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The female dung beetle *Onthophagus taurus* will sometimes engage in an extreme form of kleptoparasitism by stealing the brood ball of another female beetle, destroying the existing eggs, and replacing their own egg in the brood ball. Beetles will sometimes guard the brood balls they produce to prevent this. But guarding is a time consuming behavior that is not always beneficial. We develop a game theoretic model to determine when a dung beetle should enter and leave a dung pat and when a beetle should steal. We determine the fitness, or reproductive success, of each strategy. We show that no Evolutionary Stable Strategy exists among our strategies. We investigate long term evolution of a population under discrete replicator dynamics.

**MODEL OF KLEPTOPARASITISM IN THE *ONTHOPHAGUS*
TAURUS: WHEN TO ENTER AND LEAVE A DUNG PAT**

by

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CHAPTER I

INTRODUCTION

The *Onthophagus taurus* dung beetle is an interesting beetle to study because of its tendencies to kleptoparasitize. Not only does the beetle kleptoparasitize but it has been documented to steal from its own kind, an intraspecific kleptoparasitism. It is much more common for animals to steal from other species instead of their own [8]. In this thesis we will explore the behaviors of the *O. taurus* dung beetle that play a role in kleptoparasitism and develop a game theoretic model to predict which behaviors will benefit the dung beetle the most.

To begin our study we will first introduce mathematical modeling in chapter 2. Since our model will represent an idea from ecology, we are mainly focused on evolutionary modeling and why it is necessary to develop models for ecological events.

In chapter 3 we will introduce game theory. Game theory was first used to model economics, but has recently gained a lot of interest in ecology. Games model conflicts between players who each use different strategies. Among evolu-

tionary game theorists the existence of an evolutionary stable strategy is of great interest. We then investigate discrete replicator dynamics of game models to see how dynamics show how certain strategies develop over time.

Chapter 4 will introduce kleptoparasitism and how our dung beetles fit into the study of kleptoparasitism. Previous studies have been done that investigate the reasons why a dung beetle may choose to steal from its own species, but we focus on beetles who have a choice of strategies to choose from. The beetle will have a choice of when to enter a dung pat, whether to steal or not steal, and when to leave the dung pat. This leads to several different strategies to explore. The fitness of each strategy will be determined so we can compare it to the others in chapter 5.

We first want to determine if an evolutionary stable strategy exists. In chapter 6 we compare populations that consist of a single strategy, and see how that strategy fares against a rare mutant strategy that arises.

We then examine the replicator dynamics of our population in chapter 7. We state and prove Theorem 7.3, that takes into account the different possible mixtures of strategies to see if any strategy will force the others to diminish over time, so that a single strategy or mix of strategies then takes over the whole of the population.

CHAPTER II

MATHEMATICAL MODELING FOR ECOLOGISTS

2.1 Modeling

The term modeling can be applied in many different ways. In figure 2.1 we can see three different types of models. The first model is a three-dimensional representation of the capital city of the Czech Republic, Prague, built by Google Earth. The second model is a mathematical description of the dynamics of a predator and prey species. Both of these represent something, hence why they are all referred to as a model.

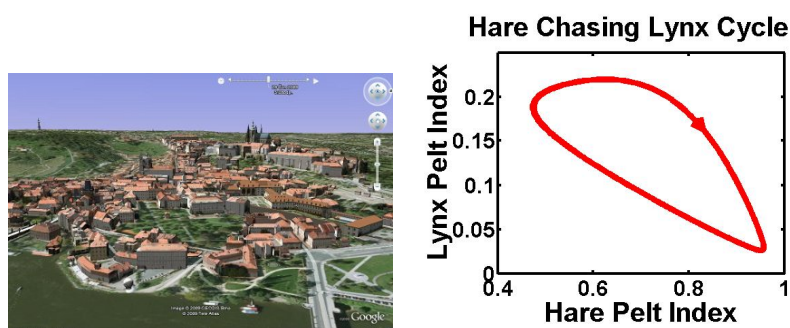


Figure 2.1: *Two Models. (a) A 3-D model of Prague, the capital city of the Czech Republic, as simulated from Google Earth (b) Hare-lynx cycle described by Lotka–Volterra equations as seen in [12].*

Modeling is used to display characteristics or behaviors of certain subjects.

Models are only useful to those that need certain information. For example consider

figure 2.2. This is a map of the rivers and counties of North Carolina. If we were to consider a person that is trying to find the route from the mountains to the beach by road, they certainly wouldn't use this map. It does not contain any information about highways. The map is not incorrect, but for the road traveler it is considered incomplete. This 'model' of North Carolina would be useful for people such as kayakers or fisherman, but it is certainly not useful for everyone. In that sense models must be useful to those that use them [20]. They can not possibly contain every bit of information possible. A map of North Carolina that contains all the rivers, lakes, roads, highways, county borders, and cities would be impossible to read.



Figure 2.2: *Map of the rivers of North Carolina, provided by www.geology.com*

2.2 Modeling for behavioral and evolutionary ecologists

Ecology is a science that investigates the abundance and distribution of organisms. The study of ecology is used to determine how organisms interact. When doing so, ecologists must determine the causes of why certain organisms grow and decline in a population, not just measure the actual growth in a population. Because evolution drives the behavior of all organisms, when trying to understand the causes of population growth and decline, evolutionary aspects must be taken into account. Behavioral and evolutionary ecology are the sciences that study the evolutionary and ecological driving forces that cause individuals to behave the way they do [20].

Behavioral and evolutionary ecology studies a very complex web of interactions. It seems that everything interacts with everything else; a hatching turtle must combat weather conditions to find the ideal time to hatch, then find its way to the ocean through a vast amount of predators, then, if it survives, make its way to the ocean, grow to an adult and find its way back to the beach to lay a nest of eggs in hopes they too will find their way to the ocean. All of this is governed by genes that influence the turtle's behavior in a multitude of ways. Modeling such a system would be impossible because of all of the complexities that are involved. This is why most models only focus on very minute details of ecology. Otherwise ecologists would get lost in the results [20].

A difference can be made between an experimental ecologist and one that develops models. An experimentalist is trying to determine if a certain behavior really happens in nature. A modeler is figuring out whether a hypothesis about something that happens in nature is feasible. A modeler will not investigate whether the hypothesis holds true in nature. Models are used to investigate the validity of one's own thinking and determine if an argument seems plausible. So models can be thought of as "thinking aids" about something that could happen in nature, not as actual investigations of nature. A good model narrows down the hypotheses that are thought to be true so that an experimentalist can then go find out the truth in nature [20].

Experimentalist and modelers are operating in an idealized world. An experimentalist will either work in a lab or draw conclusions from a random sample of ecology, but there is no way of drawing conclusions about every type of organism in a certain species. In the same sense, modelers will often overlook some, but not all, aspects of biology that an experimentalist will find important to be able to draw decisive conclusions from the model. For this reason models are idealized simplified versions of the real world.

Mathematical modeling can help answer questions about the reasons why certain behaviors of organisms occur in nature. At times the behaviors that we

see within certain species seem less beneficial than others that might be adopted.

A model can help answer our questions of why certain habits are adopted before others.

CHAPTER III

EVOLUTIONARY GAME THEORY

3.1 Game Theory

The mathematical theory of games was first developed as a model for situations of conflict [26]. It gained widespread recognition in the early 1940's because of its applications to the theoretical study of economics. In 1994 the Nobel Prize was bestowed upon John Nash for his application of game theory to economics [26]. The scope of game theory has broadened to include cooperative interactions and has been applied to the theoretical aspects of many of the social sciences.

Situations of conflict and interactions are called games and their participants are called players. The existence of a conflict is usually due to the desire of each player to improve his or her circumstances, usually by acquiring a limited number of resources. In most games each player's gain is another player's loss. Each player is assumed to have several strategies that he can use to gain a portion of the resources [26]. The success of any particular strategy is dependent on the frequencies of all the other strategies in a population, not just on the individual.

3.2 Evolutionary Game Theory

The initial purpose of game theorists was to find reasoning for certain behavior by using thought experiments. These thought experiments involved fictitious players who were assumed to know the reasoning for a certain behavior and to know that fictitious co-players would use it [16]. Initially game theory was based on decisions made by using rational thought processes. Evolutionary game theory develops games based on the idea that the Darwinian process of natural selection drives organisms to select strategies that will optimize their reproductive success [15]. Evolutionary game theory does not assume the players are making rational decisions, just decisions based on what their genetic traits have told them to do.

In evolutionary game theory, strategies are thought to be inherited traits that control an individual's behavior. A typical game investigates a population of organisms of the same species as players. These players interact generation after generation in a game situation. Those with a higher reproductive success are the ones whose strategies are carried on to the next generation. Most evolutionary game theory looks to see where a stable equilibrium of strategies is reached, but there has also been research done about games that do not reach a stable equilibrium [15].

The payoff of a certain strategy in a biological game is usually determined by reproductive success, more commonly called fitness. In many cases the fitness

of an individual can be described as the expected number of offspring [15]. Fitness could be measured as the amount of resources acquired by an individual, but the number of offspring is much easier to determine than the amount of food a certain organism acquires.

In biology, game situations emphasize strategies more than players. If we are investigating how well a certain strategy does in a population we are less interested in knowing which players play which strategies. It is important to know the relative frequencies of strategies [15]. For this reason we must be specific on how a game is defined by the strategies and the payoff of each strategy. Let \vec{P} be the frequency distribution of strategies in a population.

In this thesis, we consider only games with finitely many strategies $\Omega = \{x_1, x_2, \dots, x_n\}$. In general, \vec{P} is a measure on Ω and thus we can consider $\vec{P} \in \mathbb{R}^n$; where the i^{th} coordinate of \vec{P} corresponds to the proportion of individuals using strategy x_i . Thus given $P_i > 0$, for all $i \in 1, \dots, n$ we have $\sum_{i=1}^n P_i = 1$.

Definition 3.1 *A population game G is a pair $G = (\Omega, f)$ where Ω is a set of strategies available for the population and $f = f(x : \vec{P})$ is the payoff function, determining the fitness of a strategy $x_i \in \Omega$ in the population described by \vec{P} .*

3.3 Evolutionary Stable Strategy

The existence of evolutionary stability amongst a population of different strategies is of interest to evolutionary game theorists. To determine if there exists an evolutionary stable strategy we consider a population that consists of only one strategy, $p \in \Omega$. Then a very infrequent mutant strategy $q \in \Omega$ arises in that population. Strategy p is **stable** against strategy q if the fitness of p is greater than that of q . Strategy p is **evolutionarily stable** if it is stable against any mutant strategy that may arise in the population [24].

For the purpose of determining the stability of a strategy p we will look at the fitness of the strategy p , in a population that consists mostly of individuals using strategy p (i.e. with frequency $1 - \varepsilon$, $\varepsilon \in [0, 1]$) and a small number of individuals using a mutant strategy q (with frequency ε). This population state is described with a triple $[p, q, \varepsilon]$. Note that $[p, q, 0]$ is a population consisting entirely of individuals using strategy p and it is thus independent of q , i.e. $[p, q, 0] = [p, r, 0]$ for all $p, q, r, \in \Omega$. We then define $f(r : [p, q, 0])$ as the following.

Definition 3.2 $f(r : [p, q, 0]) = \lim_{\varepsilon \rightarrow 0^+} f(r : [p, r, \varepsilon])$

With this definition we can see that $f(r : [p, q, 0])$ represent a fitness of a small number of individuals (almost just one) using a strategy r in a population

where everybody else uses a strategy p .

Definition 3.3 *A strategy $r \in \Omega$ is a best reply to p if it maximizes the payoff function $f(x : [p, q, 0])$; i.e.*

$$f(r : [p, q, 0]) = \max\{f(x : [p, q, 0]); x \in \Omega\}. \quad (3.1)$$

Definition 3.4 [15] *A strategy p for $G = (\Omega, f)$ is evolutionarily stable if the following two conditions are satisfied:*

1. Equilibrium condition; p is a best reply to p .
2. Stability condition; For every best reply q to p such that $q \neq p$, there exists $\varepsilon_q > 0$ such that for all $0 < \varepsilon < \varepsilon_q$

$$f(p : [p, q, \varepsilon]) > f(q : [p, q, \varepsilon]). \quad (3.2)$$

3.4 Evolutionary Game Dynamics

The above definition of an evolutionary stable strategy is a static concept. Once all individuals adopt the ESS no mutant strategy can invade, and the population is stuck in the ESS forever. We want to know if every individual in the population can adopt the ESS. To answer that, we need a dynamic approach that models the evolution of the population, \vec{P} over time.

In our population of strategies we are interested in determining the payoff each strategy has when interacting with populations of other strategies. Strategies with a higher payoff will spread throughout the population [15]. In our case, the strategies with higher payoff will spread by passing their genetics on to the next generation that will then inherit the strategies of the previous generation.

We define payoff as the fitness of each individual using a certain strategy. The fitness depends on the actions of the other players and hence on the frequencies of other strategies within the population [16]. The frequencies of the population will change from generation to generation, yielding a feedback loop. The dynamics of this feedback loop is the main focus of evolutionary game theory [17].

We will investigate a discrete generation model. The individual fitness is determined by the number of offspring it brings into the next generation. For this reason the fitness will always be nonnegative. It can be 0, but once the fitness has reached 0 relative to the current distribution of strategies, that individual's strategy will never be passed on to another generation.

Let i be a strategy in a certain population. P_i is the proportion of type i in the population. Let $f_i(x)$ be the fitness of strategy i (which is dependent on the

population) [23]. Then the discrete replicator equation can be defined as

$$P_j(t+1) = \frac{P_j(t)f_j(t)}{\sum_{i=1}^n P_i(t) \cdot f_i(t)}. \quad (3.3)$$

CHAPTER IV

KLEPTOPARASITISM AND *ONTHOPHAGUS TAURUS***4.1 Overview**

In the animal kingdom, resource gathering is a behavior necessary for life. Resources can be considered items that contribute to an organism's food supply, territory, acquiring of mates, producing offspring, etc. It may be easier for an individual to steal resources from another individual if these resources are difficult to acquire. This stealing of resources from another individual is commonly called kleptoparasitism [8].

Kleptoparasitism occurs among many species. One of the most well documented types of kleptoparasitism is among seabirds. Sea birds, such as the Sandwich Tern, collect fish to eat or to feed to offspring. Breeding Sandwich Terns are often victims of kleptoparasitism by other gulls that steal the fish the tern has caught [10]. Recently kleptoparasitism has also been observed among large carnivorous mammals [5], fish [14], and spiders [1].

When individuals of the same species parasitize one another, this is known

is intraspecific parasitism. Cases when resources are stolen for parental care are of particular interest. Parental care includes preparation of a nesting site, allocation of food, and guarding of the nesting site. The theft of parental care is called brood parasitism. Intraspecific brood parasitism is often difficult to detect and quantify and evidence for it is relatively scarce [22].

Since most organisms produce so few offspring compared to the amount of food they consume, a single act of brood parasitism is an action that has much more impact than the taking of food. Brood parasitism has been studied among some birds, but it has also been documented among spiders and insects. Empirical evidence on brood parasitism can be more easily gathered from insects because they have life cycles that can be studied in a very small amount of time. It is much less costly to study insects than to study larger species, such as birds [8]. For this reason, the study of brood parasitism among insects can help to uncover patterns and perhaps even motives for the use of kleptoparasitism within a species.

4.2 *Onthophagus taurus* dung beetle

Dung beetles are found around the world, especially where large animals graze. Dung beetles play an important role in nature by aiding in the decomposition of animal manure, adding nutrients to the soil, aerating soil, and by competing for

nesting habitat and food resources with dung flies [3].

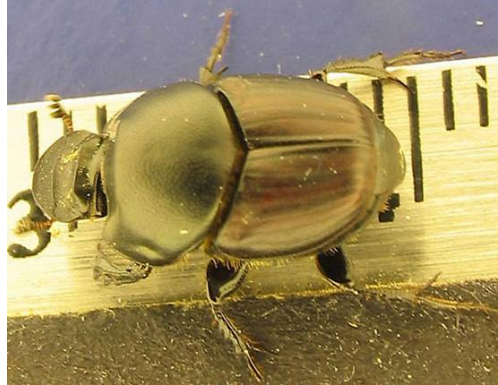


Figure 4.1: *Onthophagus taurus* dung beetle, (picture provided by Dr. Mary Crowe, University of N.C. Greensboro)

The *Onthophagus taurus* beetle, see figure 4.1, reproduces by provisioning cow or horse dung to provide food and shelter for themselves and their young [22]. The *O. taurus* dung beetle is a paracoprid dung beetle, which means the females lay their eggs in carefully constructed tunnels in the soil beneath a dung pat deposited by a large herbivore [8]. The dung beetle typically removes portions of dung from the dung pat and packs it into the blind end of the tunnels. A single egg is then deposited into an egg chamber and sealed. One egg and the dung packed around it constitutes a brood ball [13]. These brood balls provide shelter and food for the developing larvae inside.

The *O. taurus* dung beetle has been studied because of its brood parasitic behavior. It has been documented that female dung beetles will routinely access

brood balls made by other females and replace existing eggs with their own [22]. The dung beetles have been documented to stand at the the top of the tunnel and guard their brood balls against thieving beetles [18], despite the fact that parental care is rare among invertebrates.

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 [21]. Tunneling and brood ball production has been documented to require at least several hours [18]. Therefore climatic conditions that lead to evaporation of moisture in dung can affect the rate at which beetles can produce brood balls. Female dung beetles that were exposed to rapidly drying dung were more likely to kleptoparasitize brood balls already present in the environment rather than make their own [22]. For this reason we believe that the age of dung that a female dung beetle lands on will influence whether the payoff to kleptoparasitize is higher than producing her own brood ball.

We develop a game theoretic model that will develop strategies based on three choices that a female dung beetle will make. She will choose when to enter and leave a dung pat, and once she lands she will decide whether to steal or not steal. The time between depositing an egg in a complete brood ball and the time when she leaves will be considered guarding time.

Choosing to kleptoparasitize is influenced by the strategy adopted by others. If too many beetles choose to kleptoparasitize then there will be no beetles left to actually make balls, and if too few kleptoparasitize then the payoff for those who steal is much higher than for those that only prepare [8]. For this reason there has been a large body of theory focused on predicting if the use of kleptoparasitism can be evolutionarily stable [4].

CHAPTER V

OUR MODEL

5.1 Overview

Our model will investigate how the reproductive success of a female dung beetle is affected by the strategy she carries out in a dung pat. The strategies will focus on when a beetle should enter and leave a dung pat, and once arriving on the dung pat, whether to steal or not steal.

Based on the biological research we assume a dung beetle should arrive on a dung pat within 3 days of the deposition of dung in order to be able to produce brood balls [22]. For simplicity, we consider that our beetles have a genetically predetermined preference to land on day 1, day 2, or day 3 dung. Day 1 dung is the freshest dung and that which is best for producing brood balls. Day 2 dung is aging dung that beetles can still use to produce brood balls. Day 3 dung is almost or completely diminished, which is not useable to make a brood ball. We assume there is no dung that is useable to produce a brood ball after more than 3 days of its deposition. We assume cows regularly deposit dung pats so that the amount of

dung and its age distribution are constant over 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, $y \in \{x + 1, \dots, 4\}$
- whether it kleptoparasitizes or only prepares her own ball, κ or π

We will denote each strategy as (x_π, y) or (x_κ, y) . A dung beetle following strategy (x_κ, y) enters dung of age x . It searches for any ball it can steal. Those balls can come only from beetles that came to the dung earlier and leave 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. Then it will work on preparing a brood ball of her own, a process that takes a substantial amount of time (which is needed for another egg to develop inside the beetle, yet less than a day) [22]. If no ball is found by the beetle using (x_κ, y) it proceeds directly to making her own ball. In any case, the day after the dung beetle enters the dung pat, the same dung pat will have age $x + 1$, a beetle using strategy (x_κ, y) will have made one ball of her own and possibly stolen one ball 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(s) and making the ball(s) virtually invulnerable to stealing attempts of other beetles.

A strategy (x_π, y) behaves similarly to (x_κ, y) , only the beetle does not attempt to steal and prepares her own egg right away.

Since beetles can come only at day 1, 2, or 3 it makes no sense to leave or arrive later than day 4. The only strategies that will be able to produce and steal a brood ball will be those that land on day 2 dung. Those that land on day 1 dung have no one to steal from, so we do not consider $(1_\kappa, 2)$, $(1_\kappa, 3)$, and $(1_\kappa, 4)$. Those that land on day 3 dung cannot produce a brood ball, since the dung is too diminished, so we do not consider $(3_\pi, 4)$.

This leads us to eight strategies:

$$\Omega = \left\{ (1_\pi, 2), (1_\pi, 3), (1_\pi, 4), (2_\pi, 3), (2_\kappa, 3), (2_\pi, 4), (2_\kappa, 4), (3_\kappa, 4) \right\} \quad (5.1)$$

5.2 Determining Fitness

We will denote the fitness, or reproductive success, of a strategy $(x_*, y) \in \Omega$ by $f((x_*, y) : \vec{P})$, where $\vec{P} = \{P_\omega, \omega \in \Omega\}$. The fitness will be the number of undamaged brood balls that a beetle using strategy (x_*, y) can possess on average per unit time in a population described by \vec{P} .

$P_{(x_*, y)}$ will denote the proportion of the population using strategy (x_*, y) in a

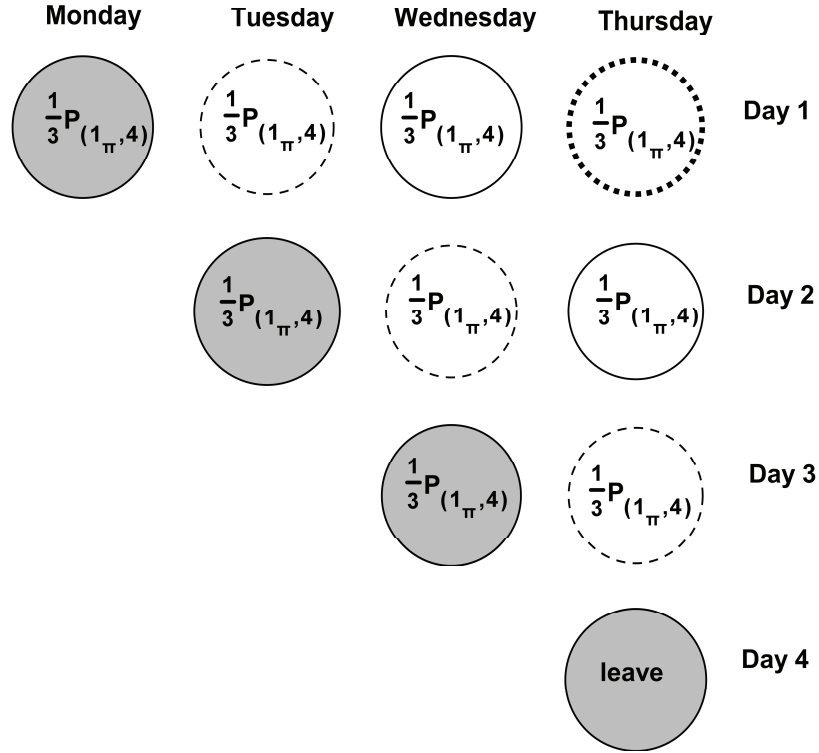


Figure 5.1: The gray circles represent dung that was distributed on Monday. Strategy $(1_\pi, 4)$ stays on that pat until day 4. The striped circles represent beetles that land on dung distributed on Tuesday and stay 3 days, and the solid circles represent those that land on Wednesday. As evident from this picture on any one pat only $\frac{1}{3}$ of the population is on each pat at a time, since the same population occupies 3 pats at one time, which can clearly be seen on Wednesday.

population consisting of a total of N beetles. 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 $x, x + 1, \dots, y - 1$ day old, see figure 5.1. We assume that the beetles are equally distributed. The effective number of beetles using strategy (x_*, y) , denoted $N_{(x_*, y)}^e$

that can be found on a single dung pat is

$$N_{(x_*,y)}^e = \frac{P_{(x_*,y)} \cdot N}{y - x}. \quad (5.2)$$

Equation (5.2) gives us the portion of the total number of beetles using strategy (x_*, y) that be be found on a single dung pat for each day $n \in [x, y - x]$.

This yields the formula for fitness of a strategy to be

$$f((x_*, y) : \vec{P}) = \frac{B_{(x_*,y)}^3}{N_{(x_*,y)}^e \cdot (y - x)} = \frac{B_{(x_*,y)}^3}{P_{(x_*,y)} \cdot N}. \quad (5.3)$$

$B_{(x_*,y)}^3$ is the number of undamaged brood balls beetles using strategy (x_*, y) have in their possession at the end day 3. $B_{(x_*,y)}^3$ is determined by the number of brood balls produced by beetles using strategy (x_*, y) , plus the number of brood balls kleptoparasitized by those beetles minus the number of brood balls stolen from them. When the day x beetles come to the dung pat, they can potentially steal brood balls of others and then make their own brood ball and since no balls are stolen from them on that day, we have

$$B_{(x_*,y)}^x = M_{(x_*,y)} + K_{(x_*,y)}; \quad (x_*, y) \in \Omega. \quad (5.4)$$

where $M_{(x_*,y)}$ and $K_{(x_*,y)}$ represent the number of brood balls made or kleptoparasitized by strategy (x_*, y) (on x -day old dung). For the simplicity of notation, we

set

$$B_{(x_*,y)}^n = 0; \quad n < x. \quad (5.5)$$

In the following days, beetles using strategy (x_*, y) do not make or kleptoparasitize any more balls, only other beetles can steal their balls and thus we have

$$B_{(x_*,y)}^n = B_{(x_*,y)}^{n-1} - S_{(x_*,y)}^n; \quad n > x. \quad (5.6)$$

where $S_{(x_*,y)}^n$ represent the number of balls stolen from strategy (x_*, y) on n -day old dung. Again for simplicity of notation we set,

$$S_{(x_*,y)}^n = 0; n < x. \quad (5.7)$$

Consequently

$$B_{(x_*,y)}^n = M_{(x_*,y)} + K_{(x_*,y)} - \sum_{i=1}^n S_{(x_*,y)}^i; \quad 1 \leq n \leq 3. \quad (5.8)$$

Each beetle using strategy (x_*, y) makes one brood ball on the day they arrive, the x^{th} day. The number of stolen balls will be 0, if $n \leq y$, since the beetles will still be guarding until day y . So by the overview we get that

$$M_{(x_*,y)} = \begin{cases} N_{(x_*,y)}^e; & (x_*, y) \in \Omega \setminus (3_\kappa, 4) \\ 0; & (x_*, y) = (3_\kappa, 4) \end{cases} \quad (5.9)$$

$$S_{(x_*,y)}^n = 0; n \leq y \quad (5.10)$$

$$K_{(x_\pi,y)} = 0 \quad (5.11)$$

Hence, by (5.6), (5.8), and (5.9)

$$B_{(x_\pi, y)}^i = N_{(x_\pi, y)}^e; \quad x = 1, 2, i < y \quad (5.12)$$

and thus, by (5.3), (5.6), and (5.12)

$$f((x_\pi, 4) : \vec{P}) = \frac{1}{4-x}, \text{ where } x \in \{1, 2\}, \text{ for any } \vec{P}. \quad (5.13)$$

To determine fitness of the remaining strategies, we will have to carry out a more careful analysis of the stealing on a day by day basis as done in the next section.

5.3 Determining $B_{(x_*, y)}^3$ for each strategy

5.3.1 Day 1

The number of balls beetles have on the 1 day old dung is determined by equations (5.4) and (5.12). In particular,

$$B_{(x_*, y)}^1 = \begin{cases} N_{(1_\pi, y)}^e, & x = 1, y \in \{2, 3, 4\}, \text{ and } * = \pi \\ 0, & \text{otherwise} \end{cases} \quad (5.14)$$

5.3.2 Day 2

Strategies $(1_\pi, 3)$ and $(1_\pi, 4)$ 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 $(1_\pi, 2)$; and the only beetles that can steal those balls are using a strategy $(2_\kappa, 3)$ or

Table 5.1: Summary of Notation

(x_*, y)	Strategy that arrives on day x and leaves on day y .
(x_κ, y)	Strategy that arrives on day x and leaves on day y and kleptoparasitizes and prepares a brood ball on day x .
(x_π, y)	Strategy that arrives on day x and leaves on day y and only prepares a brood ball on day x .
N	Total number of beetles in population.
Ω	The set of all 8 strategies, (5.1).
$\Omega_{y<4}$	Strategies that leave the dung pat before or at the beginning of day 3, i.e. $\{(1_\pi, 2), (1_\pi, 3), (2_\pi, 3), (2_\kappa, 3)\}$.
$\overline{\Omega_{y<4}}$	Strategies that leave the dung pat before or at the beginning of day 3, i.e. $\{(1_\pi, 2), (1_\pi, 3), (2_\pi, 3)\}$.
$P_{(x_*, y)}$	The proportion of beetles of the population, N , that land on day x and leave on day y and follows $*$.
\vec{P}	Frequency distribution of strategies in a population, i.e. $\vec{P} = (P_\omega, \omega \in \Omega)$
$N_{(x_*, y)}^e$	Number of beetles using strategy (x_*, y) that land in the same age dung pat on day x .
$M_{(x_*, y)}$	The number of brood balls a strategy (x_*, y) prepares on x day old dung.
$K_{(x_*, y)}$	The number of brood balls a strategy (x_*, y) kleptoparasitizes in x day old dung.
$S_{(x_*, y)}^n$	The number of brood balls that have been stolen from a strategy (x_*, y) in n day old dung.
$B_{(x_*, y)}^n$	The number of undamaged brood balls in possession of beetles using strategy (x_*, y) in n day old dung.
V^3	The sum of vulnerable brood balls on day 3, i.e. $V^3 = \sum_{(x_*, y) \in \Omega_{y<4}} B_{(x_*, y)}^2$.
$f((x_*, y) : \vec{P})$	Fitness of strategy (x_*, y) relative to \vec{P} .

$(2_\kappa, 4)$. Hence, there are $B_{(1_\pi, 2)}^1$ balls to be stolen by $(N_{(2_\kappa, 3)}^e + N_{(2_\kappa, 4)}^e)$ beetles and thus

$$S_{(1_\pi, 2)}^2 = \min\{B_{(1_\pi, 2)}^1, (N_{(2_\kappa, 3)}^e + N_{(2_\kappa, 4)}^e)\} \quad (5.15)$$

We will assume that beetles come one by one from either strategy in random order and will steal without replacement. The number of balls stolen by a given strategy is thus given by hypergeometric distribution [9]. On average,

$$K_{(2_\kappa, 3)} = \frac{N_{(2_\kappa, 3)}^e}{N_{(2_\kappa, 3)}^e + N_{(2_\kappa, 4)}^e} \cdot S_{(1_\pi, 2)}^2 \quad (5.16)$$

$$K_{(2_\kappa, 4)} = \frac{N_{(2_\kappa, 4)}^e}{N_{(2_\kappa, 3)}^e + N_{(2_\kappa, 4)}^e} \cdot S_{(1_\pi, 2)}^2 \quad (5.17)$$

5.3.3 Day 3

Strategies $(1_\pi, 4)$, $(2_\pi, 4)$, and $(2_\kappa, 4)$ continue to guard. The strategies that can be potentially stolen from we will denote as $\Omega_{y < 4}$ where

$$\Omega_{y < 4} = \{(x'_*, y') \in \Omega, y' < 4\} = \{(1_\pi, 2), (1_\pi, 3), (2_\pi, 3), (2_\kappa, 3)\}. \quad (5.18)$$

The number of brood balls that are vulnerable to kleptoparasitism on the third day we will denote as V^3 where,

$$V^3 = \sum_{(x_*, y) \in \Omega_{y < 4}} B_{(x_*, y)}^2 = (B_{(1_\pi, 2)}^2 + B_{(1_\pi, 3)}^2 + B_{(2_\pi, 3)}^2 + B_{(2_\kappa, 3)}^2). \quad (5.19)$$

The only beetles that can steal those balls are using strategy $(3_\kappa, 4)$. Thus,

$$K_{(3_\kappa, 4)} = \min(N_{(3_\kappa, 4)}^e, V^3). \quad (5.20)$$

As before, proportions of stolen balls are given by multivariate hypergeometric distribution, [9]. On average,

$$S_{(x_*, y)}^3 = \frac{B_{(x_*, y)}^2}{V^3} \cdot K_{(3_\kappa, 4)}; \quad (x_*, y) \in \Omega_{y < 4}. \quad (5.21)$$

Now we know that

$$B_{(x_*, y)}^3 = B_{(x_*, y)}^2 - S_{(x_*, y)}^3 \quad (5.22)$$

$$= B_{(x_*, y)}^2 \cdot \left[1 - \min\left(\frac{N_{(3_\kappa, 4)}^e}{V^3}, 1\right) \right]. \quad (5.23)$$

Since we know $B_{(x_*, y)}^3$ for each strategy (x_*, y) we can determine the fitness of each strategy by (5.3).

CHAPTER VI
EVOLUTIONARY STABLE STRATEGY

We will now analyze our eight strategies, (5.1) to determine if any evolutionary stable strategies exists. Our analysis will use definitions 3.3 and 3.4 as stated in section 3.3.

6.1 Leaving before the last day is not an ESS

To determine which strategies cannot be an ESS, we will start by looking at strategies $\Omega_{y < 4} = \{(1_\pi, 2), (1_\pi, 3), (2_\pi, 3), (2_\kappa, 3)\}$. These are the beetles that leave at or before the beginning of the 3rd day.

Let $p = (x_*, y) \in \Omega_{y < 4}$ be given and let $q = (3_\kappa, 4)$. We will consider a population $z = [p, q, \varepsilon]$, $\varepsilon \in [0, 1)$. Using equations (5.8) and (5.9) we can see that for each p ,

$$B_{(x_*, y)}^2 = M_{(x_*, y)} = N_{(x_*, y)}^e = (1 - \varepsilon) \cdot N. \quad (6.1)$$

Then on day 3 an ε portion of the population of beetles from strategy $(3_\kappa, 4)$ arrives and steals an ε portion brood balls from p . If $\varepsilon < \frac{1}{2}$ we have $\varepsilon < 1 - \varepsilon$ and thus by

equation (5.20)

$$B_{(3_\kappa, 4)}^3 = K_{(3_\kappa, 4)} = \varepsilon \cdot N. \quad (6.2)$$

Hence by equations (5.8) and (5.21)

$$B_{(x_*, y)}^3 = (1 - 2\varepsilon) \cdot N \quad (6.3)$$

and

$$f(q : [p, q, \varepsilon]) = \frac{B_{(3_\kappa, 4)}^3}{P_{(3_\kappa, 4)} \cdot N} = \frac{\varepsilon \cdot N}{\varepsilon \cdot N} = 1, \quad (6.4)$$

$$f(p : [p, q, \varepsilon]) = \frac{B_{(x_*, y)}^3}{P_{(x_*, y)} \cdot N} = \frac{(1 - 2\varepsilon) \cdot N}{(1 - \varepsilon) \cdot N} = 1 - \frac{\varepsilon}{(1 - \varepsilon)} \leq 1. \quad (6.5)$$

Thus,

$$f(p : [p, q, \varepsilon]) \leq f(q : [p, q, \varepsilon]) \quad (6.6)$$

with strict inequality in (6.5) whenever $\varepsilon \in (0, 1/2)$. Thus $p = (x_*, y) \in \Omega_{y < 4}$ is not ESS because it is either not the best reply to itself, or if it is, by (6.6), $q = (3_\kappa, 4)$ is best reply to p as well and, by (6.5), p does not satisfy the stability condition (3.2) of the ESS.

6.2 Staying for more than one day is not an ESS

We will show that none of the strategies that stays for more than one day is ESS.

It was shown in the above section that the strategy $(1_\pi, 3)$ is not the ESS. Now, let $p = (x_*, y) \in \{(1_\pi, 4), (2_\pi, 4), (2_\kappa, 4)\}$ and $q = (2_\pi, 3)$. In the population $z = [p, q, \varepsilon]$, $\varepsilon \in [0, 1]$, there is no stealing and thus using equations (5.3), (5.9), (5.20), and (5.21) we can see that

$$f(p : [p, q, \varepsilon]) = \frac{1}{y - x} \leq 1/2 < 1 \quad (6.7)$$

$$f(q : [p, q, \varepsilon]) = 1. \quad (6.8)$$

Hence, $p = (x_*, y) \in \{(1_\pi, 4), (2_\pi, 4), (2_\kappa, 4)\}$ is not the best reply to itself and thus it is not an ESS.

6.3 Coming too late is not an ESS

The only strategy that remains to investigate is $p = (3_\kappa, 4)$. Let $q = (1_\pi, 4)$. Since beetles using strategy $p = (3_\kappa, 4)$ cannot make their own balls and cannot steal from $q = (1_\pi, 4)$, we have by equations (5.8) and (5.20), for $\varepsilon \in (0, 1]$

$$f(p : [p, q, \varepsilon]) = 0, \quad (6.9)$$

$$f(q : [p, q, \varepsilon]) = 1/3 \quad (6.10)$$

and thus the strategy $p = (3_\kappa, 4)$ is not the best reply to itself. Hence, it is not an ESS.

CHAPTER VII
REPLICATOR DYNAMICS

7.1 Overview

Replicator dynamics describe a selection process where more successful strategies spread in the population [16]. The replicator equation, (3.3), can be written as

$$P_{(x'_*, y')}(t+1) = \frac{P_{(x'_*, y')}(t) \cdot f((x'_*, y') : \vec{P})}{\sum_{(x_*, y) \in \Omega} P_{(x_*, y)} \cdot f((x_*, y) : \vec{P})}. \quad (7.1)$$

Equation (7.1) yields

$$\frac{P_{(x'_*, y')}(t+1)}{P_{(x_*, y)}(t+1)} = \frac{P_{(x'_*, y')}(t)}{P_{(x_*, y)}(t)} \cdot \frac{f((x'_*, y') : \vec{P})}{f((x_*, y) : \vec{P})}. \quad (7.2)$$

We will first introduce two lemmas that will be used in analyzing the replicator dynamics.

Lemma 7.1 *Let $t_0 \in \mathbb{N}$, $\alpha \in \mathbb{R}$, and $i, j \in \Omega$ be such that $P_j(0) > 0$ and*

$\frac{f(i : \vec{P})}{f(j : \vec{P})} < \alpha < 1$ for all $t > t_0$ and all \vec{P} . Then $\frac{P_i(t)}{P_j(t)} \rightarrow 0$ as $t \rightarrow \infty$. Consequently,

since $P_j(t) \in [0, 1]$, $P_i(t) \rightarrow 0$ as $t \rightarrow \infty$.

Proof. Let $\gamma_n = \frac{P_i(n)}{P_j(n)}$ and $f_n = \frac{f(i : \vec{P})(n)}{f(j : \vec{P})(n)}$. Note that γ_0 is defined and if

γ_n is defined then either γ_{n+1} is defined by (7.2) or $\gamma_{n+1} = 0$. By our assumption $f_n < \alpha < 1$ and thus, by induction,

$$0 \leq \gamma_n < f_n \cdot \gamma_{n-1} < \alpha^n \cdot \gamma_0. \quad (7.3)$$

So as $n \rightarrow \infty$, $\gamma_n \rightarrow 0$ since $\alpha^n \rightarrow 0$.

Lemma 7.2 Let $t_0 \in \mathbb{N}$, $\alpha \in \mathbb{R}$, and $I, J \subset \Omega$ be such that $I \cap J = \emptyset$, $\sum_{j \in J} P_j(0) > 0$,

and $\frac{f(i : \vec{P})}{f(j : \vec{P})} < \alpha < 1$, all $i \in I$, all $j \in J$ and all $t > t_0$. Then

$$\frac{\sum_{i \in I} P_i(t)}{\sum_{j \in J} P_j(t)} \rightarrow 0 \text{ as } t \rightarrow \infty. \quad (7.4)$$

Consequently, since $\sum_{j \in J} P_j(t) \leq 1$, then $\sum_{i \in I} P_i(t) \rightarrow 0$ as $t \rightarrow \infty$.

Proof.

By (7.1)

$$\sum_{i \in I} P_i(t+1) = \frac{\sum_{i \in I} P_i(t) \cdot f(i : \vec{P})(t)}{\sum_{(x_*, y) \in \Omega} P_{(x_*, y)} \cdot f((x_*, y) : \vec{P})} \quad (7.5)$$

$$\sum_{j \in J} P_j(t+1) = \frac{\sum_{j \in J} P_j(t) \cdot f(j : \vec{P})(t)}{\sum_{(x_*, y) \in \Omega} P_{(x_*, y)} \cdot f((x_*, y) : \vec{P})}. \quad (7.6)$$

Thus

$$\frac{\sum_{i \in I} P_i(t+1)}{\sum_{j \in J} P_j(t+1)} = \frac{\sum_{i \in I} P_i(t) f(i : \vec{P})(t)}{\sum_{j \in J} P_j(t) f(j : \vec{P})(t)} \quad (7.7)$$

$$\leq \frac{\max \{f(i : \vec{P})\}}{\min \{f(j : \vec{P})\}} \cdot \frac{\sum_{i \in I} P_i(t)}{\sum_{j \in J} P_j(t)} < \alpha \cdot \frac{\sum_{i \in I} P_i(t)}{\sum_{j \in J} P_j(t)}. \quad (7.8)$$

The conclusions follows by the same proof as in the Lemma 7.1.

7.2 Main Theorem

Most strategies in the population are affected by the presence of other strategies. Those that guard are not vulnerable to kleptoparasitism until they leave. Those that do not guard are susceptible to kleptoparasitism when they leave. The presence or absence of different mixes of these strategies has an affect on how the different strategies fare over time. The following theorem summarizes the evolutionary outcomes of different initial mixtures of strategies over time.

Theorem 7.3 *The long term evolution of the population is characterized as follows:*

1. Let $P_{(3\kappa,4)}(0) > 0$.

(a) If $P_{(2\kappa,4)}(0) + P_{(2\pi,4)}(0) > 0$, then $P_{(2\kappa,4)}(t) + P_{(2\pi,4)}(t) \rightarrow 1$ as $t \rightarrow \infty$.

(b) If $P_{(2\kappa,4)}(0) = P_{(2\pi,4)}(0) = 0$ and $P_{(1\pi,4)}(0) > 0$, then $P_{(1\pi,4)}(t) \rightarrow 1$ as $t \rightarrow \infty$.

(c) If $P_{(2\kappa,4)}(0) = P_{(2\pi,4)}(0) = P_{(1\pi,4)}(0) = 0$, then there exists t_0 such that for all $t > t_0$, $\vec{P}(t) = 0$.

2. Let $P_{(3\kappa,4)}(0) = 0$.

(a) If $P_{(2\kappa,3)}(0) > 0$, then $P_{(2\kappa,3)}(t) + P_{(2\pi,3)}(t) \rightarrow 1$ as $t \rightarrow \infty$.

(b) If $P_{(2\kappa,3)}(0) = 0$, $P_{(2\kappa,4)}(0) > 0$ and $P_{(2\pi,3)}(0) > 0$, then $P_{(2\pi,3)}(t) \rightarrow 1$ as $t \rightarrow \infty$.

(c) If $P_{(2\kappa,3)}(0) = P_{(2\pi,3)}(0) = 0$ and $P_{(2\kappa,4)}(0) > 0$, then $P_{(2\kappa,4)}(t) + P_{(2\pi,4)}(t) + P_{(1\pi,3)}(t) \rightarrow 1$ as $t \rightarrow \infty$.

(d) If $P_{(2\kappa,3)}(0) = P_{(2\kappa,4)}(0) = 0$ and $P_{(2\pi,3)}(0) + P_{(1\pi,2)}(0) > 0$, then $P_{(2\pi,3)}(t) + P_{(1\pi,2)}(t) \rightarrow 1$ as $t \rightarrow \infty$.

(e) If $P_{(2\kappa,3)}(0) = P_{(2\kappa,4)}(0) = P_{(2\pi,3)}(0) = P_{(1\pi,2)}(0) = 0$, and $P_{(1\pi,3)}(0) + P_{(2\pi,4)}(0) > 0$, then $P_{(1\pi,3)}(t) + P_{(2\pi,4)}(t) \rightarrow 1$ as $t \rightarrow \infty$.

(f) If $P_{(x_*,y)}(t) = 0$ for all $(x_*, y) \in \Omega \setminus \{(1\pi, 4)\}$, then $P_{(1\pi,4)}(t) = 1$ for all $t > 0$.

Theorem 7.3 takes into account the evolutionary outcome given certain initial amounts of population of different strategies. We do need to make sure that every possible scenario is covered to be sure Theorem 7.3 to be complete. In order to do this we need to make sure that all mixes are considered where a strategy is either in the population or not in the population. This will result in $2^8 = 256$ possibilities. We narrow this list down by first considering if $P_{(3,\kappa,4)}(0) > 0$. When we prove part 1 of Theorem 7.3 it will be evident that if $P_{(3,\kappa,4)}(0) > 0$ the only strategies that will do well are those that stay until the fourth day. Likewise if $P_{(3,\kappa,4)}(0) = 0$ and $P_{(2,\kappa,3)}(0) > 0$ then eventually $(2,\kappa,3)$ will make up the whole of the population (this will be proven in part a of section 2 of Theorem 7.3). We also won't consider strategy $(1,\pi,4)$ as part of the possible mixtures because it will always be part of the population, but most of the time it will be almost 0 compared to the other strategies, except when it is the only strategy in the population.

This will narrow our possible strategy mixes down to $2^5 = 32$ possible combinations. Table 7.1 show the possible combinations and how they are covered by Theorem 7.3.

Before we prove Theorem 7.3, we will first investigate the evolution of strategy $(1,\pi,2)$ over time. We will show that if any stealing strategy is present, then $(1,\pi,2)$ will become extinct in finite time.

$P_{(1,\pi,2)}$	$P_{(1,\pi,3)}$	$P_{(2,\pi,3)}$	$P_{(2,\pi,4)}$	$P_{(2,\kappa,4)}$	Theorem 7.3 section 2, part:
1	1	1	1	1	b
1	1	1	0	1	b
1	0	1	1	1	b
1	0	1	0	1	b
0	1	1	1	1	b
0	1	1	0	1	b
0	0	1	1	1	b
1	1	0	1	1	c
1	1	0	0	1	c
1	0	0	1	1	c
1	0	0	0	1	c
0	1	0	1	1	c
0	1	0	0	1	c
0	0	1	0	1	c
0	0	0	1	1	c
0	0	0	0	1	c
1	1	1	1	0	d
1	1	1	0	0	d
1	1	0	1	0	d
1	1	0	0	0	d
1	0	1	1	0	d
1	0	1	0	0	d
1	0	0	1	0	d
1	0	0	0	0	d
0	1	1	1	0	d
0	1	1	0	0	d
0	0	1	1	0	d
0	0	1	0	0	d
0	1	0	1	0	e
0	1	0	0	0	e
0	0	0	1	0	e
0	0	0	0	0	f

Table 7.1: **Theorem 7.3 applied to all initial mixtures of strategies.** This table shows all possible initial mixtures of strategies except for $(3_\kappa, 4)$, $(2_\kappa, 3)$, and $(1_\pi, 4)$. A 1 denotes $P_{(x_*,y)}(0) > 0$ and a 0 denotes $P_{(x_*,y)}(0) = 0$. The right hand column shows which part of Theorem 7.3, section 2, the mixture is described.

7.3 Strategy $(1_\pi, 2)$ goes extinct

Theorem 7.4 *If $P_{(2_\kappa, 4)}(0) + P_{(2_\kappa, 3)}(0) + P_{(3_\kappa, 4)}(0) > 0$ then there exists $t_0 > 0$ such that for all $t > t_0$ $P_{(1_\pi, 2)}(t) = 0$.*

Moreover, if $P_{(3_\kappa, 4)}(0) > 0$, then there exists t_0 such that

$$\sum_{(x, y) \in \Omega_{y < 4}} P_{(x, y)}(t) = 0 \text{ for all } t \geq t_0. \quad (7.9)$$

Proof.

7.3.1 Case $P_{(2_\kappa, 4)}(0) > 0$

If

$$P_{(1_\pi, 2)}(t_0) \leq P_{(2_\kappa, 3)}(t_0) + \frac{1}{2}P_{(2_\kappa, 4)}(t_0) \text{ for some } t_0 > 0 \quad (7.10)$$

then by (5.8), (5.9), and (5.15)

$$M_{(1_\pi, 2)}(t) = P_{(1_\pi, 2)}(t) \cdot N \quad (7.11)$$

$$B_{(1_\pi, 2)}^2(t) = M_{(1_\pi, 2)}(t) - S_{(1_\pi, 2)}^2(t) = (P_{(1_\pi, 2)}(t) - P_{(1_\pi, 2)}(t)) \cdot N = 0. \quad (7.12)$$

Thus $P_{(1_\pi, 2)}(t_0 + 1) = 0$ and thus $P_{(1_\pi, 2)}(t) = 0$ for all $t > t_0$. If (7.10) is not true,

then we can assume

$$P_{(1_\pi, 2)}(t) > P_{(2_\kappa, 3)}(t) + \frac{1}{2}P_{(2_\kappa, 4)}(t), \text{ for all } t > 0. \quad (7.13)$$

We will show that if $P_{(2\kappa,4)}(0) > 0$ then (7.13) leads to a contradiction and hence (7.10) holds and $P_{(1\pi,2)}$ goes extinct in a finite time as shown above. By (5.8), (5.15), and (5.17),

$$B_{(1\pi,2)}^2(t) \leq \left(P_{(1\pi,2)}(t) - \frac{1}{2}P_{(2\kappa,4)}(t) \right) \cdot N \quad (7.14)$$

$$B_{(2\kappa,4)}^2(t) \geq \frac{1}{2}P_{(2\kappa,4)}(t) \cdot N. \quad (7.15)$$

Since $B_{(1\pi,2)}^3 \leq B_{(1\pi,2)}^2$ and $B_{(2\kappa,4)}^3 \leq B_{(2\kappa,4)}^2$, by (5.3) we find that

$$\frac{f((1\pi, 2) : \vec{P})(t)}{f((2\kappa, 4) : \vec{P})(t)} = \frac{B_{(1\pi,2)}^3(t)}{P_{(1\pi,2)}(t) \cdot N} \cdot \frac{\frac{1}{2}P_{(2\kappa,4)}(t) \cdot N}{B_{(2\kappa,4)}^3(t)} \quad (7.16)$$

$$\leq \frac{P_{(1\pi,2)}(t) - \frac{1}{2}P_{(2\kappa,4)}(t)}{P_{(1\pi,2)}(t)} \quad (7.17)$$

$$\leq 1 - \frac{\frac{1}{2}P_{(2\kappa,4)}(t)}{P_{(1\pi,2)}(t)}. \quad (7.18)$$

Hence, $\frac{f((1\pi, 2) : \vec{P})(t)}{f((2\kappa, 4) : \vec{P})(t)} < 1$ for all $t > 0$ and thus, by (7.2), $\frac{P_{(1\pi,2)}(t)}{P_{(2\kappa,4)}(t)}$ is not

increasing, i.e. $\frac{P_{(2\kappa,4)}(t)}{P_{(1\pi,2)}(t)}$ is not decreasing. Thus,

$$\frac{f((1\pi, 2) : \vec{P})(t)}{f((2\kappa, 4) : \vec{P})(t)} \leq 1 - \frac{1}{2} \frac{P_{(2\kappa,4)}(t)}{P_{(1\pi,2)}(t)} \quad (7.19)$$

$$\leq 1 - \frac{1}{2} \frac{P_{(2\kappa,4)}(0)}{P_{(1\pi,2)}(0)} \quad (7.20)$$

$$< 1. \tag{7.21}$$

Thus by Lemma 7.1,

$$\frac{P_{(1\pi,2)}(t)}{P_{(2\kappa,4)}(t)} \rightarrow 0 \text{ as } t \rightarrow \infty \tag{7.22}$$

which is a contradiction to assumption (7.13).

7.3.2 Case $P_{(2\kappa,3)}(0) > 0$

Here we will show that if $P_{(2\kappa,3)}(0) > 0$ then equation (7.13) leads to a contradiction, thus equation (7.10) holds true, and strategy $(1\pi, 2)$ goes extinct. So we will assume that equation (7.13) holds true.

By equations (5.8), (5.15), and (5.16) we know that

$$B_{(1\pi,2)}^2(t) \leq (P_{(1\pi,2)}(t) - P_{(2\kappa,3)}(t)) \cdot N \tag{7.23}$$

$$B_{(2\kappa,3)}^2(t) \geq P_{(2\kappa,3)}(t) \cdot N. \tag{7.24}$$

On the third day strategy $(3\kappa, 4)$ will steal as much as possible from each strategy. By equation (5.22) we know that

$$B_{(1\pi,2)}^3(t) = B_{(1\pi,2)}^2(t) \left[1 - \min \left(1, \frac{N_{(3\kappa,4)}^e(t)}{V^3(t)} \right) \right] \tag{7.25}$$

$$B_{(2\kappa,3)}^3(t) = B_{(2\kappa,3)}^2(t) \left[1 - \min \left(1, \frac{N_{(3\kappa,4)}^e(t)}{V^3(t)} \right) \right]. \tag{7.26}$$

Using the fitness equation, (5.3), we know that

$$\frac{f((1_\pi, 2) : \vec{P})(t)}{f((2_\kappa, 3) : \vec{P})(t)} = \frac{B_{(1_\pi, 2)}^3(t)}{P_{(1_\pi, 2)}(t) \cdot N} \cdot \frac{P_{(2_\kappa, 3)}(t) \cdot N}{B_{(2_\kappa, 3)}^3(t)} \quad (7.27)$$

$$\leq \frac{P_{(1_\pi, 2)}(t) - P_{(2_\kappa, 3)}(t)}{P_{(1_\pi, 2)}(t)} \quad (7.28)$$

$$\leq 1 - \frac{P_{(2_\kappa, 3)}(t)}{P_{(1_\pi, 2)}(t)}. \quad (7.29)$$

Hence, similarly as in section 7.3.1,

$$\frac{P_{(1_\pi, 2)}(t)}{P_{(2_\kappa, 3)}(t)} \rightarrow 0 \text{ as } t \rightarrow \infty \quad (7.30)$$

which is a contradiction to (7.13).

7.3.3 Case $P_{(3_\kappa, 4)}(0) > 0$

Since we have addressed what happens when $P_{(2_\kappa, 3)}(0) > 0$ and $P_{(2_\kappa, 4)}(0) > 0$ in the previous proofs, we will now assume $P_{(2_\kappa, 3)}(0) = P_{(2_\kappa, 4)}(0) = 0$, so strategy $(1_\pi, 2)$ cannot be kleptoparasitized on the second day. As we assumed $P_{(3_\kappa, 4)}(0) > 0$, the strategy $(1_\pi, 2)$ can be kleptoparasitized on the third day.

In this case $P_{(3_\kappa, 4)}$ will steal as many vulnerable brood balls as it can. Since $P_{(2_\kappa, 3)}(0) = 0$ the only vulnerable brood balls are from strategies $(1_\pi, 2)$, $(1_\pi, 3)$, and $(2_\pi, 3)$. Let $\overline{\Omega_{y < 3}} = \{(1_\pi, 2), (1_\pi, 3), (2_\pi, 3)\}$ be the set of strategies that are vulnerable to kleptoparasitism on day 3.

If

$$P_{(3\kappa,4)}(t_0) \geq P_{(1\pi,2)}(t_0) + \frac{1}{2}P_{(1\pi,3)}(t_0) + P_{(2\pi,3)}(t_0) \text{ for some } t_0 > 0, \quad (7.31)$$

then by equation (5.21)

$$P_{(1\pi,2)}(t) + \frac{1}{2}P_{(1\pi,3)}(t) + P_{(2\pi,3)}(t) = 0 \text{ for all } t \geq t_0. \quad (7.32)$$

If this is not true, then we will assume that

$$P_{(3\kappa,4)}(t) < P_{(1\pi,2)}(t) + \frac{1}{2}P_{(1\pi,3)}(t) + P_{(2\pi,3)}(t) \text{ for all } t > 0. \quad (7.33)$$

We will find the fitness of each strategy $(x_*, y) \in \overline{\Omega_{y < 3}}$ so that we can apply lemma (7.2).

By equation (5.8), (5.9), and (5.20) we know that

$$M_{(x_*,y)}(t) = N_{(x_*,y)}^e(t) \leq P_{(x_*,y)}(t) \cdot N \quad (7.34)$$

$$B_{(x_*,y)}^2(t) \leq P_{(x_*,y)}(t) \cdot N \quad (7.35)$$

$$B_{(x_*,y)}^3(t) \leq B_{(x_*,y)}^2(t) \left[1 - \frac{P_{(3\kappa,4)}(t)}{V^3(t)} \right] \quad (7.36)$$

$$B_{(3\kappa,4)}^3(t) = N_{(3\kappa,4)}^e(t). \quad (7.37)$$

By (5.3)

$$\frac{f((x_*, y) : \vec{P})}{f((3\kappa, 4) : \vec{P})} = \frac{B_{(x_*,y)}^3(t)}{P_{(x_*,y)} \cdot N} \cdot \frac{P_{(3\kappa,4)}(t) \cdot N}{B_{(3\kappa,4)}^3(t)} \quad (7.38)$$

$$\leq 1 - \frac{N_{(3\kappa,4)}^e(t)}{V^3(t)}. \quad (7.39)$$

Using a similar argument that was used in the previous sections 7.3.1 and ?? we can see that $\frac{N_{(3\kappa,4)}^e(t)}{V^3(t)}$ is non-decreasing for all $(x_*, y) \in \overline{\Omega_{y < 4}}$.

Thus $\frac{f((x_*, y) : \vec{P})}{f((3\kappa, 4) : \vec{P})} < \alpha < 1$. Therefore by lemma (7.2) we can conclude

that

$$\frac{P_{(x_*, y)}(t)}{P_{(3\kappa, 4)}(t)} \rightarrow 0 \text{ as } t \rightarrow \infty \text{ for all } (x_*, y) \in \overline{\Omega_{y < 4}}. \quad (7.40)$$

This is a contradiction to our assumption (7.33), thus (7.31) holds true. Thus for some $t_0 > 0$

$$P_{(1\pi, 2)}(t_0) + \frac{1}{2}P_{(1\pi, 3)}(t_0) + P_{(2\pi, 3)}(t_0) = 0. \quad (7.41)$$

It can also be shown that eventually strategies from $\Omega_{y < 4} = \{(1\pi, 2), (1\pi, 3), (2\pi, 3), (2\kappa, 3)\}$ will also diminish over time since they are all vulnerable to kleptoparasitism from $(3\kappa, 4)$. Then for some $t_0 > 0$

$$P_{(3\kappa, 4)}(t_0) \geq P_{(1\pi, 2)}(t_0) + \frac{1}{2}P_{(1\pi, 3)}(t_0) + P_{(2\pi, 3)}(t_0) + P_{(2\kappa, 3)}(t_0). \quad (7.42)$$

Thus,

$$P_{(1\pi, 2)}(t) + \frac{1}{2}P_{(1\pi, 3)}(t) + P_{(2\pi, 3)}(t) + P_{(2\kappa, 3)}(t) = 0 \text{ for all } t \geq t_0. \quad (7.43)$$

Note that as soon as $\Omega_{y < 4}$ are no longer strategies in the population then in the very next generation $P_{(3_\kappa, 4)}(t+1) = 0$ since the only way for strategy $(3_\kappa, 4)$ to have brood balls is by stealing. Thus $P_{(3_\kappa, 4)}(t) = 0$ for all $t > t_0$. On the other hand $(3_\kappa, 4)$ will never go extinct before those that it kleptoparasitizes.

7.4 Proof of Theorem 7.3: Case $P_{(3_\kappa, 4)}(0) > 0$

Here we will determine what happens to the overall population when $P_{(3_\kappa, 4)}(0) > 0$. No assumptions will be made about the proportions of the other strategies unless stated.

From theorem 7.4 we already know that whenever strategy $(3_\kappa, 4)$ is in the population that $P_{(1_\pi, 2)}(t) = 0$ for all $t > t_0$, where t_0 is the time strategy $(1_\pi, 2)$ goes extinct. Since strategy $(1_\pi, 2)$ is eventually not present then strategies $(2_\kappa, 3)$ and $(2_\kappa, 4)$ have no vulnerable eggs to steal from. Because of this there is eventually no distinction between strategies $(2_\kappa, 3)$ and $(2_\kappa, 4)$ and their respective non-stealing strategies $(2_\pi, 3)$ and $(2_\pi, 4)$.

7.4.1 Case $P_{(2_\kappa, 4)}(0) + P_{(2_\pi, 4)}(0) > 0$

By Theorem 7.4 whenever $P_{(3_\kappa, 4)}(0) > 0$ then for some $t_0 > 0$, $P_{(x_*, y)}(t) = 0$ for all $t > t_0 + 1$ and strategies $(x_*, y) \in \Omega_{y < 4}$. So at some finite amount of time, t_0 , the

only strategies left in the population are $(1_\pi, 4)$, $(2_\pi, 4)$, and $(2_\kappa, 4)$.

These strategies will always be present in the population since no other strategies will steal from them and they are not dependent on other strategies for brood balls.

Here we will let $I = \{(2_\kappa, 4), (2_\pi, 4)\}$, and let $J = \{(1_\pi, 4)\}$.

Since there are no balls to steal from, by equation (5.13)

$$f((x_*, y) : \vec{P}) = \frac{1}{2}, \text{ for all } (x_*, y) \in I \quad (7.44)$$

$$f((1_\pi, 4) : \vec{P}) = \frac{1}{3} \quad (7.45)$$

$$\frac{f((1_\pi, 4) : \vec{P})}{f((x_*, y) : \vec{P})} = \frac{2}{3} < 1. \quad (7.46)$$

Thus using lemma 7.2 $\frac{P_{(1_\pi, 4)}(t)}{\sum_{(x_*, y) \in I} P_{(x_*, y)}(t)} \rightarrow 0$ as $t \rightarrow \infty$.

Therefore $P_{(2_\kappa, 4)}(t) + P_{(2_\pi, 4)}(t) \rightarrow 1$ as $t \rightarrow \infty$.

7.4.2 Case $P_{(2_\kappa, 4)}(0) = P_{(2_\pi, 4)}(0) = 0$, $P_{(1_\pi, 4)}(0) > 0$

If $P_{(2_\kappa, 4)}(0) = P_{(2_\pi, 4)}(0) = 0$ then by Theorem 7.4, since $P_{(3_\kappa, 4)}(0) > 0$, then eventually the only strategy present is $(1_\pi, 4)$. Thus, $P_{(1_\pi, 4)}(t) \rightarrow 1$ as $t \rightarrow \infty$ whenever $t > t_0$.

7.4.3 Case $P_{(2\pi,4)}(0) = P_{(2\kappa,4)}(0) = P_{(1\pi,4)}(0) = 0$

If we have a population of strategies that includes no beetles that guard until the end of day 3, then the entire population will eventually die off. Strategy $(3_\kappa, 4)$ will eventually steal all of the available brood balls, which will lead to its own demise. Thus over some finite amount time, t , there will be no strategies present in the population.

7.5 Proof of Theorem 7.3: Case $P_{(3_\kappa,4)}(0) = 0$

If there is no initial population of strategy $(3_\kappa, 4)$ then there are no beetles that are vulnerable to kleptoparasitism on the third day. This leaves the only beetles subject to kleptoparasitism to be $(1_\pi, 2)$ by strategies $(2_\kappa, 3)$ and $(2_\kappa, 4)$.

7.5.1 Case $P_{(2_\kappa,3)}(0) + P_{(2_\kappa,4)}(0) > 0$

Assume $P_{(2_\kappa,3)}(0) + P_{(2_\pi,3)}(0) > 0$. If strategies $(2_\kappa, 3)$ and $(2_\kappa, 4)$ are present in the population then we have already shown by theorem 7.4 that there exists a t_0 such that for all $t \geq t_0$, $P_{(1_\pi,2)}(t) = 0$. Thus in this case we will only consider the strategies from sets $I = \{(1_\pi, 3), (1_\pi, 4), (2_\pi, 4), (2_\kappa, 4)\}$ and $J = \{(2_\kappa, 3), (2_\pi, 3)\}$

We will show that $\sum_{i \in I} P_{(x_*, y)}(t) \rightarrow 0$ as $t \rightarrow \infty$ for all $(x_*, y) \in I$.

There is no stealing at times $t \geq t_0$ as stated above. Thus the fitness of each

strategy is easily calculated by equation (5.13).

$$f((1_\pi, 3) : \vec{P}) = f((2_\pi, 4) : \vec{P}) = f((2_\kappa, 4) : \vec{P}) = \frac{1}{2} \quad (7.47)$$

$$f((1_\pi, 4) : \vec{P}) = \frac{1}{3} \quad (7.48)$$

$$f((2_\kappa, 3) : \vec{P}) = f((2_\pi, 3) : \vec{P}) = 1. \quad (7.49)$$

By Lemma 7.2, $\frac{\sum_{(x', y') \in I} P_{(x', y')}(t)}{\sum_{(x, y) \in J} P_{(x, y)}(t)} \rightarrow 0$ as $t \rightarrow \infty$. Therefore $P_{(2_\kappa, 3)}(t) +$

$P_{(2_\pi, 3)}(t) \rightarrow 1$ as $t \rightarrow \infty$.

7.5.2 Case $P_{(2_\kappa, 3)}(0) = P_{(2_\pi, 3)}(0) = 0$

Now there are only strategies that will guard for more than one day. As in before in 7.5.4 we will see that those that stay longer will eventually do worse than those that guard for less time. As shown by Theorem 7.4, if $P_{(2_\kappa, 4)}(0) > 0$ then $P_{(1_\pi, 2)}(t) = 0$ for some finite amount of time t .

Here we will let $I = \{(1_\pi, 4)\}$ and $J = \{(1_\pi, 3), (2_\pi, 4), (2_\kappa, 4)\}$. The fitnesses of each strategy will be the same as was determined by equations (7.47), (7.48), and (7.49).

Thus by lemma 7.2, $P_{(1_\pi, 4)}(t) \rightarrow 0$ as $t \rightarrow \infty$ and $P_{(1_\pi, 3)}(t) + P_{(2_\pi, 4)}(t) + P_{(2_\kappa, 4)}(t) \rightarrow 1$ as $t \rightarrow \infty$.

7.5.3 Case $P_{(2_\kappa,3)}(0) = 0$

Here we will assume that $P_{(2_\kappa,4)}(0) > 0$ as well. By section 7.5.1 we know that $P_{(2_\kappa,3)}(t) + P_{(2_\pi,3)}(t) \rightarrow 1$ as $t \rightarrow \infty$. If $P_{(2_\kappa,3)}(0) = 0$ then it follows that $P_{(2_\pi,3)} \rightarrow 1$ as $t \rightarrow \infty$.

7.5.4 Case $P_{(2_\kappa,3)}(0) = P_{(2_\kappa,4)}(0) = 0$

Since $P_{(2_\kappa,3)}(0) = P_{(2_\kappa,4)}(0) = P_{(3_\kappa,4)}(0) = 0$ then no strategy is susceptible to kleptoparasitism. The preparing strategies that don't guard will thus do better than those that do guard, since they spend less time with the brood balls.

Now we will define two groups, those that guard, $I = \{(1_\pi, 3), (1_\pi, 4), (2_\pi, 4)\}$, and those that don't guard, $J = \{(1_\pi, 2), (2_\pi, 3)\}$.

Using (5.13), $f((1_\pi, 2) : \vec{P}) = 1$ and using (7.47), (7.48), and (7.49), Lemma 7.2 shows that $P_{(1_\pi,2)}(t) + P_{(2_\pi,3)}(t) \rightarrow 1$ as $t \rightarrow \infty$.

7.5.5 Case $P_{(x_*,y)}(0) = 0$ for all $(x_*, y) \in \Omega \setminus (1_\pi, 4)$

If there are no other strategies present besides strategy $(1_\pi, 4)$, then there will always be a population of this strategy. Thus $P_{(1_\pi,4)}(t) = 1$ for all $t > 0$.

CHAPTER VIII

CONCLUSION

We developed a game theoretic model of kleptoparasitic behavior of the *O. taurus* dung beetle. Strategies took into account a beetle's genetic predetermination to land on dung of a certain age, steal or not steal, and guard or not guard. We calculated fitness of each strategy based on how many offspring each strategy could produce on average. We used the fitness equation (5.3) and definitions 3.3 and 3.4 to determine that there is no evolutionary stable strategy in our model.

We investigated the replicator dynamics of this population using Theorem 7.3. This theorem is a summary of the long term evolution of the population. A goal in developing Theorem 7.3 is to see what strategies a population of dung beetles will adopt over time. These strategies should be those that result in a higher fitness for the individual beetle, thus a higher reproductive success. These strategies will thus spread in the population.

It is clear that beetles should not wait to arrive until the dung is too dry to produce their own brood ball, so that stealing is the only option. This behavior is

not beneficial to beetles adopting it because they cannot be certain that there are other beetles in the population that are not guarding. Also if too much of a population adopts this habit, then eventually they will diminish the entire population of beetles that do not guard until the last day, so that no beetles will be available to kleptoparasitize. But this also proves that beetles should guard as long as possible because of the chance of stealers arriving in the same dung pat. We showed in chapter 6 that no strategy is evolutionarily stable, thus vulnerable strategies will decrease their fitness even if a small amount of stealers arrive. Guarding does result in less eggs being produced over time, but keeping the eggs safe against kleptoparasitism will help the strategy survive into the next generation.

We can also see that stealing is more productive than not stealing, when the stealers arrive early enough. This can be seen in strategies that arrive and leave the same day. Those that steal, whatever they can, will have a higher reproductive success than those that only prepare. If there is no population to steal from they will at least have the same fitness as those that only prepare.

The benefits of stealing prove that staying to protect brood balls is beneficial. But arriving between the days when dung is first usable and the day when dung is not usable at all will be more beneficial than arriving early or late. Those that arrive early can only prepare and those that arrive late can only steal. Those that

arrive in between can do both, resulting in a higher reproductive success.

In Theorem 7.3 we summarize the different initial mixture of strategies, but some of these initial mixtures aren't plausible, and some don't have plausible outcomes. Dung beetles have been shown to kleptoparasitize ([22], [18], [8]), which is why we're interested in them. Thus when we investigate the dynamics only initial mixtures with stealers present is plausible. When we investigate the ESS mixtures without an initial population of stealers, stealers could appear as mutants in later generations. Because of the benefits of stealing, eventually we should see the number of stealers grow. If stealers are in the population then beetles should guard at least until the time that the stealers arrive. This way if guarders sometimes leave earlier than usual, a stealer can benefit.

Though stealing is beneficial, all of the outcomes in Theorem 7.3 do not have stealers in them. Over time the stealers cause those that can be stolen from to go extinct, so that there is no way to distinguish between stealers and non-stealers. This is not compatible with what is seen in field observations. This can be explained by the simplified nature of our model. We only consider beetles that arrive at the beginning of the first, second, and third day. We do not consider beetles that may arrive before or after the start of the day. If we did consider different arrival times in a certain day then stealers may have a better chance to steal eggs that should

have been guarded.

The outcomes that seem the most plausible are those in parts 2c, 2d, and 2e of Theorem 7.3. These outcomes have different arrival and departure times, which has been observed to occur in nature. (The other strategies all have outcomes that have strategies that arrive and depart the dung pat at the same time.) Among these three strategies 2d and 2e don't have final mixtures that have stealers in them. From the previous argument, this is not plausible.

The dynamics do show that strategies that will do well over time are consistent in the amount of time they spend in a dung pat. This shows that over time a population of beetles will eventually tend to adopt the same guarding habits, even though there may not be any stealing behavior in the population. To determine whether beetles guard the same amount of time in a dung pat could be tested in the field.

This leads us to believe that the most plausible situation that would occur in nature is 2c of Theorem 7.3. In the outcome of this mixture there are beetles that arrive on the first day and guard two days, as well as beetles that arrive the second day, steal or not steal, and then guard until the fourth day. This outcome shows beetles guarding but there is still a chance, though a small one, of kleptoparasitism.

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