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1 **Perceptual advertisement by the prey of stalking or ambushing predators**
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13 **Abstract**

14 There has been previous theoretical explorations of the stability of signals by prey that

15 they have detected a stalking or ambush predator, where such perceptual

16 advertisement dissuades the predator from attacking. Here we use a game theoretical

17 model to extend the theory to consider some empirically-motivated complexities: (i)

18 many perceptual advertisement signals appear to have the potential to vary in

19 intensity, (ii) higher intensity signals are likely to be most costly to produce, and (iii)

20 some high-cost signals (such as staring directly at the predator) can only be utilized if

21 the prey is very confident of the existence of a nearby predator (that is, there are

22 reserved or unfakable signals). We demonstrate that these complexities still allow for

23 stable signalling. However, we do not find solutions where prey use a range of signal

24 intensities to signal different degrees of confidence in the proximity of a predator;

25 with prey simply adopting a binary response of not signalling or always signalling at

26 the same fixed level. However this fixed level will not always be the cheapest possible

27 signal, and we predict that prey that require more certainty about proximity of a

28 predator will use higher cost signals. The availability of reserved signals does not

29 prohibit the stability of signalling based on lower-cost signals, but we do also find

30 circumstances where only the reserved signal is used. We discuss the potential to

31 empirically test our model predictions, and to develop theory further to allow

32 perceptual advertisement to be combined with other signalling functions.

33

34 Keywords: intraspecific-communication; predator-prey signalling, stotting, costly

35 signalling, evolutionarily stable strategy

36

## 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]

3

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 vental 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.

112     2. The costs of signalling are not so high that signalling is never profitable

113     3. The value of the stimulus $x$ provides some information (albeit imperfect) about

114         the likelihood of predator presence, such that those prey most "concerned"

115         about predation are actually those most at risk.

116     4. Prey that strongly suspect the presence of the predator are more difficult to

117         capture than those with lower levels of suspicion, so that the signal actually

118         conveys meaningful information to the predator.

119     5. The cost to the predator of attacking is not so high that it is never profitable for

120         the predator to attack.

121

122 Here we explore a development of the model of Bergstrom & Lachmann [19] that

123 allows for greater levels of signal complexity. Specifically, the signal considered in

124 the previous model was a simple binary response. Although the focal prey individual

125 could vary in its expectation of the risk of predation (with that expectation rising with

126 increasing stimulus value $x$), this variation in expectation influenced whether the

127 signal was given or not, but not the nature of the signal. However, it seems

128 biologically plausible that many of the real-world signals considered to be perceptual

129 advertisement could vary in intensity in a way that could potentially convey

130 information about the prey's certainty of the close proximity of the predator. For

131 example, tail flicking, foot drumming and vocalizations could all vary in their

132 frequency. The last two could vary in the intensity of individual elements (e.g. the

133 loudness of a bark) as well as frequency, and it seems plausible that such flexibility

134 could be used to convey the prey's degree of confidence in the presence of the

135 predator. Here we will explore the evolutionary stability of perceptual advertisement

136 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

234     strongly suspect the presence of a predator are more difficult to capture than those that

235     have lower levels of suspicion.

236

237     If a predator is present we assume that there is a non-zero probability of it revealing

238     itself with certainty, $P[x=2]>0$, and otherwise $x$ has a probability density f(x). If there

239     is no predator $x=2$ cannot occur, but other cues $x_o$ have density $f_o(x)$. We assume that

240     predators arrive at an average rate of one per unit time, but that other cues occur at

241     rate $r$. We assume that $f(x)/f_o(x)$ increases with $x$. That is, the higher the value of the

242     cue $x$ the more likely it is to be indicative of a predator. This is analogous to Bergstom

243     & Lachmann [19]'s assumption that the value of the stimulus $x$ provides some

244     indication (albeit imperfect) of the presence of a predator.

245

246     We further assume that

247

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

249

250     In fact we do not technically need this derivative to exist at all, as long as the term in

251     brackets is an increasing function of $x$. $f(x)/(f(x)+rf_o(x))$ is the probability that a cue of

252     strength $x$ received by a prey individual actually comes from a predator (recall that

253     $w(x)$ is the cost to a prey of an attack coming from a predator that sends cue $x$). This

254     condition means that (if predators always attack) then the higher the value of the cue $x$

255     received, the higher the expected cost to the prey. Thus, the higher the value of cue $x$

256     that the prey receives, the greater its incentive to discourage attack from the predator.

257     The prey can discourage such an attack by signalling to the predator that it has been

258    detected. Again, this is analogous to Bergstrom & Lachman [19]'s assumption that

259    those prey most concerned about predation are actually those at greatest risk of an

260    attack.

261

262    **3. Results: stable solutions of the model**

263    In general, the rewards to the predator $R_Q$ and the prey $R_P$ in terms of expected

264    energetic gain are given by the expressions below:

265

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

267

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

$$-r\int_0^1 f_0(x)u(s(x))dx.$$

269

270    We define the following two predator choices: choice 0 is the choice not to attack and

271    choice 1 is the choice to attack. Thus $w(x) > 0$ is the cost to the prey of the predator

272    making choice 1.

273

274    For a stable solution, the prey must play $min(A_0)$ or $min(A_1)$ in every situation

275    (otherwise it could change to a lower signal within the same set and so reduce its cost

276    without affecting the predator response).

277

278    We also need $min(A_1) < min(A_0)$, whenever both sets are non-empty and $min(A_1)$ is

279    sometimes chosen by the prey, since otherwise switching to a lower-cost signal could

280 prevent an attack. This means that min($A_l$) = 0 unless $A_1$ is the empty set (or at least a

281 signal never employed by the prey).

282

283 Note that if there exists a value $s$ that is a member of $A_0$ where $s \leq 1$, then the

284 unfakable signal (s = 2) cannot be stable.

285

286 Thus the possible stable solutions are:

287 1) $A_0 = [0,1] \cup \{2\}$, so that there are no attacks and prey always give the lowest-

288 cost signal: $s(x) = 0$ for all $x$.

289 2) $A_l = [0,1] \cup \{2\}$, and $A_0$ equals the empty set, so that there is always an attack

290 whenever the predator is present and prey always give the lowest-cost signal:

291 $s(x) = 0$ for all $x$.

292 3) $A_0 = \{2\}$, so only the restricted unfakable signal prevents an attack in this case.

293 There are two possibilities:

294 either (a) $s(2) = 2$ and $s(x) = 0$ for all $x \leq 1$, so that only the unfakable signal is

295 given when the predator is spotted;

296 or (b) $s(x) = 0$ for all $x$ and so no signal is ever given and there is always an attack.

297 4) $2 \in A_0$, $A_0 \setminus \{2\} \neq \Phi$ so the predator will respond to sufficiently strong signals

298 below the unfakable one. There are four cases labelled a-d, depending on the

299 signals given by the prey (these cases will be explored in turn below).

300

301 We consider case 1 below to illustrate our methodology, and each of the other seven

302 cases (2, 3a, 3b, 4a, 4b, 4c and 4d) described above are considered in Appendix A.

303

13

304  *Case 1: $A_0 = [0,1] \cup \{2\}$, and s(x) = 0 for all x. There are no attacks and the prey*

305  *always gives the lowest-cost signal, regardless of x.*

306  Substituting the above values into equations (2a) and (2b) we obtain

307  $R_Q = 0$,                                                                    (3a)

308

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

310

311  This strategy pair is stable with respect to the predators' strategy if any change in

312  predator strategy reduces the reward to the predator. The only change in strategy that

313  the predator can make is to switch to attacking when a signal $s = 0$ is received, i.e.

314  moving the signal 0 from set $A_0$ to $A_1$. We shall denote such a change by the shorthand

315  $0 \rightarrow A_1$ (and other strategy changes will be similarly denoted in Appendix A). This

316  change reduces the predator payoff if

317

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

319

320  We summarise all of the important conditions in a logical sequence as we see in

321  Appendix A. We denote the condition in inequality (4) by $(C3^c)$. In general conditions

322  denoted by a C relate to a change of the predator response to a signal, and conditions

323  denoted by a D relate to a change in prey strategy.

324

325  The strategy pair is clearly stable with respect to the prey's strategy, since changing $s$

326  can only increase the cost without affecting the outcome.

327

14

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

378    without modifying predator behaviour, and thus would not be selected. For the

379    predators, as long as all prey are not signalling, then there is no intrinsic difference

380    that the predator can detect between interactions with prey, so the only rational

381    strategy is to always or never attack (whichever leads to the highest average reward).

382    This occurs because we have assumed that the prey but not the predator can perceive

383    the value of the stimulus $x$ in any interaction, hence in the absence of a signal from the

384    prey the predator does not have any information on whether a particular prey

385    individual has become aware of its presence or not. Biologically, this seems plausible

386    in many situations. Consider a lion stalking a gazelle, the lion might be aware of the

387    sound of dry vegetation snapping under its body as it creeps forward, but it would

388    often not be able to judge effectively whether those sounds have carried to and been

389    detected by the gazelle (in the absence of any behavioural change – perception

390    advertisement – by the gazelle). We would expect an analogous non-signalling

391    equilibrium to exist in other coevolved signalling systems where receivers have no

392    way of differentiating signallers in the absence of signals.

393

394    Such a non-signalling equilibrium is not only logically plausible, it meets with

395    biological observation: while examples of perceptual advertisement are widespread

396    taxonomically, they are not ubiquitous and it seems that only a minority of vertebrate

397    prey seem to use them to stalking or ambush predators. Although the non-signalling

398    equilibrium is stable to the appearance of any single mutant, it is possible to imagine

399    scenarios where evolution away from this equilibrium is possible. Imagine the

400    equilibrium strategy is for prey never to signal, and predators not to respond to signals

401    and always attack. If the prey population remains unchanged, so no signals occur,

402    then other strategies can drift into the predator population provided those strategies

17

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-

18

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

19

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

502  kangaroo rat system where often the prey has visually detected a specific snake prior

503  to the onset of its foot thumping signal.

504

505  In this paper we have strived to further cement the theoretical underpinning of the

506  interpretation of perceptual advertisement signals from prey to ambushing or stalking

507  predators. We have shown that such signals seem evolutionarily stable in a wider

508  range of circumstances than previous explored, and that the predicted signals accord

509  well with empirical observation of such signals in natural systems. However, it is

510  important to note that although there seems good evidence that some systems feature

511  signals by prey that function primarily in informing predators of their detection, such

512  a signal may have a number of other functions: such as informing predators of the

513  intrinsic quality of the signaller [22], warning other prey individuals of the danger

514  [23], and (most speculatively) attracting mesopredators that might be a threat to the

515  focal predator. Further, the signal may also be subject to sexual selection [24][25].

516  Hence there is a need to build on existing theory and explore the influence of such

517  multiple selection pressures on the existence and form of signals between prey and

518  predators. We hope that this work will provide a useful foundation for such further

519  development.

520

521

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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

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

602

603

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

604

26

605

606 This solution is stable with respect to predator strategy if $0 \to A_0$ (i.e. predators

607 switching to not attack when receiving the minimum-cost signal) reduce their payoff,

608 i.e. if

609

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

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 $x \le 1$. 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

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

623

624

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

626

627 This is stable with respect to the predator if $2 \to A_1$ (predators switching to attacking

628 when receiving the maximum-cost signal) reduces their payoff: i.e. if

629

630   $P[X = 2]v(2) < 0$

631                                                                              (8)

632   which we denote by (C5$^c$),

633

634   and if $0 \rightarrow A_0$ (predators switching to not attacking when given the minimum cost

635   signal) reduce their payoff, ie. if

636

637   $\int_0^1 f(x)v(x)dx > 0$                                                   (9)

638

639   which we denote by (C2).

640

641   It is stable with respect to prey strategy if $s(2) \rightarrow 0$ (switching to using the minimum

642   cost signal in response to the reserved cue $x = 2$) reduces the prey payoff; i.e. if

643

644   $w(2) + u(0) - u(2) > 0.$                                                   (10)

645

646   We denote this condition by D2(2).

647

648   All other changes of $s$ would increase the cost of signalling to prey without affecting

649   the outcome of the signal (in terms of predator behaviour).

650

651   *Case 3b: $A_0 = \{2\}$, s(x) = 0 for all x. The maximum-cost signal would deter an*

652   *attack, but prey always use the minimum cost signal:*

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

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

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

$$w(2)+u(0)-u(2) < 0.$$ (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).

677    There are four different variations of case 4 where the predator will respond to

678    sufficiently strong signals below the unfakable one.

679

680    *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*

681    *minimum-cost signal in response to cue values below a critical threshold ($x_{crit}$) and*

682    *a single higher-cost signal ($a_o$) to all other cues. The higher-cost signal deters*

683    *attack but the minimum-cost one does not:*

684

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

686

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

688

689    This solution is stable with respect to predator strategy if $a_o \to A_1$ reduces the

690    predator's payoff, i.e. if

691

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

693

694    which we denote by $C4^c(a_o)$,

695

696    and if $0 \to A_o$ reduces the payoff: i.e. if

697

30

698 $$\int_0^{x_{crit}} f(x)v(x)dx > 0 \qquad\qquad (16)$$

699

700 which we denote by C1($a_o$).

701

702 The strategy is in equilibrium regarding a change in prey strategy if a small change in

703 $x_{crit}$ has no effect: i.e.

704

705 $$f(x_{crit})w(x_{crit}) + (f(x_{crit}) + rf_o(x_{crit}))(u(0) - u(a_o)) = 0. \qquad\qquad (17)$$

706

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

708

709 All changes not involving ($s(x) \rightarrow a_o$ & $x < x_{crit}$) or ($s(x) \rightarrow 0$ & $x \geq x_{crit}$) increase costs

710 without changing outcomes (or do worse than changes involving them) and those

711 involving either of these reduce the payoff, because of the equation (D1($a_o$)) and

712 condition (1). The condition D1($a_o$) finds the unique value of $x_{crit}$ associated with $a_o$,

713 and, from condition (1), the larger $a_o$, the larger $x_{crit}$. It is easy to see that a pair ($a_o$,

714 $x_{crit}$) (and generally many such pairs) always exists, and so D1($a_o$) always holds for

715 some $a_o$, by noting that substituting $x_{crit} = 0$ in the left hand side of (17) gives a

716 negative value, and that letting $a_o$ tend to zero makes the second term on the left hand

717 side of (17) arbitrarily small, so a corresponding $x_{crit}$ can clearly be found that satisfies

718 (17) (we note this would not necessarily be true if there was a minimum registerable

719 non-zero signal with non-zero cost).

720

31

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

722  conditions for each $a_o$.

723

724  *Case 4b: $A_o = [a_o, 1] \cup \{2\}$, $s(x) = 0$ for all $x$. Prey never signal, despite the fact that*

725  *high (but unreserved) values of the signal and the reserved signal would both deter*

726  *attack:*

727

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

729

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

731

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

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

734

735  This is condition (C3) again.

736

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

738

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

740

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

742  implies that

743

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

32

745 so that if (D2ᶜ(aₒ)) holds then the strategy is also stable against any $s(x) \to a_o$ when

746 $x \leq 1$).

747

748 ***Case 4c: $A_o = [a_o, 1] \cup \{2\}$, $s(2) = a_o$, $s(x) = 0$ for $x \leq 1$. High (but unreserved)***

749 ***values of the signal and the reserved signal would both deter attacks. However, the***

750 ***prey always adopts the lowest-cost signal (thus always induces an attack if the***

751 ***predator is present), unless the highest value cue (x=2) is detected, in which case***

752 ***the prey signals with the lowest-cost signal that is still sufficient to deter an attack:***

753

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

(22a)

756

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

(22b)

759

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

761 $$\int_0^1 f(x)v(x)dx > 0$$

(23)

762

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

764

765 $$P[x = 2]v(2) < 0$$

(24)

766

767 which is condition (C5ᶜ).

768

33

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

770

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

772

773    which is condition D2($a_o$), and if $s(1) \to a_0$ reduces the payoff, i.e. if

774

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

776

777    which we denote by condition $D3^c(a_o)$. (We again note that if ($D3^c(a_o)$) holds, then

778    from inequality (1) the bracketed expression is negative for all $x \leq 1$).

779

780    *Case 4d: $A_o = [a_o,1] \cup \{2\}$, $s(x) = a_o$ for all x. High (but unreserved) values of the*

781    *signal and the reserved signal both deter attacks. The prey always signals with the*

782    *lowest-cost signal that is still sufficient to deter an attack, regardless of the cue*

783    *received:*

784

$$R_Q 7850, \tag{27a}$$

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

787

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

789

$$P[x = 2]v(2) + \int_0^1 f(x)v(x)dx < 0. \tag{28}$$
790
791

34

792

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

794

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

796

797    Assuming that it is not worth giving a signal to a zero cue, e.g. if $f(0) = 0$, which we

798    shall assume, then this last condition can never be met and Case 4d is never stable.

799

800    Assuming that the bigger the cue $x$ the lower the reward to the predator should it

801    attack, as we have done, we have the following relationships between the A

802    conditions for any $a < b$:

803

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

805

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

807

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

809

810    Note that Case 1 occurs if $C3^c$ holds and Case 2 occurs if $C3$ holds, so exactly one of

811    these always holds.

812

813    Cases 2, 3b and 4b all involve a population which does not signal, where and thus

814    there are always attacks. Case 4b occurs when $D2^c(a_o) \cap C3$ holds, which implies

815    $D2^c(1) \cap C3$ and Case 3b which implies Case 2. Thus even though there are

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

835

836    and equation (31). This gives $C2 \cap C5^c \cap D3^c(1)$.

837

**Table 1** — D3(1), D2(2)

| | D3(1) | D2(2) | |
|---|---|---|---|
| ↑C5 | 2 | 2 | 2 |
| ↑C4 | 2,5 | 2 | 2,3 |
| ↑C3 | 2,4,5 | 2,4 | 2,3,4 |
| ↑C2 | 1,4,5 | 1,4 | 1,3,4 |
| ↑C1 | 1,4 | 1,4 | 1,4 |
| | 1 | 1 | 1 |

**Table 2** — D3(1), D2(2)

| | D3(1) | D2(2) | |
|---|---|---|---|
| ↑C5 | 2 | 2 | 2 |
| ↑C4 | 2,3 | 2,3,5 | 2,5 |
| ↑C3 | 2,3,4 | 2,3,4,5 | 2,4,5 |
| ↑C2 | 1,3,4 | 1,3,4,5 | 1,4,5 |
| ↑C1 | 1,4 | 1,4 | 1,4 |
| | 1 | 1 | 1 |