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Perceptual advertisement by the prey of stalking or ambushing predators

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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 utilized 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 do 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.

Keywords: intraspecific-communication; predator-prey signalling, stotting, costly signalling, evolutionarily stable strategy

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 defense, 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 [1] 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 this to predators [2]. 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 can signal to detected predators (dissuading them from attacking). Such signals are called *perception advertisement*, an idea whose origin is variously credited to [3], [4] or [5]. 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 [6]

62 discusses directed staring in the direction of the predator as such a signal, suggesting
63 that that for many birds and mammals this is combined with idiomatic postures that
64 involve elevating the head, craning the neck and becoming immobile. The brown hare
65 is a particularly commonly-cited example of this, with hares responding to stalking
66 foxes by standing pipedally with their ears erect and their white ventral surface
67 directed towards the fox [7], and foxes being less likely to attack hares adopting this
68 posture. Tail flicking (raising and lowering of the tail, often to show flashes of a
69 conspicuous underside) is reported as perceptual advertisement in a number of
70 waterbirds [5][8] as well as some deer and antelope [6]. Some deer and squirrels keep
71 the tail continuously lifted in response to a nearby predator, exposing a brightly
72 contrasting underside (a behavior called *tail flagging*) and this too is considered to be
73 perceptual advertising [9][10]. Many artiodactyls (even toed ungulates: e.g. pigs, deer,
74 antelopes, sheep, goats, and cattle) emit calls (often describes as snorts or barks) that
75 are also interpreted as perceptual advertisement (see [10][11] for reviews). Such calls
76 can often be supplemented by foot stamping. A number of primates have been
77 recorded using characteristic perceptual advertising calls to stalking predators (that
78 might be expected to break off attacks when detected) such as leopards, but not to
79 pursuit predators such as chimpanzees (which should care less about being detected)
80 [6]. Some perceptual advertisements signals involve the repeated close approach and
81 backing away from the predator: such inspection behaviour has been reported in a
82 range of fish, birds and mammals (e.g. [12][13][14]) and, although it may have
83 additional functions, is generally considered to be perceptual advertisement. Foot
84 drumming behaviour in a number of species of desert-living kangaroo rats is generally
85 considered to inform nearby snakes that they have been detected [15][16]. Finally
86 some species of antelope, gazelle, sheep, goat, cattle, deer and pronghorn all show a

87 characteristic jumping behaviour involving all of the legs being stretched out
88 downwards at the top of the spring (so called *stotting*) that is considered to function as
89 a mixture of perception advertisement and quality advertisement; with the relative
90 importance of the two varying between species and ecological situations [6][17][18].
91
92 Although both parties can potentially gain from such signalling, its evolutionary
93 stability is not trivial, because there can be an opportunity for prey to cheat and signal
94 that they have detected the predators on occasions when they suspect that a predator is
95 around but they are not certain. Bergstrom and Lachmann [19] developed a game
96 theoretical model to explore the conditions required for evolutionary stability in the
97 face of such a danger of cheating (this model was later refined by [20]). Bergstrom
98 and Lachmann [19] envisage prey receiving a stimulus of value x at a certain time.
99 This stimulus may be produced by a predator but may also come from other
100 environmental sources; crucially the higher the value of x, the more likely the
101 stimulus is to be predator-generated. Thus the stimulus (the value of x) provides an
102 imperfect but still meaningful indication of the presence of a predator. For the
103 evolutionarily stable strategy there is a critical value of x. If the prey detects a value of
104 the stimulus above the critical value, then it signals and the predator (if present) aborts
105 its attack; for stimulus values below the critical value, the prey does not signal and the
106 predator (if present) does attack. Bergstrom & Lachmann [19] demonstrate that such a
107 signal can be stable provided a number of conditions are met. These can be interpreted
108 biologically as follows:
109
110 1. There is a cost to prey of signalling, a cost that is paid whether the predator is
111 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 & Lachmann [19] 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 vocalizations 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.

137

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

150

151 Associated with our interest in greater variation in signal expression, we also consider
152 greater variation in signal costs. Again this is biologically driven, as it seems likely
153 that the variety of perceptual advertisement signals observed in the natural world vary
154 in their costliness. For example, some (such as foot stamping or tail flicking) can be
155 carried out without requiring a break from foraging, whereas directed staring and
156 vocalizations likely generally require such an opportunity cost. Stotting is highly
157 likely to be much more energetically expensive that tail flagging. If the cost is paid in
158 terms of risk of informing predators other than the focal predator being signalled of
159 the presence of the prey, this may be more costly for vocalizations (which can be
160 detected over long distances) than (for example) tail flicking. Hence, our final novel

161 model elaboration will be to allow variation in signal costs to be associated with the
162 variation in signal forms possible.
163
164 **2. Methods: Description of the model**
165 We consider a population of prey individuals and a population of predator individuals.
166 Within each population, all individuals are of identical quality. We use evolutionary
167 game theory to analyze the predator and prey signalling behavior that we might expect
168 to see.
169
170 As a predator approaches a prey individual the prey receives some cue x, for instance
171 it hears a noise. We assume that prey are approached by predators on average once
172 per unit time following a Poisson process, and that the intensity x of the cue received
173 follows a specific probability distribution, which we denote by f, e.g. x could be
174 continuous with density function $f(x)$. In addition, prey receive non-predator-derived
175 cues x_o, following a different probability distribution f_o. These assumptions are
176 effectively the same as used by Bergstrom & Lachmann [19].
177
178 Upon receiving cue x, a prey individual will send a signal $s(x)$, which the predator (if
179 present) can detect. The (energetic) cost of sending signal s to the prey is $u(s)$, which
180 increases with s but is independent of x (except for the indirect effect that x has
181 through influencing the value of s); it is paid regardless of whether a predator is
182 present or not. We shall assume that $u(s)$ is strictly increasing with s. If this was not
183 the case, and there were a number of signals of equal cost, then it is reasonable to
184 assume that the prey would always prefer the highest intensity signal amongst them. If

185 the predator receives signal s, it can choose to either continue the attack or respond to
186 the signal and not attack.
187
188 That the prey have a range of potential signals open to them is our first crucial
189 departure from the assumptions of Bergstrom & Lachmann [19], who assume a simple
190 binary signal, with only two possible values (on or off). Following the methodology
191 of [21], we divide all possible signals into A_0 that will prevent an attack and A_1 that
192 will not. The prey's strategy is $s(x)$ for $x \in C$, the set of possible cues; and the
193 predator's strategy is a choice of $A_0 \subseteq S$, the set of possible signals.
194
195 We shall seek evolutionarily stable strategy pairs; namely, choices of A_0 and $s(x)$
196 which when either the prey or the predator change strategy, means that they would
197 perform strictly worse. We note that some formal strategy changes do not influence
198 behaviour, and hence rewards, at all (for example if the predator changes the response
199 it would give to a signal that the prey does not use). We thus in practice seek strategy
200 pairs where any change which leads to an actual change in behaviour gives a strictly
201 smaller reward. Thus in Section 3 (and in the associated Appendix A) we consider all
202 plausible potential stable strategy pairs, and find the conditions under which they are
203 stable, i.e. in which *any* change in strategy which leads to a behavioural change would
204 cause the type changing strategy to perform worse.
205
206 We assume that some signals cannot be given to weak (low x) cues (e.g. prey cannot
207 stare straight at a predator whose presence – and hence location - they are highly
208 uncertain of). In general we define the function $T(x)$ to give the allowable signals.
209 When x is received, the only allowable signals are $s \leq T(x)$.

210

211 In this paper we allow a range of values of $x \in [0,1]$ which indicates the potential
212 presence of a predator and a single strong signal $x=2$ which reveals the predator with
213 certainty. We also allow a range of unrestricted signals of increasing strength $s \in [0,1]$
214 and one restricted signal s=2. Thus we have $C=S=[0,1] \cup \{2\}$, and we set $T(x) = 1$ for
215 $x \leq 1$ and $T(2) = 2$. Thus for any cue $x \leq 1$ (which contains information about a
216 predator but not certainty) the prey give any signal except the restricted signal (staring
217 at the predator). If $x = 2$ and the prey knows where the predator is, it can stare at it
218 using the most expensive signal ($s(2) = 2$) or choose any other (cheaper) signal.
219

220 If a predator attacks a prey individual when it has given the cue x, then the reward to
221 the predator is $v(x)$ which decreases with increasing x. This reward can be interpreted
222 as the expected energetic gain to the predator (probability of prey capture multiplied
223 by value of the prey minus energy expended). The (average) cost to the prey of an
224 attack is $w(x)$, which again decreases with increasing x. This again can be interpreted
225 as an expected energy loss (probability of capture multiplied by the cost of death plus
226 the value of energy expended if death does not occur). We note that cost of death in
227 particular would depend upon the state of the individual (a young healthy individual
228 has more to lose), but that for simplicity all prey individuals in our model are assumed
229 to be identical; the only asymmetry is in the strength of the cue received, and
230 potentially the strategy played. Thus predators which induce higher values of the cue
231 x are less likely to be successful in an attack. This assumption is fundamental to
232 perceptual advertisement, and indicates that the predator benefits from remaining
233 undetected. It is analogous to Bergstrom & Lachmann [19]'s 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 Bergstom & Lachmann [19]'s assumption that the value of the stimulus x provides some indication (albeit imperfect) of the presence of a predator.

We further assume that

$$\frac{d}{dx}\left(\frac{w(x)f(x)}{f(x)+rf_0(x)}\right)>0. \qquad (1)$$

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 & Lachman [19]'s 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:

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

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

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) $2 \in A_0$, $A_0 \setminus \{2\} \neq \Phi$ 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 equations (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.

328 ***Summary of evolutionarily stable strategies***

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

334

335 (S1): No attacks or costly signals (*s* values above 0) occur when $C3^c$ holds (inequality
336 4 holds).

337

338 (S2): No costly signals (*s* values above zero) are given and attacks always occur when
339 C3 holds (inequality 4 does not hold).

340

341 (S3): Attacks always occur unless the predator is unambiguously spotted, when the
342 prey gives the unfakable signal (s=1), when the combination of conditions represented
343 by $C5^c \cap C2 \cap D2(2)$ holds (equivalently inequalities 8,9 and 10 hold, see Appendix A).

344

345 (S4): Medium-cost signals (*s* values between zero and one) occur for sufficiently
346 strong cues, and these deter attacks, while attacks occur when no signal is given (s =
347 0). The precise conditions when such signals occur are given in Appendix B.

348

349 (S5): Medium level signals occur only when the predator is unambiguously spotted
350 and this is enough to deter the predator. Otherwise attacks occur. The precise
351 conditions when such signals occur are again given in Appendix B.

352

353

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

357

358 That is, five different solution types are possible, and for a given set of parameter
359 values more than one of these five may be possible. Indeed, for some parameter
360 values four of the five are possible. We list the set of possible solutions for a given
361 situation separated by commas in the figure. The 5 criteria C1,...C5 are always in the
362 same order. However, the criteria D2(2) and D3(1) can occur in either order, hence, to
363 find the possible solutions for a given set of parameter values, one must first evaluate
364 the order of these and select whichever of the two tables in Figure 1 is appropriate to
365 that ordering. One then identifies which of the 18 cells in the table the parameter
366 value combination implies, and the list of possible solutions for that set of parameter
367 values will be given in that cell. In particular, at the bottom of the diagrams in Figure
368 1, attacks are unattractive to predators and so no signal is needed to deter them; at the
369 top attacks are so attractive that no signal can deter them.

370

371 **4. Discussion**

372

373 The first thing to note about our model predictions is that (for any combination of
374 parameter values) a single non-signalling equilibrium will exist where the prey do not
375 signal (in our model this is equivalent to using the lowest-cost signal $s = 0$), and all
376 predators either always attack or never attack. Clearly when predators always or never
377 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

403 include the condition of always attacking when no signal is given. That is, all such
404 predator strategies with respect to other signals will be equivalent in payoffs as long
405 as no signals are given. If after some such predator strategies have drifted into the
406 population a mutant signalling prey individual occurs, then that mutant may (but need
407 not necessarily – and in most causes likely will not) do better than the non-signalling
408 "field" individuals. Thus if predators are susceptible to such stimuli, this is a potential
409 way for signalling strategies to begin.
410
411 It is important to see that evolution away from the non-signalling equilibrium is
412 possible (as discussed above), since otherwise the other signalling equilibria predicted
413 by our model could not be reached. One type of signalling equilibrium predicted is
414 exactly analogous to that predicted by the model of Bergstrom and Lachman [19].
415 Specifically, there is a critical value of x, for stimulus values below which prey
416 respond by not signalling (i.e. using the lowest-cost signal s =0). However for all x
417 values greater than the threshold, prey emit the same higher-cost signal. Thus, despite
418 the greater flexibility of signalling introduced in our model (with a range of signal
419 intensities open to the prey: all values of s from zero to one inclusive) they adopt an
420 essential binary signal, exploiting only two of the continuum of signal levels open to
421 them. The biological interpretation of this is that we do not expect perceptual
422 advertisements to be informative about the prey's confidence in the proximity of the
423 predator. That is, we do not expect an individual prey type to modulate say foot-
424 drumming intensity or tail-flicking frequency to indicate to the predator how
425 confident the prey is in having detected the predator. Such a strategy does not appear
426 evolutionarily stable in our model. We note that this prediction relies on the
427 assumption that all individuals are essentially identical. Significant between-

428 individual variation in predators and/or prey could perhaps generate different such
429 intensities. We would expect this result to hold more widely in coevolved signalling
430 systems. Specifically, where receivers are limited to a binary response (e.g. whether to
431 mate or not, whether to flee or not, whether to attack or not) signallers will often be
432 expected to utilize only two signal levels.
433
434 The range of possible signals available in our model gives a larger range of possible
435 scenarios where signalling can occur than in [19], since the region associated with
436 strategy (S4) is larger than for any fixed value of signal a_o. On the other hand, regions
437 (S3) and (S5) overlap with regions (S1), (S2) and (S4) so that it is possible that
438 situations may occur where only unfakeable signals are used when in the absence of
439 this possibility either there would be no signalling or there would be signalling with
440 fakable signals (in this latter case the overall level of signalling would be significantly
441 reduced). Thus overall in our model there are more types of signalling possibilities
442 and signalling would occur in more scenarios, but sometimes the actual amount of
443 signalling that would be observed would be a lot less, than in the model of Bergstrom
444 and Lachman [19].
445
446 However, the model also demonstrates that prey will not necessarily always adopt the
447 cheapest signal to indicate that it suspects a predator is near. That is, the non-zero
448 signal used by prey at this equilibrium ($s = a_o$) is not the minimum cost signal that can
449 be differentiated from $s = 0$. If fact we predict not just one equilibrium of this type for
450 a given set of parameter values but a continuum of such equilibria, for each critical
451 value of the stimulus (x_c) there will be a different value of signal intensity a_o. We
452 would expect x_c and a_o to be the same across individual animals within a set of

453 interacting predators and prey populations; but would expect variation in these values
454 between sets of populations. Thus globally, we would not expect that the intensity of
455 vocalizations produced by artiodactyls as perceptual advertising to be strongly
456 constrained; however at a local level we would expect such uniformity in the type of
457 signals given by different prey individuals or the same individual on different
458 occasions. We would predict that higher confidence in predator presence needed
459 before signalling (higher x_c) will be associated with more intense and costly signals
460 (higher a_o). Thus a clear prediction of our model is that prey populations that require
461 less certainty before advertising perception will signal more often when no predator is
462 in fact present and will also use lower cost signals. This prediction should be
463 amenable to empirical testing across populations. We would also expect analogous
464 situations in other coevolved signalling systems, with signallers that utilize more
465 expensive signals using them less frequently than in analogous populations where
466 signalling is cheaper.
467
468 It is important to note that this "medium-cost equilibrium" predicted by Bergstrom &
469 Lachman [19] also occurs in our model despite the introduction of the reserved signal
470 that is high-cost and can only be given when the prey is very sure of the existence of a
471 nearby predator. Thus the potential for such an unfakable high-cost signal does not
472 prevent the occurrence of the previously-described equilibrium. Our model predicts
473 the existence of yet another type of equilibrium where the prey never signals and the
474 predator always attacks, unless the prey is very sure of the presence of the predator (x
475 = 2 in our model) and gives the reserved, unfakable, high-cost signal which deters the
476 predator (if one is present). We note that, as with all our signalling equilibria, the
477 prey's behaviour is a binary response between two alternatives. Biologically, this

478 equilibrium means that we predict that sometimes perceptual advertisement signals
479 may be very expensive, but such signals will only be used (indeed in some cases can
480 only be used) when the prey is very sure of the existence of the predator nearby. An
481 example of such an unfakable signal may be the directed staring as described in hares
482 in the Introduction. Note our prediction is that prey that use such high-cost signals
483 will not also use lower cost signalling. Hence we would not expect hares to also on
484 some occasions use a lower-cost signal (e.g. foot thumping or tail flagging) when they
485 have reduced confidence in the proximity of a predator. Caro [6] argues that
486 perception advertising signals are generally low-cost (compared to signals of
487 individual quality). He admits that the apparent perceptual advertisement function of
488 stotting behaviour does not fit well with this generalization. Our models predict that
489 such high cost signals can be predicted, but they will be paired with very high
490 confidence in the proximity of a predator. Again this is empirically testable, and we
491 would predict that costly-perceptual advertisement by stotting or directed staring is
492 very rarely triggered by non-predatory environmental stimuli (in comparison to lower
493 cost signals). Generally across co-evolved signalling systems we would expect high
494 cost signals to be used more sparingly and more judiciously (with less signalling to
495 inappropriate receivers – e.g. sexual signalling to heterospecific females).
496
497 The model also predicts one final type of equilibrium where prey only signal when
498 they have maximal confidence in the proximity of a predator, but do not use the
499 reserved signal to do this but rather a lower unreserved signal. Biologically this means
500 that even when prey have detected predators with certainty they may not use
501 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 [22], warning other prey individuals of the danger [23], and (most speculatively) attracting mesopredators that might be a threat to the focal predator. Further, the signal may also be subject to sexual selection [24][25]. 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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580

581 **Figure Caption**

582

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

596

597 **Appendix A**

598

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

601

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

602

603

604 $$R_P = -P[X=2](w(2)+u(0)) - \int_0^1 f(x)w(x)dx - u(0)\int_0^1 (f(x)+rf_o(x))dx. \qquad (5b)$$

605

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

609

610 $$P[X=2]v(2)+\int_0^1 f(x)v(x)dx>0. \qquad (6)$$

611

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

614

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

617

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

621

622

$$R_Q = \int_0^1 f(x)v(x)dx, \qquad (7a)$$

623

624

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

625

626

627 This is stable with respect to the predator if $2 \rightarrow A_1$ (predators switching to attacking
628 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°),

and if $0 \rightarrow A_0$ (predators switching to not attacking when given the minimum cost signal) reduce their payoff, ie. 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 $0 \to A_0$ (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 $s(2) \to 2$ (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: $A_0 = [a_o,1] \cup \{2\}$, $s(x) = 0$, $x < x_{crit}$; $s(x) = a_o$, $x \geq x_{crit}$. 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:

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

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

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

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

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.

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

We denote this equality condition by D1(a_o).

All changes not involving ($s(x) \rightarrow a_o$ & $x < x_{crit}$) or ($s(x) \rightarrow 0$ & $x \geq x_{crit}$) increase costs without changing outcomes (or do worse than changes involving them) and those involving either of these reduce the payoff, because of the 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_{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 $0 \to A_0$ 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 $s(2) \to a_o$ 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 $s(x) \to a_o$ 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 $0 \to A_0$ reduces the payoff, i.e. if

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

which is condition (C2), and if $a_o \to A_1$ 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 $s(2) \to 0$ reduces the payoff, i.e. if

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

which is condition D2(a_o), and if $s(1) \to a_o$ 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 $x \le 1$).

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

$$f(0)w(0) + (f(0) + f_o(0))(u(0) - u(a_o)) > 0. \quad (29)$$

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 A conditions for any $a < b$:

$$C5 \Rightarrow C4(b) \Rightarrow C4(a) \Rightarrow C3 \Rightarrow C2 \Rightarrow C1(b) \Rightarrow C1(a). \quad (30)$$

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

$$D3(a) \Rightarrow D2(a), \quad D2(b) \Rightarrow D2(a), \quad D3(b) \Rightarrow D3(a). \quad (31)$$

Note that Case 1 occurs if $C3^c$ 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 $D2^c(a_o) \cap C3$ holds, which implies $D2^c(1) \cap C3$ 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

817 observable behaviours of both predators and prey (always attack, never signal) are the
818 same in each case.
819
820 **Appendix B**
821
822 The solution represented by case (S4) occurs when the combination of conditions
823 represented by $C4^c(a_o) \cap C1(a_o) \cap D1(a_o)$ holds for a given value of a_o. There will be a
824 solution to $D1(a_o)$ provided that $D3^c(1)$ holds (we can see this by considering all
825 possible combinations of a_o and x and realizing there is no solution only if $u(a_o)$ is too
826 small even for its maximum value of $a_o = 1$).
827
828 The solution represented by case (S5) occurs when the combination of conditions
829 represented by $C2 \cap C5^c \cap D2(a_o) \cap D3^c(a_o)$ holds for a given value of a_o. There will be
830 such an a_o if
831
832 $\cup_{a_o \in (0,1)} \left(D2(a_o) \cap D3^c(a_0) \right) \equiv$ $D3^c(1)$ from the fact that
833
834 $$D2(a_o) \cap D3^c(a_o) \equiv -w(2) < u(0) - u(a_o) < -\frac{w(1) f(1)}{f(1) + r f_0(1)}$$
835
836 and equation (31). This gives $C2 \cap C5^c \cap D3^c(1)$.
837

D3(1) ↦ D2(2) ↤

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	

D3(1) ↤ D2(2) ↦

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	