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Optimal Investment Across Different Aspects of Anti-predator Defences

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1 **Abstract**

2 We present a simple model of investment across a suite of different anti-predatory
3 defences. Defences can incur an initial construction cost and and/or may be costly
4 each time they are utilised. Our aim is to use a simple, but general, mathematical
5 model to explore when prey that face a single predatory threat where each attack is of
6 the same nature should invest only in a single defence, and when they should spread
7 their investment across more than one defence. This should help to explain the
8 observed variety of defences that a single prey individual may employ during repeated
9 attacks of a similar nature or even at different stages during one attack. Previous
10 verbal reasoning suggested that prey should specialise in investment in defences that
11 can be utilised early in the predation sequence. Our quantitative model predicts that
12 (depending of the relatively properties of different defences), there may be
13 concentrated investment in early-acting, or in late-acting defences, or a spread of
14 investment across both defence types. This variety of predictions is in agreement with
15 the variation in defences shown by natural organisms subjected to repeated predatory
16 attack.

17

18 Keyword: predation, predator-prey, investment in defences, optimal strategy, costs of
19 defences

20

20

21

22 **Introduction**

23 Predation is an almost ubiquitous process in the natural world, and very few animals
24 are immune to the risk of predation for at least part of their life history. Since
25 predation is responsible for a large proportion of mortality in many species, it is no
26 surprise that anti-predatory defences are also widespread and intensively studied by
27 behavioural ecologists (see Ruxton et al. 2004 and Caro 2005 for reviews). Caro
28 identified one of the ten most pressing questions in the study of anti-predatory
29 defences as “how can we explain patterns of morphological and physiological
30 defences across taxa?” There is indeed tremendous variety between species in the
31 forms of anti-predatory defences employed. However, there is even substantial
32 variability within an individual in the defences they employ against different attacks
33 (Buskirk 2001 and references therein). The conventional explanation of this variation
34 is that many individuals face risk of predation from a suite of different predatory types
35 for which different defences might be required. For example, a single caterpillar
36 might face attack by avian predators, predatory social wasps, parasitic wasps and flies,
37 ants, spiders, and even insectivorous rodents. Whilst visual crypsis may be an
38 effective defence against detection by birds, it is unlikely to be as effective against
39 ants that rely more on tactile, vibrational and olfactory cues to locate their prey.
40 However, variation in predatory threat (while certainly part of the answer) cannot be
41 the sole driver of within-individual variation in defences, since a single individual can
42 use different defences against the same type of predator in different attacks (reviewed
43 in section 13.6 of Caro 2005).

44

45 That a single individual can utilise a suite of different defences is noteworthy for at
46 least two reasons. Firstly, defences are likely to be costly and each defence added to
47 the prey's portfolio potentially adds an associated cost. Secondly, there can be
48 interference between different defences such that implementation of one may impair
49 the performance of another. The different costs of different defences are considered in
50 depth in Chapter 5 of Ruxton et al. 2004. For our purposes, we differentiate between
51 two general types of cost, those that are paid "up-front" such that the cost is paid
52 whether or not attacks occur and regardless of the number of attacks (often called
53 constitutive defences), and costs that are incurred each time the defence is used. For
54 example, a caterpillar that defends itself against birds by being difficult to detect
55 visually pays up-front costs. There may be physiological costs to the production of
56 pigments required to produce the desired appearance. Alternatively or additionally,
57 there may be opportunity costs associated with restricted use of microhabitats and
58 restricted movement required to maximise crypsis. These costs are paid regardless of
59 the number of attacks that an individual caterpillar experiences. In contrast some costs
60 occur whenever the defence is employed in a specific attack (Higginson & Ruxton
61 (2009) call these 'responsive' defences) . For example, some insects (notably many
62 ladybirds) exhibit reflex bleeding where toxin-laced blood is exuded from joints in the
63 exoskeleton in response to handling by a potential predator. This blood may deter the
64 predator from pursuing its attack, but the exuded blood and its toxins have been lost,
65 and have to be replaced. Replacement of these is likely to be physiologically costly,
66 and the total cost of using this defence will increase with the number of times it is
67 deployed (Grill and Moore 1998). Notice that this reflex bleeding defence may also
68 incur up-front costs as well, since there may be physiological costs associated with the
69 storage of toxins in a way that avoids autotoxicity, and gaps in the exoskeleton that

70 allow reflex blood to leave may impose costs in terms of, for example, water loss or
71 risk of fungal disease. Other examples of responsive defences are regurgitation
72 (Bowers 1993), gland secretions (Eisner et al. 2004), urticating hairs (Bowers 1993),
73 ink release by cephalopods (Derby 2007), and the explosive defence of the
74 bombardier beetle (Eisner 1958).

75

76 Investment in, or deployment of, one defence can reduce the effectiveness of another
77 defence. For example investment in a tough spiny exterior may provide mechanical
78 protection against handling by predators, but it may make the prey individual more
79 conspicuous (decreasing the effectiveness of camouflage as a defence) and may make
80 it more difficult for the prey to choose to flee from predators that may be able to
81 circumvent the anti-handling defence. Flight and crypsis are two classically
82 interfering defences. If a predator has not yet detected a predator, the prey may
83 increase the chances of remaining undetected by remaining still and trusting to their
84 cryptic appearance. However, if the predator inadvertently comes close to the prey
85 before detecting it, the close spatial proximity of the two individuals will reduce the
86 effectiveness of fleeing by the prey to escape the predator. Conversely, if the prey
87 flees early in the predatory sequence before detection has occurred, then the
88 effectiveness of crypsis is likely to be greatly reduced as the fleeing animal is more
89 vulnerable to detection than when sitting still (Broom & Ruxton 2005).

90

91 Implicit in our description above is that an interaction between a prey individual and a
92 predatory individual is generally a sequence of different phases. The most commonly
93 used articulation of this is the sequence laid out by Endler (1991), who suggested that
94 a predation event involves a sequence of six stages: encounter, detection,

95 identification, approach, subjugation and consumption. Defences differ in which of
96 these stages they can be utilised in. Clearly crypsis only works in the initial
97 “encounter” stage prior to detection of the prey by the predator. In contrast, anti-
98 predatory vigilance to allow detection of the predator by the prey may be of use to the
99 prey throughout all of the first four of Endler’s six stages. Here we will simplify
100 Endler’s six stages: subsuming the first four into a “pre-capture” stage and the last
101 two into “post-capture. Our aim is to use a simple, but general, mathematical model to
102 explore when prey that face a simple predatory threat, where each attack is of the
103 same nature, should invest only in a single defence; and when they should spread their
104 investment across more than one defence.

105

106 **Methods**

107 *Model description*

108 The key to our model is the idea that to successfully exploit an encountered prey item,
109 the predator must capture it and then subdue and consume it. Thus, successful
110 predation requires success at each of a sequence of stages. Different defences act at
111 different stages of the predation process, and we will simply characterise these as pre-
112 capture and post-capture defences, simplifying predation to a two stage process.

113

114 Pre-capture defences minimise the probability that a predator that comes spatially
115 close to (hereafter, “encounters”) the prey is able to capture it. These might be
116 defences that minimise the chance that the prey is detected and recognised (such as
117 camouflage or disguise) or defences that reduce the chance that an attack will lead to
118 capture (swiftness of movement, vigilance, manoeuvrability). We characterise all
119 these pre-capture defences in a single parameter D_1 . D_1 is a non-negative number

120 indicating the investment in pre-capture defences, with increasing values indicating
121 increasing investment. The probability that an encounter with a predator leads to
122 capture (P_1) is a decreasing function of D_1 . That is, increasing investment in pre-
123 encounter defences reduces the probability that the prey individual will be
124 successfully captured by any predator that encounters it.

125

126 Post-capture defences involve such things as fighting ability, venomous stings,
127 armoured integument and production of mucus. All these defences have in common
128 the fact that they reduce the probability (P_2) that capture leads to the death (and thus
129 consumption) of the prey (i.e. capture leads to successful predation). We describe
130 increasing investment in post-capture defences by increasing values of D_2 , with P_2
131 declining with increasing values of D_2 . That is, increasing investment in post-capture
132 defences reduces the probability that a predator that physically captures the prey is
133 able to subdue, kill and consume it.

134

135 We are interested in finding the optimal strategy in terms of investment in these two
136 defences. There are costs, as well as benefits, to investment in defence. We first of all
137 assume that there are fixed costs to the creation of the defences. Thus, even if the prey
138 individual never encounters a predator, it pays a cost for its investment in defences.
139 This occurs because these defences are constitutive (at least in part). The fecundity of
140 an individual that never encounters any predators is given by $F(D_1, D_2)$ where F
141 declines with increasing values of both D_1 and D_2 . This represents the fixed costs of
142 investment in the two types of defence. As investment in a defence increases so the
143 fitness cost increases.

144

145 However, as well as fixed costs, we assume that there can be additional costs every
 146 time a defence is used. For example, for pre-capture defences, we can imagine that
 147 there is a fixed cost to building and maintaining the muscle structure required for fast
 148 escape, but there is an additional cost (say in energy expended and/or feeding time
 149 lost) every time that defence is used and the prey has to flee. Specifically we assume
 150 that if the prey encounters a predator on a number of occasions N_a , then it has to use
 151 its pre-capture defence on N_a occasions. The cost of these encounters is represented
 152 by multiplying the fecundity of the prey individual by $[C_1(D_1)]^{N_a}$, where $C_1(0) = 1$
 153 (that is unaffected if there is no investment in defence) and C_1 declines with
 154 increasing values of D_1 (and thus fecundity declines both the investment in defence
 155 and with how often the defences are used). This formulation captures the assumptions
 156 that the costs of using pre-capture defences increase both with the number of times
 157 these defences are used and with the extent of these defences. That is, greater
 158 investment in pre-capture defence reduces the risk of capture, but also incurs higher
 159 fixed costs and costs that increase with the number of time these defences are used.

160

161 Let us assume that of these N_a encounters, a number N_c lead to capture of the prey and
 162 a number N_n lead to no capture and the prey escaping. Thus, we assume that to
 163 successfully survive these attacks the prey will have to successfully use its post-
 164 capture defences on N_c occasions ($N_c \leq N_a$). The cost of these is represented by
 165 multiplying the fecundity of the prey individual by $[C_2(D_2)]^{N_c}$.

166

167 Where $C_2(0) = 1$ and C_2 declines with increasing values of D_2 . This formulation
 168 captures the assumptions that the costs of using post-capture defences increases both
 169 with the number of times these defences are used and with the extent of these

170 defences. That is greater investment in post-capture defence reduces the risk that
 171 capture leads to death, but also incurs both higher fixed costs and higher costs each
 172 time these defences are used.

173

174 If a number of encounters with predators occur, then the fecundity of the prey
 175 individual is zero if it is killed in any one of these. The probability of it not being
 176 killed in any of the encounters is $(1-P_2)^{N_c}$.

177

178 Thus, the total payoff to an individual playing a certain strategy (in terms of
 179 investment across its two possible defences) is given by the fecundity multiplied by
 180 the probability of surviving:

181

$$182 \quad R = FC_1^{N_a} C_2^{N_c} (1 - P_2)^{N_c}$$

$$= FC_1^{N_n} [C_1 C_2 (1 - P_2)]^{N_c}$$

183 where for notational convenience, we have omitted writing out functional
 184 dependences on D_1 and D_2 .

185

186 However, N_c (and so N_n) depends upon the value of D_1 . Let us assume that encounters
 187 with a predator occur as a Poisson process at rate ε , and that reproduction requires that
 188 an individual first avoid being consumed by a predator for a time period T . From the
 189 general properties of the Poisson process, this can be broken down into two
 190 independent Poisson processes. Namely, encounters that lead to capture (which are
 191 Poisson with rate εP_1) and encounters that do not lead to capture (which are Poisson
 192 with rate $\varepsilon(1-P_1)$). Thus N_c takes values drawn from a Poisson distribution with mean
 193 $\varepsilon P_1 T$, and N_n from a Poisson distribution with mean $\varepsilon(1-P_1)T$.

194

195 Since N_c and N_n are generated by independent processes, we can write the payoff as

196

197
$$R = FE[C_1^{N_n}]E[\{C_1C_2(1-P_2)\}^{N_c}],$$

198

199 where $E[\cdot]$ denotes the expectation of a stochastic process.

200

201 From the properties of the Poisson process, if x is Poisson with mean λ , then

202

203
$$E[t^x] = \exp(\lambda(t-1)).$$

204

205 and using this, we can eliminate N_n and N_c from our expression for the payoff, giving

206

207
$$R = F \exp(\varepsilon(1-P_1)T(C_1-1)) \exp(\varepsilon P_1 T(C_1C_2(1-P_2)-1)).$$

208

209 If we take logs and divide by εT , we can simplify this to

210

211
$$R_i = \frac{\ln(R)}{\varepsilon T} = \frac{\ln(F)}{\varepsilon T} - 1 + C_1(1-P_1) + P_1C_1C_2(1-P_2) \quad (1)$$

212

213 Maximising the above function, maximises the payoff. In order to make further

214 progress, we must now specify the following functional forms.

215

216 $F(D_1, D_2) = F_{\max} \exp(-f_1D_1 - f_2D_2)$. Thus, we assume that maximum fecundity217 (before any predator encounters) is a decreasing decelerating function of both D_1 and

218 D_2 . The higher the values of f_1 and f_2 , the higher the fixed costs of pre-capture and
 219 post-capture defences respectively.

$$220 \quad P_1 = \max(0, 1 - p_1 D_1)$$

$$221 \quad P_2 = \max(0, 1 - p_2 D_2)$$

222 That is, we assume that the probability of an attack succeeding decreases linearly with
 223 investment in defences. The higher the values of p_1 and p_2 the higher the anti-
 224 predatory efficacy of pre-capture and post-capture defences respectively.

$$225 \quad C_1 = \max(0, 1 - c_1 D_1)$$

$$226 \quad C_2 = \max(0, 1 - c_2 D_2)$$

227 We assume that the cost of defences increases linearly with the investment in
 228 defences. The higher the values of c_1 and c_2 the higher the per-use costs of pre-capture
 229 and post-capture defences respectively.

230

231

232 These are perhaps the simplest functions that have the required properties outlined in
 233 the description above. Clearly, this restricts investment in defences such that $p_1 D_1$,
 234 $p_2 D_2$, $c_1 D_1$ and $c_2 D_2$ must all be less than one for the model to give sensible
 235 predictions. Thus as D_1 approaches $1/c_1$ for example, any use of the first defence
 236 would cost an individual almost all of its fitness. Provided that p_1 is not much smaller
 237 than c_1 , and p_2 not much smaller than c_2 , these upper boundaries will not be
 238 approached for any reasonable strategy.

239

240 **Model predictions**

241 We begin by identifying the types of different solutions (in terms of investment across
 242 the two defences) that are optimal in different circumstances. We define the following
 243 two terms that are central to the work that follows.

244

$$245 \quad \beta_1 = \frac{f_1}{p_1 \varepsilon T} - 1$$

246

$$247 \quad \beta_2 = \frac{f_2}{p_2 \varepsilon T} - 1$$

248

249 β can be thought of as the ratio of the constitutive cost to the benefit of defences. Note
 250 that it immediately follows that $\beta_1 \geq -1$ and $\beta_2 \geq -1$. First, let us ask if it is ever
 251 optimal for the prey never to make any investment in these costly defences. In all
 252 analyses we explore the effect of f_1 and f_2 , which control the constitutive impact of
 253 defences on maximum fecundity.

254

255 **No investment:** $(D_1, D_2) = (0, 0)$.

256 This occurs when both the derivatives of equation (1) with respect to D_1 and D_2 are
 257 negative at $(0, 0)$. It is easy to show that this occurs whenever we satisfy two
 258 conditions:

259

$$260 \quad \beta_1 > 0 \tag{2}$$

261

262 and

263

$$264 \quad \beta_2 > 0 \tag{3}$$

265

266 For this solution, the stability condition is the same as the existence condition, so
 267 whenever this solution is valid it is also stable. The above conditions are equivalent to

268

$$269 \quad f_1 > p_1 \varepsilon T \text{ and } f_2 > p_2 \varepsilon T .$$

270

271 This is shown graphically in Figure 1 with example values for parameters. These
 272 conditions make intuitive sense. Increasing the f values increases the constitutive cost
 273 of defence. If the p value is small then the effectiveness of the associated defence is
 274 low, if ε is small then attacks rarely occur, and if T is small then individuals only have
 275 a short pre-reproductive period to survive: all of which should make investment in
 276 defences less attractive. That is, if the constitutive cost of defence has a larger impact
 277 on fitness than the increase in the probability of survival, prey should never invest in
 278 defences. Notice, that the occurrence of this no-defence equilibrium is influenced only
 279 by the constitutive costs of defence (f_1 and f_2) not by the costs of utilising the defences
 280 (c_1 and c_2).

281

282 ***Investment only in pre-attack defences: $(D_1, D_2) = (D_1, 0)$.***

283 This occurs when both the derivative of equation (1) with respect to D_1 is zero and the
 284 derivative with respect to D_2 is negative at $(D_1, 0)$. Evaluation of these derivatives
 285 leads to two conditions again:

286

287 Firstly, the derivative with respect to D_2 gives

288

$$289 \quad \frac{-f_2}{\varepsilon T} + (1 - p_1 D_1)(1 - c_1 D_1) p_2 < 0$$

290

291 Expressed in terms of β_1 and β_2 this becomes

292

$$293 \quad \beta_2 > \left(\frac{p_1 \beta_1}{4c_1} \right) \left(\beta_1 + 2 + \frac{2c_1}{p_1} \right) = \left(\frac{\beta_1}{4a_1} \right) (\beta_1 + 2 + 2a_1) \quad (4)$$

294

$$295 \quad \text{where } a_1 = \frac{c_1}{p_1}$$

296

297 The derivative with respect to D_1 gives

298

$$299 \quad \frac{-f_1}{\varepsilon T} + p_1 - 2p_1 c_1 D_1 = 0.$$

300

301 Expressed in terms of β_1 and β_2 this becomes

302

$$303 \quad D_1 = \frac{-\beta_1}{2c_1},$$

304

305 which is positive providing $\beta_1 < 0$.

306

307 For $(D_1, 0)$ to be stable we need the second derivative of R with respect to D_1 to be

308 negative at $(D_1, 0)$. It is easy to demonstrate that this is always true. Thus, again this

309 solution is stable any time that it is valid. So, biologically we can conclude that it is
 310 also possible for all investment to be concentrated in pre-attack defences.

311

312 However there are further conditions on β_1 , since the optimal level of investment in
 313 defence in this case is given by

314

$$315 \quad D_1 = \frac{-\beta_1}{2c_1}$$

316

317 The condition $c_1 D_1 < 1$, together with $\beta_1 \geq -1$, leads to the restriction $-1 < \beta_1 < 0$;

318 and the condition $p_1 D_1 < 1$ leads to the restriction $-2a_1 < \beta_1 < 0$.

319 This gives

320

$$321 \quad -2\min(0.5, a_1) < \beta_1 < 0 \quad (5)$$

322

323 which in addition to (4) gives the conditions for the $(D_1, 0)$ solution.

324

325 These conditions are summarised graphically in Figure 1. Again, the results make
 326 intuitive sense. From our arguments in the previous section, this solution is more
 327 likely to occur under conditions where β_1 is negative and β_2 is positive (or only just
 328 negative). The other parameter group that affects the likelihood of obtaining this
 329 solution is a_1 . a_1 takes a high value if the costs of using pre-attack defences is high
 330 and/or if the effectiveness of such defences is low. Hence, it is logical that increasing
 331 a_1 restricts the area of (β_1, β_2) space where such solutions occur. From the arguments
 332 laid out already it is no surprise that the level of investment in pre-attack defences

333 only increases as β_1 becomes more negative (because constitutive costs decrease or
 334 benefits increase) and/or as c_1 is reduced (because responsive costs decrease).

335

336

337 ***Investment only in post-capture defences: $(D_1, D_2) = (0, D_2)$***

338 This occurs when the derivative of equation (1) with respect to D_1 is negative and the
 339 derivative with respect to D_2 is zero at $(0, D_2)$. Evaluation of these derivatives leads to
 340 two conditions again:

341

342 Firstly, the derivative with respect to D_1 gives

343

$$344 \quad \frac{-f_1}{\varepsilon T} + p_1 - (p_1 + c_1)(1 - c_2 D_2) p_2 D_2 < 0$$

345

346 Expressed in terms of β_1 and β_2 this becomes

347

$$348 \quad \beta_1 > \left(\frac{p_2}{4c_2} \right) \left(1 + \frac{c_1}{p_1} \right) \beta_2 (\beta_2 + 2) = \left(\frac{1 + a_1}{4a_2} \right) \beta_2 (\beta_2 + 2) \quad (6)$$

349

350 where $a_2 = \frac{c_2}{p_2}$.

351

352 The derivative with respect to D_2 gives

353

$$354 \quad \frac{-f_2}{\varepsilon T} + p_2 - 2p_2 c_2 D_2 = 0.$$

355

356 Expressed in terms of β_1 and β_2 this becomes

357

358
$$D_2 = \frac{-\beta_2}{2c_2},$$

359

360 which is positive providing $\beta_2 < 0$.

361

362 For this solution to be stable we need the second derivative of R with respect to D_2 to
 363 be negative at $(0, D_2)$. It is easy to demonstrate that this is always true, and thus again
 364 this solution is always stable when it exists. This means that it is possible to find
 365 combinations of parameter values where investment in post-attack defences occurs
 366 without any investment in pre-capture defence.

367

368 Since this is the mirror image of the case above, it will not be surprising to find very
 369 analogous conditions for this case. The conditions for the existence of this solution are

370

$$371 \begin{aligned} & -1 < \beta_2 < 0 \\ & -2a_2 < \beta_2 < 0 \end{aligned}$$

372

$$373 \text{ giving } -2\min(0.5, a_2) < \beta_1 < 0 \quad (7)$$

374

375 which together with (6) gives the conditions for the $(0, D_2)$ solution.

376

377 These limits can again be interpreted intuitively as above, and are shown graphically
 378 in Figure 1.

379

380 Note, however, a significant difference between conditions (4) & (6); whilst a_2 had no
 381 effect on the boundaries of the pre-attack only case, a_1 (as well as a_2) does affect the
 382 boundaries of the post-attack only case. This asymmetry arises from the fundamental
 383 asymmetry between the two types of defences, pre-attack defences occur before post-
 384 attack defences, and thus influence the frequency with which post-attack defences are
 385 used. However, post-attack defences do not affect the frequency with which pre-
 386 attack defences are used. Increasing a_1 (increasing the costs of utilising a pre-attack
 387 defence or decreasing its efficacy) increases the extent of (β_1, β_2) space where this
 388 post-attack only investment strategy occurs – again this is just as we would expect.

389

390 *Non-zero investment in both forms of defence*

391 At such a solution, the derivatives of equation (1) with respect to both D_1 and D_2 will
 392 be zero. Substituting the specific functional forms and differentiating gives:

393

$$394 \quad \frac{-f_1}{\epsilon T} + p_1 - 2p_1c_1D_1 + (2p_1c_1D_1 - p_1 - c_1)(1 - c_2D_2)p_2D_2 = 0 \quad (8)$$

395

$$396 \quad \frac{-f_2}{\epsilon T} + (1 - p_1D_1)(1 - c_1D_1)(p_2 - 2p_2c_2D_2) = 0 \quad (9)$$

397

398 These can be solved simultaneously for the non-zero combination of D_1 and D_2 that
 399 maximises the payoff.

400

401 Using (9) we can get an expression for D_2 in terms of D_1 :

402

$$403 \quad D_2 = \left(\frac{1}{2c_2} \right) \left(1 - \frac{f_2}{p_2 \varepsilon T (1 - p_1 D_1)(1 - c_1 D_1)} \right) \quad (10)$$

404

405 Using this substitution, and rearranging equation (8) gives

406

$$407 \quad \left(\frac{p_2}{4c_2} \right) \left(1 - \left[\frac{f_2}{p_2 \varepsilon T (1 - p_1 D_1)(1 - c_1 D_1)} \right]^2 \right) = \frac{\frac{f_1}{\varepsilon T} - p_1(1 - 2c_1 D_1)}{c_1 + p_1(1 - 2c_1 D_1)} \quad (11)$$

408

409 It is relatively easy to show that as D_1 increases the RHS of this always increases,
 410 because the nominator gets larger and the denominator gets smaller, and the LHS
 411 always decreases (providing $c_1 D_1 < 1$ and $p_1 D_1 < 1$: which we have assumed to hold
 412 earlier). Thus there can be at most one solution where the two sides balance and so at
 413 most one solution with $D_1 > 0$ and $D_2 > 0$.

414

415 Thus, for any parameter value combination, if a solution (D_1, D_2) exists, then this
 416 solution is unique.

417

418 Using the standard methodology of considering the determinant of the Hessian matrix,
 419 the solution will be stable when this determinant is negative, so that

420

$$421 \quad \frac{\partial^2 R_1}{\partial D_1^2} \frac{\partial^2 R_1}{\partial D_2^2} > \left(\frac{\partial^2 R_1}{\partial D_1 D_2} \right)^2, \frac{\partial^2 R_1}{\partial D_1^2} < 0, \frac{\partial^2 R_1}{\partial D_2^2} < 0$$

422

423 at the solution values (D_1, D_2) . We obtain

424

$$425 \quad \frac{\partial^2 R_1}{\partial D_1^2} = 2p_1c_1(p_2D_2(1 - c_2D_2) - 1)$$

$$426 \quad \frac{\partial^2 R_1}{\partial D_2^2} = -2p_2c_2(1 - p_1D_1)(1 - c_1D_1)$$

$$427 \quad \frac{\partial^2 R_1}{\partial D_1 D_2} = (2p_1c_1D_1 - p_1 - c_1)(p_2 - 2p_2c_2D_2)$$

428

429 It is clear that both second derivatives are negative and so we only need the first

430 condition to be solved. Substituting for D_2 in (8) and tidying yields

$$431 \quad 4p_1c_1p_2c_2v_1 - p_2^2p_1c_1v_1 + \left(\frac{f_2}{\varepsilon T v_1}\right)^2 (p_1c_1v_1 - (p_1 + c_1 - 2p_1c_1D_1)^2) > 0 \quad (12)$$

432

433 where D_1 is given by the solution of (11) and $v_1 = (1 - p_1D_1)(1 - c_1D_1)$.

434

435 Thus a stable non-zero investment occurs if the solutions of (10) and (11) yield values

436 of D_1 and D_2 such that

$$437 \quad 0 < D_1 < \min\left(\frac{1}{p_1}, \frac{1}{c_1}\right), \quad 0 < D_2 < \min\left(\frac{1}{p_2}, \frac{1}{c_2}\right)$$

438

439 and (12) holds. An unstable solution occurs if (10) and (11) yield such values and (12)

440 does not hold. Unlike the other strategies discussed so far, this mixed-defences

441 strategy is not guaranteed to be stable whenever it exists.

442

443 **Co-existence of solutions**

444 We consider the five possible solutions Stable (D_1, D_2) ; Unstable (D_1, D_2) ; $(D^*_1, 0)$;

445 Stable $(0, D^*_2)$; $(0, 0)$ where we use D^*_1 and D^*_2 to indicate that if one of these single

446 defence solutions were to coexist for the same parameters as (D_1, D_2) , the levels
 447 would in general be different to that of the same defence in the two-defence solution.

448

449 It is clear from equations (2), (3), (5) and (7) that $(0,0)$ cannot co-exist with either of
 450 the single defence strategies, and by noticing that the left hand side of equation (9)
 451 decreases with increasing levels of either defence, it is also clear that it cannot co-
 452 exist with either of the two-defence solutions (either the two-defence solution is stable
 453 when it exists or it is unstable).

454

455 We shall now consider the two single-defence solutions. The lower boundary to the
 456 pre-attack only solution $(D_1,0)$ is given when the inequality in (4) is replaced by an
 457 equality i.e.

$$458 \quad \beta_2 = \left(\frac{\beta_1}{4a_1} \right) (\beta_1 + 2 + 2a_1). \quad (13)$$

459

460 The left-most boundary of the post-attack-only solution in Figure 1 is attained using
 461 (6) in a similar way to give:

462

$$463 \quad \beta_1 = \left(\frac{1+a_1}{4a_2} \right) \beta_2 (\beta_2 + 2). \quad (14)$$

464

465 The gradient $d\beta_2/d\beta_1$ of the boundary of the $(D_1,0)$ solution, evaluated at the origin is
 466 simply $1/(2a_1)$. For the left-most boundary to the $(0,D_2)$ solution, the gradient $d\beta_1/d\beta_2$
 467 evaluated at the origin is simply $(1+a_1)/(2a_2)$. Thus, the gradient $d\beta_2/d\beta_1$ at this point
 468 is $2a_2/(1+a_1)$.

469

470 From Figure 1, we can see that there will be an area of overlap of the two regions if
 471 the gradient of the $(0,D_2)$ boundary is less steep than at the of the $(D_1,0)$ boundary at
 472 the origin, i.e. if

473

$$474 \quad \frac{2a_2}{1+a_1} < \frac{1}{2a_1}. \quad (15)$$

475

476 However if (15) is not satisfied for a particular set of parameter values then the two
 477 single-defence-only solutions cannot co-exist.

478

479 From before, the conditions for a solution $(0,D_2)$ are given by (6) and (7) and the
 480 conditions for a solution $(D_1,0)$ are given by (4) and (5). If we look at the simplifying
 481 case where $a_2 = a_1 = 0.5$, then (4) becomes

482

$$483 \quad \beta_2 > \frac{\beta_1}{2}(\beta_1 + 3)$$

484

485 (5) becomes $-1 < \beta_1 < 0$,

486

487 (6) becomes

488

$$489 \quad \beta_1 > \frac{3\beta_2}{4}(\beta_2 + 2),$$

490

491 and (7) becomes $-1 < \beta_1 < 0$.

492

493 In general, $\beta_1 > -1$ and $\beta_2 > -1$ is the allowable region if $c_1 \geq 0.5 p_1$, $c_2 \geq 0.5 p_2$ and
 494 $p_1 \beta_1 > -2c_1$ (or $p_2 \beta_2 > -2c_2$) if $c_1 < 0.5 p_1$ ($c_2 < 0.5 p_2$). So if $p_1 \leq 2c_1$ and $p_2 \leq 2c_2$ then
 495 the full range of possible β s are valid (and so any parameter sets of this type give
 496 solutions as above), but if $p_1 > 2c_1$ and/or $p_2 > 2c_2$ then there will be parameter
 497 combinations that we cannot solve in this way; these cases correspond to defences
 498 which are so effective that a reasonable investment can reduce the probability of
 499 capture to zero, and we ignore this possibility here.

500

501 We now show that (D_1, D_2) cannot occur with $(D^*_1, 0)$. For both of these to be
 502 solutions, each must satisfy equation (8), and we can see from this that $D^*_1 > D_1$.
 503 For (D_1, D_2) to be a solution we need these values to solve (10) and (11). For $(D^*_1, 0)$
 504 we need equation (11) to be solved with the left-hand side replaced by 0. However
 505 this means that in this second solution the left-hand term is less than in the first, but
 506 the right-hand term is greater than the first ($D^*_1 > D_1$ and the right-hand term increases
 507 with D_1); which yields a contradiction. Thus the two solutions cannot occur for the
 508 same parameters.

509

510 Hence (D_1, D_2) can only occur together with $(0, D_2)$ (see Figure 1), or as a unique
 511 solution.

512

513 In all of our numerical calculations (see the following section) a stable solution of this
 514 type (with investment in both defences) exists whenever none of the other three types
 515 do, although we have been unable to prove that this must always be the case.

516

517 We have shown there are five possible equilibrium solutions, four of which are ESSs
 518 $((0,0), (D_1,0), (0,D_2), \text{stable } (D_1,D_2))$, together with the unstable (D_1,D_2) which is not
 519 an ESS). Thus without restrictions, there would be 32 possible combinations of
 520 solutions. However, we have shown that $(0,0)$ can only exist as the sole solution, and
 521 that there can never be more than one solution from $(D_1,0)$, stable (D_1,D_2) and
 522 unstable (D_1,D_2) . This leaves nine possible combinations, which we consider below.
 523 The following five combinations are all observed in Figure 1: $(0,0)$; $(D_1,0)$; $(0,D_2)$;
 524 stable (D_1,D_2) ; $(0,D_2)$, stable (D_1,D_2) . In addition to some of these, both $(D_1,0)$, $(0,D_2)$
 525 and $(0,D_2)$, unstable (D_1,D_2) are observed in Figure 3. This leaves the two possibilities
 526 of only unstable (D_1,D_2) and no solution, which are the two possibilities leading to no
 527 ESS. We have been unable to prove that these cannot occur, but have not observed
 528 them in any of our numerical investigations.

529

530 Numerical Investigation of the Model

531

532 Recall our definitions:

$$533 \quad \beta_1 = \frac{f_1}{p_1 \varepsilon T} - 1$$

534 and

$$535 \quad \beta_2 = \frac{f_2}{p_2 \varepsilon T} - 1.$$

536 We know that $(0,0)$ occurs when β_1 and β_2 are both positive, and under these
 537 circumstances $(0,0)$ can be the only solution. This translates to conditions $f_1 > p_1 \varepsilon T$
 538 and $f_2 > p_2 \varepsilon T$.

539

540 For all of the examples that follow we assume the values $p_1 = 0.1$, $p_2 = 0.1$, $\varepsilon T = 10$
 541 and $c_2 = 0.2$. Then $(0,0)$ is the unique solution when $f_1 > 1$ and $f_2 > 1$. The boundaries
 542 of these conditions are shown by the dotted lines in Figure 1, and the region of no
 543 investment in defences lies above both these boundary values of f_1 and f_2 in the top
 544 right corner of Figure 1 (note the dotted lines will be partially covered by other lines).

545

546

547 For the situation where the prey should invest only in pre-capture defences, there are
 548 two restrictions on f_1 : $-2 < \beta_1 < 0$ and $-2a_1 < \beta_1 < 0$. As before, the prey should not
 549 invest in post-capture defences where $f_2 > p_2 \varepsilon T$. Under our default parameters
 550 values, $c_1 = 0.2$, and thus $a_1 = 2$, since $a_1 = c_1/p_1$. and therefore the most restrictive
 551 condition is that not involving a_1 . The region of (f_1, f_2) parameter space where only
 552 pre-capture defences are predicted therefore occurs when β_1 is negative and (by re-
 553 arrangement) $f_1 > p \varepsilon T$. Since $f_1 = p_1 \varepsilon T \beta_1 + 1$, for our default values these fall at f_1
 554 values of 1 and -1. However, we are only interested in non-negative values of f_1 and
 555 f_2 , so the critical f_2 values become 0 and 1.

556

557 There is also a restriction on f_2 given by

558

$$559 \quad \beta_2 > \left(\frac{\beta_1}{4a_1} \right) (\beta_1 + 2 + 2a_1)$$

560

561 In order to find this line, we simply take a range of f_1 values, between the two extreme
 562 values (0 and 1), convert these to β_1 values, and hence to β_2 values, before converting
 563 these to f_2 values. Since

564

565
$$f_2 = p_2 \epsilon T \beta_2 + 1,$$

566

567 we need to specify the value of p_2 . We assume this takes the value 0.1. Thus, the
 568 curved broken line and the vertical lines at f_1 equals 0 and 1 in Figure 1 enclose the
 569 region where investment in pre-capture defences makes post-capture unnecessary.

570 This is the top, left region of Figure 1.

571

572 A very similar situation occurs for the $(0, D_2)$ solution. Here, there are two restrictions
 573 on f_2 : $-2 < \beta_2 < 0$ and $-2a_2 < \beta_2 < 0$. Let us assume that $c_2 = 0.3$, and thus $a_1 = 3$, since
 574 $a_2 = c_2/p_2$. Thus, the most restrictive condition does not involve a_2 .

575 Since $f_2 = p_2 \epsilon T \beta_2 + 1$, for our default values these fall at f_2 values of 1 and -1.

576 However, we are only interested in non-negative values of f_1 and f_2 , so the critical f_2
 577 values become 0 and 1.

578

579 There is then a restriction on f_1 given by

580

581
$$\beta_1 > \left(\frac{1 + a_1}{4a_1} \right) \beta_2 (\beta_2 + 2)$$

582

583 In order to find this line, we simply take a range of f_2 values, between the two extreme
 584 values, convert these to β_2 values, and hence to β_1 values, before converting these to f_1
 585 values. Thus, the solid curved line and the horizontal lines at $f_2 = 0$ and $f_2 = 1$ to the
 586 right of the curved line enclose the parameter values that yield this solution (in the
 587 bottom, right part of Figure 1).

588

589 Lastly, we show the solution where investment is spread across both defences, these
590 must be solved numerically, and are only valid if both D values are positive, and that
591 all four P and C values are positive. All these solutions are shown in Figure 1; the
592 situation where non-zero investment in both defences is shown as a hatched region.
593 Notice that to the right of the solid curved lines there are parameter combinations
594 where the both-defences solution co-exists with another solution involving investment
595 only in post-attack defences.

596

597 In order to explore the nature of the mixed solution, in Figure 2 we plot the D_1 and D_2
598 values for the mixed solution along a transect of f_1 values where we hold f_2 at the
599 value 0.6. We observe that for f_1 values close to zero there is no valid mixed solution,
600 since simultaneous solution for non-zero D_1 and D_2 values predicts a negative D_2
601 value. In this region the only solution is for zero investment in D_2 and all investment
602 to be channelled into D_1 . At around f_1 values of 0.4 we do begin to get a mixed
603 solution with initially very low investment in D_2 . The D_1 value at this point shown on
604 Figure 2 is close to the value 1.5 predicted for the solution with zero investment in D_2
605 at $f_1 = 0.4$. Generally as f_1 increases, so D_2 increases and D_1 decreases. Eventually, at
606 an f_1 value around 1.05 the D_1 value falls to zero, when this occurs, then Figure 2
607 predicts the D_2 value to be close to the 0.667 value predicted for the solution with no
608 investment in D_1 at this point.

609

610 In Figure 3 we present the result of the same evaluation as in Figure 1 but where c_2 is
611 reduced six-fold to 0.05. Although the predictions are superficially similar, there are
612 several interesting differences. Firstly, there is now a region of f_1 - f_2 space where both

613 the $(0, D_2)$ and $(D_1, 0)$ solutions are valid and stable. We must also consider the
614 stability of the solution of investment across both defences. In figure 3, we only plot
615 such solutions where they are stable. In Figure 1, the interior solution is stable
616 whenever it exists. This is not true for the parameters chosen for Figure 3. As in
617 Figure 1, when $f_1 < 1$, the interior solution exists for all f_2 values below the broken
618 line marking the region of $((D_1, 0)$ solutions. However, it is only stable for a subset of
619 lower f_2 values. Thus, there can be a region where both $(0, D_2)$ and (D_1, D_2) are
620 potential solutions but only the first of these is stable. As we have seen in Figure 1, it
621 is possible also to find regions of parameter space where both solutions are stable
622 simultaneously.

623

624 Discussion

625 In his influential work, Endler (1991) suggested that it may be more attractive for prey
626 to interrupt the predation sequence as early as possible (see also Planque et al (2002)
627 who argue the same relating to successive defences against brood parasitism). He
628 argues this for a number of reasons. Firstly, failure of a later defence may be more
629 likely to be catastrophic for the prey. Secondly, later in the sequence the performance
630 of the prey may be weakened or exhausted by implementation of defences earlier in
631 the sequence. Thirdly, the lost time and energy spent in repelling the attack will be
632 reduced if the attack is resolved early in the sequence. Finally, investment in defences
633 later in the sequence may be inefficient, if these defences are seldom used because
634 defences used earlier in the sequence are generally successful in repelling attacks
635 before the later-acting defences are implemented. The last point especially argues that
636 we should expect investment in early (pre-capture) defences, but not in later defences.

637

638 Furthermore, early defences are more often constitutive, in that the prey does not have
639 to detect the predator to be undetected, and so predator encounters might not affect the
640 cost of early defences . In contrast, post-encounter defences are more often
641 responsive, involving defensive behaviours or other physiological costs, such as
642 regurgitation or reflex bleeding that are triggered by a specific attack.

643

644 Our model predicts that there can be circumstances where it is optimal for the prey to
645 invest in neither defence. This occurs if the constitutive costs of the defences are high,
646 if the defences have low efficacy (per unit of investment), if attacks are rare and if the
647 period during which the prey is exposed to predation is short. There are also
648 circumstances where we predict investment in pre-capture defences but not post
649 capture defences. This solution is more likely to occur under conditions where β_I is
650 negative and β_2 is positive (or only just negative). The parameter β for a given
651 defence can be seen as a description of the cost-benefit ratio of the defences: β
652 becomes larger (more positive) if the constitutive costs of the defence are high. β also
653 becomes larger if the attack rate, the period that must be survived by the prey and/or
654 the efficacy of the defence are low. Whether or not we predict investment in pre-
655 capture defences only is also affected by the value of a_I . This parameter takes a high
656 value if the costs of using pre-capture defences are high and/or if the effectiveness of
657 pre-attack defences is low. Increasing a_I restricts the area of (β_I, β_2) space where
658 investment only in pre-capture defences is optimal. The level of investment in pre-
659 capture defences increases as β_I becomes more negative and/or as c_I is reduced.

660

661 In circumstances where the asymmetry of the cost/benefit ratios are opposite (that is
662 β_S is negative and β_I is positive (or only just negative), then we get investment in

663 post-attack defences only. Where the two β values are generally similar and not too
664 large and positive, we predict investment across both defences. Indeed, such solutions
665 are likely where f_1 and f_2 are small, which might be reasonable for defences such as
666 colouration and sequestering of defences. Many defences serve other, perhaps primary
667 functions, such as catching or subduing prey, and so their marginal canonical costs in
668 terms of defence might be small. We find that the costs of one defence affects the
669 likelihood of investment in the other (cf Figure 3 and 1).

670

671 Further, there are combinations of parameter values for which different strategies are
672 both stable. In such circumstances the strategy to which the population settles will
673 depend on the history of the population. Thus, the model predicts that it is difficult to
674 make generalisations about how many and which defences a certain prey type will
675 invest in without quantitative evaluation of the different properties of each of the
676 alternative defences, as we discuss above. Our model might therefore provide insight
677 in to, for example, the evolution of aposematism in the lepidoptera. Many closely
678 related species have differing defensive strategies, with some investing heavily in pre-
679 capture defences (excellent crypsis paying opportunity costs) and others having both
680 pre-capture (warning coloration) and post-capture (aversive chemistry) defences. Our
681 model shows how easily these might be equally fit, and so divergent selection might
682 occur based initially on very minor differences, or even genetic drift.

683

684 There is a significant difference between the two types of defence, in that pre-attack
685 defences occur before post-attack defences, and thus influence the extent to which
686 post-attack defences are used. However, post-attack defences do not affect the
687 frequency with which pre-attack defences are used. This results in the co-existence of

688 solutions in both defences and in only post-attack defences, but not in both defences
689 and only pre-attack defences.

690

691 An interesting extension of our model would be to include a range of predator types
692 (or equivalently a range of different predatory situations), with different defences
693 differing in their rank order of efficacy against these different predators. In particular,
694 this would allow exploration of generalism and specialism in defences and in
695 particular the general trend (noted by both Endler 1991 & Caro 2005) that defences
696 used later in the predation sequence are more likely to be specialised for a particular
697 type of predator than more general defences used earlier in the sequence. Again, the
698 role of multi-functional defences was identified by Caro (2005) as another of his ten
699 most pressing questions in predator-prey interactions.

700

701 Endler's (1991) categorisation of different anti-predatory defences in animals has
702 been highly influential, but development of theoretical underpinning for his
703 predictions and empirical testing of these predictions has been lacking. We hope our
704 work will be a useful early step in developing a more solid theoretical base for
705 understanding diversity of anti-predatory traits. There have been developments on the
706 empirical side. Low (1998) carefully demonstrated investment across a range of
707 defences by the leaf-mining larvae of a moth (*Antispila nysaefoiella*) against a
708 specialist parasitoid. Langridge et al (in prep) demonstrated that the anti-predatory
709 behaviours of cuttlefish (*Sepia officinalis*) accords with three of Endler's specific
710 predictions: that later in the sequences of an attack, defences become more predator-
711 specific, more risky if unsuccessful in deterring attack and more costly to mount.
712 More empirical and theoretical work to explore and develop these predictions would

713 be valuable. In this, an important resource may be the comparatively much more
714 extensive literature seeking to understand the diversity of anti-herbivore traits shown
715 by plants (e.g. Biere et al, 2004, Ode 2006). We suggest that a useful next
716 development for our understanding of anti-predator behaviours would be to explore
717 how applicable current understanding of anti-herbivore defences is to the different
718 system.

719

720 The diversity of possible solutions to investment across only two defences in our
721 simple model where prey face only one type of attack demonstrates that a general
722 understanding of the diversity of anti-predatory suites used by different prey will be a
723 challenge. However, to meet that challenge, we feel that we have demonstrated that
724 simple verbal reasoning will be insufficient and models that allow quantitative
725 evaluation of a complex of different costs and benefits (as well as interaction between
726 the effectiveness of defences, not considered here) will be required.

727

728

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- 764
- 765

765

766

767 **Figure captions**

768

769 **Figure 1:** Different optimal solutions in terms of investment in pre-capture and post-770 capture defences for different combinations of values of the parameters f_1 and f_2 . The771 higher the values of f_1 and f_2 , the higher the fixed costs of pre-capture and post-772 capture defences respectively. Other parameter values: $\varepsilon T = 10$, $p_1 = 0.1$, $p_2 = 0.1$, $c_1 =$ 773 0.2 , $c_2 = 0.3$. When both f_1 and f_2 are greater than 1 (top right quarter of this figure),774 then zero investment in both defences is predicted. There is a region where f_1 is less775 than 1 and f_2 is sufficiently high where investment only in pre-capture defences is776 predicted. This region is bounded by the vertical dotted line at $f_1 = 1$ and the curved

777 broken line that separates this region from a hatched region below. The hatched

778 region indicates parameter combinations for which investment across both defences is

779 predicted. Note this solution can co-exist for some parameter combinations with

780 investment only in the later-acting (post-capture) defence. The both-defences solution

781 is plotted only when it is stable (although it is stable in all cases where it exists for this

782 figure, this is not true in general). The region where only investment in post-capture

783 defences is optimal occurs in the bottom right of the figure and is bounded by the

784 horizontal broken line at $f_2 = 1$ and the curved solid line that cuts through the middle

785 of the hatched region.

786

787 **Figure 2:** D_1 (broken line) and D_2 (solid line) values for the mixed solution shown in788 Figure 1 along a transect of f_1 values where we hold f_2 at the value 0.6. All other

789 values are as in Figure 1. Clearly, only combinations where both D_1 and D_2 are non-
790 negative are valid.

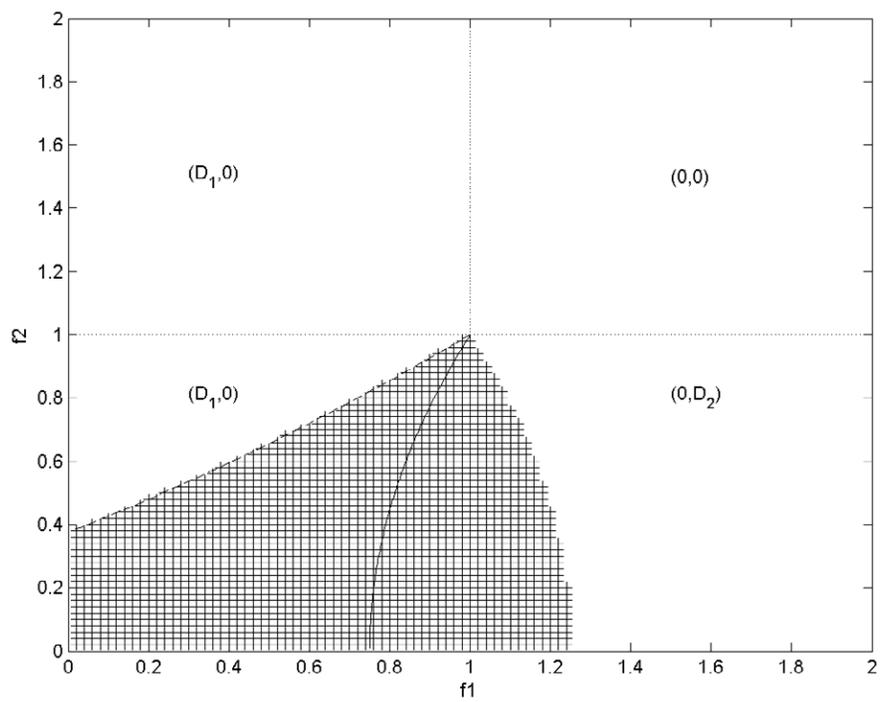
791

792 **Figure 3:** Different optimal solutions in terms of investment in pre-capture and post-
793 capture defences for different combinations of values of the parameters f_1 and f_2 . The
794 higher the values of f_1 and f_2 , the higher the fixed costs of pre-capture and post-
795 capture defences respectively. The values of the other parameters are the same as
796 those used for Figure 1, except $c_2 = 0.05$. When both f_1 and f_2 are greater than 1 (top
797 right quarter of this figure), then zero investment in both defenses is predicted. There
798 is a region where f_1 is less than 1 and f_2 is sufficiently high when investment only in
799 pre-capture defences is predicted. This region is bounded by the vertical dotted line at
800 $f_1 = 1$ and the curved dotted line. The hatched region indicates parameter
801 combinations for which investment across both defences is predicted and this solution
802 is stable. However, this solution is not stable everywhere where it is valid, and so this
803 solution is substantially less commonly predicted than in Figure 1. Note that this
804 solution can co-exist for some parameter combinations with investment only in the
805 later-acting (post-capture) defence. The region where only investment in post-capture
806 defences is optimal occurs in the bottom right of the figure and is bounded by the
807 horizontal broken line at $f_2 = 1$ and the curved solid line. Between the two curved
808 lines there is a region labelled “both”, where both the solution with investment only in
809 post-capture defences and the solution with investment only in pre-capture defences
810 are possible.

811

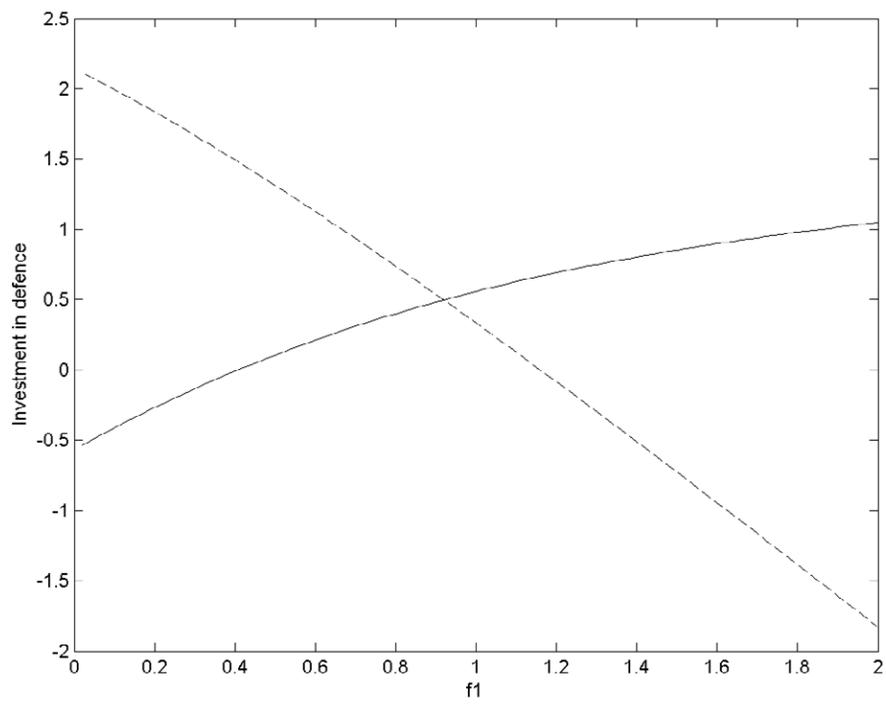
812

813

813 **Fig. 1**814
815

Accepted m.

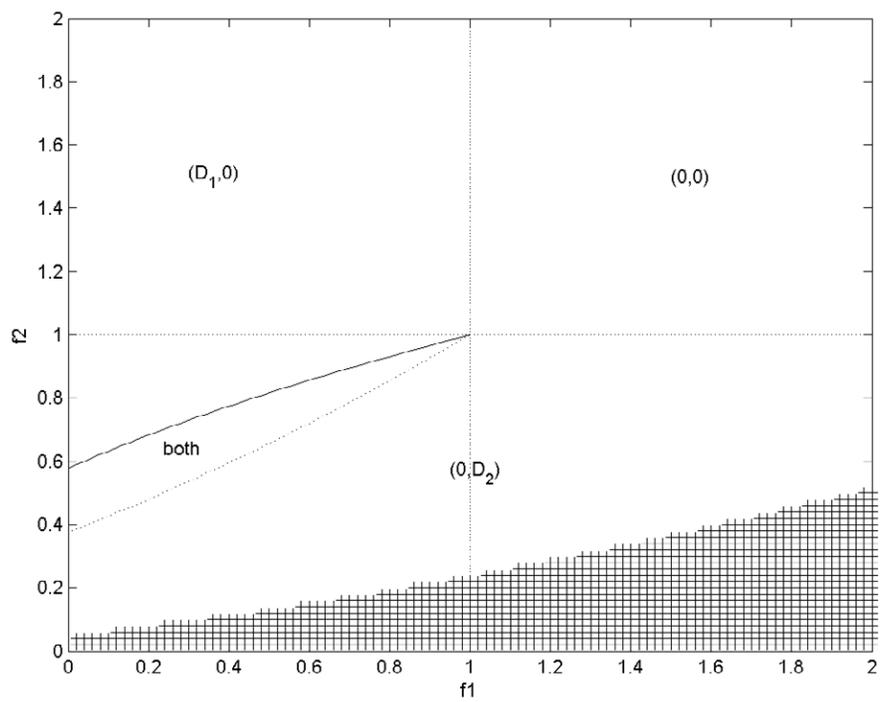
815 **Fig. 2**
816



817
818

Accepted m.

818 **Fig. 3**
819



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Accepted m.