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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.

Keywords: Kleptoparasitism, game theory, Brood parasitism,

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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 parasities 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.

2. Model

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 Recent laboratory data (Mary Crowe et al., unpublished manuscript) also suggests that breeding pairs or females remain in the proximity of the brood balls for an extended period of time.

A beetle's strategy is determined by

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

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

$$\Omega = \Big\{(1,2),(1,3),(1,4),(2,3),(2,4),(3,4)\Big\}. \tag{1}$$

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

2.1. Model of stealing the ball

Here we describe the mechanism/ model of how the ball is stolen. Consider a case where N beetles are trying to steal a ball in a dung pat where there are B balls in total. We assume that the beetles are not 100% effective in finding the balls and introduce a parameter κ that is related to the success rate of kleptoparasitism. During a small period of time $\mathrm{d}t$, each ball could be found by N beetles and will thus be stolen with probability $\kappa N \mathrm{d}t$. Hence,

$\kappa N B \mathrm{d}t$ balls will be stolen in total. Once a beetle steals a ball, it does not attempt to steal another one. Hence

$$N - B = N_0 - B_0 \tag{2}$$

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

$$\frac{\mathrm{d}B}{\mathrm{d}t} = -\kappa N B = -\kappa B(B + N_0 - B_0). \tag{3}$$

The solution of (3) is

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

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

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

balls left, while the beetles have stolen

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

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

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

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

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

$$B(1) \approx B_0 \tag{8}$$

$$B_0 - B(1) \approx N_0, \tag{9}$$

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

2.2. Determining Fitness

We will denote the fitness, or reproductive success, of a strategy $(x, y) \in \Omega$ by f_{xy}. The fitness is the (average) rate at which brood balls produced by a beetle using strategy (x, y) reach maturity in a population described by $\vec{P}$ minus any costs involved in producing a brood ball. Here $\vec{P} = \langle P_\omega, \omega \in \Omega \rangle$, where P_{xy} is the proportion of the population using strategy (x, y). Evolution favours individuals with the greatest fitness, which depends upon the composition of the population. The composition of the population will change through time according to this fitness, on a timescale that is long in comparison to the three day interactions that we describe. We investigate such changes, and in particular look for stable population mixtures, evolutionarily stable strategies (ESSs).

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

$$N^e_{xy} = \frac{P_{xy} \cdot N}{y - x}. \tag{10}$$

This yields the formula for fitness of a strategy to be

$$f_{xy} = \frac{B^3_{xy}}{P_{xy} \cdot N} - \varepsilon \rho_{x,y} = \frac{B^3_{xy}}{N^e_{xy} \cdot (y - x)} - \varepsilon \rho_{x,y} \tag{11}$$

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

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

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

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

2.2.1. Day 1

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

$$B^1_{xy} = \begin{cases} N^e_{1y}, & y \in \{2,3,4\} \\ 0, & \text{otherwise} \end{cases} \tag{12}$$

2.2.2. Day 2

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

$$B^2_{12} = N^e_{12} \cdot (1-\sigma_2), \tag{13}$$

where

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

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

$$B^2_{xy} = N^e_{xy}, \quad x \in \{1,2\}, y \in \{3,4\}. \tag{15}$$

2.2.3. Day 3

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

$$V_3 = B_{12}^2 + B_{13}^2 + B_{23}^2 \tag{16}$$

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

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

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

$$\begin{aligned}
B_{12}^3 &= B_{12}^2 - S_3 \cdot \frac{B_{12}^2}{V_3} = N_{12}^e \cdot (1-\sigma_2) \cdot \left(1 - \frac{S_3}{V_3}\right), && (18)\\
B_{23}^3 &= B_{23}^2 - S_3 \cdot \frac{B_{23}^2}{V_3} = N_{23}^e \cdot \left(1 - \frac{S_3}{V_3}\right), && (19)\\
B_{13}^3 &= B_{13}^2 - S_3 \cdot \frac{B_{13}^2}{V_3} = N_{13}^e \cdot \left(1 - \frac{S_3}{V_3}\right), && (20)\\
B_{24}^3 &= N_{24}^e, && (21)\\
B_{14}^3 &= N_{14}^e, && (22)\\
B_{34}^3 &= S_3. && (23)
\end{aligned}$$

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

3. ESS analysis

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

$$f_{14} < f_{24}. \tag{24}$$

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

$$f_{13} < f_{23}. \tag{25}$$

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

$$f_{12} < f_{23}. \tag{26}$$

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

The fitness of the respective beetles becomes

$$\begin{aligned} f_{24} &= \frac{1}{2} - \varepsilon, && (27) \\ f_{23} &= \frac{N^e_{34} - N^e_{23}}{N^e_{34} e^{\kappa(N^e_{34} - N^e_{23})} - N^e_{23}} - \varepsilon = \frac{P_{34} - P_{23}}{P_{34} e^{\kappa'(P_{34} - P_{23})} - P_{23}} - \varepsilon, && (28) \\ f_{34} &= \frac{N^e_{23} e^{\kappa(N^e_{34} - N^e_{23})} - N^e_{23}}{N^e_{34} e^{\kappa(N^e_{34} - N^e_{23})} - N^e_{23}} = \frac{P_{23} e^{\kappa'(P_{34} - P_{23})} - P_{23}}{P_{34} e^{\kappa'(P_{34} - P_{23})} - P_{23}}, && (29) \end{aligned}$$

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

$$\kappa' = \kappa N. \tag{30}$$

3.1. Pure strategies

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

$$f_{23} = 1 - \varepsilon, \tag{31}$$

$$f_{24} = 1/2 - \varepsilon, \tag{32}$$

$$f_{34} = 1 - e^{-\kappa'} \tag{33}$$

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

$$\kappa' < -\ln(\varepsilon). \tag{34}$$

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

$$f_{23} = e^{-\kappa'} - \varepsilon, \tag{35}$$

$$f_{24} = 1/2 - \varepsilon, \tag{36}$$

$$f_{34} = 0. \tag{37}$$

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.

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

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

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

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

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

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

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

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

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

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

Rearranging (38) gives

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

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

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

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

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

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

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

3.3. Mixtures of all three pure strategies

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

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

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

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

Substituting (47) into (48) we obtain

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

Thus we have,

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

which substituted into (47) gives

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

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

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

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

$$P_{24} = 1 - P_{23} - P_{34} \tag{54}$$

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

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

We believe that this equilibrium is also an ESS in all cases, as suggested by our numerical results, but we have not been able to prove this.

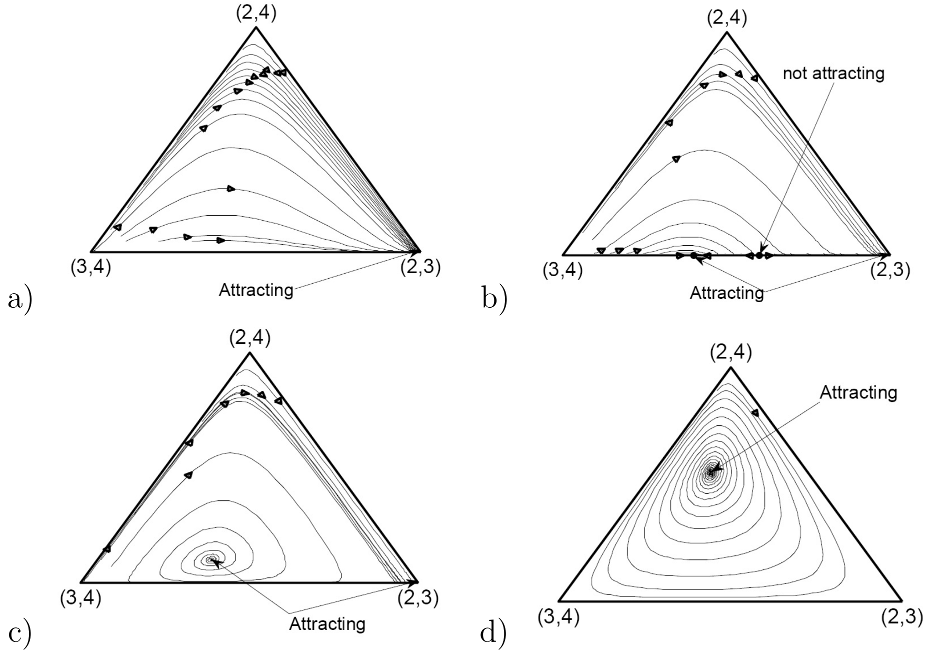

Figure 1: Diagram of the dynamics for $\varepsilon = 0.2$ and a) $\kappa' = 1 < \frac{2(1-\varepsilon)}{1+\varepsilon}$, b) $\frac{2(1-\varepsilon)}{1+\varepsilon} < \kappa' = 1.34 < \frac{1-\varepsilon}{\varepsilon}\ln(1+2\varepsilon)$, c) $\frac{1-\varepsilon}{\varepsilon}\ln(1+2\varepsilon) < \kappa'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

3.4. Dynamics

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

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

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

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

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

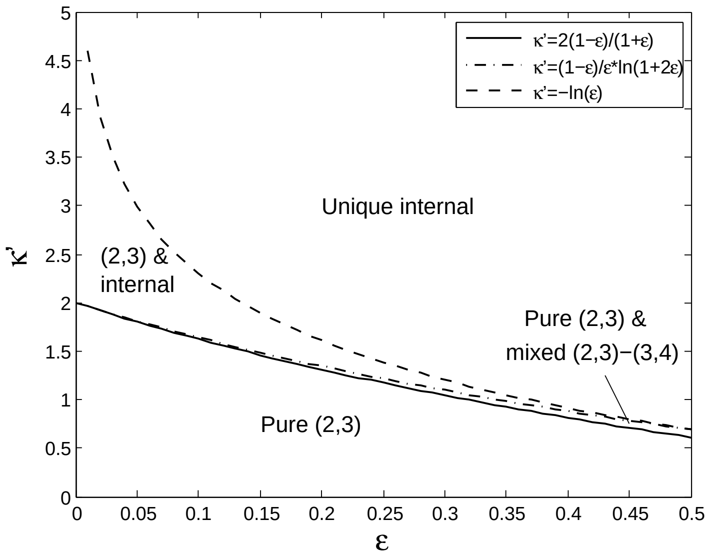

Figure 2: Outcomes for different model parameters, the cost of making own ball, ε and the (scaled) effectiveness to find a ball, κ'.

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

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

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

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

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

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

then there are again two solutions, a pure $(2, 3)$ ESS and an internal equilibrium combining all three strategies. Finally if

$$-\ln(\varepsilon) < \kappa' \tag{60}$$

there is a unique internal equilibrium.

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

5. Discussion

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

The key factors which affect the mixture of individuals are two key parameters, the ease of finding brood balls to steal, and the cost of making your own ball. The harder balls are to find, and the lower the cost of making a ball, the more the strategy $(2, 3)$ prevails in the population. This strategy is always present in some numbers, and for sufficiently low cost of ball making and high difficulty of finding difficulty all beetles play this strategy. As these parameters change (cost of ball making increases, difficulty of finding a ball decreases), then the parasitic individuals can appear, and at more extreme values the individuals that use considerable time resources defending their brood balls can appear.

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

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

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 understanding of these important and fascinating animals.

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