e. willingness to escalate) provided that the opponent does not withdraw. At the honest equilibrium, individuals using signal A are strong and willing to escalate; thus, as long as the honest strategy is an ESS there is a perfect correlation between the two functions. What can destroy this correlation? Obviously, on the one hand, weak individuals pretending to be strong, that is, using high-intensity threat and then attacking, or, on the other hand, strong individuals pretending to be weak, that is, using low-intensity threat and then withdrawing when threatened, can both do this. The first strategy has the same fitness as the 'cheater' strategy ($S_b$), so as long as cheaters cannot spread, this strategy cannot spread either. It is easy to show (see Appendix) that the ‘cheater’ strong strategy cannot spread either, as long as the expected value of the resource is greater than the cost of fighting for strong individuals fighting each other (i.e. $0.5V > C_{SS}$, which is one of the assumptions of the model). All in all, a strong correlation is expected between strength and willingness to fight as long as strength is variable in the population, the inequality $0.5V > C_{SS}$ holds, and communication takes place within the honest striking distance.

Endurance displays convey information about the signaller’s stamina and condition. In this case there is a direct correlation between the quality being advertised and signal form. Individuals in poor condition cannot perform the same signals as individuals in good condition. That is why Hurd & Enquist (2005) called these types of display ‘performance signals’ and Grafen (1990) called them ‘revealing handicaps’. It is important that endurance displays can be one-to-many signals, that is, one signaller can broadcast to many receivers, and these displays can be given, and are expected to be given, outside the striking distance. Matching of endurance displays is also possible if the challenger’s identity is clear. Note that while endurance displays are used in the context of aggressive communication, these are not threat displays: they do not convey information about the probability of impending attack.

Dominance displays advertise ownership or social dominance within groups. The form of these displays is often such that it serves to exaggerate the size of the signaller, as size is usually a good predictor of fighting ability. Dominance displays are usually one-to-many (broadcast) signals, although if the challenger’s identity is known then dominance displays can be addressed to one specific receiver (i.e. towards the challenger). The range of dominance displays can vary, depending on the signal type, that is, auditory, visual or chemical. Some dominance displays, such as birdsong, can have an exceptionally large

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**Figure 4.** Examples of steep and smooth $f(x)$ functions with the corresponding $x_{HSD}$ (solid line) and $x_{DSD}$ (dashed line) thresholds (same parameters, unless specified otherwise, are used as in Fig. 1). (a) A steep $f(x)$ function, $b = 0.8$, (c) with the corresponding $x_{HSD}$ and $x_{DSD}$ thresholds. (b) A smooth $f(x)$ function, $b = 0.05$, (d) with the corresponding $x_{HSD}$ and $x_{DSD}$ thresholds. Note that in the first case the $x_{HSD}$ and $x_{DSD}$ thresholds are very close to each other, that is, there is a sharp transition between honest signalling and no signalling.
range. Dominance displays are given far outside the striking distance. Given that the function of dominance displays is to advertise ownership and dominance, they do not convey information about the probability of an impending attack. Since dominance displays are not always enough to deter rivals, a transition between dominance and threat displays is expected and it is the usual sequence of escalation in animal fights in general. For example, Walther’s (1984) observations on Grant’s gazelle, Gazella granti clearly show this: only 2.6% of the dominance displays were followed immediately by a fight, in contrast to threat displays, where this number was as high as 77.5%.

All in all, both endurance and dominance displays have a different function from threat displays and are given outside the striking distance. As the contest escalates and opponents get closer and closer to each other, the frequency of threat displays should increase. Once the opponents reach the honest striking distance they should switch to threat displays or submissive displays (depending on the repertoire of the species) or flee (if possible).

**Predictions**

1. The honest use of threat displays is evolutionarily stable only within a certain distance between signaller and receiver, named the honest striking distance.
2. This range of honesty depends on weaponry and species-specific fighting style. The longer the reach of the weapons and the more mobile the fighting style the larger is the range within which the use of honest threat displays is an ESS.
3. There may or may not be a zone within which a mixture of honest and dishonest displays is used. This zone should be more prominent in species where the probability of a successful attack is a gradually decreasing function of distance.
4. Outside these zones threat displays are unreliable and should thus not be attended to, and as a consequence are not expected to be used, and even if used are expected to be ignored.
5. Approaching, that is, closing the distance between signaller and receiver, is a threat in itself. Crossing the honest striking distance has a forcing effect, as it forces the signaller to switch to honest threat displays (or to give up and flee).
6. If there is a gradation of threat displays then the most intense and the most efficient form should be the one displayed closest to the opponent, within striking distance, with weaponry fully displayed in a ready-to-use form.

There is already strong support for some of these predictions in the literature. It is clear that distance plays a crucial role: an escalated contest implies closer range and more aggressive individuals are more willing to close the range between the contestants. For example, Bossema & Burgler (1980) found while investigating feeder interactions in European jays, Garrulus glandarius, that the probability of attack was higher at short distances than at large ones. Furthermore, this probability was lowest if the receiver reacted with retreat and highest when it showed behaviour indicating approach. Matching song types is a signal of aggressive intentions in song sparrows, Melospiza melodia (Vehrencamp 2001). In playback experiments, song sparrow males that type-matched spent more time closer to the speaker (Vehrencamp 2001), and the distance to the speaker was a significant predictor of attack (i.e. the closer they were the more likely they were to attack, Searcy et al. 2006). The same correlation was found in swamp sparrows, Melospiza georgiana: those males that eventually attacked the speaker were significantly closer to it on average than those that never attacked (Ballentine et al. 2008). In anolis lizards, Anolis carolinensis, the A and B type headbob displays predict impending attack (Hurd 2004); most variation in headbob displays was found in the close to mid range (<60 cm) where the frequencies of A and B type headbob displays increased compared to the C type. Male collared lizards, Crotaphytus collaris, can exchange aggressive signals from as far away as 30 m but when the contest escalates they approach to within 0.5 m and switch to close-range signals (Lappin et al. 2006). In cave-dwelling little blue penguins, Eudyptula minor, distance and escalation were also correlated (Waas 1991b): the closer they were the higher intensity signal they used. Moreover, Waas (1991b) found that stationary displays were much less effective in deterring opponents than distance-reducing displays. Whereas stationary displays implied only the use of distance-reducing displays if the opponent failed to retreat, distance-reducing displays predicted an escalation to contact behaviour (Waas 1991b).

Many, if not all, species have graded threat displays of increasing intensity. Usually, the mildest form of threat is a ‘pointer’, a signal with which the opponent can be picked out of the crowd. The simplest of such displays is probably staring (e.g. little blue penguins: Waas 1991b) as it can unambiguously identify the receiver, but, for example, song type matching (Vehrencamp 2001) can serve the same purpose. However, the most intense threat in all known cases is approaching the opponent within striking distance and displaying weaponry in a full ready-to-use form. For example, in cave-dwelling little blue penguins the highest intensity (noncontact) threat is the so-called ‘flipper spread approach’ (Waas 1990); all higher intensity threats involve direct contact with the opponent (i.e. ‘bill to bill’, ‘bill slap’, etc., Waas 1990). Both song and swamp sparrow threat displays (i.e. those displays that predict attack) involve ‘wing-wave’ and a low-amplitude soft song (Vehrencamp 2001; Ballentine et al. 2008); wing-wave derives from the fighting technique, whereas soft songs can be perceived only at a close distance (Vehrencamp 2001; Ballentine et al. 2008). In collared lizards, gaping, that is, showing of weaponry and muscles, is a close-range threat display (Lappin et al. 2006).

In fulmars, Fulmarus glacialis, the honest striking distance is known. Enquist et al. (1985) studied the behaviour of fulmars competing for food on the surface of the sea. The bird in possession of the food is the owner and the others are potential challengers. Wing displays affected the behaviour of the challengers only if they were within 2 m. The rate of challenging against owners
showing full wing display was half the rate of challenging against owners not showing it. However, if the potential challengers were outside the 2 m radius then no differences in challenging rate were found. Enquist et al. (1985) gave no explanation for this finding, but, as we have seen, this is exactly what is expected based on the proximity risk model.

Finally, some observations can be related to the zone of mixed cheating. In American goldfinches, Carduelis tristis, the lowest intensity threat is the so-called ‘Low-intensity head forward’ display, whereas the highest intensity is the ‘Wing flap’ display (Popp 1987). The highest intensity threat is the most effective in driving away rivals but it is also the riskiest as it provokes the highest rate of attack from the receivers. Popp (1987) found that subordinates occasionally (10.9% and 9.3% in two groups, respectively) tried to bluff against dominants by initiating encounters with the highest intensity threat but they lost the majority of these encounters. The prediction of the proximity risk model is that these bluffing attempts were made in the zone of mixed cheating, that is, between the honest and dishonest striking distances. Thus, by simply plotting the distance between subordinates and dominants when these bluffing attempts are made, one can map out the zone of mixed cheating and estimate both the honest and the dishonest striking distance thresholds.

The proximity risk principle holds for humans as well. The range and form of threat displays are determined by the type and range of weapons the potential opponents possess. A swordsman has a higher honest striking distance than a bare-handed fighter, a gun has a higher one than a swordsman, etc. For obvious reasons intercontinental ballistic missiles have the highest values. In addition, displaying the ability and willingness to use these weapons are just as important as for nonhuman animals, hence the importance of displaying marksmanship, missile testing, military demonstrations, etc.

Conclusions

It is clear that threat displays are not handicaps. All known examples of threat displays are related to weaponry and fighting technique. More specifically it is usually the first step in the species-specific fighting technique that is used as a threat display, often in a ‘frozen’ form, that is, holding it much longer then necessary to send a clear message (Walther 1984). This use of the first step of the species-specific fighting technique as a threat display is evolutionarily stable and cannot be invaded by either cost-free signals or handicaps (Számádó 2003). The reliability of these displays (sensu Enquist 1985) is maintained by the risk inherent in the situation when a threat is made towards an individual who might retaliate. However, the threat of retaliation is credible only if the opponents are sufficiently close to each other; this is what I call, ‘proximity risk’. This proximity risk crucially depends on the weaponry of the species and on the species-specific fighting technique. I have shown that the honest use of threat displays is evolutionarily stable only within a threshold (the honest striking distance) within which this proximity risk is sufficiently large. Outside this distance the threat is not large enough to make the honest use of threat displays stable but a zone might be expected (depending on weaponry and fighting technique) in which a mixture of honest and dishonest threats is used. Finally, outside this zone (the dishonest striking distance) threat displays are unreliable, they confer no information about future choice of action and/or strength and thus even if given should be ignored. The model has testable predictions as discussed above; basically, it predicts a strong relation between weaponry, fighting technique and the range within which honest threat displays are evolutionarily stable.

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References


### Appendix

The fitness of a strong individual playing strategy $S_a$ is as follows:

$$E(S_a, S_a) = (1 - q) \left( \frac{1}{2} V - C_{SS} \right) + qV \quad (A1)$$

The fitness of a strong individual playing as a weak individual (denoted $S_c$) is as follows:

$$E(S_c, S_a) = (1 - q) 0 + q(V - C_{SW}) \quad (A2)$$

$S_c$ can spread in a population where strong individuals are playing $S_a$ if:

$$-C_{SW} > (1 - q) \left( \frac{1}{2} V - C_{SS} \right) \quad (A3)$$

Thus we can see that $S_c$ will not spread as long as the expected benefit from the fight ($0.5V$) is greater than the cost of fighting between strong individuals ($C_{SS}$).