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A game theoretic model of kleptoparasitism with strategic arrivals and departures of beetles at dung pats

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Abstract

Dung beetles *Onthophagus taurus* lay their eggs in brood balls within dung pats. The dung that is used must be sufficiently fresh, and so beetles must keep moving from pat to pat to find fresh dung. If another beetle finds a brood ball it will usually eat the egg inside and lay its own egg in the brood ball instead of constructing its own ball. Thus beetles will often stay near their eggs to guard them. We model a population of beetles where the times of arrival and departure from pats are strategic choices, and investigate optimal strategies depending upon environmental conditions, which can be reduced to two key parameters, the cost of brood ball construction and the easiness of finding balls to parasitise. We predict that beetles should follow one of three distinct behaviours; stay in patches for only short periods, arrive late and be purely parasitic, remain in pats for longer periods in order to guard their brood balls. Under different conditions populations can consist of the

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first of these types only, a combination of the first and second types, or a combination of all three types.

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1. Introduction

Kleptoparasitism, the stealing of resources, is a common behaviour in the natural world. It has been observed, for example, in wild dogs (Carbone et al., 2005), seabirds (Dies and Dies, 2005), insects (Reader, 2003), fish (Hamilton and Dill, 2003) and lizards (Cooper and Perez-Mellado, 2003). For an excellent review of this behaviour see Iyengar (2008).

When is it beneficial for animals to engage in kleptoparasitism, and why does kleptoparasitism occur in some situations and not others which are superficially similar? A series of game theoretical models has investigated this question, starting with Broom and Ruxton (1998) (see also Ruxton and Broom, 1999; Broom and Ruxton, 2003; Broom et al., 2004; Broom and Rychtář, 2007).

All of these models are generic, and there have been few models that focus on a particular species. One of these was Crowe et al. (2009) which modelled the stealing behaviour of the dung beetle *Onthophagus taurus*.

O. taurus is a common dung beetle on many continents, originally across Southern Europe, North Africa and Asia Minor, being introduced to North America and Australia in the twentieth century (Hunt et al., 1999; Fincher and Woodruff, 1975). *O. taurus* have been extensively studied because the species exhibits a male dimorphism in the expression of beetle horns (see e.g. Moczek, 1996; Emlen and Nijhout, 1999; Moczek and Emlen, 2000; Emlen

et al., 2007). Here, we will focus on female behavior. The females of *O. taurus* lay eggs in carefully constructed tunnels under the soil's surface and beneath a dung pat deposited by a large herbivore (Crowe et al., 2009). The time that a given dung pat is usable is dependent on climatic conditions, particularly temperature and humidity. This time can range from a few hours to several days (Moczek et al., 2002). Potential parasites can benefit from stealing a ball in two ways. They can gain nourishment by eating the egg of the previous owner, and they can save time in preparing their own ball by using the existing one for their own egg, if the dung is not too old. It has been documented that female dung beetles will routinely access brood balls made by other females and replace existing eggs with their own (Moczek and Cochrane, 2006). Female dung beetles have been documented to guard their brood balls against thieving beetles (Hunt and Simmons, 2002).

Crowe et al. (2009) modelled this situation as a random process, focusing on a population of beetles on a single dung pat. They concluded that in general if stealing opportunities presented themselves then they should be taken, and that guarding may or may not be the best strategy depending upon ecological conditions. However, the model of Crowe et al. (2009) did not consider the time aspect at all. Beetles usually use all the dung from a dung pat within a period of four days (Bertone et al., 2006), and do not spend large periods of time on a single dung pat, but move from pat to pat. This is thus a dynamic process, where timing of beetles behavior can be very important. In contrast to Crowe et al. (2009), in this paper we model the situation where arrival and departure times at given dung pats are strategic choices.

47 2. Model

48 In this paper we consider a model of dung pats visited by a large (effec-
 49 tively infinite) population of beetles. It is assumed that it is always in the
 50 interest of beetles to steal if they get the opportunity (i.e. if they encounter
 51 the brood ball of a beetle which has already left the pat), but that beetles
 52 can vary their time of arrival and departure at a pat, and that any particular
 53 beetle will enter (and leave) a pat when the dung in the pat reaches a cer-
 54 tain age. The strategies in our model will thus consist of a pair of numbers,
 55 which are the choice of the age of the dung when a beetle arrives and departs
 56 a patch. For simplicity we consider only the day of arrival and the day of
 57 departure, so that strategies are pairs of positive integers, and we assume
 58 that a beetle must stay at least one day. Whilst this is a simplification, it
 59 is not an unreasonable one. Beetles need some time (roughly a day on av-
 60 erage, calculated from results published in Hunt et al., 2002) after laying an
 61 egg for the subsequent egg to develop to be ready to lay. It is logical that
 62 during this time the beetle should stay close to the egg (and thus guard it)
 63 as opposed to going elsewhere. Recent laboratory data (Mary Crowe et al.,
 64 unpublished manuscript) also suggests that breeding pairs or females remain
 65 in the proximity of the brood balls for an extended period of time.

66 A beetle's strategy is determined by

- 67 • the age of dung (in days) when it enters a dung pat, $x \in \{1, 2, 3\}$
- 68 • the age of dung (in days) when it leaves a dung pat, $y \in \{x + 1, \dots, 4\}$

69 We will denote each strategy as (x, y) . We thus have six strategies:

$$\Omega = \left\{ (1, 2), (1, 3), (1, 4), (2, 3), (2, 4), (3, 4) \right\}. \quad (1)$$

70 A dung beetle following strategy (x, y) enters dung of age x . If $x = 1$, the
 71 beetle makes her own ball. If $x > 1$, the beetle searches for any ball it can
 72 steal. Such balls can come only from beetles that came to the dung earlier
 73 and left no later than on day x , i.e. only from beetles using a strategy (x', y')
 74 for $x' < y' \leq x$. If the beetle finds a ball it can steal, it eats the other beetle's
 75 egg and lays her own egg in the ball. If no ball is found and the dung is not
 76 too old (i.e. $x < 3$, so $x = 2$), the beetle will work on preparing a brood ball
 77 of her own. A beetle that prepares its own ball incurs a fitness cost ε (so if
 78 there is an opportunity to steal it should be taken, as we assume above). In
 79 any case (for $x \leq 2$), the day after the dung beetle enters the dung pat, the
 80 same dung pat will have age $x + 1$, a beetle using strategy (x, y) will have
 81 one ball with an egg of her own; the ball was possibly stolen from a beetle
 82 using strategy (x', y') for $x' < y' \leq x$. If $y = x + 1$, the beetle now leaves
 83 the dung pat to find a dung pat of age x . Otherwise, it stays in the same
 84 dung pat until it is of age y , guarding her ball and making the ball virtually
 85 invulnerable to the stealing attempts of other beetles. Beetles coming on day
 86 3 cannot make their own balls as the dung is too old already. If they do not
 87 steal the ball, they will have no ball of their own.

88 *2.1. Model of stealing the ball*

89 Here we describe the mechanism/ model of how the ball is stolen. Con-
 90 sider a case where N beetles are trying to steal a ball in a dung pat where
 91 there are B balls in total. We assume that the beetles are not 100% effective
 92 in finding the balls and introduce a parameter κ that is related to the success
 93 rate of kleptoparasitism. During a small period of time dt , each ball could
 94 be found by N beetles and will thus be stolen with probability $\kappa N dt$. Hence,

95 $\kappa NBdt$ balls will be stolen in total. Once a beetle steals a ball, it does not
 96 attempt to steal another one. Hence

$$N - B = N_0 - B_0 \quad (2)$$

97 where $B_0(N_0)$ is the number of balls (beetles) at time 0. Hence, N is the
 98 solution of the differential equation

$$\frac{dB}{dt} = -\kappa NB = -\kappa B(B + N_0 - B_0). \quad (3)$$

99 The solution of (3) is

$$B(t) = \begin{cases} (N_0 - B_0) \cdot \frac{B_0}{N_0 e^{\kappa t(N_0 - B_0)} - B_0}, & B_0 \neq N_0 \\ \frac{B_0}{\kappa t B_0 + 1}, & B_0 = N_0. \end{cases} \quad (4)$$

100 Note that the second formula is a limit of the first when $B_0 - N_0 \rightarrow 0$. We
 101 will thus use the first formula (and approach the appropriate limit where
 102 necessary). Up to scaling (in κ), we may assume that beetles have time $t = 1$
 103 to steal the eggs. Thus after N beetles have come to a dung pat with B
 104 balls, there will be

$$B(1) = (N_0 - B_0) \cdot \frac{B_0}{N_0 e^{\kappa(N_0 - B_0)} - B_0} \quad (5)$$

105 balls left, while the beetles have stolen

$$B_0 - B(1) = N_0 B_0 \cdot \frac{e^{\kappa(N_0 - B_0)} - 1}{N_0 e^{\kappa(N_0 - B_0)} - B_0} \quad (6)$$

106 balls in total. Note that the above formulae approach the right numbers in
 107 the limiting cases, when the numerator and denominator both tend to zero.

108 When κ approaches ∞ (i.e. when beetles are very effective in finding and
109 stealing the balls) then

$$B(1) \approx \begin{cases} 0, & N_0 \geq B_0 \\ B_0 - N_0, & N_0 < B_0, \end{cases} \quad (7)$$

110 which means that the beetles find and steal all the balls (if there are more
111 beetles than balls) or that every beetle steals one ball for herself (if there
112 are more balls than beetles). Similarly, as B_0 approaches ∞ (and $\kappa > 0$, i.e.
113 there is some chance of stealing), we get

$$B(1) \approx B_0 \quad (8)$$

$$B_0 - B(1) \approx N_0, \quad (9)$$

114 which means that every beetle gets to steal a ball for her own egg (while leav-
115 ing the total number of balls effectively constant). Finally, as N_0 approaches
116 ∞ , we get that $B(1) \approx 0$, meaning that beetles find and steal every possible
117 egg.

118 2.2. Determining Fitness

119 We will denote the fitness, or reproductive success, of a strategy $(x, y) \in \Omega$
120 by f_{xy} . The fitness is the (average) rate at which brood balls produced by
121 a beetle using strategy (x, y) reach maturity in a population described by $\vec{P}$
122 minus any costs involved in producing a brood ball. Here $\vec{P} = \langle P_\omega, \omega \in \Omega \rangle$,
123 where P_{xy} is the proportion of the population using strategy (x, y) . Evolution
124 favours individuals with the greatest fitness, which depends upon the com-
125 position of the population. The composition of the population will change

126 through time according to this fitness, on a timescale that is long in com-
 127 parison to the three day interactions that we describe. We investigate such
 128 changes, and in particular look for stable population mixtures, evolutionarily
 129 stable strategies (ESSs).

130 A beetle using strategy (x, y) works for $y - x$ days on provisioning (stealing
 131 and/or making a brood ball plus potential guarding). This also means that
 132 beetles using strategy (x, y) can be found in pats that are $x, x + 1, \dots, y - 1$
 133 days old. We assume that dung pats are produced at a constant rate, and
 134 that the beetles are equally distributed in time and space. Thus, the effective
 135 number of beetles using strategy (x, y) , denoted N_{xy}^e , that can be found on
 136 a single dung pat of age between x and $y - 1$ is

$$N_{xy}^e = \frac{P_{xy} \cdot N}{y - x}. \quad (10)$$

137 This yields the formula for fitness of a strategy to be

$$f_{xy} = \frac{B_{xy}^3}{P_{xy} \cdot N} - \varepsilon \rho_{x,y} = \frac{B_{xy}^3}{N_{xy}^e \cdot (y - x)} - \varepsilon \rho_{x,y} \quad (11)$$

138 where B_{xy}^i is the number of undamaged brood balls beetles using strategy
 139 (x, y) have in their possession in a dung pat of age i , and $\rho_{x,y}$ is the probability
 140 that an individual using (x, y) made its own brood ball.

141 B_{xy}^3 is determined by the number of brood balls produced (made or stolen)
 142 by beetles using strategy (x, y) , minus the number of brood balls stolen from
 143 them. In order to determine B_{xy}^3 (which is necessary to find f_{xy}) for each
 144 strategy, we will determine B_{xy}^1 and B_{xy}^2 .

145 Note that we have assumed that there is effectively no cost in searching
 146 for new cow pats. Field data indicates that the density of pats is over 0.5 pats
 147 per m^2 and that beetles can search over $5m^2$ per second (Crowe et al., 2009).

148 However, according to Moczek and Cochrane (2006) the time expended on
 149 tunneling and brood ball production in *O. Taurus* requires several hours (see
 150 also Hunt and Simmons, 2002, 2004).

151 2.2.1. Day 1

152 Only beetles using strategies (1, 2), (1, 3), (1, 4) come on the first day of
 153 the dung pat. There is nothing to steal and they all make their own balls.
 154 We thus have

$$B_{xy}^1 = \begin{cases} N_{1y}^e, & y \in \{2, 3, 4\} \\ 0, & \text{otherwise} \end{cases} \quad (12)$$

155 2.2.2. Day 2

156 Strategies (1, 3) and (1, 4) continue to guard their brood balls, so their
 157 brood balls will not be stolen. The only brood balls that can be stolen come
 158 from strategy (1, 2); and the only beetles that can steal these balls are using a
 159 strategy (2, 3) or (2, 4). Hence, there are B_{12}^1 balls to be stolen by $(N_{23}^e + N_{24}^e)$
 160 beetles to steal them, we use 5 and get

$$B_{12}^2 = N_{12}^e \cdot (1 - \sigma_2), \quad (13)$$

161 where

$$(1 - \sigma_2) = \frac{(N_{23}^e + N_{24}^e) - N_{12}^e}{(N_{23}^e + N_{24}^e)e^{\kappa t((N_{23}^e + N_{24}^e) - N_{12}^e)} - N_{12}^e}. \quad (14)$$

162 Above, σ_2 denotes the fraction of the balls that got stolen (using 6). Note
 163 that (2, 3) and (2, 4) may steal, but those beetles that did not steal can
 164 make a ball of their own. In total, each such beetle will have a ball in their
 165 possession. Thus, we get

$$B_{xy}^2 = N_{xy}^e, \quad x \in \{1, 2\}, y \in \{3, 4\}. \quad (15)$$

166 *2.2.3. Day 3*

167 Strategies (1, 4) and (2, 4) continue to guard their brood balls, so their
 168 brood balls will not be stolen. The brood balls that can be stolen come from
 169 strategies (1, 2), (1, 3) and (2, 3); and the only beetles that can steal those
 170 balls are using a strategy (3, 4). No new balls can be made on day 3. There
 171 are thus in total

$$V_3 = B_{12}^2 + B_{13}^2 + B_{23}^2 \quad (16)$$

172 vulnerable balls that can be stolen on day 3 by a total of N_{34}^e beetles. Thus,
 173 by (6), beetles using strategy (3, 4) will steal

$$S_3 = N_{34}^e V_3 \cdot \frac{e^{\kappa(N_{34}^e - V_3)} - 1}{N_{34}^e e^{\kappa(N_{34}^e - V_3)} - V_3} \quad (17)$$

174 balls. Assuming that stolen balls are selected at random, the fraction B_{12}^2/V_3
 175 of those stolen balls belonged to (1, 2) beetles and similarly for other strate-
 176 gies. We thus get

$$B_{12}^3 = B_{12}^2 - S_3 \cdot \frac{B_{12}^2}{V_3} = N_{12}^e \cdot (1 - \sigma_2) \cdot \left(1 - \frac{S_3}{V_3}\right), \quad (18)$$

$$B_{23}^3 = B_{23}^2 - S_3 \cdot \frac{B_{23}^2}{V_3} = N_{23}^e \cdot \left(1 - \frac{S_3}{V_3}\right), \quad (19)$$

$$B_{13}^3 = B_{13}^2 - S_3 \cdot \frac{B_{13}^2}{V_3} = N_{13}^e \cdot \left(1 - \frac{S_3}{V_3}\right), \quad (20)$$

$$B_{24}^3 = N_{24}^e, \quad (21)$$

$$B_{14}^3 = N_{14}^e, \quad (22)$$

$$B_{34}^3 = S_3. \quad (23)$$

177 The corresponding fitnesses then follow from (11), although this still involves
 178 the unknown term $\rho_{x,y}$. It turns out from the analysis below that we do not
 179 need to evaluate $\rho_{x,y}$, but we note here that $\rho_{1,y} = 1$ for $y = 2, 3, 4$ and
 180 $\rho_{3,4} = 0$.

181 3. ESS analysis

182 First, we establish that none of the strategies $(1, 2)$, $(1, 3)$, $(1, 4)$ can be an
 183 ESS or even involved in an evolutionarily stable mixture. Indeed, it follows
 184 from (11), (21) and (22) that, under any circumstances,

$$f_{14} < f_{24}. \quad (24)$$

185 Now we compare strategies $(1, 3)$ and $(2, 3)$. Each has the same probability
 186 of losing any brood ball that they make (if it is stolen by a $(3, 4)$ individual).
 187 $(2, 3)$ has no greater cost per ball, as $(1, 3)$ can never steal, and $(2, 3)$ makes
 188 balls at a faster rate than $(1, 3)$ (taking one day instead of two). Thus, as long
 189 as the expected cost per brood ball is less than the expected reward (which
 190 we assume, as otherwise the population would not be viable), we have that

$$f_{13} < f_{23}. \quad (25)$$

191 Finally, since $\kappa > 0$ (i.e. beetles can steal something), we get that $\sigma_2 > 0$
 192 and thus since $\rho_{2,3} \leq \rho_{1,2} = 1$,

$$f_{12} < f_{23}. \quad (26)$$

193 This means that we can restrict ourselves to the analysis of the case where
 194 only $(2, 3)$, $(2, 4)$ and $(3, 4)$ are present. In this situation, beetles using $(3, 4)$
 195 can steal balls coming from $(2, 3)$ only and no other stealing takes place.
 196 Thus $(2, 3)$, $(2, 4)$ must make their own brood balls and $\rho_{2,y} = 1$ for $y = 3, 4$.

197 The fitness of the respective beetles becomes

$$f_{24} = \frac{1}{2} - \varepsilon, \quad (27)$$

$$f_{23} = \frac{N_{34}^e - N_{23}^e}{N_{34}^e e^{\kappa(N_{34}^e - N_{23}^e)} - N_{23}^e} - \varepsilon = \frac{P_{34} - P_{23}}{P_{34} e^{\kappa'(P_{34} - P_{23})} - P_{23}} - \varepsilon, \quad (28)$$

$$f_{34} = \frac{N_{23}^e e^{\kappa(N_{34}^e - N_{23}^e)} - N_{23}^e}{N_{34}^e e^{\kappa(N_{34}^e - N_{23}^e)} - N_{23}^e} = \frac{P_{23} e^{\kappa'(P_{34} - P_{23})} - P_{23}}{P_{34} e^{\kappa'(P_{34} - P_{23})} - P_{23}}, \quad (29)$$

198 where the new factor κ' is just a rescaling of the original factor κ ,

$$\kappa' = \kappa N. \quad (30)$$

199 3.1. Pure strategies

200 We shall first consider each pure strategy in turn, assuming the popu-
 201 lation consists almost entirely of individuals of that type, together with a
 202 small invading group comprising individuals from the other types. When the
 203 population consists of almost all (2, 3) strategists, the fitnesses of the three
 204 strategies are

$$f_{23} = 1 - \varepsilon, \quad (31)$$

$$f_{24} = 1/2 - \varepsilon, \quad (32)$$

$$f_{34} = 1 - e^{-\kappa'} \quad (33)$$

205 so that (2, 3) is an ESS when f_{23} is the largest of the three fitnesses i.e.

$$\kappa' < -\ln(\varepsilon). \quad (34)$$

206 When the population consists of almost all (3, 4) strategists, the fitnesses of
 207 the three strategies are

$$f_{23} = e^{-\kappa'} - \varepsilon, \quad (35)$$

$$f_{24} = 1/2 - \varepsilon, \quad (36)$$

$$f_{34} = 0. \quad (37)$$

For $(3, 4)$ to be an ESS we need $\varepsilon > \max(1/2, e^{-\kappa'})$. Note that such a population is not realistic, since it consists only of individuals who arrive too late to lay their own eggs, and so no eggs are ever laid. Provided that the cost of egg laying is not unfeasibly large, then this is not an ESS, and we shall discount it. In general we shall assume that $\varepsilon < 1/2$.

Finally when the population consists of almost all $(2, 4)$ strategists, the fitnesses of $(2, 4)$ is $f_{24} = 1/2 - \varepsilon$. It can thus be invaded by $(2, 3)$ strategists whose fitness is $f_{23} = 1 - \varepsilon$. Thus, $(2, 4)$ is never an ESS.

3.2. *Mixtures of two pure strategies*

We shall first consider populations consisting of two of the three strategies only. For any particular mixture to be an ESS, the payoffs to the two strategies involved must be equal, and greater than the payoff to the third strategy

First we consider a pair including $(2, 3)$ and $(2, 4)$. We have $p_{34} = 0$, so that $f_{23} = 1 - \varepsilon, f_{24} = 1/2 - \varepsilon$. Thus $f_{23} > f_{24}$, which means that no such mixture can be an ESS.

Now we consider a pair including $(2, 4)$ and $(3, 4)$. We have $p_{23} = 0$, so that $f_{24} = 1/2 - \varepsilon, f_{34} = 0$. Thus $f_{24} > f_{34}$, which means that no such mixture can be an ESS.

227 To have a pair including (2, 3) and (3, 4) we need $f_{23} = f_{34}$ which, by (27)
 228 and (28) implies that

$$h(P_{23}) = f_{23} - f_{34} = \frac{(1 - P_{23}) - P_{23}e^{\kappa'(1-2P_{23})}}{(1 - P_{23})e^{\kappa'(1-2P_{23})} - P_{23}} - \varepsilon = 0. \quad (38)$$

229 For stability against small changes in the relative frequency of the two types
 230 in the equilibrium we need $h'(P_{23}) < 0$ where the differentiation is with
 231 respect to P_{23} . It happens if and only if

$$1 - e^{2\kappa'(1-2P_{23})} + 2\kappa'(1 - 2P_{23})e^{\kappa'(1-2P_{23})} < 0. \quad (39)$$

232 It is easy to show that the left hand side of (39) is zero at $P_{23} = 1/2$, positive
 233 when $P_{23} > 1/2$ and negative when $P_{23} < 1/2$. This, together with the fact
 234 that $h(0) = h(1) = e^{-\kappa'} - \varepsilon$, in turn means that there are either no roots to
 235 (38) or there are exactly two, with an unstable root with $P_{23} > 1/2$ and a
 236 stable (against changes in P_{23} and P_{34}) root with $P_{23} < 1/2$. There are two
 237 such roots when $h(0) > 0 > h(1/2)$ i.e.

$$\frac{2(1 - \varepsilon)}{1 + \varepsilon} < \kappa' < -\ln(\varepsilon). \quad (40)$$

238 In addition we need stability against invasion by P_{24} . We will first evalu-
 239 ate the mean fitness in a mixture satisfying (38). Since pats are visited daily
 240 by all females, the ratio of the number of brood balls hatching daily to the
 241 number of females is simply the proportion of females building balls, P_{23} .
 242 This is also the proportion of females who pay the costs of building a brood
 243 ball. Hence, $f_{23} = f_{34} = P_{23}(1 - \varepsilon)$. Thus, $f_{23} > f_{24} = 1/2 - \varepsilon$ is equivalent
 244 to

$$P_{23} > \frac{1 - 2\varepsilon}{2(1 - \varepsilon)}. \quad (41)$$

245 This inequality defines a region in parameter space which has a boundary
 246 defined by when $>$ is replaced by $=$ in (41). This boundary thus occurs when
 247 $P_{23} = \frac{1-2\varepsilon}{2(1-\varepsilon)}$ and thus when

$$\frac{P_{23}}{1 - P_{23}} = 1 - 2\varepsilon \quad \text{and} \quad 1 - 2P_{23} = \frac{\varepsilon}{1 - \varepsilon}. \quad (42)$$

248 Rearranging (38) gives

$$e^{\kappa'(1-2P_{23})} = \frac{1 + \frac{P_{23}}{1-P_{23}}\varepsilon}{\frac{P_{23}}{1-P_{23}} + \varepsilon} \quad (43)$$

249 which using the rearrangements in (42) leads to the boundary condition as

$$\kappa' = \frac{1 - \varepsilon}{\varepsilon} \ln(1 + 2\varepsilon). \quad (44)$$

250 It is clear that invasion by P_{24} is resisted if and only if κ' lies on one side
 251 of the critical value given by (44), and simple verification indicates that the
 252 required condition is

$$\kappa' < \frac{1 - \varepsilon}{\varepsilon} \ln(1 + 2\varepsilon). \quad (45)$$

253 The right-hand term of (45) always lies between the two limits of (40) for
 254 $\varepsilon < 0.5$ so that we have a pair (2, 3) and (3, 4) if and only if

$$\frac{2(1 - \varepsilon)}{1 + \varepsilon} < \kappa' < \frac{1 - \varepsilon}{\varepsilon} \ln(1 + 2\varepsilon). \quad (46)$$

255 3.3. Mixtures of all three pure strategies

256 For an internal equilibrium we require the fitness of all three strategies
 257 to be identical. By (27) and (28), $f_{23} = f_{24}$ if and only if

$$e^{\kappa'(P_{34}-P_{23})} = 2 - \frac{P_{23}}{P_{34}}. \quad (47)$$

258 By (28) and (29), $f_{23} = f_{34}$ if and only if

$$\varepsilon = \frac{P_{34} - P_{23}e^{\kappa'(P_{34}-P_{23})}}{P_{34}e^{\kappa'(P_{34}-P_{23})} - P_{23}}. \quad (48)$$

259 Substituting (47) into (48) we obtain

$$\varepsilon = \frac{P_{34} - P_{23}(2 - \frac{P_{23}}{P_{34}})}{P_{34}(2 - \frac{P_{23}}{P_{34}}) - P_{23}} = \frac{P_{34} - P_{23}}{2P_{34}}. \quad (49)$$

260 Thus we have,

$$P_{23} = P_{34}(1 - 2\varepsilon), \quad (50)$$

261 which substituted into (47) gives

$$P_{34} - P_{23} = \frac{1}{\kappa'} \ln(1 + 2\varepsilon). \quad (51)$$

262 Rearranging (50) and (51) we obtain an internal equilibrium when

$$P_{23} = \frac{1 - 2\varepsilon}{2\kappa'\varepsilon} \ln(1 + 2\varepsilon), \quad (52)$$

$$P_{34} = \frac{1}{2\kappa'\varepsilon} \ln(1 + 2\varepsilon), \quad (53)$$

$$P_{24} = 1 - P_{23} - P_{34} \quad (54)$$

263 whenever the three terms are all positive, which (assuming $\varepsilon < 1/2$) occurs

264 if and only if

$$\kappa' > \frac{1 - \varepsilon}{\varepsilon} \ln(1 + 2\varepsilon). \quad (55)$$

265 We believe that this equilibrium is also an ESS in all cases, as suggested by

266 our numerical results, but we have not been able to prove this.

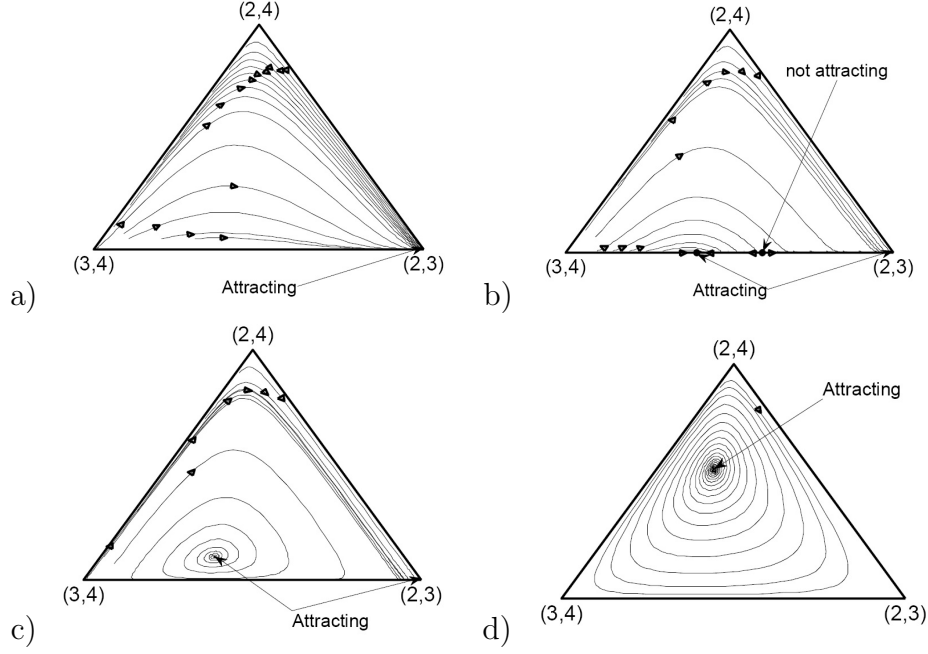


Figure 1: Diagram of the dynamics for $\varepsilon = 0.2$ and a) $\kappa' = 1 < \frac{2(1-\varepsilon)}{1+\varepsilon}$, b) $\frac{2(1-\varepsilon)}{1+\varepsilon} < \kappa' = 1.34 < \frac{1-\varepsilon}{\varepsilon} \ln(1+2\varepsilon)$, c) $\frac{1-\varepsilon}{\varepsilon} \ln(1+2\varepsilon) < \kappa' = 1.5 < -\ln(\varepsilon)$, d) $-\ln(\varepsilon) < \kappa' = 3$.

267 3.4. Dynamics

268 We consider evolutionary dynamics, using the classical replicator equation
 269 (Hofbauer and Sigmund, 1998)

$$\frac{d}{dt}P_{xy} = P_{xy}(f_{xy} - \bar{f}), \quad (56)$$

270 where $\bar{f}$ is the mean payoff in the population. The dynamics yields four
 271 different outcomes, as in the ESS analysis above, see Figure 1.

272 It is hard to prove results regarding the replicator dynamics in a case
 273 with non-linear payoffs as in this paper, and we shall restrict ourselves to
 274 observing the outcome of simulations.

275 When there was a unique solution, this was either a pure ESS or an

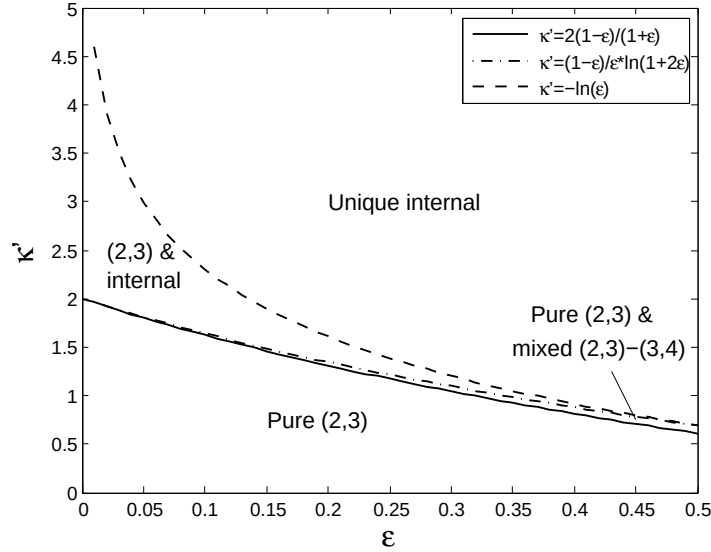


Figure 2: Outcomes for different model parameters, the cost of making own ball, ε and the (scaled) effectiveness to find a ball, κ' .

internal equilibrium, and so in each case a rest point of the dynamics. In each case the numerical results showed that this was a global attractor so that starting with any population mixture, the population always finished at the unique rest point. When there were two rest points, where the population finished depended upon the initial population composition, but generally each had a substantial basin of attraction.

4. Results summary

There are four distinct cases, based upon comparing the value of κ' with three progressively larger functions of ε . We illustrate these in Figure 2.

If

$$\kappa' < \frac{2(1-\varepsilon)}{1+\varepsilon} \quad (57)$$

286 then there is a unique pure (2, 3) ESS which is globally stable. If

$$\frac{2(1 - \varepsilon)}{1 + \varepsilon} < \kappa' < \frac{1 - \varepsilon}{\varepsilon} \ln(1 + 2\varepsilon), \quad (58)$$

287 then there are two ESSs, a pure (2, 3) ESS and a mixed ESS combining the
288 two strategies (2, 3) and (3, 4). If

$$\frac{1 - \varepsilon}{\varepsilon} \ln(1 + 2\varepsilon) < \kappa' < -\ln(\varepsilon), \quad (59)$$

289 then there are again two solutions, a pure (2, 3) ESS and an internal equilib-
290 rium combining all three strategies. Finally if

$$-\ln(\varepsilon) < \kappa' \quad (60)$$

291 there is a unique internal equilibrium.

292 We can thus see that when brood balls are difficult to find (when com-
293 pared to the cost of production) then all individuals should spend as short a
294 time on the dung pat as possible before leaving, and create their own brood
295 balls. When they become easier to find, then this strategy remains an ESS,
296 but there is also an alternative mixed ESS comprising both individuals of the
297 original type and pure parasites which arrive late in the hope of exploiting
298 these individuals after they have left by stealing their brood balls. If finding
299 brood balls becomes even easier, then whilst the first solution is still an ESS,
300 the mixed solution involves a third strategy which arrives early and waits for
301 a long time guarding its brood balls as a defence against the late arriving
302 parasites. Finally for brood balls that are very easy to find, the pure strategy
303 is no longer an ESS, and the mixture of three is the unique solution.

304 5. Discussion

305 In this paper we have considered a dynamic model of the creation, par-
306 asitism and defence of brood balls by a common species of dung beetle. As
307 the quality of dung quickly declines over a small period of days, beetles must
308 move between pats to give their offspring a good chance of survival. We have
309 shown that under different circumstances, three distinct strategies can sur-
310 vive in some combinations. The first type are individuals $(2, 3)$ which arrive
311 early on dung pats but leave quickly; whilst they would parasitise others if
312 the opportunity arose, they are not on the dung pat at the right time to do
313 so. Thus if the population only consists of individuals of this type, there
314 is no parasitism. The second type are purely parasitic $(3, 4)$ beetles which
315 arrive later, after those of the first type have left, and who parasitise their
316 brood balls. Finally there are $(2, 4)$ individuals who arrive early and stay for
317 a long time to guard their own eggs from parasitic individuals. The second
318 type can clearly only exist if there are individuals of the first type, and the
319 defensive strategy of the third type is only effective if the second type are
320 present.

321 The key factors which affect the mixture of individuals are two key pa-
322 rameters, the ease of finding brood balls to steal, and the cost of making your
323 own ball. The harder balls are to find, and the lower the cost of making a
324 ball, the more the strategy $(2, 3)$ prevails in the population. This strategy is
325 always present in some numbers, and for sufficiently low cost of ball making
326 and high difficulty of finding difficulty all beetles play this strategy. As these
327 parameters change (cost of ball making increases, difficulty of finding a ball
328 decreases), then the parasitic individuals can appear, and at more extreme

329 values the individuals that use considerable time resources defending their
330 brood balls can appear.

331 Our model predicts that very new pats should not be used for brood balls.
332 This seems to agree with reality. Crowe et al. (unpublished manuscript)
333 conducted an experiment which documented the density of *O. taurus* beetles
334 on dung pats every 12 hrs from creation. Data suggests that dung beetles
335 are found in the pat at fairly consistent levels at 12, 24, 36 and 48 hrs but
336 after 48hrs there are very few beetles in the pat (probably because the pat is
337 relatively dried out at that point). The number of beetles in the soil below
338 the pat is significantly lower than the numbers in the pat and that beetles
339 do not make their way below the pat until about 24hrs after pat creation.
340 The data also indicates that the act of burying dung (to create brood balls)
341 does not begin until the pat is at least 12 hrs old. Thus *O. taurus* likely uses
342 different aged pats for different things. Although the density may be high
343 in newly created dung pats (12 hrs or less old) the adults are likely to be
344 feeding (not all feeding beetles use a dung pat for brood ball production as
345 the density of beetles found below a dung pat is significantly lower than the
346 number of beetles within the dung pat).

347 A key assumption of our model is that all beetles are potential parasites
348 and whether they parasitise or not is governed by their arrival and departure
349 strategies. In real populations beetles do indeed arrive and depart at very
350 different times (Crowe, 2011) and it seems reasonable to assume that they
351 would take the opportunity to parasitise if the chance presented itself (Crowe
352 et al., 2009).

353 Our model predicts that although parasitism is an effective strategy for

the beetles to employ, we cannot necessarily expect it to occur at high frequency or, in some cases, at all. In real populations parasitism generally occurs at a low frequency (roughly 13%, Moczek and Cochrane, 2006) which might correspond to the type of situation that we predict to occur when balls are easy to find (e.g. see Figure 1d).

We have also assumed that beetles only arrive or leave at discrete times, and this is clearly a simplification as in real populations they arrive and depart throughout the day. However, our aim was to make the model tractable whilst retaining the key features of beetles being able to arrive or depart at early or late times, and stay for short or long periods. Similarly the beetles search for brood balls is idealized, effectively assuming random searching with balls spread evenly across the search area; we again retain the key feature of balls being either easy or hard to find. Finally we assumed that dung was usable if sufficiently young, and not after a cut-off point. If dung deteriorated in quality, then it may be possible that arrival on the first day could be a playable strategy.

It would be of great interest to obtain realistic estimates of our two key parameters ε and κ' from real populations to see how well our predictions match reality. One can extend the model by incorporating another parameter, the effectiveness of guarding (treated as 100% in the current model). The parameter may be negatively correlated with the cost of egg production and depend on to what degree a female can guard the brood ball and feed simultaneously. Further model developments including using continuous rather than discrete arrival and departure times, and potentially more complex searching strategies for the beetles, would also help improve our

379 understanding of these important and fascinating animals.

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