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Game theoretic model of brood parasitism in a dung beetle *Onthophagus taurus*

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Abstract We present a game theoretic model of brood parasitism in the dung beetle *Onthophagus taurus*. Female *O. taurus* engage in brood parasitism when they attack a brood ball made by another female, destroy the existing egg and place one of their own eggs to develop within the existing dung ball. Brood parasitism is more costly than other forms of kleptoparasitism because an individual loses the total investment in an offspring. In this paper, we outline the behaviors involved in brood ball production and provide time estimates of those behaviors. The model is then used to predict when it is beneficial to steal the brood ball created by another female and when it is beneficial for a female to create her own. We also investigate how long a female should guard her eggs.

Introduction

Resource gathering (be the resource food, mates, territory—to name a few) is a fundamental aspect of the behavior of animals. Thus the study of resource gathering has been and remains a central interest of behavioral ecologists (see Stephens et al. 2007, for a recent review). If resources are difficult and/or expensive to acquire then, except for the most solitary of taxa, it may be attractive to try and steal resources already acquired by another. This stealing of resources is commonly called kleptoparasitism. This process occurs across a great diversity of taxa, with recent observations from large carnivorous mammals (Carbone et al. 2005), birds (Dies and Dies 2005; Bertran and Margalida 2004), lizards (Cooper and Perez-Mellado 2003), fish (Hamilton and Dill 2003), insects (Reader 2003), snails (Iyengar 2002) and spiders (Agnarsson 2002). Since not all species that seem capable of kleptoparasitism exhibit it, and since there is strong variation between species

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and between individuals within a species in the extent to which this tactic is used, there is a real need for a predictive theoretical basis to explain this variation in terms of fitness or fitness-related traits. This is a problem that we found to be particularly well-suited for the use of game theory as a tool in behavioral ecology.

The attractiveness of kleptoparasitism as a strategy will be influenced by the strategies adopted by others. If more individuals adopt kleptoparasitism rather than searching for undiscovered resources, this will depress the availability of kleptoparasitic opportunities and increase the frequency with which resources gained by the focal individual (either by kleptoparasitism or conventional means) will be stolen by another. Hence there has been a considerable body of theory aimed at predicting the evolutionarily stable use of kleptoparasitism in different ecological circumstances (Barnard and Sibly 1981; Stillman et al. 1997; Broom and Ruxton 1998, 2003; Ruxton and Broom 1999; Sirot 2000; Hamilton 2002; Broom and Rychtář 2007). However, there has been very little testing of this theoretical work. One likely reason for this is that the theoretical models have focused on aggressive interactions over small food parcels, generally in large avian systems. The fitness benefit or cost of gaining or losing a single food item is very difficult to quantify when individuals may gather hundreds of such food parcels over a day, and hundreds of thousands over a lifetime.

One type of kleptoparasitism where this problem should be reduced is the theft of parental care (generally called brood parasitism). Parental care can be considered as the allocation of resources to offspring to enhance offspring survival and fecundity (Krebs and Davies 1993). If an individual can be caused to divert such parental care from its own offspring to those of another, then the host individual is the victim of kleptoparasitism. Parental care (which includes preparation and maintenance of a nesting site, guarding this site, and provisioning offspring with food) is taxonomically diverse, and so, unsurprisingly, is brood parasitism (Clutton-Brock 1992). Since the overwhelming majority of animals produce far fewer offspring than the number of food parcels they consume, the costs of a single act of brood parasitism is generally likely to be much more dramatic than a single act of food stealing. Furthermore, the number and growth rates of offspring are easier for biologists to monitor than the number, type and intake of every meal. Although brood parasitism has been particularly well-studied in large avian systems (Smith et al. 2000; Zink 2000; Anderson and Hauber 2007; Yom-Tov 2001), with some cuckoo species being famously obligate brood parasites (Davies and deBrooke 1998; Servidio and Lande 2003) it has been documented in invertebrates that exhibit extensive parental care, including spiders (Fink 1986) and insects (Moczek and Cochrane 2006; Muller et al. 1990). Insects that exhibit brood parasitism should provide particularly appropriate study systems for the empirical investigation of kleptoparasitism, since many insects have life-histories that allow them to be kept in breeding colonies in laboratory conditions, where variables can be carefully manipulated and confounding factors avoided. Furthermore, the small size and low expense of many insect colonies allows replication of studies. While there are inherent difficulties in studying any population under labs conditions, the study of insects can be far less costly than studying the behavior of avian systems both in terms of time consumption and economy.

The majority of models of brood parasitism have focused on loss of parental care by the addition of parasitic eggs to a nest. The predictive output of the model is therefore focused on egg rejection and acceptance behavior by a parasitized host. These have included population genetics models (May and Robinson 1985), quantitative genetic models (Servidio and Lande 2003) and game theoretical models (Lotem and Rothstein 1995; Lotem and Nakamura 1998; Davies et al. 1996). Generally, these models have focused on the host and the benefits and costs on their fitness. In contrast, our model describes the benefits and costs to the individual following a kleptoparasitic, brood stealing strategy

versus provisioning the brood themselves, following the behavior from the perspective of the stealing individual as well as the potential host. Here we present the first game theoretic model of brood parasitic behavior purposely designed to allow comparison with an appropriate insect species: the dung beetle *Onthophagus taurus*.

Onthophagus taurus, is a widely dispersed dung beetle, originally distributed across Central and Southern Europe, North Africa and Asia Minor, ranging from Spain to Morocco, Turkey and Iran. It was introduced and successfully spread across pasture lands of North America and Australia (Hunt et al. 1999; Fincher and Woodruff 1975). *O. taurus* is a paracoprid dung beetle, which means the female lays her eggs in a carefully constructed and supplied tunnel under the soil's surface and beneath a dung pat deposited by a large herbivore. Once a female finds a suitable dung pat, she will create a tunnel and prepare a brood ball, a sausage shaped dung ball placed at the end of the tunnel. A single egg is laid in the dung ball, and the tunnel is then sealed up with soil to prevent brood parasitism from conspecifics (Moczek and Cochrane 2006) or other species, such as those from the genus Aphodius (Moczek and Cochrane 2006) This protection may be enhanced by guarding by the adults (González-Megías and Sánchez-Pinero 2003). Guarding is expensive in that it prevents an individual from obtaining resources needed for further offspring production and provisioning. See Halffter and Edmunds (1982) for more detail on the nesting behaviors of this and other related species. It should also be noted that there are many factors that may prevent a brood from developing even if guarded, for example a genetic problem or adverse weather conditions. We assume that all such factors act in the same way for guarded as well as unguarded eggs and do not include them in our model.

Onthophagus taurus is a particularly well suited species to use in the study of brood parasitism because the costs of different behaviors can be understood in terms of time. Adults have a short lifespan of less than 40 days (Hunt et al. 2002), and they require fresh dung both for adult feeding (to produce eggs) and for reproduction. Further, brood parasitism has aspects that simplify the quantification of the costs and benefits of the strategy. A brood parasite saves itself the time required to make a dung ball on its own but must invest the time required to dig down to the brood ball of another (presumably detected by the substrate disturbance involved in digging the tunnel). We assume for the purposes of our model that the beetle is searching for both suitable dung to provision a brood ball, as well as existing brood balls to steal, and making use of whichever it locates first. The timing of both behaviors can be studied in the lab under close to natural conditions in terms of substrate and moisture. Further parasitism generally involves the killing of the original egg and the replacement of this with the parasite's own egg. This one-for-one swap again aids in quantification of the costs and benefits: if an individual suffers brood parasitism then it loses all fitness benefits from that brood ball (since its single egg from the ball is destroyed by the parasite).

We will first formalize this behavior in a mathematical model and then formally solve this model, in order to make predictions for the strategy that optimizes fitness of adult females both in terms of their use of brood parasitism as a facultative reproductive strategy and their use of egg guarding as a means of reducing their risk of brood parasitism.

Model of *O. taurus*'s life history

For modeling purposes, we consider females only and simplify their life history as follows. Each beetle is initially engaged in a resting period. During the time period the beetle is resting and feeding in order to gain energy, mating and replenishing resources. Once

sufficiently rested, on average in time T_R, it starts searching for dung to make a brood ball. We assume that beetles find dung at rate vd where d is the density of dung and v is the area the beetle can search in a unit time. When dung is found, the beetle prepares a ball (in time T_P), and once the ball is ready, it lays an egg (in time T_L).

When looking for dung, beetles may find already prepared balls with eggs produced by others. In this case, they can steal the ball and kill the other egg. When a prepared ball is found, it takes time T_K to steal it and to kill the residing egg. It is generally assumed that $T_K < T_P$ but we will solve the situation in full generality (i.e. even for $T_K > T_P$).

Once a beetle lays an egg, it has an option to regain energy (in preparation for laying another egg) or to guard the last egg to prevent the theft of the brood ball by other beetles. Not all balls are suitable for stealing. After being laid, the egg is vulnerable for the time T_V. Vulnerable means that (a) the ball can be found, i.e. it is placed in a relatively fresh dung so that the dung still attracts other beetles and (b) the egg is not too developed. Once the egg is mature enough, or it is beneath a dung pat that is so dry that it will be ignored by other beetles, it is considered invulnerable and a new beetle will eventually arise from it. We assume $T_K \ll T_V$, so that we can consider the vulnerable egg to be killed the moment it is found.

To summarize, we assume that beetles are always involved in exactly one of the following activities:

(1)   resting
(2)   searching for a dung and/or a brood ball
(3)   preparing a brood ball
(4)   stealing a brood ball
(5)   laying an egg
(6)   guarding

and that there are potentially 3 different kinds of eggs

(I)   vulnerable and unguarded (can be killed if found)
(II)   vulnerable and guarded (cannot be killed)
(III)   invulnerable (cannot be killed)

The model parameters and the notation are summarized in Table 1.

For the sake of generality, we will assume that beetles may steal any fraction $s \in [0,1]$ of eggs they find and which are suitable for stealing. Similarly, we assume that beetles may guard their eggs for an arbitrary length of time and that guarding is 100% effective when employed. We also assume that they guard mainly against other beetles. Since it does not give any advantage to guard an egg that is no longer vulnerable, beetles just have to choose $g \in [0,1]$, corresponding to guarding an egg for the time $T_G = gT_V$. Thus, beetles employ a strategy σ described by a pair $(s,g) \in [0,1]^2$. The success of a strategy is measured by the number of invulnerable eggs the beetles are able to produce per unit of time, a measure of fitness.

To steal or not to steal?

In this section we will investigate the conditions under which it is beneficial to steal.

Assume a mixture of beetles using any possible strategies. First, consider the case $T_K < T_P$; the case $T_K > T_P$ is analogous. As long as there is at least one beetle using a strategy $\sigma' = (s',g')$, $g' \neq 1$ (this is equivalent to saying that there is a nonzero density of

Table 1 Model parameters (upper portion) and notation (lower portion)

	Meaning	Typical value, Reference
D	Density of female population	88 females/m^2 (unpublished data)
d	Density of dung	0.63 pads/m^2 (unpublished data)
v	Area beetles search for dung in 1 s	5.5 m^2/s (unpublished data)
T_R	Average resting time	2–5 days Hunt and Simmons (2000, 2002a) Moczek and Cochrane (2006)
T_P	Average time needed to make a ball	10–17 h Hunt et al. (2000) Hunt and Simmons (2004)
T_K	Average time needed to steal a ball	<1 h, est. from Moczek and Cochrane (2006)
T_L	Average time needed to lay an egg	2–7 days Hunt and Simmons (2000) Hunt et al. (2002) Moczek and Cochrane (2006)
T_V	Average time an egg is vulnerable	2.6 days Steinbauer and Wardhaugh (1995)
σ	Beetles' strategy	$\sigma = (s, g) \in [0,1]^2$
s	Probability to steal a ball	In [0,1]
g	Fraction of T_V beetles guard their egg	In [0,1]
T_G	Guarding time	$T_G = gT_V$
R	Density of resting beetles	
S	Density of searchers	
P	Density of beatles preparing their own balls	
K	Density of kleptoparasiting beetles	
L	Density of beetles laying the eggs	
G	Density of guarding beetles	
E	Density of unguarded vulnerable eggs	

unguarded vulnerable eggs), then a strategy $\sigma_1 = (1,g)$, does better than any strategy $\sigma = (s,g)$, $s \neq 1$, for any $g \in [0,1]$.

We can compare the times strategies σ_1 and σ need to produce an egg. In order to make an egg, a beetle has to

- find a dung pat and then spend a time T_P to prepare for laying and a time T_L to lay an egg, or
- find an already prepared brood ball, steal it (in time T_K) and then lay an egg (in time T_L).

Since $s < 1$, the strategy σ_1 is able to lay an egg in a shorter time (as there are some unguarded eggs and the beetles using strategy σ_1 steal every possible egg). Next, both strategies spend the same expected time in laying, guarding and resting. It is possible that not all eggs survive to the invulnerable stage due to outside influences, but chances of surviving are the same for eggs of both strategies. Thus, a strategy σ_1 produces an invulnerable egg in a shorter time and results in higher fitness.

We must also consider what happens when the mixture contains only beetles that guard the eggs for the full time T_V. From the mathematical point of view, in such a mixture, all strategies do equally well because there are no unguarded eggs, and thus no opportunity to steal anything. (I.e. the time to produce an egg will always consist of time T_R to rest, time needed to find a dung, time T_P to prepare a ball, and time T_L to lay the egg.) However, even in such mixtures, a biologically more realistic model would be to assume that, for various reasons, a beetle may occasionally and inadvertently leave an egg slightly earlier than when it becomes invulnerable. Hence, in biologically realistic mixtures, there are always some unguarded eggs, giving an advantage either to stealing strategies (if $T_K < T_P$), or to non-stealing strategies (if $T_K > T_P$).

In conclusion, there is always only one best strategy for stealing. If $T_K < T_P$, it is best to steal every unguarded egg that is found. If $T_K > T_P$, then it is best not to steal at all.

To guard or not to guard?

In this section we give the criteria for when it is beneficial to guard an egg and when it is not. If there are no beetles that steal, it is not beneficial to guard. However, based on the above section, we may assume that all beetles are stealing at every opportunity because $T_K < T_P$ in a biologically realistic setting (Moczek and Cochrane 2006). We will consider a mixture of strategies $(1,g)$ in order to estimate how well or poorly a particular strategy does in such a mixture. All individuals in our mixture, using any strategy, will need exactly the same time T to produce an egg, because they all employ the same stealing strategy. The exact value of T not needed for our analysis, but the formula for T is provided in the Sect. 5.

A strategy $(1,g)$ spends an additional time gT_V in guarding, and thus spends in total a time $T + gT_V$ before it is ready to start producing another egg. Not all eggs may actually survive. Eggs have to survive a time $(1-g)T_V$ without being killed by other beetles. We may assume that an unguarded vulnerable is turning into an invulnerable egg with the rate $1/((1-g)T_V)$; while it is being killed with a rate $v\,S$ (which corresponds to a rate at which it is being found by searching beetles). Consequently, only a fraction

$$\frac{\frac{1}{(1-g)T_V}}{\frac{1}{(1-g)T_V} + vS} = \frac{1}{1 + (1-g)T_V vS}$$

of unguarded vulnerable eggs survive. In total, an individual using a strategy $(1,g)$ produces an invulnerable egg in time

$$T(g) = (T + gT_V)(1 + (1-g)T_V vS)$$

The above is a quadratic function in g. Since the leading term is negative, the minimum on an interval [0,1] is attained either at $g = 0$ or at $g = 1$. The minimum is attained at $g = 0$ (no guarding at all) if

$$T(0) < T(1)$$

and it is attained at $g = 1$ (guarding for the whole vulnerable time) otherwise. By evaluating, this is equivalent to

$$T(1 + T_V vS) < T + T_V$$

which is the same as

$$T < \frac{1}{vS} \qquad (4.1)$$

In conclusion, it is better not to guard the egg at all if and only if one can produce a new egg faster than others can find the old one. Once the others can find the egg faster than one can produce a new one, it is better to guard the vulnerable egg for the whole time until it becomes invulnerable.

Results

Consider a population in which all beetles use a strategy $\sigma = (s, g)$. We first calculate the density of searchers in such a population. Using the standard arguments and reasoning (Broom and Ruxton 1998; Broom et al. 2007) the diagram in Fig. 1 yields S as a positive solution of

$$D = S[1 + vd(T_R + T_P + T_L + gT_V)] + S^2 \left[sv^2 d(1-g)T_V(T_R + T_K + T_L + gT_V) \right]$$

and other quantities can be calculated as follows:

$$E = vdS(1-g)T_V$$
$$P = vdST_P$$
$$K = svSET_K$$
$$L = (vdS + svSE)T_L$$
$$G = (vdS + svSE)gT_V$$
$$R = (vdS + svSE)T_R$$

Second, we calculate the time T to produce one egg in such a population. Production of an egg consists of a resting period, searching period, preparation for egg laying (either making its own ball or stealing one that is already made) and laying period. The time can be calculated using the diagram in Fig. 1.
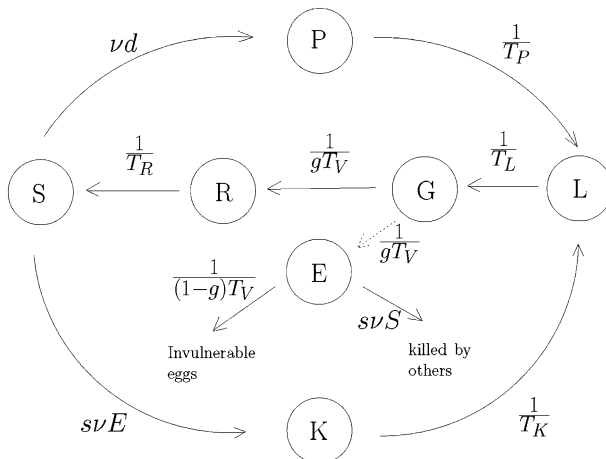

Fig. 1 Life cycle of female beetles *Onthophagus taurus*

$$T(s, g) = T_R + \frac{1}{vd + svE} + \frac{vdT_P}{vd + svE} + \frac{svET_K}{vd + svE} + T_L + gT_V.$$

As seen in Fig. 2, if the parameters of the model are in the range specified in Table 1, the time to produce an egg is always greater than the time an egg can be found by others. Hence, one should guard as much as possible. We can also see from Fig. 2 that as g increases from 0 to 1, the interlaying interval steadily increases (mainly due to the fact that beetles have to guard longer and longer) and also that other variables change more or less linearly. When g is close to 1, the behavior changes due to the drop in the number of unguarded eggs. When no or only a few unguarded eggs are around, a beetle has to prepare more balls of its own (increase of P), cannot steal as much as it used to (drop in K), and mainly, it takes much longer to find dung or a prepared brood ball—causing sharp increase in S. This increase in S means that vulnerable eggs are found faster, leading to even fewer vulnerable eggs in the population.

Also one should note that the number of searchers in the population is negligible. This corresponds to findings in the field where the vast majority of beetles are found in the dung pats.

Figure 3 shows the case where the density of beetles is very small, corresponding to the situation in which the beetles are just arriving at the pasture. One can see from Fig. 3d that now the beetles actually have a choice, and that the choice of a focal individual depends on the choice of others. If g is low and no beetles protect their eggs for very long, it is
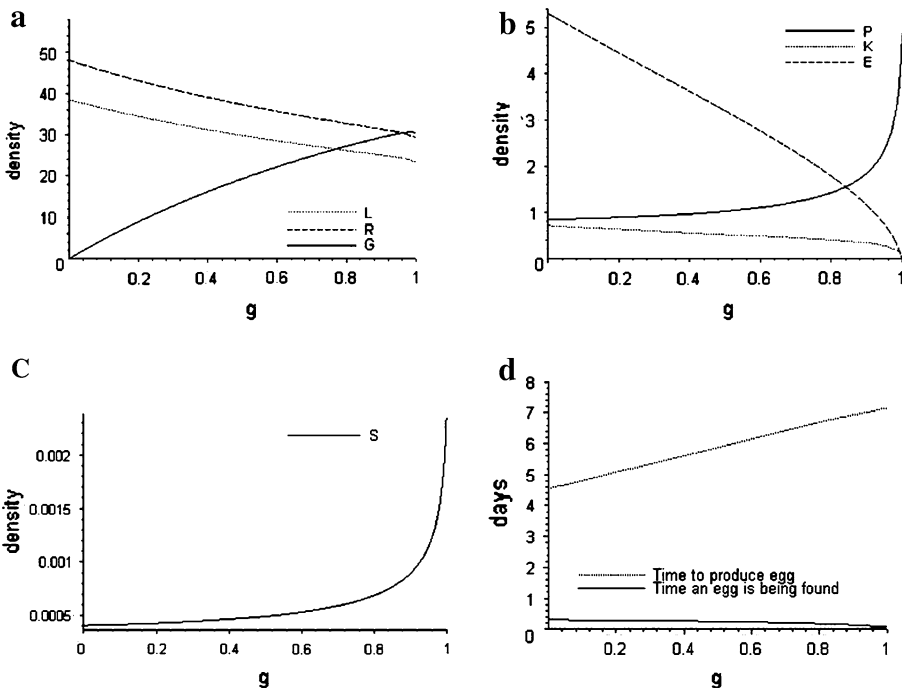

Fig. 2 Population with natural densities of beetles. (**a**)–(**c**) Densities of female beetles and vulnerable eggs, (**d**) comparison of time needed to produce egg versus time in which an egg is found. For all figures, $T_R = 2.5$ days, $T_L = 2$ days, $T_P = 10$ h, $T_K = 1$ h, $T_V = 2.6$ days, $D = 88$ females/m^2, $d = 0.63$ pads/m^2, $v = 5.5$ m^2/s, $s = 1$
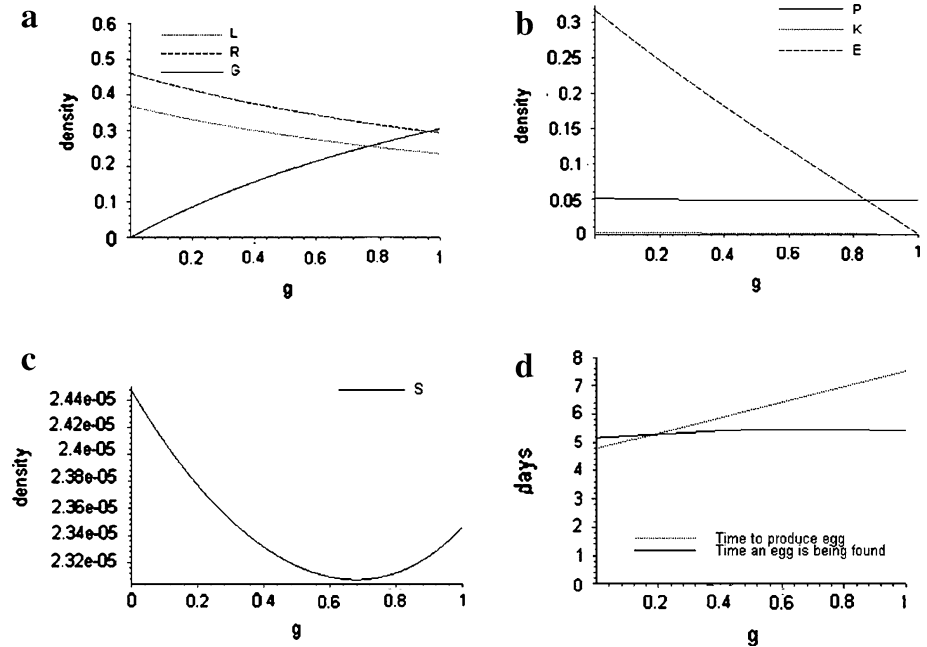
Fig. 3 Population with low densities of beetles. (**a**)–(**c**) Densities of female beetles and vulnerable eggs, (**d**) comparison of time needed to produce egg versus time in which an egg is found. For all figures, $T_R = 2.5$ days, $T_L = 2$ days, $T_P = 10$ h, $T_K = 1$ h, $T_V = 2.6$ days, $D = 0.8$ females/m^2, $d = 0.63$ pads/m^2, $v = 5.5$ m^2/s, $s = 1$

advantageous not to protect as well, while when g is high, it is advantageous to protect as well. Also, in a low density population, there are almost no brood parasites, since there are not so many eggs relative to dung pats. Thus, dung pats are found with a much higher rate than are brood balls; once a dung pat is found, it very likely does not contain a brood ball with an egg yet.

In a population with an even smaller density of beetles ($D < 0.65$ if other parameters are as in Figs. 2 and 3), the time required to find an egg is larger than the time in which one can produce a new egg since there are almost no beetles who could find the egg). Consequently, for very low beetle densities, one should not guard the eggs at all.

Discussion

Our model makes clear and empirically testable predictions. We first consider brood parasitism and predict that there should be no mixed strategies; individuals should either attempted to usurp every buried brood ball that they detect or none. Further, individuals should attempt to usurp brood balls if the time taken to usurp is less than the expected time required from that point to assemble and provision a brood ball of their own. Based on previous empirical research and our own field measurements (references in Table 1), we expect the time taken to usurp to be an order of magnitude less than the time taken to create a viable brood ball. Thus, we would expect brood parasitism to be strongly favored, and for individuals to take every chance to steal that is offered. This prediction invites empirical

testing. If variation between individuals were found with respect to adopting this tactic, it would suggest variation between individuals with respect to the relative time required for preparation of brood balls versus stealing, perhaps because smaller females are unable to compete successfully for dung to make a brood ball of their own, especially under high desiccation conditions. However, we note that Moczek and Cochrane (2006) found no size variation in likelihood of brood parasitism.

If empirical work were to find a mixed strategy where individuals sometimes but not always exhibit brood parasitism behavior, this would suggest that there is intrinsic variation between different opportunities in terms of either the value of the brood ball or the costs of reaching it. The second of these is entirely plausible, since González-Megías and Sánchez-Pinero (2004) report variation in the extent to which burrows are sealed following oviposition on the brood-ball. Clearly the less extensively the burrow is refilled, the more vulnerable offspring are in terms of both being discovered by a brood parasite and being quickly and cheaply accessed by the parasite after discovery. It may be that there is a trade-off for the female, in that these costs associated with kleptoparasitism might be traded off against the costs to the offspring in terms of digging its way out when it is ready to emerge. This trade-off could be explored under laboratory conditions, and any such trade-off would lead to the prediction that in a between-site comparison refilling of burrows would be less extensive in situations where the risk of brood parasitism is lower (e.g. because population density of beetles is lower).

Our predictions for defending eggs are also clear and testable. First, we predict that if any guarding does occur, then it should be for the whole time that the egg is vulnerable to brood parasitism. Further, we predict that a female will either guard all of her eggs for the full time until the offspring are sufficiently developed to be invulnerable or none of them. As with parasitism, the decision to guard or not is predicted to be governed by the comparison between two times. In this case, the first time is the total time required to produce an egg (including the time taken to forage sufficiently to develop an egg, dig a tunnel and provision that tunnel with a dung ball, lay the egg, then refill the tunnel); the second time is the expected time that an undefended egg would remain undisturbed by brood parasites. If the second time is longer, then no guarding should occur, whereas if it is shorter, then all eggs should be defended. This could easily be tested by between-site comparison or experimental manipulation; as the local density of beetles declines, the expected time until an unguarded egg is discovered should lengthen, and there should be a critical population size below which no guarding occurs and above which all eggs are guarded.

In order to extend our model beyond the specific dung beetle species, it is useful to consider the rejection costs to avian hosts mentioned earlier. Just as the time spent guarding can decrease or increase the fitness of a beetle dependant of the density of kleptoparasites in the population, rejection of a potential parasite egg or nestling from a host nest can increase or decrease fitness based of the density of parasites in the area. If an egg is lost to a beetle when it is found and unguarded that beetle loses in fitness. If a parasitized bird is allowed to grow in a nest it often will push all of its co-nesting out of the nest when it is large enough (Servidio and Lande 2003; Smith et al. 2000) also resulting in a comparable lose of fitness. When looking at the reverse, if all a beetle's time is spent guarding this is a loss in fitness due to decrease in future eggs. In an avian systems, rejection of an egg that is not parasitic is also a lose in time spent and the energy costs of developing that egg.

Although already useful both to insect and avian kleptoparasite researchers, our model could be further elaborated. The most obvious extension is to introduce intrinsic variation

between individuals. Within-population size variation is strong in this species, and it has been demonstrated that larger females can produce larger dung balls and that, in turn, dung ball size has a strong influence on the body size and fecundity of the offspring (Hunt and Simmons 2002b). It is perhaps surprising, then, that female body size is not a strong indicator of propensity to kleptoparasitise (Moczek and Cochrane 2006). An elaboration of our model with heterogeneity in individuals would be useful for producing hypotheses for how these empirical results could be reconciled. There is also strong size variation in males, and since males can also contribute to dung ball creation, Hunt and Simmons (2002c), then elaboration of the model to study the effects of male phenotype on brood parasitism and guarding would also be interesting.

Moczek and Cochrane (2006) also note that females sometimes increase the size of a dung ball that they obtain by kleptoparasitism, before they commit their egg to it. Another useful extension of our model would be to make predictions about the circumstances in which this behavior might be expected to be shown. More generally we believe that development of this model and associated experiments on this and similar species of dung beetle should be an effective combination for improving our general understanding of the taxonomic and ecological distribution of brood parasitism in particular and kleptoparasitism in general.

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