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Perceptual advertisement by the prey of stalking or ambushing predators

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HIGHLIGHT

- We model signals by prey that they have detected a stalking or ambush predator.
- Such perceptual advertisement dissuades the predator from attacking.
- Such signals appear to have the potential to vary in intensity and cost.
- Some signals can only be given if the predator is detected with certainty.
- We show that such complexities still allow for stable, low cost reliable signalling.

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ABSTRACT

There has been previous theoretical explorations of the stability of signals by prey that they have detected a stalking or ambush predator, where such perceptual advertisement dissuades the predator from attacking. Here we use a game theoretical model to extend the theory to consider some empirically-motivated complexities: (i) many perceptual advertisement signals appear to have the potential to vary in intensity, (ii) higher intensity signals are likely to be most costly to produce, and (iii) some high-cost signals (such as staring directly at the predator) can only be utilised if the prey is very confident of the existence of a nearby predator (that is, there are reserved or unfakable signals). We demonstrate that these complexities still allow for stable signalling. However, we do not find solutions where prey use a range of signal intensities to signal different degrees of confidence in the proximity of a predator; with prey simply adopting a binary response of not signalling or always signalling at the same fixed level. However this fixed level will not always be the cheapest possible signal, and we predict that prey that require more certainty about proximity of a predator will use higher-cost signals. The availability of reserved signals does not prohibit the stability of signalling based on lower-cost signals, but we also find circumstances where only the reserved signal is used. We discuss the potential to empirically test our model predictions, and to develop theory further to allow perceptual advertisement to be combined with other signalling functions.

1. Introduction

When a predator attacks its prey, there may be a cost to the prey even if the attack is unsuccessful and the prey escapes with its life. This cost may be on opportunity cost of the lost time that might have been invested in other activities but that must be spent in evading the predator, the energetic costs of evasion, injury, depletion of resources (such as toxins) used in defence, or the risk that evading one predator can increase the conspicuousness of the prey to other predators. Unsuccessful attacks can be costly to the predator too, in terms of time and/or energy lost, risk of injury, or costs associated with betraying its presence to other prey or its own predators. Hence both prey and predators can benefit if predators can be dissuaded by a signal from the prey from attacking in situations where the chance of an attack succeeding is low. One such situation is aposematism, where there is variation between prey species in their level of defence, and highly defended prey species signal those defences to predators with conspicuous displays (see Ruxton et al., 2004 for an overview). Another situation where such signalling might be advantageous is where there is within-species variation in the ease of capture of prey individuals because of variation in intrinsic quality (e.g. running speed), and particularly high-quality individuals signal their quality to predators (Vega-Redondo and Hasson, 2003). Lastly, many ambush or stalking predators need to come near to the prey without being detected by that prey in order to facilitate capture; thus prey can signal to

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detected predators (dissuading them from attacking). Such signals are called *perception advertisement*, an idea whose origin is variously credited to Zahavi (1977), Baker and Parker (1979) or Woodland et al. (1980). It is this last type of prey–predator signalling that we will focus on here.

A number of empirical studies have reported perceptual advertisement signals of a diversity of forms from a diversity of vertebrate prey. In a recent review, Caro (2005) discusses directed staring in the direction of the predator as such a signal, suggesting that that for many birds and mammals this is combined with idiomatic postures that involve elevating the head, craning the neck and becoming immobile. The brown hare is a particularly commonly-cited example of this, with hares responding to stalking foxes by standing pipedally with their ears erect and their white vental surface directed towards the fox (Holley, 1993), and foxes being less likely to attack hares adopting this posture. Tail flicking (raising and lowering of the tail, often to show flashes of a conspicuous underside) is reported as perceptual advertisement in a number of waterbirds (Woodland et al., 1980; Alvarez, 1993) as well as some deer and antelope (Caro, 2005). Some deer and squirrels keep the tail continuously lifted in response to a nearby predator, exposing a brightly contrasting underside (a behaviour called *tail flagging*) and this too is considered to be perceptual advertising (Caro et al., 1995, 2004). Many artiodactyls (even toed ungulates: e.g. pigs, deer, antelopes, sheep, goats, and cattle) emit calls (often describes as snorts or barks) that are also interpreted as perceptual advertisement (see Caro et al., 2004; Reby et al., 1999 for reviews). Such calls can often be supplemented by foot stamping. A number of primates have been recorded using characteristic perceptual advertising calls to stalking predators (that might be expected to break off attacks when detected) such as leopards, but not to pursuit predators such as chimpanzees (which should care less about being detected) (Caro, 2005). Some perceptual advertisements signals involve the repeated close approach and backing away from the predator: such inspection behaviour has been reported in a range of fish, birds and mammals (e.g. Godin and Davis, 1995; Godin and Davis, 1995; Randall and King, 2001) and, although it may have additional functions, is generally considered to be perceptual advertisement. Foot drumming behaviour in a number of species of desert-living kangaroo rats is generally considered to inform nearby snakes that they have been detected (Randall et al., 1995; Randall, 2000). Finally some species of antelope, gazelle, sheep, goat, cattle, deer and pronghorn all show a characteristic jumping behaviour involving all of the legs being stretched out downwards at the top of the spring (so called *stotting*) that is considered to function as a mixture of perception advertisement and quality advertisement; with the relative importance of the two varying between species and ecological situations (Caro, 2005, 1986a, 1986b).

Although both parties can potentially gain from such signalling, its evolutionary stability is not trivial, because there can be an opportunity for prey to cheat and signal that they have detected the predators on occasions when they suspect that a predator is around but they are not certain. Bergstrom and Lachmann (2001) developed a game theoretical model to explore the conditions required for evolutionary stability in the face of such a danger of cheating (this model was later refined by Getty (2002)). Bergstrom and Lachmann (2001) envisage prey receiving a stimulus of value x at a certain time. This stimulus may be produced by a predator but may also come from other environmental sources; crucially the higher the value of x, the more likely the stimulus is to be predator-generated. Thus the stimulus (the value of x) provides an imperfect but still meaningful indication of the presence of a predator. For the evolutionarily stable strategy there is a critical value of x. If the prey detects a value of the stimulus above the critical value, then it signals and the predator (if present) aborts its attack; for stimulus values below the critical value, the prey does not signal and the predator (if present) does attack. Bergstrom and Lachmann (2001) demonstrate that such a signal can be stable provided a number of conditions are met. These can be interpreted biologically as follows:

1. There is a cost to prey of signalling, a cost that is paid whether the predator is present or not.
2. The costs of signalling are not so high that signalling is never profitable.
3. The value of the stimulus x provides some information (albeit imperfect) about the likelihood of predator presence, such that those prey most “concerned” about predation are actually those most at risk.
4. Prey that strongly suspect the presence of the predator are more difficult to capture than those with lower levels of suspicion, so that the signal actually conveys meaningful information to the predator.
5. The cost to the predator of attacking is not so high that it is never profitable for the predator to attack.

Here we explore a development of the model of Bergstrom and Lachmann (2001) that allows for greater levels of signal complexity. Specifically, the signal considered in the previous model was a simple binary response. Although the focal prey individual could vary in its expectation of the risk of predation (with that expectation rising with increasing stimulus value x), this variation in expectation influenced whether the signal was given or not, but not the nature of the signal. However, it seems biologically plausible that many of the real-world signals considered to be perceptual advertisement could vary in intensity in a way that could potentially convey information about the prey's certainty of the close proximity of the predator. For example, tail flicking, foot drumming and vocalisations could all vary in their frequency. The last two could vary in the intensity of individual elements (e.g. the loudness of a bark) as well as frequency, and it seems plausible that such flexibility could be used to convey the prey's degree of confidence in the presence of the predator. Here we will explore the evolutionary stability of perceptual advertisement in the face of this biologically-driven increase in the flexibility of signalling possible.

Further, it may be that some signals are only possible when the prey has a very high degree of confidence in the presence of the predator. For example, the directed staring of the hares discussed above and the predator inspection behaviour necessarily require that the predator has been detected and its position localised. Directed staring in particular has been widely observed across taxa, and we will also use our model to explore the evolutionary stability of such “reserved” signals that can only be given in special circumstances but provide very reliable information to the predator. Such signals are “unfakable” in that the prey must have good information about not just the presence but the position of the predator in order to perform them. We will also explore the consequence of the potential for such signals for the evolutionary stability of signals that do not have this restriction (such as vocalisations) and hence are potentially less inherently reliable.

Associated with our interest in greater variation in signal expression, we also consider greater variation in signal costs. Again this is biologically driven, as it seems likely that the variety of perceptual advertisement signals observed in the natural world vary in their costliness. For example, some (such as foot stamping or tail flicking) can be carried out without requiring a break from foraging, whereas directed staring and vocalisations likely generally require such an opportunity cost. Stotting is highly likely to be much more energetically expensive that tail flagging.

If the cost is paid in terms of risk of informing predators other than the focal predator being signalled of the presence of the prey, this may be more costly for vocalisations (which can be detected over long distances) than (for example) tail flicking. Hence, our final novel model elaboration will be to allow variation in signal costs to be associated with the variation in signal forms possible.

2. Methods: description of the model

We consider a population of prey individuals and a population of predator individuals. Within each population, all individuals are of identical quality. We use evolutionary game theory to analyse the predator and prey signalling behaviour that we might expect to see.

As a predator approaches a prey individual the prey receives some cue x, for instance it hears a noise. We assume that prey are approached by predators on average once per unit time following a Poisson process, and that the intensity x of the cue received follows a specific probability distribution, which we denote by f, e.g. x could be continuous with density function $f(x)$. In addition, prey receive non-predator-derived cues x_o, following a different probability distribution f_o. These assumptions are effectively the same as used by Bergstrom and Lachmann (2001).

Upon receiving cue x, a prey individual will send a signal $s(x)$, which the predator (if present) can detect. The (energetic) cost of sending signal s to the prey is $u(s)$, which increases with s but is independent of x (except for the indirect effect that x has through influencing the value of s); it is paid regardless of whether a predator is present or not. We shall assume that $u(s)$ is strictly increasing with s. If this was not the case, and there were a number of signals of equal cost, then it is reasonable to assume that the prey would always prefer the highest intensity signal amongst them. If the predator receives signal s, it can choose to either continue the attack or respond to the signal and not attack.

That the prey have a range of potential signals open to them is our first crucial departure from the assumptions of Bergstrom and Lachmann (2001), who assume a simple binary signal, with only two possible values (on or off). Following the methodology of Broom and Ruxton (2011), we divide all possible signals into A_0 that will prevent an attack and A_1 that will not. The prey's strategy is $s(x)$ for $x \in C$, the set of possible cues; and the predator's strategy is a choice of $A_0 \subseteq S$, the set of possible signals.

We shall seek evolutionarily stable strategy pairs; namely, choices of A_0 and $s(x)$ which when either the prey or the predator change strategy, means that they would perform strictly worse. We note that some formal strategy changes do not influence behaviour, and hence rewards, at all (for example if the predator changes the response it would give to a signal that the prey does not use). We thus in practice seek strategy pairs where any change which leads to an actual change in behaviour gives a strictly smaller reward. Thus in Section 3 (and in the associated Appendix A) we consider all plausible potential stable strategy pairs, and find the conditions under which they are stable, i.e. in which *any* change in strategy which leads to a behavioural change would cause the type changing strategy to perform worse.

We assume that some signals cannot be given to weak (low x) cues (e.g. prey cannot stare straight at a predator whose presence—and hence location—they are highly uncertain of). In general we define the function $T(x)$ to give the allowable signals. When x is received, the only allowable signals are $s \leq T(x)$.

In this paper we allow a range of values of $x \in [0,1]$ which indicates the potential presence of a predator and a single strong signal $x=2$ which reveals the predator with certainty. We also allow a range of unrestricted signals of increasing strength $s \in [0,1]$ and one restricted signal $s=2$. Thus we have $C=S=[0,1] \cup \{2\}$, and we set $T(x)=1$ for $x \leq 1$ and $T(2)=2$. Thus for any cue $x \leq 1$ (which contains information about a predator but not certainty) the prey give any signal except the restricted signal (staring at the predator). If $x=2$ and the prey knows where the predator is, it can stare at it using the most expensive signal ($s(2)=2$) or choose any other (cheaper) signal.

If a predator attacks a prey individual when it has given the cue x, then the reward to the predator is $v(x)$ which decreases with increasing x. This reward can be interpreted as the expected energetic gain to the predator (probability of prey capture multiplied by value of the prey minus energy expended). The (average) cost to the prey of an attack is $w(x)$, which again decreases with increasing x. This again can be interpreted as an expected energy loss (probability of capture multiplied by the cost of death plus the value of energy expended if death does not occur). We note that cost of death in particular would depend upon the state of the individual (a young healthy individual has more to lose), but that for simplicity all prey individuals in our model are assumed to be identical; the only asymmetry is in the strength of the cue received, and potentially the strategy played. Thus predators which induce higher values of the cue x are less likely to be successful in an attack. This assumption is fundamental to perceptual advertisement, and indicates that the predator benefits from remaining undetected. It is analogous to Bergstrom and Lachmann's (2001) condition that prey that strongly suspect the presence of a predator are more difficult to capture than those that have lower levels of suspicion.

If a predator is present we assume that there is a non-zero probability of it revealing itself with certainty, $P[x=2]>0$, and otherwise x has a probability density $f(x)$. If there is no predator $x=2$ cannot occur, but other cues x_o have density $f_o(x)$. We assume that predators arrive at an average rate of one per unit time, but that other cues occur at rate r. We assume that $f(x)/f_o(x)$ increases with x. That is, the higher the value of the cue x the more likely it is to be indicative of a predator. This is analogous to Bergstrom and Lachmann's (2001) assumption that the value of the stimulus x provides some indication (albeit imperfect) of the presence of a predator.

We further assume that

$$\frac{d}{dx}\left(\frac{w(x)f(x)}{f(x)+rf_o(x)}\right) > 0 \tag{1}$$

In fact we do not technically need this derivative to exist at all, as long as the term in brackets is an increasing function of x. $f(x)/(f(x)+rf_o(x))$ is the probability that a cue of strength x received by a prey individual actually comes from a predator (recall that $w(x)$ is the cost to a prey of an attack coming from a predator that sends cue x). This condition means that (if predators always attack) then the higher the value of the cue x received, the higher the expected cost to the prey. Thus, the higher the value of cue x that the prey receives, the greater its incentive to discourage attack from the predator. The prey can discourage such an attack by signalling to the predator that it has been detected. Again, this is analogous to Bergstrom and Lachmann's (2001) assumption that those prey most concerned about predation are actually those at greatest risk of an attack.

3. Results: stable solutions of the model

In general, the rewards to the predator R_Q and the prey R_P in terms of expected energetic gain are given by the expressions below:

$$R_Q = P[X=2]v(2)1_{s(2)\in A_1} + \int_{s(x)\in A_1} f(x)v(x)dx \tag{2a}$$

$$R_P = -P[x=2](w(2)1_{s(2)\in A_1}+u(s(2))) - \int_0^1 f(x)(w(x)1_{s(x)\in A_1}+u(s(x)))dx$$
$$-r\int_0^1 f_0(x)u(s(x))dx \tag{2b}$$

We define the following two predator choices: choice 0 is the choice not to attack and choice 1 is the choice to attack. Thus $w(x)>0$ is the cost to the prey of the predator making choice 1.

For a stable solution, the prey must play $\min(A_0)$ or $\min(A_1)$ in every situation (otherwise it could change to a lower signal within the same set and so reduce its cost without affecting the predator response).

We also need $\min(A_1) < \min(A_0)$, whenever both sets are non-empty and $\min(A_1)$ is sometimes chosen by the prey, since otherwise switching to a lower-cost signal could prevent an attack. This means that $\min(A_1)=0$ unless A_1 is the empty set (or at least a signal never employed by the prey).

Note that if there exists a value s that is a member of A_0 where $s \leq 1$, then the unfakable signal ($s=2$) cannot be stable.

Thus the possible stable solutions are

1) $A_0=[0,1] \cup \{2\}$, so that there are no attacks and prey always give the lowest-cost signal: $s(x)=0$ for all x.
2) $A_1=[0,1] \cup \{2\}$, and A_0 equals the empty set, so that there is always an attack whenever the predator is present and prey always give the lowest-cost signal: $s(x)=0$ for all x.
3) $A_0=\{2\}$, so only the restricted unfakable signal prevents an attack in this case. There are two possibilities:
   either (a) $s(2)=2$ and $s(x)=0$ for all $x \leq 1$, so that only the unfakable signal is given when the predator is spotted;
   or (b) $s(x)=0$ for all x and so no signal is ever given and there is always an attack.
4) $2 \in A_0$, $A_0 \backslash \{2\} \neq \Phi$ so the predator will respond to sufficiently strong signals below the unfakable one. There are four cases labelled (a–d), depending on the signals given by the prey (these cases will be explored in turn below).

We consider case 1 below to illustrate our methodology, and each of the other seven cases 2, 3a, 3b, 4a, 4b, 4c and 4d described above are considered in Appendix A.

Case 1. $A_0=[0,1]\cup\{2\}$, and $s(x)=0$ for all x. There are no attacks and the prey always gives the lowest-cost signal, regardless of x.

Substituting the above values into Eqs. (2a) and (2b) we obtain

$$R_Q = 0 \tag{3a}$$

$$R_P = -u(0)\left\{ p[X=2] + \int_0^1 (f(x)+rf_o(x))dx \right\} \tag{3b}$$

This strategy pair is stable with respect to the predators' strategy if any change in predator strategy reduces the reward to the predator. The only change in strategy that the predator can make is to switch to attacking when a signal $s=0$ is received, i.e. moving the signal 0 from set A_0 to A_1. We shall denote such a change by the shorthand $0 \rightarrow A_1$ (and other strategy changes will be similarly denoted in Appendix A). This change reduces the predator payoff if

$$P[X=2]v(2) + \int_0^1 f(x)v(x)dx < 0 \tag{4}$$

We summarise all of the important conditions in a logical sequence as we see in Appendix A. We denote the condition in inequality (4) by ($C3^c$). In general conditions denoted by a C relate to a change of the predator response to a signal, and conditions denoted by a D relate to a change in prey strategy.

The strategy pair is clearly stable with respect to the prey's strategy, since changing s can only increase the cost without affecting the outcome.

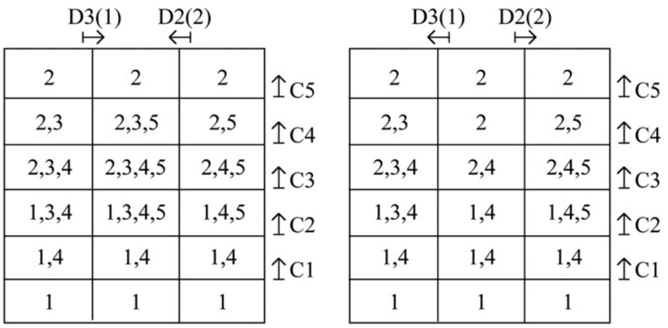
3.1. Summary of evolutionarily stable strategies

Although there are technically eight cases, there are only five distinct cases where the observable behaviour can be different. Note that we give the conditions for when a given solution can occur, and it is not guaranteed that this will be the solution observed in a particular population, as there can be more than one solution for an identical set of parameter values.

S1: No attacks or costly signals (s values above 0) occur when $C3^c$ holds (inequality (4) holds).
S2: No costly signals (s values above zero) are given and attacks always occur when C3 holds (inequality (4) does not hold).
S3: Attacks always occur unless the predator is unambiguously spotted, when the prey gives the unfakable signal ($s=1$), when the combination of conditions represented by $C5^c \cap C2 \cap D2(2)$ holds (equivalently inequalities (8)–(10) hold, see Appendix A).
S4: Medium-cost signals (s values between zero and one) occur for sufficiently strong cues, and these deter attacks, while attacks occur when no signal is given ($s=0$). The precise conditions when such signals occur are given in Appendix B.
S5: Medium level signals occur only when the predator is unambiguously spotted and this is enough to deter the predator. Otherwise attacks occur. The precise conditions when such signals occur are again given in Appendix B.

Where the different solutions hold depends on D2(2), D3(1) and C1–C5 (see Appendix A) for the cases numbered 1–5 above, and we present these solutions graphically in Fig. 1.

That is, five different solution types are possible, and for a given set of parameter values more than one of these five may be possible. Indeed, for some parameter values four of the five are possible. We list the set of possible solutions for a given situation separated by commas in the figure. The 5 criteria C1,…,C5 are always in the same order. However, the criteria D2(2) and



2	2	2	↑C5
2,3	2,3,5	2,5	↑C4
2,3,4	2,3,4,5	2,4,5	↑C3
1,3,4	1,3,4,5	1,4,5	↑C2
1,4	1,4	1,4	↑C1
1	1	1	

2	2	2	↑C5
2,3	2	2,5	↑C4
2,3,4	2,4	2,4,5	↑C3
1,3,4	1,4	1,4,5	↑C2
1,4	1,4	1,4	↑C1
1	1	1	

Fig. 1. The potential evolutionarily stable solutions to the model. Which of the different solutions holds depends on which of the conditions D2(2), D3(1) and C1–C5 hold. Whilst there is a defined order to conditions C1–C5, the order of the other two conditions depends on the parameter values, and we include two tables for the two possible orderings. In some situations more than one type of solution is possible. In all, five different types of solution are possible: (1) no costly signals (s values above 0) or attacks occur; (2) no costly signals (s values above 0) occur, but attacks always occur; (3) attacks always occur unless the predator is unambiguously spotted, when the prey gives the unfakable signal ($s=1$); (4) medium-cost signals (s values between zero and one) occur for sufficiently strong cues, and these deter attacks, while attacks occur when no signal is given ($s=0$); and (5) medium level signals occur only when the predator is unambiguously spotted and this is enough to deter the predator, otherwise attacks occur.

D3(1) can occur in either order, hence, to find the possible solutions for a given set of parameter values, one must first evaluate the order of these and select whichever of the two tables in Fig. 1 is appropriate to that ordering. One then identifies which of the 18 cells in the table the parameter value combination implies, and the list of possible solutions for that set of parameter values will be given in that cell. In particular, at the bottom of the diagrams in Fig. 1, attacks are unattractive to predators and so no signal is needed to deter them; at the top attacks are so attractive that no signal can deter them.

4. Discussion

The first thing to note about our model predictions is that (for any combination of parameter values) a single non-signalling equilibrium will exist where the prey do not signal (in our model this is equivalent to using the lowest-cost signal $s=0$), and all predators either always attack or never attack. Clearly when predators always or never attack any mutant prey that used a higher-cost signal would incur greater costs without modifying predator behaviour, and thus would not be selected. For the predators, as long as all prey are not signalling, then there is no intrinsic difference that the predator can detect between interactions with prey, so the only rational strategy is to always or never attack (whichever leads to the highest average reward). This occurs because we have assumed that the prey but not the predator can perceive the value of the stimulus x in any interaction, hence in the absence of a signal from the prey the predator does not have any information on whether a particular prey individual has become aware of its presence or not. Biologically, this seems plausible in many situations. Consider a lion stalking a gazelle, the lion might be aware of the sound of dry vegetation snapping under its body as it creeps forward, but it would often not be able to judge effectively whether those sounds have carried to and been detected by the gazelle (in the absence of any behavioural change—perception advertisement—by the gazelle). We would expect an analogous non-signalling equilibrium to exist in other coevolved signalling systems where receivers have no way of differentiating signallers in the absence of signals.

Such a non-signalling equilibrium is not only logically plausible, it meets with biological observation: while examples of perceptual advertisement are widespread taxonomically, they are not ubiquitous and it seems that only a minority of vertebrate prey seem to use them to stalking or ambush predators. Although the non-signalling equilibrium is stable to the appearance of any single mutant, it is possible to imagine scenarios where evolution away from this equilibrium is possible. Imagine the equilibrium strategy is for prey never to signal, and predators not to respond to signals and always attack. If the prey population remains unchanged, so no signals occur, then other strategies can drift into the predator population provided those strategies include the condition of always attacking when no signal is given. That is, all such predator strategies with respect to other signals will be equivalent in payoffs as long as no signals are given. If after some such predator strategies have drifted into the population a mutant signalling prey individual occurs, then that mutant may (but need not necessarily—and in most causes likely will not) do better than the non-signalling "field" individuals. Thus if predators are susceptible to such stimuli, this is a potential way for signalling strategies to begin.

It is important to see that evolution away from the non-signalling equilibrium is possible (as discussed above), since otherwise the other signalling equilibria predicted by our model could not be reached. One type of signalling equilibrium predicted is exactly analogous to that predicted by the model of Bergstrom and Lachmann (2001). Specifically, there is a critical value of x, for stimulus values below which prey respond by not signalling (i.e. using the lowest-cost signal $s=0$). However for all x values greater than the threshold, prey emit the same higher-cost signal. Thus, despite the greater flexibility of signalling introduced in our model (with a range of signal intensities open to the prey: all values of s from zero to one inclusive) they adopt an essential binary signal, exploiting only two of the continuum of signal levels open to them. The biological interpretation of this is that we do not expect perceptual advertisements to be informative about the prey's confidence in the proximity of the predator. That is, we do not expect an individual prey type to modulate say foot-drumming intensity or tail-flicking frequency to indicate to the predator how confident the prey is in having detected the predator. Such a strategy does not appear evolutionarily stable in our model. We note that this prediction relies on the assumption that all individuals are essentially identical. Significant between-individual variation in predators and/or prey could perhaps generate different such intensities. We would expect this result to hold more widely in coevolved signalling systems. Specifically, where receivers are limited to a binary response (e.g. whether to mate or not, whether to flee or not, whether to attack or not) signallers will often be expected to utilise only two signal levels.

The range of possible signals available in our model gives a larger range of possible scenarios where signalling can occur than in (Bergstrom and Lachmann, 2001), since the region associated with strategy (S4) is larger than for any fixed value of signal a_o. On the other hand, regions (S3) and (S5) overlap with regions (S1), (S2) and (S4) so that it is possible that situations may occur where only unfakeable signals are used when in the absence of this possibility either there would be no signalling or there would be signalling with fakable signals (in this latter case the overall level of signalling would be significantly reduced). Thus overall in our model there are more types of signalling possibilities and signalling would occur in more scenarios, but sometimes the actual amount of signalling that would be observed would be a lot less, than in the model of Bergstrom and Lachmann (2001).

However, the model also demonstrates that prey will not necessarily always adopt the cheapest signal to indicate that it suspects a predator is near. That is, the non-zero signal used by prey at this equilibrium ($s=a_o$) is not the minimum cost signal that can be differentiated from $s=0$. If fact we predict not just one equilibrium of this type for a given set of parameter values but a continuum of such equilibria, for each critical value of the stimulus (x_c) there will be a different value of signal intensity a_o. We would expect x_c and a_o to be the same across individual animals within a set of interacting predators and prey populations; but would expect variation in these values between sets of populations. Thus globally, we would not expect that the intensity of vocalisations produced by artiodactyls as perceptual advertising to be strongly constrained; however at a local level we would expect such uniformity in the type of signals given by different prey individuals or the same individual on different occasions. We would predict that higher confidence in predator presence needed before signalling (higher x_c) will be associated with more intense and costly signals (higher a_o). Thus a clear prediction of our model is that prey populations that require less certainty before advertising perception will signal more often when no predator is in fact present and will also use lower cost signals. This prediction should be amenable to empirical testing across populations. We would also expect analogous situations in other coevolved signalling systems, with signallers that utilise more expensive signals using them less frequently than in analogous populations where signalling is cheaper.

It is important to note that this "medium-cost equilibrium" predicted by Bergstrom and Lachmann (2001) also occurs in our model despite the introduction of the reserved signal that is high-cost and can only be given when the prey is very sure of the existence of a nearby predator. Thus the potential for such an unfakable high-cost signal does not prevent the occurrence of the previously-described equilibrium. Our model predicts the existence of yet another type of equilibrium where the prey never signals and the predator always attacks, unless the prey is very sure of the presence of the predator ($x=2$ in our model) and gives the reserved, unfakable, high-cost signal which deters the predator (if one is present). We note that, as with all our signalling equilibria, the prey's behaviour is a binary response between two alternatives. Biologically, this equilibrium means that we predict that sometimes perceptual advertisement signals may be very expensive, but such signals will only be used (indeed in some cases can only be used) when the prey is very sure of the existence of the predator nearby. An example of such an unfakable signal may be the directed staring as described in hares in the Introduction. Note our prediction is that prey that use such high-cost signals will not also use lower cost signalling. Hence we would not expect hares to also on some occasions use a lower-cost signal (e.g. foot thumping or tail flagging) when they have reduced confidence in the proximity of a predator. Caro (2005) argues that perception advertising signals are generally low-cost (compared to signals of individual quality). He admits that the apparent perceptual advertisement function of stotting behaviour does not fit well with this generalisation. Our models predict that such high cost signals can be predicted, but they will be paired with very high confidence in the proximity of a predator. Again this is empirically testable, and we would predict that costly-perceptual advertisement by stotting or directed staring is very rarely triggered by non-predatory environmental stimuli (in comparison to lower cost signals). Generally across co-evolved signalling systems we would expect high cost signals to be used more sparingly and more judiciously (with less signalling to inappropriate receivers—e.g. sexual signalling to heterospecific females).

The model also predicts one final type of equilibrium where prey only signal when they have maximal confidence in the proximity of a predator, but do not use the reserved signal to do this but rather a lower-cost unreserved signal. Biologically this means that even when prey have detected predators with certainty they may not use unfakable signals such as directed staring. It is likely that this is what occurs in the kangaroo rat system where often the prey has visually detected a specific snake prior to the onset of its foot thumping signal.

In this paper we have strived to further cement the theoretical underpinning of the interpretation of perceptual advertisement signals from prey to ambushing or stalking predators. We have shown that such signals seem evolutionarily stable in a wider range of circumstances than previous explored, and that the predicted signals accord well with empirical observation of such signals in natural systems. However, it is important to note that although there seems good evidence that some systems feature signals by prey that function primarily in informing predators of their detection, such a signal may have a number of other functions: such as informing predators of the intrinsic quality of the signaller (Zahavi, 1990), warning other prey individuals of the danger (Blumsein and Armitage, 1997), and (most speculatively) attracting mesopredators that might be a threat to the focal predator. Further, the signal may also be subject to sexual selection (Cresswell, 1994; Leal, 1999). Hence there is a need to build on existing theory and explore the influence of such multiple selection pressures on the existence and form of signals between prey and predators. We hope that this work will provide a useful foundation for such further development.

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Appendix A

Case 2. $A_1=[0,1]\cup\{2\}$, and $s(x)=0$ for all x. Thus attacks always occur and the prey always gives the lowest-cost signal:

$$R_Q = P[X=2]v(2) + \int_0^1 f(x)v(x)dx \tag{5a}$$

$$R_P = -P[X=2](w(2)+u(0)) - \int_0^1 f(x)w(x)dx - u(0)\int_0^1 (f(x)+rf_o(x))dx \tag{5b}$$

This solution is stable with respect to predator strategy if $0\rightarrow A_0$ (i.e. predators switching to not attack when receiving the minimum-cost signal) reduce their payoff, i.e. if

$$P[X=2]v(2) + \int_0^1 f(x)v(x)dx > 0 \tag{6}$$

This is clearly the opposite of the condition from (4), and we denote this condition by (C3).

It is clearly stable with respect to prey strategy, since changing s increases the cost without affecting the outcome.

Case 3a. $A_0=\{2\}$, $s(2)=2$, $s(x)=0$ for all $x\leq 1$. Only the maximum-cost signal prevents attack; prey give this signal in response to obtaining the "special" cue $x=2$, and otherwise give the lowest-cost signal:

$$R_Q = \int_0^1 f(x)v(x)dx \tag{7a}$$

$$R_P = -P[X=2]u(2) - \int_0^1 f(x)w(x)dx - u(0)\int_0^1 (f(x)+rf_o(x))dx \tag{7b}$$

This is stable with respect to the predator if $2\rightarrow A_1$ (predators switching to attacking when receiving the maximum-cost signal) reduces their payoff: i.e. if

$$P[X=2]v(2) < 0 \tag{8}$$

which we denote by (C5^c), and if $0\rightarrow A_0$ (predators switching to not attacking when given the minimum cost signal) reduce their payoff, i.e. if

$$\int_0^1 f(x)v(x)dx > 0 \tag{9}$$

which we denote by (C2).

It is stable with respect to prey strategy if $s(2)\rightarrow 0$ (switching to using the minimum cost signal in response to the reserved cue $x=2$) reduces the prey payoff; i.e. if

$$w(2)+u(0)-u(2) > 0 \tag{10}$$

We denote this condition by D2(2).

All other changes of s would increase the cost of signalling to prey without affecting the outcome of the signal (in terms of predator behaviour).

Case 3b. $A_0=\{2\}$, $s(x)=0$ for all x. The maximum-cost signal would deter an attack, but prey always use the minimum cost signal:

$$R_Q = P[X=2]v(2) + \int_0^1 f(x)v(x)dx \tag{11a}$$

$$R_P = -P[X=2](w(2)+u(0)) - \int_0^1 f(x)w(x)dx - u(0)\int_0^1 (f(x)+rf_o(x))dx \tag{11b}$$

This is stable with respect to predator strategy if $0\rightarrow A_0$ (predators switching to not attacking when receiving the minimum-cost signal) reduce their payoff, i.e. if

$$P[X=2]v(2)+\int_0^1 f(x)v(x)dx>0 \tag{12}$$

This is again condition (C3).

It is stable with respect to prey strategy if $s(2)\rightarrow 2$ (giving the maximum-cost signal in response to the reserved cue $x=2$) reduces the prey's payoff, i.e. if

$$w(2)+u(0)-u(2)<0 \tag{13}$$

This is the complement to the condition from inequality (10), $D2(2)^c$.

All other changes of s would increase the cost of signalling to the prey without affecting the outcome (i.e. without changing predator attack decisions).

There are four different variations of case 4 where the predator will respond to sufficiently strong signals below the unfakable one.

Case 4a. $A_0=[a_o,1]\cup\{2\}$, $s(x)=0$, $x<x_{\text{crit}}$; $s(x)=a_o$, $x\geq x_{\text{crit}}$. That is, prey give a minimum-cost signal in response to cue values below a critical threshold (x_{crit}) and a single higher-cost signal (a_o) to all other cues. The higher-cost signal deters attack but the minimum-cost one does not:

$$R_Q=\int_0^{x_{crit}} f(x)v(x)dx \tag{14a}$$

$$R_P=-\int_0^{x_{\text{crit}}} f(x)w(x)dx-u(0)\int_0^{x_{\text{crit}}}(f(x)+rf_o(x))dx-u(a_o)\times\left[P[x=2]+\int_{x_{\text{crit}}}^1(f(x)+rf_o(x))dx\right] \tag{14b}$$

This solution is stable with respect to predator strategy if $a_o\rightarrow A_1$ reduces the predator's payoff, i.e. if

$$\int_{x_{crit}}^1 f(x)v(x)dx+P[x=2]v(2)<0 \tag{15}$$

which we denote by $C4^c(a_o)$, and if $0\rightarrow A_o$ reduces the payoff: i.e. if

$$\int_0^{x_{crit}} f(x)v(x)dx>0 \tag{16}$$

which we denote by $C1(a_o)$.

The strategy is in equilibrium regarding a change in prey strategy if a small change in x_{crit} has no effect: i.e.

$$f(x_{\text{crit}})w(x_{\text{crit}})+(f(x_{\text{crit}})+rf_o(x_{\text{crit}}))(u(0)-u(a_o))=0 \tag{17}$$

We denote this equality condition by $D1(a_o)$.

All changes not involving ($s(x)\rightarrow a_o$ and $x<x_{\text{crit}}$) or ($s(x)\rightarrow 0$ and $x\geq x_{\text{crit}}$) increase costs without changing outcomes (or do worse than changes involving them) and those involving either of these reduce the payoff, because of equation ($D1(a_o)$) and condition (1). The condition $D1(a_o)$ finds the unique value of x_{crit} associated with a_o, and, from condition (1), the larger a_o, the larger x_{crit}. It is easy to see that a pair (a_o, x_{crit}) (and generally many such pairs) always exists, and so $D1(a_o)$ always holds for some a_o, by noting that substituting $x_{\text{crit}}=0$ in the left hand side of (17) gives a negative value, and that letting a_o tend to zero makes the second term on the left hand side of (17) arbitrarily small, so a corresponding x_{crit} can clearly be found that satisfies (17) (we note this would not necessarily be true if there was a minimum registerable non-zero signal with non-zero cost).

Note that there is an x_{crit} for each a_o (potentially), so there is a different set of conditions for each a_o.

Case 4b. $A_o=[a_o,1]\cup\{2\}$, $s(x)=0$ for all x. Prey never signal, despite the fact that high (but unreserved) values of the signal and the reserved signal would both deter attack:

$$R_Q=P[x=2]v(2)+\int_0^1 f(x)v(x)dx \tag{18a}$$

$$R_p=-P[x=2](w(2)+u(0))-\int_0^1 f(x)w(x)dx-u(0)\int_0^1(f(x)+rf_o(x))dx \tag{18b}$$

This is stable with respect to predator strategy if $0\rightarrow A_0$ reduces the payoff, i.e. if

$$P[x=2]v(2)+\int_0^1 f(x)v(x)dx>0 \tag{19}$$

This is condition (C3) again.

It is stable with respect to prey strategy if $s(2)\rightarrow a_o$ reduces the payoff: i.e. if

$$w(2)+u(0)-u(a_o)<0 \tag{20}$$

We denote this condition by $D2^c(a_o)$. (Note that from (1) it is clear that ($D2^c(a_o)$) implies that

$$f(x)w(x)+(f(x)+rf_o(x))(u(0)-u(a_o))<0 \tag{21}$$

so that if ($D2^c(a_o)$) holds then the strategy is also stable against any $s(x)\rightarrow a_o$ when $x\leq 1$).

Case 4c. $A_o=[a_o,\ 1]\cup\{2\}$, $s(2)=a_o$, $s(x)=0$ for $x\leq 1$. High (but unreserved) values of the signal and the reserved signal would both deter attacks. However, the prey always adopts the lowest-cost signal (thus always induces an attack if the predator is present), unless the highest value cue ($x=2$) is detected, in which case the prey signals with the lowest-cost signal that is still sufficient to deter an attack:

$$R_Q=\int_0^1 f(x)v(x)dx \tag{22a}$$

$$R_P=-P[x=2]u(a_o)-\int_0^1 f(x)w(x)dx-u(0)\int_0^1(f(x)+rf_o(x))dx \tag{22b}$$

This is stable with respect to predator strategy if $0\rightarrow A_0$ reduces the payoff, i.e. if

$$\int_0^1 f(x)v(x)dx>0 \tag{23}$$

which is condition (C2), and if $a_o\rightarrow A_1$ reduces the payoff, i.e. if

$$P[x=2]v(2)<0 \tag{24}$$

which is condition ($C5^c$).

It is stable with respect to prey strategy if $s(2)\rightarrow 0$ reduces the payoff, i.e. if

$$w(2)+u(0)-u(a_o)>0 \tag{25}$$

which is condition $D2(a_o)$, and if $s(1)\rightarrow a_o$ reduces the payoff, i.e. if

$$f(1)w(1)+(f(1)+rf_o(1))(u(0)-u(a_o))<0 \tag{26}$$

which we denote by condition $D3^c(a_o)$. (We again note that if ($D3^c(a_o)$) holds, then from inequality (1) the bracketed expression is negative for all $x\leq 1$).

Case 4d. $A_o=[a_o,1]\cup\{2\}$, $s(x)=a_o$ for all x. High (but unreserved) values of the signal and the reserved signal both deter attacks. The prey always signals with the lowest-cost signal that is still sufficient to deter an attack, regardless of the cue received:

$$R_Q=0 \tag{27a}$$

$$R_P=-u(a_o)\left\{P[x=1]+\int_0^1(f(x)+rf_o(x))dx\right\} \tag{27b}$$

This is stable with respect to predator strategy if $a_o \to A_1$ reduces the payoff, i.e. if

$$P[x=2]v(2)+\int_0^1 f(x)v(x)dx<0 \tag{28}$$

It is stable with respect to prey strategy if $s(x)\to 0$ reduces the payoff at $x=0$, i.e. if

$$f(0)w(0)+(f(0)+f_o(0))(u(0)-u(a_o))>0 \tag{29}$$

Assuming that it is not worth giving a signal to a zero cue, e.g. if $f(0)=0$, which we shall assume, then this last condition can never be met and Case 4d is never stable.

Assuming that the bigger the cue x the lower the reward to the predator should it attack, as we have done, we have the following relationships between the C conditions for any $a<b$:

$$\mathrm{C5} \Rightarrow \mathrm{C4}(b) \Rightarrow \mathrm{C4}(a) \Rightarrow \mathrm{C3} \Rightarrow \mathrm{C2} \Rightarrow \mathrm{C1}(b) \Rightarrow \mathrm{C1}(a) \tag{30}$$

Similarly we have the following relationships for any $a<b$,

$$\mathrm{D3}(a) \Rightarrow \mathrm{D2}(a),\mathrm{D2}(b) \Rightarrow \mathrm{D2}(a),\mathrm{D3}(b) \Rightarrow \mathrm{D3}(a) \tag{31}$$

Note that Case 1 occurs if $\mathrm{C3}^c$ holds and Case 2 occurs if C3 holds, so exactly one of these always holds.

Cases 2, 3b and 4b all involve a population which does not signal, where and thus there are always attacks. Case 4b occurs when $\mathrm{D2}^c(a_o)\cap\mathrm{C3}$ holds, which implies $\mathrm{D2}^c(1)\cap\mathrm{C3}$ and Case 3b which implies Case 2. Thus even though there are distinctions worth noting, we will list all three as examples of Case 2, since the observable behaviours of both predators and prey (always attack, never signal) are the same in each case.

Appendix B

The solution represented by case (S4) occurs when the combination of conditions represented by $\mathrm{C4}^c(a_o)\cap\mathrm{C1}(a_o)\cap\mathrm{D1}(a_o)$ holds for a given value of a_o. There will be a solution to $\mathrm{D1}(a_o)$ provided that $\mathrm{D3}^c(1)$ holds (we can see this by considering all possible combinations of a_o and x and realizing there is no solution only if $u(a_o)$ is too small even for its maximum value of $a_o=1$).

The solution represented by case (S5) occurs when the combination of conditions represented by $\mathrm{C2}\cap\mathrm{C5}^c\cap\mathrm{D2}(a_o)\cap\mathrm{D3}^c(a_o)$ holds for a given value of a_o. There will be such an a_o if $\cup_{a_o\in(0,1)}(D2(a_o)\cap D3^c(a_0))\equiv \mathrm{D3}^c(1)$ from the fact that

$$D2(a_o)\cap D3^c(a_o)\equiv -w(2)<u(0)-u(a_o)<-\frac{w(1)f(1)}{f(1)+rf_0(1)}$$

and Eq. (31). This gives $\mathrm{C2}\cap\mathrm{C5}^c\cap\mathrm{D3}^c(1)$.

References

Alvarez, F, 1993. Alertness signalling in two rail species. Anim. Behav. 46, 1229–1231.

Baker, R.P., Parker, G.A., 1979. The evolution of bird coloration. Philos. Trans. R. Soc. London B 287, 63–130.

Bergstrom, C.T., Lachmann, M., 2001. Alarm calls as costly signals of antipredatory vigilance: the watchful babbler game. Anim. Behav. 61, 535–543.

Blumsein, D.T., Armitage, K.B., 1997. Does sociality drive the evolution of communication complexity? A comparative test with ground-dwelling sciurid alarm calls. Am. Nat. 150, 179–200.

Broom, M., Ruxton, G.D., 2011. Some mistakes go unpunished: the evolution of all or nothing signalling. Evolution 65, 2743–2749.

Caro, T.M., 1986a. The functions of stotting: a review of the hypotheses. Anim. Behav 34, 649–662.

Caro, T.M., 1986b. The functions of stotting in Thomson's gazelles: some tests of the predictions. Anim. Behav. 34, 663–684.

Caro, T.M., 2005. Antipredator Defenses in Birds and Mammals. University of Chicago Press, Chicago.

Caro, T.M., Lombardo, L., Goldizen, A.W., Kelly, M, 1995. Tail flagging and other anti-predatory signals in white-tailed deer: new data and synthesis. Behav. Ecol. 6, 442–450.

Caro, T.M., Graham, C.M., Stoner, C.J., Vargas, J.K., 2004. Adaptive significance of antipredator behaviour in artiodactyls. Anim. Behav. 67, 205–228.

Cresswell, W., 1994. Song as a pursuit-deterrent signal, and its occurrence relative to other anti-predator behaviours of skylark (*Alauda arvensis*) on attack by merlins (*Falco columbarius*). Behav. Ecol. Sociobiol. 23, 217–223.

Getty, T., 2002. The discriminating babbler meets the optimal diet hawk. Anim. Behav. 63, 397–402.

Godin, J.-G.J., Davis, S.A., 1995. Who dares, benefits: predator approach behaviour in the guppy (*Poecilia reticulata*) deters predator pursuit. Proc. R. Soc. London B 259, 193–200.

Godin, J.-G.J., Davis, S.A., 1995. Boldness and predation deterrence: a reply to Milinski and Boltshauser. Proc. R. Soc. London B 262, 107–112.

Holley, A.J.F., 1993. Do brown hares signal to foxes. Ethology 94, 21–30.

Leal, M., 1999. Honest signalling during prey-predator interactions in the lizard Anolis cristatellus. Anim. Behav. 58, 521–526.

Randall, J.A., 2000. Why do desert animals drum their feet? Am. Zool. 40, 1182–1183.

Randall, J.A, King, D.K.B., 2001. Assessment and defence of solitary kangaroo rats under risk of predation by snakes. Anim. Behav. 61, 579–587.

Randall, J.A, Hatch, S.M., Hekkala, E.R., 1995. Interspecific variation in antipredator behaviour in sympatric species of kangaroo rat. Behav. Ecol. Sociobiol. 36, 243–250.

Reby, D., Cargnelutti, B., Hewison, A.J.M., 1999. Contexts and possible functions of barking in roe deer. Anim. Behav. 57, 1121–1128.

Ruxton, G.D., Speed, M.P., Sherratt, T.M.T.M., 2004. Avoiding Attack. University Press, Oxford.

Vega-Redondo, F., Hasson, O., 2003. A game-theoretic model of predator–prey signalling. J. Theor. Biol. 162, 309–319.

Woodland, D.J., Jaafar, Z., Knight, M.L., 1980. The pursuit deterrent function of alarm calls. Am. Nat. 115, 748–753.

Zahavi, A., 1977. Reliability of communication systems and the evolution of altruism. In: Stonehouse, B., Perrins, C.M. (Eds.), Evolutionary Ecology, 1977. McMillan, London, pp. 253–259.

Zahavi, A., 1990. A Arabian babblers: the quest for social status in a cooperative breeder. In: Stacey, P.B., Koenig, W.D. (Eds.), Cooperative Breeding in Birds: Long Terms Studies of Ecology and Behaviour. Cambridge University Press, Cambridge, pp. 105–130.