



## City Research Online

### City, University of London Institutional Repository

---

**Citation:** Yates, G. E. & Broom, M. (2007). Stochastic models of kleptoparasitism. *Journal of Theoretical Biology*, 248(3), pp. 480-489. doi: 10.1016/j.jtbi.2007.05.007

This is the unspecified version of the paper.

This version of the publication may differ from the final published version.

---

**Permanent repository link:** <https://openaccess.city.ac.uk/id/eprint/981/>

**Link to published version:** <https://doi.org/10.1016/j.jtbi.2007.05.007>

**Copyright:** City Research Online aims to make research outputs of City, University of London available to a wider audience. Copyright and Moral Rights remain with the author(s) and/or copyright holders. URLs from City Research Online may be freely distributed and linked to.

**Reuse:** Copies of full items can be used for personal research or study, educational, or not-for-profit purposes without prior permission or charge. Provided that the authors, title and full bibliographic details are credited, a hyperlink and/or URL is given for the original metadata page and the content is not changed in any way.

# Stochastic models of kleptoparasitism

G.E. Yates                      M. Broom

April 24, 2007

## Abstract

In this paper we consider a model of kleptoparasitism amongst a small group of individuals, where the state of the population is described by the distribution of its individuals over three specific types of behaviour (handling, searching for or fighting over, food). The model used is based upon earlier work which considered an equivalent deterministic model relating to large, effectively infinite, populations. We find explicit equations for the probability of the population being in each state. For any reasonably sized population, the number of possible states, and hence the number of equations, is large. These equations are used to find a set of equations for the means, variances, covariances and higher moments for the number of individuals performing each type of behaviour. Given the fixed population size, there are five moments of order one or two (two means, two variances and a covariance). A normal approximation is used to find a set of equations for these five principal moments. The results of our model are then analysed numerically, with the exact solutions, the normal approximation and the deterministic infinite population model compared. It is found that the original deterministic models approximate the stochastic model well in most situations, but that the normal approximations are better, proving to be good approximations to the exact distribution, which can greatly reduce computing time.

## 1 Introduction

There are many biological situations in which a population is divided amongst a number of sites. These sites may be physical locations, such as patches of food, or may categorise the population in some way, perhaps by their activity or whether they have a particular disease or not. The rates at which individuals leave each site depend on the current location of the individual in question, and are also often dependent on the location of other members of the population.

A feature of interest in such situations is the expected proportion of the population at each site at equilibrium. This is often calculated using a deterministic model, which assumes that the population is large. Individual movements in a small population have a much larger effect on transition rates than in a large population, and can also result in large differences between the expected proportion of the population on each site given by the two models. As a result of this, stochastic models are generally more appropriate when considering small populations. The use of stochastic models also enables the variance of the number of individuals at each site to be calculated, which is not possible using deterministic models. Examples of such models include:

- 1) The SIS epidemic. This is one of the simplest epidemic models, in which individuals are either susceptible or infective, and once they recover from the disease they are immediately susceptible again (see Weiss and Dishon 1971; Nasell 1996, 1999; Kryscio and Lefevre 1989).
- 2) Coagulation-fragmentation processes. The model population contains  $N$  individuals who are grouped into clusters of various sizes, where possible events are the merging of two groups into one and the separation of a group into two smaller groups. These processes have many applications including animal grouping; see Durrett et al (1998) and Durrett et al (1999) and their references.
- 3) The Ideal Free Distribution (Fretwell and Lucas 1970) which describes the distribution of animals among a number of patches of a resource, such as prey or mates (see, for example, Jackson et al 2004; Hugie and Grand 1998; Houston and McNamara 1988; Yates and Broom 2005).

We focus in this paper on the modelling of food stealing, or *kleptoparasitism*. Many authors have observed various animals stealing food from others. For example Brockmann and Barnard (1979) reviewed literature from the previous 40 years and found such occurrences among a variety of bird species. Such kleptoparasitic behaviour can be intraspecific, when food is stolen from members of the same species, or interspecific, when food is stolen from members of a different species. Although kleptoparasitism is particularly well documented among birds, it occurs in many species. For example, Vollrath (1979) conducted both field and laboratory research into the theridiid spider, which steals from two other spider species, while Homer et. al. (2002) have observed the behaviour in hyenas.

Recently a series of game-theoretic models of kleptoparasitic behaviour (e.g. Broom and Ruxton, 2003; Luther and Broom, 2004; Broom, Luther and Ruxton, 2004) have been developed investigating the strategic choices of individuals in a variety of circumstances. They took as their basis the paper Ruxton and Moody (1997) where behaviour was completely deterministic in character, due to the large population assumed and the lack of decisions of the individuals involved, and its refinement in Broom and Ruxton (1998). Indeed, conditional

on individuals' decisions, all of these models were essentially deterministic. In this paper we consider the refinement of Ruxton and Moody (1997) in Broom and Ruxton (1998) where no decisions are allowed by individuals, and introduce a stochastic version of this model, comparing the large population situation to the non-deterministic stochastic version.

## 2 The models

We first recall the structure of the basic model from Ruxton and Moody (1997) and Broom and Ruxton (1998).

They considered a population where the density of individuals is  $P$ . This population is divided into three different activities; searching for food items, which we label state  $S_1$  (state  $S$  in the original papers), handling a food item, state  $S_2$  (originally state  $H$ ), and involved in an aggressive contest, state  $S_3$  (originally state  $A$ ). We shall label the number of individuals in  $S_i$  as  $X_i$  for  $i = 1, 2$  and the number of *fighting pairs* in  $S_3$  as  $X_3$ . Thus if the total population size is  $n$ , then

$$X_1 + X_2 + 2X_3 = n$$

The number of available food items per unit area is given by  $f$ . Individuals were able to search an area  $\nu_f$  for food in unit time, so that the rate at which individual searchers found food (and so moved from state  $S_1$  to  $S_2$ ) was  $\lambda_{12} = \nu_f f$ . At the end of handling, the handler resumed searching. It was assumed that food items take a time to handle drawn from an exponential distribution with mean  $t_h$ , so that individuals move from state  $S_2$  to  $S_1$  at rate  $\lambda_{21} = 1/t_h$ . Individuals also searched for handlers, being able to search an area of size  $\nu_h$  per unit time. When a searcher encountered a handler, it challenged for the food item and a fight ensued, and one individual from each of  $S_1$  and  $S_2$  moved to the fighting state  $S_3$ , this occurred at rate  $\lambda_{13} = \nu_h$  per pair of individuals. Contest times were drawn from an exponential distribution with mean time  $t_a/2$ . At the end of a contest, the winner started handling the food, and the loser resumed searching, so that a fighting pair splits, one of each moving from  $S_3$  to the states  $S_1$  and  $S_2$ , at rate  $\lambda_{31} = 2/t_a$ . These are summarised in Figure 1.

### 2.1 The deterministic model

We further define the proportion of individuals in state  $S_i$  as  $z_i$  for all  $i$  and thus if the total population size is  $n$ , then  $z_1 = X_1/n$ ,  $z_2 = X_2/n$  and  $z_3 = 2X_3/n$ . The transition rates are as in Figure 2.

We can thus find the large population transition rates  $\lambda'_{ij}$  in terms of  $\lambda_{ij}$  as follows:

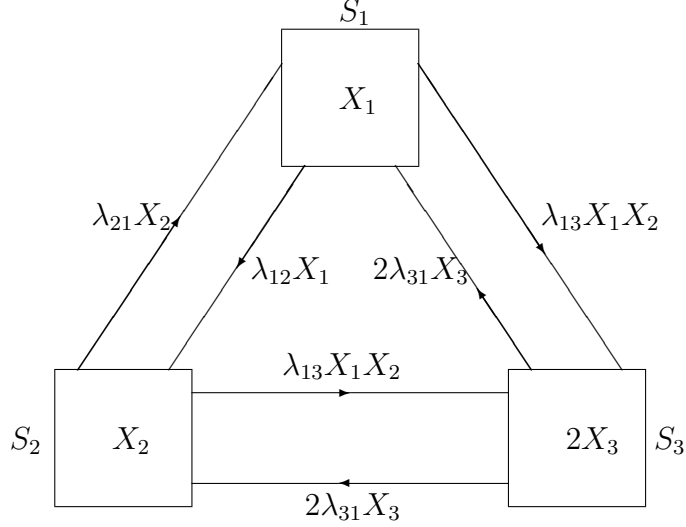


Figure 1: The Stochastic Kleptoparasitism Model. The sites are indicated by the boxes, transition rates are given on the arc with the arrow in the appropriate direction between the states. Both rates into  $S_3$  are identical, as are those leaving  $S_3$ . Individuals enter state  $S_3$  in pairs, one each from  $S_1$  and  $S_2$ . Similarly, pairs leave  $S_3$  simultaneously, with one going to each of  $S_1$  and  $S_2$ .

The transition rate from  $S_1$  to  $S_2$  is given by

$$\lambda_{12}X_1 = \lambda_{12}(nz_1) = n(\lambda'_{12}z_1) \text{ for large } n \Rightarrow \lambda'_{12} = \lambda_{12}.$$

Similarly  $\lambda'_{21} = \lambda_{21}$ ,

$$\text{while } 2\lambda_{31}X_3 = 2\lambda_{31}(nz_3/2) = n(\lambda'_{31}z_3) \text{ for large } n \Rightarrow \lambda'_{31} = \lambda_{31}$$

$$\text{and } \lambda_{13}X_1X_2 = \lambda_{13}(nz_1)(nz_2) = n(\lambda'_{13}z_1z_2) \text{ for large } n \Rightarrow \lambda'_{13} = n\lambda_{13}$$

Following Broom and Ruxton (1998) we see that for an essentially infinite population, the proportions of the population in each site satisfy the differential equations

$$\frac{dz_1}{dt} = \lambda'_{21}z_2 + \lambda'_{31}z_3 - \lambda'_{12}z_1 - \lambda'_{13}z_1z_2, \quad (1)$$

$$\frac{dz_2}{dt} = \lambda'_{12}z_1 + \lambda'_{31}z_3 - \lambda'_{21}z_2 - \lambda'_{13}z_1z_2, \quad (2)$$

$$\frac{dz_3}{dt} = 2\lambda'_{13}z_1z_2 - 2\lambda'_{31}z_3. \quad (3)$$

Note that Equation (3) can be obtained from a linear combination of Equations (1) and (2). At equilibrium  $\frac{dz_1}{dt} = \frac{dz_2}{dt} = \frac{dz_3}{dt} = 0$ , and substituting  $z_3 = 1 - z_1 - z_2$  into Equations (1) and (2) and rearranging gives

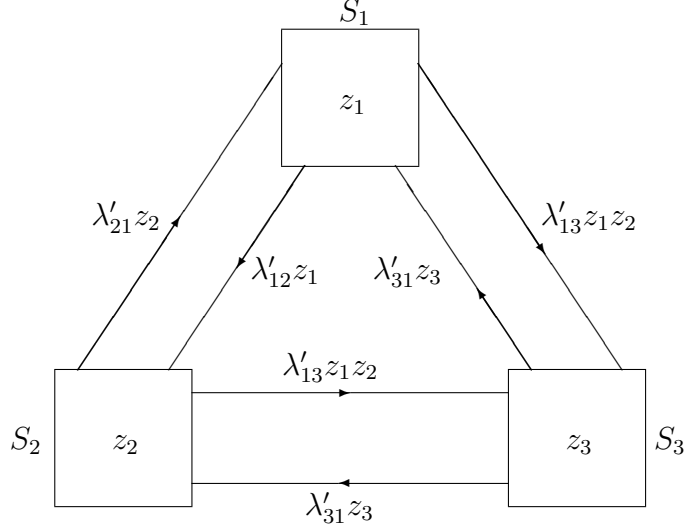


Figure 2: The Deterministic Kleptoparasitism Model. The states are indicated by the boxes, transition rates are given on the arc with the arrow in the appropriate direction between the states per individual; thus the actual transition rate of movement in a large population of size  $n$  is  $n \times$  this individual rate. Both rates into  $S_3$  are identical, as are those leaving  $S_3$ . Individuals enter state  $S_3$  in pairs, one each from  $S_1$  and  $S_2$ .

$$\begin{aligned} (\lambda'_{12} + \lambda'_{31})z_1 + (\lambda'_{31} - \lambda'_{21})z_2 + \lambda'_{13}z_1z_2 - \lambda'_{31} &= 0, \\ (\lambda'_{31} - \lambda'_{12})z_1 + (\lambda'_{21} + \lambda'_{31})z_2 + \lambda'_{13}z_1z_2 - \lambda'_{31} &= 0. \end{aligned}$$

Therefore

$$z_1 = \frac{\lambda'_{21}}{\lambda'_{12}} z_2, \quad (4)$$

while  $z_2$  solves

$$\lambda'_{13}\lambda'_{21}z_2^2 + \lambda'_{31}(\lambda'_{12} + \lambda'_{21})z_2 - \lambda'_{12}\lambda'_{31} = 0. \quad (5)$$

Since the coefficients of  $z_2^2$  and  $z_2$  in this equation are positive,  $z_2$  is given by the positive root, meaning that

$$z_2 = \frac{-\lambda'_{31}(\lambda'_{12} + \lambda'_{21}) + \sqrt{\lambda'_{31}^2(\lambda'_{12} + \lambda'_{21})^2 + 4\lambda'_{12}\lambda'_{13}\lambda'_{21}\lambda'_{31}}}{2\lambda'_{13}\lambda'_{21}}.$$

Note that  $z_2$  is the *handling ratio*, which is directly related to the food consumption rate per individual. In fact this consumption rate is  $z_2/t_h = \lambda'_{21}z_2$ .

## 2.2 The stochastic kleptoparasitism model

Following the description of transitions at the start of this section, we can see that the transition rates for this model are as shown in Figure 1. The numbers of individuals in  $S_1$  and  $S_2$  are  $X_1$  and  $X_2$  respectively, while  $X_3$  gives the number of pairs in  $S_3$ . There are only four possible movements. recall that the population size  $n$  is fixed, and that  $X_1 + X_2 + 2X_3 = n$ .

The probability that  $X_1(t) = x_1$  and  $X_2(t) = x_2$  is denoted by  $p_{x_1, x_2}(t)$ . The Kolmogorov forward equations for  $p_{x_1, x_2}(t)$  for this process are

$$\begin{aligned} \frac{d}{dt} p_{x_1, x_2}(t) &= \lambda_{13}(x_1 + 1)(x_2 + 1)p_{x_1+1, x_2+1}(t) + \lambda_{31}(n - x_1 - x_2 + 2)p_{x_1-1, x_2-1}(t) \\ &\quad + \lambda_{12}(x_1 + 1)p_{x_1+1, x_2-1}(t) + \lambda_{21}(x_2 + 1)p_{x_1-1, x_2+1}(t) \\ &\quad - [\lambda_{13}x_1x_2 + \lambda_{31}(n - x_1 - x_2) + \lambda_{12}x_1 + \lambda_{21}x_2]p_{x_1, x_2}(t). \end{aligned} \quad (6)$$

$\forall x_1, x_2 \in \{0, 1, \dots, n\}$ , where by convention  $p_{x_1, x_2} = 0$  if any of  $x_1 < 0$ ,  $x_2 < 0$  or  $x_1 + x_2 > n$  occur. In addition, since the number of individuals in  $S_3$  must be even,  $p_{x_1, x_2}(t) = 0$  if  $n - x_1 - x_2$  is odd. At equilibrium  $\frac{d}{dt} p_{x_1, x_2}(t) = 0 \forall x_1, x_2$  and these equations become a set of linear equations for the joint equilibrium distribution of  $X_1$  and  $X_2$ .

### 2.2.1 The number of distinct states of the stochastic model

Under the model,  $n - x_1 - x_2$  must be even; the number of states for which  $X_1 = x_1$  depends on whether  $n - x_1$  is odd or even. If  $n - x_1$  is odd, there are  $\frac{n-x_1+1}{2}$  such states, otherwise there are  $\frac{n-x_1}{2} + 1$  states. Since  $\frac{n-x_1+1}{2} = \frac{n-(x_1+1)}{2} + 1$ , the number of states when  $n$  is even is

$$\begin{aligned} \frac{n}{2} + 1 + \sum_{i=1}^{n/2} 2 \left( \frac{n-2i}{2} + 1 \right) &= \frac{n}{2} + 1 + \sum_{i=1}^{n/2} n - 2i + 2 = \frac{n}{2} + 1 + (n+2)\frac{n}{2} - \frac{n}{2} \left( \frac{n}{2} + 1 \right) \\ &= \left( \frac{n}{2} + 1 \right)^2. \end{aligned}$$

If  $n$  is odd the total number of states is

$$\begin{aligned} \sum_{k=1}^{(n+1)/2} 2 \left( \frac{n-(2k-1)}{2} + 1 \right) &= (n+3)\frac{n+1}{2} - 2 \sum_{k=1}^{(n+1)/2} k \\ &= (n+3)\frac{n+1}{2} - \frac{n+1}{2} \left( \frac{n+1}{2} + 1 \right) = \frac{(n+1)(n+3)}{4}. \end{aligned}$$

In either case the number of states is of order  $\frac{n^2}{4}$ .

### 2.2.2 Equations for the moments of $X_1$ and $X_2$

It is not practical to solve the equations for  $p_{x_1, x_2}$ . Instead we find equations for the principal moments of the process, namely the means, variances and the covariance of the random variables  $X_1$  and  $X_2$  (from which the moments involving  $X_3$  can also be found). We begin by obtaining a partial differential equation for the cumulant generating function of  $X_1$  and  $X_2$ , from which equations for the above moments can be derived. The cumulant generating function is denoted  $K(s_1, s_2)$  and is defined to be  $\log M(s_1, s_2)$ , where  $M(s_1, s_2)$  is the moment generating function. From this it is possible to obtain equations for the cumulants of  $X_1$  and  $X_2$ . The cumulant  $k_{i,j}$  is the coefficient of  $\frac{s_1^i s_2^j}{i!j!}$  in the series expansion of  $K(s_1, s_2)$ . The partial differential equation for  $K(s_1, s_2)$  is

$$\begin{aligned} n\lambda_{31}(e^{s_1+s_2} - 1) + [\lambda_{12}(e^{s_2-s_1} - 1) + \lambda_{31}(1 - e^{s_1+s_2})] \frac{\partial K}{\partial s_1} \\ + [\lambda_{21}(e^{s_1-s_2} - 1) + \lambda_{31}(1 - e^{s_1+s_2})] \frac{\partial K}{\partial s_2} \\ + \lambda_{13}(e^{-(s_1+s_2)} - 1) \left( \frac{\partial^2 K}{\partial s_1 \partial s_2} + \frac{\partial K}{\partial s_1} \frac{\partial K}{\partial s_2} \right) = 0. \quad (7) \end{aligned}$$

This is derived in Appendix A.

Differentiating  $K(s_1, s_2)$  with respect to  $s_1$   $i$  times and  $s_2$   $j$  times and setting  $s_1 = s_2 = 0$  in the function obtained gives the  $(i, j)$  cumulant of  $X_1$  and  $X_2$ .

For example,  $\frac{\partial K}{\partial s_1} \Big|_{s_1=s_2=0} = E(X_1)$ ,  $\frac{\partial^2 K}{\partial s_1^2} \Big|_{s_1=s_2=0} = Var(X_1)$  and  $\frac{\partial^2 K}{\partial s_1 \partial s_2} \Big|_{s_1=s_2=0} = Cov(X_1, X_2)$ .

Applying this to Equation (7) gives the following set of equations:

$$n\lambda_{31} - \lambda_{31}\mu_1 - \lambda_{31}\mu_2 - \lambda_{13}\sigma_{12} - \lambda_{13}\mu_1\mu_2 = 0, \quad (8)$$

$$\lambda_{12}\mu_1 - \lambda_{21}\mu_2 = 0, \quad (9)$$

$$\begin{aligned} n\lambda_{31} - \lambda_{31}\mu_1 + (\lambda_{21} - \lambda_{31})\mu_2 - (\lambda_{12} + \lambda_{31})\sigma_1^2 + (\lambda_{21} - \lambda_{31})\sigma_{12} - \lambda_{13}k_{2,1} - \lambda_{13}\mu_1\sigma_{12} \\ - \lambda_{13}\mu_2\sigma_1^2 = 0, \quad (10) \end{aligned}$$

$$\lambda_{12}\mu_1 + \lambda_{21}\mu_2 - \lambda_{12}\sigma_1^2 - \lambda_{21}\sigma_2^2 + (\lambda_{12} + \lambda_{21})\sigma_{12} = 0, \quad (11)$$



$$n\lambda_{31} + (\lambda_{12} - \lambda_{31})\mu_1 - \lambda_{31}\mu_2 - (\lambda_{21} + \lambda_{31})\sigma_2^2 + (\lambda_{12} - \lambda_{31})\sigma_{12} - \lambda_{13}k_{1,2} - \lambda_{13}\mu_2\sigma_{12} - \lambda_{13}\mu_1\sigma_2^2 = 0. \quad (12)$$

These 5 equations contain the 7 unknowns  $\mu_1, \mu_2, \sigma_1^2, \sigma_2^2, \sigma_{12}, k_{2,1}$  and  $k_{1,2}$ , where  $\mu_i = E(X_i)$ ,  $\sigma_i^2 = Var(X_i)$ ,  $\sigma_{12} = Cov(X_1, X_2)$ ,  $k_{2,1} = E[(X_1 - \mu_1)^2(X_2 - \mu_2)]$  and  $k_{1,2} = E[(X_1 - \mu_1)(X_2 - \mu_2)^2]$ . Further equations can be obtained, but the number of unknowns would also be increased.

It is possible to obtain expressions for  $\mu_1$  and  $\sigma_{12}$  in terms of  $\mu_2$  from the first two of these equations. These are

$$\mu_1 = \frac{\lambda_{21}}{\lambda_{12}}\mu_2 \quad (13)$$

and

$$\sigma_{12} = -\frac{\lambda_{21}}{\lambda_{12}}\mu_2^2 - \frac{\lambda_{31}(\lambda_{12} + \lambda_{21})}{\lambda_{13}\lambda_{12}}\mu_2 + \frac{n\lambda_{31}}{\lambda_{13}} \quad (14)$$

and are derived in Appendix B.

We now show two results relating these moments.

**Result 1** The signs of  $nz_1 - \mu_1$  and  $nz_2 - \mu_2$  are the same.

The proof follows from the fact that expression (4) for  $z_1$ , with the substitutions  $\lambda'_{12} = \lambda_{12}$  and  $\lambda'_{21} = \lambda_{21}$  can be rearranged to give

$$\lambda_{12}z_1 - \lambda_{21}z_2 = 0.$$

Multiplying this equation by  $n$  and subtracting (9) gives

$$\lambda_{12}(nz_1 - \mu_1) = \lambda_{21}(nz_2 - \mu_2).$$

Since  $\lambda_{12}$  and  $\lambda_{21}$  are both positive, it follows that  $nz_1 - \mu_1$  and  $nz_2 - \mu_2$  have the same sign.

Thus the number of searchers and handlers are either both overestimated or both underestimated by the deterministic model.

**Result 2** The signs of  $nz_2 - \mu_2$  and  $\sigma_{12}$  are the same (and so are also the same as that of  $nz_1 - \mu_1$ )

Making the substitutions  $\lambda'_{12} = \lambda_{12}$ ,  $\lambda'_{13} = n\lambda_{13}$ ,  $\lambda'_{21} = \lambda_{21}$  and  $\lambda'_{31} = \lambda_{31}$  into Equation (5) and multiplying by  $n$  gives

$$\lambda_{13}\lambda_{21}(nz_2)^2 + \lambda_{31}(\lambda_{12} + \lambda_{21})nz_2 - n\lambda_{12}\lambda_{31} = 0.$$

Substituting the expression for  $\mu_1$  into (8) and multiplying by  $\lambda_{12}$  gives

$$n\lambda_{12}\lambda_{31} - \lambda_{31}(\lambda_{12} + \lambda_{21})\mu_2 - \lambda_{12}\lambda_{13}\sigma_{12} - \lambda_{13}\lambda_{21}\mu_2^2 = 0.$$

Adding these two equations gives

$$\begin{aligned} & \lambda_{13}\lambda_{21}((nz_2)^2 - \mu_2^2) + \lambda_{31}(\lambda_{12} + \lambda_{21})(nz_2 - \mu_2) - \lambda_{12}\lambda_{13}\sigma_{12} = 0. \\ \Rightarrow & (nz_2 - \mu_2)(\lambda_{13}\lambda_{21}(nz_2 + \mu_2) + \lambda_{31}(\lambda_{12} + \lambda_{21})) = \lambda_{12}\lambda_{13}\sigma_{12}. \end{aligned}$$

This shows that the signs of  $nz_2 - \mu_2$  and  $\sigma_{12}$  are the same, since the  $\lambda_{ij}$ s and  $\mu_2$  are all positive.

Thus if  $X_1$  and  $X_2$  are negatively correlated, as we would naively assume should usually be the case since the total number of individuals in the three categories is fixed, then this would indicate that the deterministic model would underestimate the number of searchers and handlers.

### 2.2.3 The normal approximation

If one assumes that  $X_1$  and  $X_2$  are bivariate normal, then  $k_{2,1}$  and  $k_{1,2}$  are both 0. This method is described by Whittle (1957) and has been applied more recently by Nasell (2003) with the stochastic logistic model, of which the SIS epidemic is an example. Using this approximation it is possible to derive expressions for  $\hat{\sigma}_1^2$  and  $\hat{\sigma}_2^2$  in terms of  $\hat{\mu}_2$ , and a quartic equation for  $\hat{\mu}_2$ , where the  $\hat{\cdot}$  above each variable denotes the normal approximation. These are derived in Appendix B.

The variances are given by

$$\begin{aligned} \hat{\sigma}_1^2 = & \frac{\lambda_{21}^2}{\lambda_{12}^2}\hat{\mu}_2^2 + \frac{2\lambda_{21}(\lambda_{31} - \lambda_{21})}{\lambda_{12}\lambda_{13}}\hat{\mu}_2 + \frac{\lambda_{21} - \lambda_{31}}{\lambda_{13}} + \frac{2\lambda_{21}^2 - 3\lambda_{21}\lambda_{31} + \lambda_{31}^2}{\lambda_{13}^2} - \frac{\lambda_{21}\lambda_{31}(n+1)}{\lambda_{12}\lambda_{13}} \\ & + \frac{\lambda_{21}\lambda_{31}(\lambda_{21} - \lambda_{31})}{\lambda_{12}\lambda_{13}^2} + \frac{\lambda_{31}((2\lambda_{21} - \lambda_{31})n + \lambda_{12} + \lambda_{31}) - \lambda_{12}\lambda_{21}}{\lambda_{13}(\lambda_{12} + \lambda_{31} + \lambda_{13}\hat{\mu}_2)} \\ & + \frac{\lambda_{31}n}{\lambda_{12} + \lambda_{31} + \lambda_{13}\hat{\mu}_2} + \frac{(\lambda_{31} - \lambda_{21})(3\lambda_{21}\lambda_{31} + 2\lambda_{12}\lambda_{21} - \lambda_{31}^2 - \lambda_{12}\lambda_{31})}{\lambda_{13}^2(\lambda_{12} + \lambda_{31} + \lambda_{13}\hat{\mu}_2)} \\ & + \frac{\lambda_{21}\lambda_{31}^2(n+1)}{\lambda_{12}\lambda_{13}(\lambda_{12} + \lambda_{31} + \lambda_{13}\hat{\mu}_2)} + \frac{\lambda_{21}\lambda_{31}^2(\lambda_{31} - \lambda_{21})}{\lambda_{12}\lambda_{13}^2(\lambda_{12} + \lambda_{31} + \lambda_{13}\hat{\mu}_2)} \quad (15) \end{aligned}$$

and

$$\begin{aligned}
\hat{\sigma}_2^2 = & \hat{\mu}_2^2 + \frac{2(\lambda_{31} - \lambda_{12})}{\lambda_{13}} \hat{\mu}_2 + \frac{\lambda_{12} - \lambda_{31}}{\lambda_{13}} + \frac{2\lambda_{12}^2 - 3\lambda_{12}\lambda_{31} + \lambda_{31}^2}{\lambda_{13}^2} - \frac{\lambda_{12}\lambda_{31}(n+1)}{\lambda_{13}\lambda_{21}} \\
& + \frac{\lambda_{12}\lambda_{31}(\lambda_{12} - \lambda_{31})}{\lambda_{13}^2\lambda_{21}} + \frac{\lambda_{12}[\lambda_{31}((2\lambda_{12} - \lambda_{31})n + \lambda_{21} + \lambda_{31}) - \lambda_{12}\lambda_{21}]}{\lambda_{13}(\lambda_{21}\lambda_{12} + \lambda_{31}\lambda_{12} + \lambda_{21}\lambda_{13}\hat{\mu}_2)} \\
& + \frac{\lambda_{12}\lambda_{31}n}{\lambda_{21}\lambda_{12} + \lambda_{31}\lambda_{12} + \lambda_{21}\lambda_{13}\hat{\mu}_2} + \frac{\lambda_{12}(\lambda_{31} - \lambda_{12})(3\lambda_{31}\lambda_{12} + 2\lambda_{21}\lambda_{12} - \lambda_{31}^2 - \lambda_{21}\lambda_{31})}{\lambda_{13}^2(\lambda_{21}\lambda_{12} + \lambda_{31}\lambda_{12} + \lambda_{21}\lambda_{13}\hat{\mu}_2)} \\
& + \frac{\lambda_{12}^2\lambda_{31}^2(n+1)}{\lambda_{13}\lambda_{21}(\lambda_{21}\lambda_{12} + \lambda_{31}\lambda_{12} + \lambda_{21}\lambda_{13}\hat{\mu}_2)} + \frac{\lambda_{12}^2\lambda_{31}^2(\lambda_{31} - \lambda_{12})}{\lambda_{13}^2\lambda_{21}(\lambda_{21}\lambda_{12} + \lambda_{31}\lambda_{12} + \lambda_{21}\lambda_{13}\hat{\mu}_2)}, \quad (16)
\end{aligned}$$

while the quartic equation for  $\hat{\mu}_2$  is

$$\begin{aligned}
& 2\lambda_{13}^3\lambda_{21}^2(\lambda_{12} + \lambda_{21})\hat{\mu}_2^4 \\
& + \lambda_{13}^2\lambda_{21}(3\lambda_{31}(\lambda_{12}^2 + \lambda_{21}^2) + 2\lambda_{12}\lambda_{21}(\lambda_{12} - \lambda_{13} + \lambda_{21} + 5\lambda_{31}))\hat{\mu}_2^3 \\
& + \lambda_{13}[\lambda_{31}(\lambda_{12} + \lambda_{21})(\lambda_{31}(\lambda_{12}^2 + \lambda_{21}^2) + \lambda_{21}\lambda_{12}(3(\lambda_{12} + \lambda_{21}) - 2\lambda_{13}(n+2) + 8\lambda_{31})) \\
& \quad - 2\lambda_{12}^2\lambda_{13}\lambda_{21}^2]\hat{\mu}_2^2 \\
& + \lambda_{12}\lambda_{31}[2(\lambda_{12} + \lambda_{21})^2\lambda_{31}^2 - \lambda_{13}\lambda_{31}((\lambda_{12}^2 + \lambda_{21}^2)(n+1) + 2\lambda_{12}\lambda_{21}(3n+2)) \\
& \quad + \lambda_{31}(\lambda_{12} + \lambda_{21})^3 - \lambda_{12}\lambda_{13}\lambda_{21}(\lambda_{12} + \lambda_{21})(2n+3) + 2n\lambda_{12}\lambda_{13}^2\lambda_{21}]\hat{\mu}_2 \\
& + -\lambda_{12}^2\lambda_{31}n(\lambda_{31}(\lambda_{12} + \lambda_{21})(\lambda_{12} - \lambda_{13} + \lambda_{21} + 2\lambda_{31}) - 2\lambda_{12}\lambda_{13}\lambda_{21}) \\
& = 0. \quad (17)
\end{aligned}$$

These equations are of course rather cumbersome, but can be used to find numerical results, as we do in the following section.

### 3 Numerical evaluations

Tables 1 - 4 show the results of evaluations of both the stochastic and deterministic models, along with the normal approximation to the stochastic model, for a variety of parameter values. Those in Tables 1 and 2 were chosen specifically to give a range of sets of values, so that different features of the model might be demonstrated. The  $\lambda_{ij}$ s used in Tables 3 and 4 were randomly generated;  $\lambda_{12}, \lambda_{21}, \lambda_{31} \sim U(0, 50)$  and  $\lambda_{13} \sim U(0, 2.5)$ , the distributions chosen to ensure that the transition rates were, on average, of similar order ( $\lambda_{13}$  being associated with the only quadratic transition). Tables 1 and 3 show  $\mu_1, \mu_2, \sigma_1^2, \sigma_2^2, \sigma_{12}, k_{2,1}$  and  $k_{1,2}$ , while Tables 2 and 4 show  $\mu_3, \sigma_3^2, \sigma_{13}$  and  $\sigma_{23}$ .

Since  $\hat{\mu}_2$  satisfies a quartic equation, the normal approximation gives 4 values for  $\hat{\mu}_2$ . Only

Model	$\lambda_{12}$	$\lambda_{13}$	$\lambda_{21}$	$\lambda_{31}$	$\mu_1$	$\mu_2$	$\sigma_{12}$	$\sigma_1^2$	$\sigma_2^2$	$k_{2,1}$	$k_{1,2}$
S	1.5	2	1.5	3	7.3247	7.3247	-0.63	6.70	6.70	-0.56	-0.56
D	1.5	2	1.5	3	7.2892	7.2892					
N	1.5	2	1.5	3	7.3267	7.3267	-0.66	6.67	6.67		
S	5	2	5	3	7.3247	7.3247	-0.63	6.70	6.70	-0.56	-0.56
D	5	2	5	3	7.2892	7.2892					
N	5	2	5	3	7.3267	7.3267	-0.66	6.67	6.67		
S	1	0.06	1	1	16.7296	16.7296	-4.20	12.53	12.53	-2.62	-2.62
D	1	0.06	1	1	16.6667	16.6667					
N	1	0.06	1	1	16.7302	16.7302	-4.24	12.49	12.49		
S	50	0.06	1	1	0.9304	46.5218	-0.82	0.91	5.34	-0.80	0.56
D	50	0.06	1	1	0.9296	46.4782					
N	50	0.06	1	1	0.9304	46.5219	-0.82	0.91	5.33		
S	1	3	1	1	3.7815	3.7815	-0.15	3.63	3.63	-0.15	-0.15
D	1	3	1	1	3.7627	3.7627					
N	1	3	1	1	3.7840	3.7840	-0.17	3.61	3.61		
S	1	0.06	1	50	24.6428	24.6428	-11.97	12.67	12.67	-0.50	-0.50
D	1	0.06	1	50	24.6358	24.6358					
N	1	0.06	1	50	24.6428	24.6428	-11.97	12.67	12.67		
S	1	2	3	4	13.8421	4.6140	-0.78	11.50	4.35	-0.62	-0.73
D	1	2	3	4	13.7764	4.5921					
N	1	2	3	4	13.8448	4.6149	-0.81	11.48	4.32		

Table 1: The mean, variance and covariance of  $X_1$  and  $X_2$  for a variety of transition rates.  $n = 50$  in all cases. The letters in the Model column correspond to each of the models. S stands for stochastic, D for deterministic and N for normal approximation. The values for the deterministic model in the 'mean' columns are  $nz_1$  and  $nz_2$  respectively. The stochastic model and normal approximation are described in Sections 2.2 and 2.2.3 respectively.

Description	$\lambda_{12}$	$\lambda_{13}$	$\lambda_{21}$	$\lambda_{31}$	$\mu_3$	$\sigma_{13}$	$\sigma_{23}$	$\sigma_3^2$
S	1.5	2	1.5	3	35.3505	-6.07	-6.07	12.15
D	1.5	2	1.5	3	35.4216			
N	1.5	2	1.5	3	35.3467	-6.01	-6.01	12.01
S	5	2	5	3	35.3505	-6.07	-6.07	12.15
D	5	2	5	3	35.4216			
N	5	2	5	3	35.3467	-6.01	-6.01	12.01
S	1	0.06	1	1	16.5408	-8.33	-8.33	16.67
D	1	0.06	1	1	16.6667			
N	1	0.06	1	1	16.5396	-8.25	-8.25	16.51
S	50	0.06	1	1	2.5477	-0.09	-4.51	4.61
D	50	0.06	1	1	2.5923			
N	50	0.06	1	1	2.5477	-0.09	-4.51	4.60
S	1	3	1	1	42.4370	-3.47	-3.47	6.95
D	1	3	1	1	42.4745			
N	1	3	1	1	42.4321	-3.44	-3.44	6.87
S	1	0.06	1	50	0.7144	-0.69	-0.69	1.39
D	1	0.06	1	50	0.7283			
N	1	0.06	1	50	0.7144	-0.69	-0.69	1.39
S	1	2	3	4	31.5439	-10.72	-3.57	14.29
D	1	2	3	4	31.6315			
N	1	2	3	4	31.5403	-10.66	-3.51	14.17

Table 2: The mean and variance of the number of individuals on Site 3, along with the covariances of the number on Site 3 with the numbers of individuals on Sites 1 and 2, for a variety of transition rates.  $n = 50$  in all cases. The letters in the Model column correspond to each of the models. S stands for stochastic, D for deterministic and N for normal approximation. The value for the deterministic model in the 'mean' column is  $nz_3$ . The stochastic model and normal approximation are described in Sections 2.2 and 2.2.3 respectively.

Model	$\lambda_{12}$	$\lambda_{13}$	$\lambda_{21}$	$\lambda_{31}$	$\mu_1$	$\mu_2$	$\sigma_{12}$	$\sigma_1^2$	$\sigma_2^2$	$k_{2,1}$	$k_{1,2}$
S	26.39	1.297	23.80	11.81	13.4338	14.8958	-2.78	10.92	11.81	-2.06	-1.98
D	26.39	1.297	23.80	11.81	13.3769	14.8327					
N	26.39	1.297	23.80	11.81	13.4348	14.8968	-2.83	10.88	11.76		
S	13.50	2.380	13.96	3.281	7.1911	6.9542	-0.58	6.59	6.39	-0.52	-0.53
D	13.50	2.380	13.96	3.281	7.1562	6.9204					
N	13.50	2.380	13.96	3.281	7.1931	6.9561	-0.61	6.56	6.36		
S	17.47	2.300	32.69	30.01	20.9940	11.2195	-3.47	14.51	9.37	-1.89	-2.63
D	17.47	2.300	32.69	30.01	20.9123	11.1758					
N	17.47	2.300	32.69	30.01	20.9950	11.2200	-3.51	14.47	9.33		
S	49.44	1.516	35.76	9.751	10.7328	14.8386	-2.13	9.19	11.89	-1.72	-1.57
D	49.44	1.516	35.76	9.751	10.6853	14.7730					
N	49.44	1.516	35.76	9.751	10.7338	14.8400	-2.18	9.15	11.84		
S	46.02	1.274	46.33	4.207	10.0455	9.9783	-1.25	8.79	8.74	-1.05	-1.06
D	46.02	1.274	46.33	4.207	9.9983	9.9314					
N	46.02	1.274	46.33	4.207	10.0470	9.9798	-1.29	8.75	8.70		
S	44.00	0.2067	34.01	21.19	19.7018	25.4890	-9.16	12.62	13.64	-3.16	-1.40
D	44.00	0.2067	34.01	21.19	19.6698	25.4476					
N	44.00	0.2067	34.01	21.19	19.7019	25.4890	-9.17	12.61	13.63		
S	23.63	1.273	16.87	40.05	16.0989	22.5499	-5.91	11.88	14.27	-3.39	-2.38
D	23.63	1.273	16.87	40.05	16.0499	22.4813					
N	23.63	1.273	16.87	40.05	16.0992	22.5503	-5.94	11.85	14.25		
S	49.66	0.1327	2.763	13.47	2.5746	46.2746	-2.33	2.45	4.41	-2.10	1.79
D	49.66	0.1327	2.763	13.47	2.5735	46.2538					
N	49.66	0.1327	2.763	13.47	2.5746	46.2746	-2.33	2.44	4.42		
S	17.15	0.9662	10.15	0.9526	4.6964	7.9353	-0.42	4.45	7.22	-0.40	-0.38
D	17.15	0.9662	10.15	0.9526	4.6734	7.8964					
N	17.15	0.9662	10.15	0.9526	4.6979	7.9379	-0.45	4.43	7.18		
S	5.771	0.2995	19.09	28.51	35.3951	10.7001	-7.02	12.16	8.58	1.53	-4.44
D	5.771	0.2995	19.09	28.51	35.3468	10.6855					
N	5.771	0.2995	19.09	28.51	35.3952	10.7001	-7.03	12.18	8.56		
S	26.27	1.606	15.26	27.52	12.6004	21.6915	-4.15	10.19	14.54	-2.95	-2.08
D	26.27	1.606	15.26	27.52	12.5542	21.6120					
N	26.27	1.606	15.26	27.52	12.6008	21.6922	-4.19	10.15	14.51		

Table 3: The mean, variance and covariance of  $X_1$  and  $X_2$  for a variety of transition rates.  $n = 50$  in all cases. The letters in the Model column correspond to each of the models. S stands for stochastic, D for deterministic and N for normal approximation. The values for the deterministic model in the 'mean' columns are  $nz_1$  and  $nz_2$  respectively. The stochastic model and normal approximation are described in Sections 2.2 and 2.2.3 respectively.

Model	$\lambda_{12}$	$\lambda_{13}$	$\lambda_{21}$	$\lambda_{31}$	$\mu_3$	$\sigma_{13}$	$\sigma_{23}$	$\sigma_3^2$
S	26.39	1.297	23.80	11.81	21.6704	-8.14	-9.02	17.16
D	26.39	1.297	23.80	11.81	21.7904			
N	26.39	1.297	23.80	11.81	21.6685	-8.05	-8.93	16.98
S	13.50	2.380	13.96	3.281	35.8547	-6.01	-5.81	11.82
D	13.50	2.380	13.96	3.281	35.9235			
N	13.50	2.380	13.96	3.281	35.8508	-5.95	-5.75	11.70
S	17.47	2.300	32.69	30.01	17.7865	-11.04	-5.90	16.94
D	17.47	2.300	32.69	30.01	17.9119			
N	17.47	2.300	32.69	30.01	17.7850	-10.96	-5.82	16.78
S	49.44	1.516	35.76	9.751	24.4286	-7.06	-9.76	16.81
D	49.44	1.516	35.76	9.751	24.5417			
N	49.44	1.516	35.76	9.751	24.4263	-6.98	-9.66	16.64
S	46.02	1.274	46.33	4.207	29.9763	-7.54	-7.49	15.03
D	46.02	1.274	46.33	4.207	30.0702			
N	46.02	1.274	46.33	4.207	29.9732	-7.46	-7.41	14.87
S	44.00	0.2067	34.01	21.19	4.8092	-3.46	-4.48	7.94
D	44.00	0.2067	34.01	21.19	4.8826			
N	44.00	0.2067	34.01	21.19	4.8091	-3.44	-4.46	7.90
S	23.63	1.273	16.87	40.05	11.3511	-5.97	-8.36	14.33
D	23.63	1.273	16.87	40.05	11.4688			
N	23.63	1.273	16.87	40.05	11.3506	-5.91	-8.31	14.22
S	49.66	0.1327	2.763	13.47	1.1508	-0.12	-2.08	2.20
D	49.66	0.1327	2.763	13.47	1.1727			
N	49.66	0.1327	2.763	13.47	1.1507	-0.11	-2.09	2.20
S	17.15	0.9662	10.15	0.9526	37.3683	-4.02	-6.79	10.81
D	17.15	0.9662	10.15	0.9526	37.4301			
N	17.15	0.9662	10.15	0.9526	37.3642	-3.97	-6.73	10.70
S	5.771	0.2995	19.09	28.51	3.9048	-5.13	-1.55	6.69
D	5.771	0.2995	19.09	28.51	3.9677			
N	5.771	0.2995	19.09	28.51	3.9047	-5.14	-1.52	6.67
S	26.27	1.606	15.26	27.52	15.7081	-6.04	-10.39	16.43
D	26.27	1.606	15.26	27.52	15.8337			
N	26.27	1.606	15.26	27.52	15.7069	-5.96	-10.32	16.28

Table 4: The mean and variance of the number of individuals on Site 3, along with the covariances of the number on Site 3 with the numbers of individuals on Sites 1 and 2, for a variety of transition rates.  $n = 50$  in all cases. The letters in the Model column correspond to each of the models. S stands for stochastic, D for deterministic and N for normal approximation. The value for the deterministic model in the 'mean' column is  $nz_3$ . The stochastic model and normal approximation are described in Sections 2.2 and 2.2.3 respectively.

one of the solutions of Equation (17) was a plausible value for  $\hat{\mu}_2$  for each set of parameters used here. The normal approximation is very accurate and all of the estimates of  $\sigma_3^2$ ,  $\sigma_{13}$  and  $\sigma_{23}$  are fairly good. In particular, the normal approximation agrees more closely with the stochastic model than does the deterministic model for each parameter set.

The deterministic model, stochastic model and its normal approximation were evaluated for 400 sets of parameters with the results summarised in Tables 5 and 6. In each case the population size was either 10, 20, 30, 40 or 50. For the first 200 sets (Table 5)  $\lambda_{12}$ ,  $\lambda_{21}$  and  $\lambda_{31} \sim U(0, n)$  and  $\lambda_{13} \sim U(0, 3)$  so that the transition rates were of similar order. The covariance between  $X_1$  and  $X_2$ ,  $\sigma_{12}$ , is negative for each of these sets of parameters. In the last 200 parameter sets (Table 6)  $\lambda_{12} \sim U(0.5, 1.5)$ ,  $\lambda_{13}, \lambda_{21} \sim U(10^6, 1.0001 \times 10^{10})$  and  $\lambda_{31} \sim U(0, 0.1)$ . These distributions were chosen to give parameter sets for which  $\sigma_{12}$  may be positive. If  $\sigma_{12}$  is to be positive it must be when  $\mu_2$  is small, since expression (14) for  $\sigma_{12}$  in terms of  $\mu_2$  is decreasing in  $\mu_2$ . Also,  $\frac{n\lambda_{31}}{\lambda_{13}}$  must be larger than  $\frac{\lambda_{21}}{\lambda_{12}}\mu_2^2 + \frac{\lambda_{31}(\lambda_{12} + \lambda_{21})}{\lambda_{13}\lambda_{12}}\mu_2$ . They were chosen as a result of carrying out some evaluations for which  $\sigma_{12}$  was close to zero. When the normal approximation provided more than one set of values for the cumulants, the set which gave the means closest to those given by the deterministic model were used.

From Tables 1,3 and 5 we can see that generally the deterministic model underestimates the number of individuals in states  $S_1$  and  $S_2$ , i.e. that  $nz_1 < \mu_1$  and  $nz_2 < \mu_2$ . Thus there is a consistent bias when using the large population approximation, when the values of the transition rates are broadly comparable. Associated with this, the covariance of  $X_1$  and  $X_2$  was negative in each case (as we may expect because there is a total of  $n$  individuals to divide between these categories). However, the covariance between  $X_1$  and  $X_2$  was positive in 180 out of the 200 cases from Table 6 (which used values evaluated in order to try to make this occur). It follows from Results 1 and 2 in Section 2.2 that  $nz_1 > \mu_1$  and  $nz_2 > \mu_2$  in these cases, and so sometimes the more usual result above does not occur. Note that, as can be seen, the bias is very small and the large population approximation predicts the expectation of the number of individuals in these states well (although the variance can be quite large). The use of deterministic models for the various previous works on kleptoparasitism such as Broom and Ruxton (1998) thus seems reasonable.

The other two covariances were not positive for any of the parameter sets investigated. Thus the number in the fighting category  $S_3$  seems always negatively correlated with the numbers in either of the other categories. It was found that  $\sigma_1^2 < \sigma_2^2 \iff \mu_1 < \mu_2$  and  $\sigma_1^2 > \sigma_2^2 \iff \mu_1 > \mu_2$  for all cases evaluated. This again makes sense; the larger the expected number of a given site, the larger the magnitude of the variance of this number. We have not been able to prove the generality of these results.

For every set of parameters tested  $\mu_i \leq \hat{\mu}_i$ ,  $i=1,2$  and  $\sigma_{12} > \hat{\sigma}_{12}$ .  $\hat{\mu}_i$  and  $\hat{\sigma}_{12}$  are the



Characteristic	Number of Evaluations
Total evaluations	200
$\sigma_{12} > 0$	0
$\mu_1 < \mu_2$ and $\sigma_1^2 > \sigma_2^2$	0
$\mu_2 < \mu_1$ and $\sigma_2^2 > \sigma_1^2$	0
$\mu_1 > \hat{\mu}_1$	0
$k_{2,1} < 0$ & $\sigma_1^2 < \hat{\sigma}_1^2$	11
$k_{2,1} > 0$ & $\sigma_1^2 > \hat{\sigma}_1^2$	0
$k_{1,2} < 0$ & $\sigma_2^2 < \hat{\sigma}_2^2$	3
$k_{1,2} > 0$ & $\sigma_2^2 > \hat{\sigma}_2^2$	1
$\sigma_{13} > 0$	0
$\sigma_{23} > 0$	0
Multiple possible sets of parameters under normal approximation	7

Table 5: A summary of numerical evaluations of the model with paired movements into and out of  $S_3$ .  $n=10, 20, 30, 40$  or  $50$ .  $\lambda_{12}, \lambda_{21}, \lambda_{31} \sim U(0, n)$ ,  $\lambda_{13} \sim U(0, 3)$ .

Characteristic	Number of Evaluations
Total evaluations	200
$\sigma_{12} > 0$	180
$\mu_1 < \mu_2$ and $\sigma_1^2 > \sigma_2^2$	0
$\mu_2 < \mu_1$ and $\sigma_2^2 > \sigma_1^2$	0
$\mu_1 > \hat{\mu}_1$	0
$k_{2,1} < 0$ & $\sigma_1^2 < \hat{\sigma}_1^2$	0
$k_{2,1} > 0$ & $\sigma_1^2 > \hat{\sigma}_1^2$	17
$k_{1,2} < 0$ & $\sigma_2^2 < \hat{\sigma}_2^2$	6
$k_{1,2} > 0$ & $\sigma_2^2 > \hat{\sigma}_2^2$	2
$\sigma_{13} > 0$	0
$\sigma_{23} > 0$	0
Multiple possible sets of parameters under normal approximation	196

Table 6: A summary of numerical evaluations of the model with paired movements into and out of  $S_3$ .  $n=10, 20, 30, 40$  or  $50$ .  $\lambda_{12} \sim U(0.5, 1.5)$ ,  $\lambda_{13}, \lambda_{21} \sim U(10^6, 1.0001 \times 10^{10})$ ,  $\lambda_{31} \sim U(0, 0.1)$ .

estimates of  $\mu_i$  and  $\sigma_{12}$  under the normal approximation. Thus the normal approximation seems to always overestimate  $\mu_1$  and  $\mu_2$  (although this overestimate is very small). It has, again, not been possible to prove the generality of this result.

## 4 Discussion

This paper considers both a deterministic and a stochastic model for kleptoparasitism, along with a normal approximation to the stochastic model. The deterministic model is that of Broom and Ruxton (1998), for which explicit solutions for the equilibrium proportion of the population on each site can be found. The forward Kolmogorov equations were derived for the equilibrium distribution of the stochastic model. It is not practical to solve these explicitly, but numerical solutions have been obtained for many sets of parameters.

A partial differential equation for the cumulant generating function was derived for the stochastic model. A set of 5 equations for the means, variances and covariance of the number of individuals on sites 1 and 2 has been obtained from this. These equations contain 7 unknowns, since they also contain the cumulants  $k_{2,1}$  and  $k_{1,2}$ . The normal approximation reduces the number of unknowns, since  $k_{2,1}$  and  $k_{1,2}$  are assumed to be zero under this approximation. These equations are not linear, and the solution is given in the form of a quartic equation for  $\mu_2$  and expressions for  $\mu_1$ ,  $\sigma_1^2$ ,  $\sigma_2^2$  and  $\sigma_{12}$  in terms of  $\mu_2$ .

The stochastic model generally gave larger numbers of individuals on sites 1 and 2 than the deterministic model. This corresponds to a larger number of searchers and handlers, and a smaller number of individuals fighting. Thus, the deterministic approximation will often overestimate the number of individuals involved in a contest, and we may expect to see less conflict than is predicted by our models, especially in the case of small populations, where the differences with the infinite population approximation will be largest. One possible reason for this is as follows: if the number of individuals on  $S_1$  and  $S_2$  in equilibrium were equal, then any movement between the two would reduce the product  $X_1X_2$ , and so the rate of movement towards the fighting state  $S_3$  would generally be reduced by this variability. This argument may still hold when  $X_1$  and  $X_2$  are of similar order. The differences between stochastic and deterministic models were always small however, indicating the validity of the use of the deterministic model for these kind of systems. The difference between these values is related to the sign of the covariance between the numbers of individuals on sites 1 and 2 as shown in Section 3. There were some cases for which this covariance is positive, meaning that the deterministic model gives the larger numbers of individuals on sites 1 and 2. These were associated when the numbers in  $S_1$  and  $S_2$  were very uneven (in particular  $X_2$  was small), so the above argument may be reversed, and variability may increase  $X_1X_2$

on average.

The normal approximation performs well, particularly for estimating the means, where these were a lot closer to the means given by the stochastic model than were those given by the deterministic model. In fact the differences between the actual means and the normal approximations were almost zero. The approach of using Normal approximations to simplify the analysis of such systems seems a possible way forward. For any such system of equations we would have a multivariate normal random variable of dimension  $k$ , the total number of sites. Although the quartic equation and expressions for the variances are long, they can be evaluated numerically much more quickly than the equilibrium Kolmogorov equations can be solved. This will be especially true if, as in our kleptoparasitism model, we are interested in the distribution of the number of individuals involved in a particular behaviour, for an intermediately sized population (for a very small population, we could find numerical solutions to the Kolmogorov equations themselves).

# Appendices

## A Derivation of Equation (7)

The first step in deriving this equation is to multiply Equations (6) by  $\exp\{s_1x_1 + s_2x_2\}$  and add over all values of  $X_1$  and  $X_2$ . This gives

$$\begin{aligned} & \sum_{x_1=0}^n \sum_{x_2=0}^{n-x_1} \exp\{s_1x_1 + s_2x_2\} \frac{d}{dt} p_{x_1, x_2}(t) \\ &= \sum_{x_1=0}^n \sum_{x_2=0}^{n-x_1} \exp\{s_1x_1 + s_2x_2\} [\lambda_{13}(x_1 + 1)(x_2 + 1)p_{x_1+1, x_2+1}(t) \\ &+ \lambda_{31}(n - x_1 - x_2 + 2)p_{x_1-1, x_2-1}(t) + \lambda_{12}(x_1 + 1)p_{x_1+1, x_2-1}(t) + \lambda_{21}(x_2 + 1)p_{x_1-1, x_2+1}(t) \\ &- [\lambda_{13}x_1x_2 + \lambda_{31}(n - x_1 - x_2) + \lambda_{12}x_1 + \lambda_{21}x_2]p_{x_1, x_2}(t)]. \quad (18) \end{aligned}$$

At equilibrium, the left hand side of this equation reduces to 0, while each sum on the right can be expressed in terms of  $M(s_1, s_2)$ ,  $\frac{\partial M}{\partial s_1}$ ,  $\frac{\partial M}{\partial s_2}$  and  $\frac{\partial^2 M}{\partial s_1 \partial s_2}$ . The first term on the right hand side is equivalent to

$$\begin{aligned} & \sum_{x_1=0}^{n-2} \sum_{x_2=0}^{n-x_1-2} \lambda_{13}(x_1 + 1)(x_2 + 1)p_{x_1+1, x_2+1} \exp\{s_1x_1 + s_2x_2\} \\ &= \lambda_{13} \sum_{x_1=1}^{n-1} \sum_{x_2=1}^{n-x_1} x_1x_2p_{x_1, x_2} \exp\{s_1(x_1 - 1) + s_2(x_2 - 1)\}. \end{aligned}$$

Since

$$M(s_1, s_2) = \sum_{x_1=0}^n \sum_{x_2=0}^{n-x_1} \exp\{s_1x_1 + s_2x_2\} p_{x_1, x_2},$$

this is equivalent to

$$\lambda_{13} \exp\{-(s_1 + s_2)\} \frac{\partial^2 M}{\partial s_1 \partial s_2}.$$

The second term on the right hand side of Equation (18) is equivalent to

$$\begin{aligned} & \sum_{x_1=1}^{n-1} \sum_{x_2=1}^{n-x_1} \lambda_{31}(n - x_1 - x_2 + 2)p_{x_1-1, x_2-1} \exp\{s_1x_1 + s_2x_2\} \\ &= \lambda_{31} \sum_{x_1=0}^{n-2} \sum_{x_2=0}^{n-x_1-2} (n - x_1 - x_2)p_{x_1, x_2} \exp\{s_1(x_1 + 1) + s_2(x_2 + 1)\}. \end{aligned}$$

Since  $n - x_1 - x_2 = 0$  when  $x_1 + x_2 = n$  and  $p_{x_1, x_2} = 0$  when  $x_1 + x_2 = n - 1$ , the sum above is equivalent to

$$\begin{aligned} \lambda_{31} \sum_{x_1=0}^n \sum_{x_2=0}^{n-x_1} (n - x_1 - x_2) p_{x_1, x_2} \exp \{s_1(x_1 + 1) + s_2(x_2 + 1)\} \\ = \lambda_{31} \exp\{s_1 + s_2\} \left( nM - \frac{\partial M}{\partial s_1} - \frac{\partial M}{\partial s_2} \right). \end{aligned}$$

The third term on the right hand side of Equation (18) is equivalent to

$$\begin{aligned} \sum_{x_1=0}^{n-1} \sum_{x_2=1}^{n-x_1} \lambda_{12}(x_1 + 1) p_{x_1+1, x_2-1} \exp \{s_1 x_1 + s_2 x_2\} \\ = \lambda_{12} \sum_{x_1=1}^n \sum_{x_2=0}^{n-x_1} x_1 p_{x_1, x_2} \exp \{s_1(x_1 - 1) + s_2(x_2 + 1)\} = \lambda_{12} \frac{\partial M}{\partial s_1}. \end{aligned}$$

Similarly

$$\sum_{x_1=0}^n \sum_{x_2=0}^{n-x_1} \lambda_{21}(x_2 + 1) p_{x_1-1, x_2+1} \exp \{s_1 x_1 + s_2 x_2\} = \lambda_{21} \frac{\partial M}{\partial s_2}$$

and

$$\begin{aligned} \sum_{x_1=0}^n \sum_{x_2=0}^{n-x_1} [\lambda_{13} x_1 x_2 + \lambda_{31}(n - x_1 - x_2) + \lambda_{12} x_1 + \lambda_{21} x_2] p_{x_1, x_2} \exp \{s_1 x_1 + s_2 x_2\} \\ = \lambda_{13} \frac{\partial^2 M}{\partial s_1 \partial s_2} + \lambda_{31} \left( nM - \frac{\partial M}{\partial s_1} - \frac{\partial M}{\partial s_2} \right) + \lambda_{12} \frac{\partial M}{\partial s_1} + \lambda_{21} \frac{\partial M}{\partial s_2}. \end{aligned}$$

Inserting each of these expressions into Equation (18) gives the following partial differential equation for  $M(s_1, s_2)$ :

$$\begin{aligned} n\lambda_{31}(e^{s_1+s_2} - 1)M + [\lambda_{12}(e^{s_2-s_1} - 1) + \lambda_{31}(1 - e^{s_1+s_2})] \frac{\partial M}{\partial s_1} \\ + [\lambda_{21}(e^{s_1-s_2} - 1) + \lambda_{31}(1 - e^{s_1+s_2})] \frac{\partial M}{\partial s_2} + \lambda_{13}(e^{-(s_1+s_2)} - 1) \frac{\partial^2 M}{\partial s_1 \partial s_2} = 0. \quad (19) \end{aligned}$$

Since  $K(s_1, s_2) = \log M(s_1, s_2)$ ,

$$\frac{\partial K}{\partial s_i} = \frac{1}{M} \frac{\partial M}{\partial s_i}, \quad i = 1, 2 \quad \text{and} \quad \frac{\partial^2 K}{\partial s_1 \partial s_2} = \frac{1}{M} \frac{\partial^2 M}{\partial s_1 \partial s_2} - \frac{1}{M^2} \frac{\partial M}{\partial s_1} \frac{\partial M}{\partial s_2}.$$

Thus

$$\frac{\partial M}{\partial s_i} = M \frac{\partial K}{\partial s_i}, \quad i = 1, 2$$

and

$$\frac{\partial^2 M}{\partial s_1 \partial s_2} = M \left( \frac{\partial^2 K}{\partial s_1 \partial s_2} + \frac{1}{M^2} \frac{\partial M}{\partial s_1} \frac{\partial M}{\partial s_2} \right) = M \left( \frac{\partial^2 K}{\partial s_1 \partial s_2} + \frac{\partial K}{\partial s_1} \frac{\partial K}{\partial s_2} \right).$$

These expressions can be substituted into Equation (19) to give Equation (7).

## B Derivation of the expressions for $\mu_1$ , $\sigma_1^2$ , $\sigma_2^2$ and $\sigma_{12}$ in terms of $\mu_2$ and the quartic equation for $\mu_2$ under the normal approximation

Firstly, expressions for  $\mu_1$  and  $\sigma_{12}$  are derived from Equations (8) and (9). Since neither equation includes the terms  $k_{2,1}$  and  $k_{1,2}$ , the expressions for  $\hat{\mu}_1$  and  $\hat{\sigma}_{12}$  are identical to those for  $\mu_1$  and  $\sigma_{12}$ , except that  $\mu_2$  is replaced by  $\hat{\mu}_2$  in each. It is clear from Equation (9) that

$$\mu_1 = \frac{\lambda_{21}\mu_2}{\lambda_{12}}.$$

Substitution of this expression for  $\mu_1$  into Equation (8) gives

$$n\lambda_{31} - \lambda_{31} \frac{(\lambda_{12} + \lambda_{21})}{\lambda_{12}} \mu_2 - \frac{\lambda_{13}\lambda_{21}}{\lambda_{12}} \mu_2^2 - \lambda_{13}\sigma_{12} = 0,$$

which can be rearranged to give

$$\sigma_{12} = -\frac{\lambda_{21}}{\lambda_{12}} \mu_2^2 - \frac{\lambda_{31}(\lambda_{12} + \lambda_{21})}{\lambda_{13}\lambda_{12}} \mu_2 + \frac{n\lambda_{31}}{\lambda_{13}}.$$

Setting  $k_{2,1} = k_{1,2} = 0$  in Equations (10) - (12) gives

$$n\lambda_{31} - \lambda_{31}\hat{\mu}_1 + (\lambda_{21} - \lambda_{31})\hat{\mu}_2 - (\lambda_{12} + \lambda_{31})\hat{\sigma}_1^2 + (\lambda_{21} - \lambda_{31})\hat{\sigma}_{12} - \lambda_{13}\hat{\mu}_1\hat{\sigma}_{12} - \lambda_{13}\hat{\mu}_2\hat{\sigma}_1^2 = 0, \quad (20)$$

$$\lambda_{12}\hat{\mu}_1 + \lambda_{21}\hat{\mu}_2 - \lambda_{12}\hat{\sigma}_1^2 - \lambda_{21}\hat{\sigma}_2^2 + (\lambda_{12} + \lambda_{21})\hat{\sigma}_{12} = 0 \quad (21)$$

and

$$n\lambda_{31} + (\lambda_{12} - \lambda_{31})\hat{\mu}_1 - \lambda_{31}\hat{\mu}_2 - (\lambda_{21} + \lambda_{31})\hat{\sigma}_2^2 + (\lambda_{12} - \lambda_{31})\hat{\sigma}_{12} - \lambda_{13}\hat{\mu}_2\hat{\sigma}_{12} - \lambda_{13}\hat{\mu}_1\hat{\sigma}_2^2 = 0. \quad (22)$$

When the above expressions for  $\hat{\mu}_1$  and  $\hat{\sigma}_{12}$  are substituted into Equation (20) the fol-

lowing equation involving  $\hat{\mu}_2$  and  $\hat{\sigma}_1^2$  is obtained:

$$\begin{aligned}
& -(\lambda_{12} + \lambda_{31} + \lambda_{13}\hat{\mu}_2)\hat{\sigma}_1^2 + \frac{\lambda_{13}\lambda_{21}^2}{\lambda_{12}^2}\hat{\mu}_2^3 + \frac{\lambda_{21}(\lambda_{21}\lambda_{31} + 2\lambda_{12}\lambda_{31} - \lambda_{12}\lambda_{21})}{\lambda_{12}^2}\hat{\mu}_2^2 \\
& - \frac{\lambda_{31}(\lambda_{13}\lambda_{21}(n+1) + \lambda_{12}\lambda_{13} + \lambda_{21}^2 + \lambda_{12}\lambda_{21}) - \lambda_{31}^2(\lambda_{12} + \lambda_{21}) - \lambda_{12}\lambda_{13}\lambda_{21}}{\lambda_{12}\lambda_{13}}\hat{\mu}_2 \\
& + \frac{\lambda_{31}(\lambda_{13} + \lambda_{21} - \lambda_{31})n}{\lambda_{13}} = 0.
\end{aligned}$$

The coefficient of  $\hat{\sigma}_1^2$  in this equation is negative, since  $\lambda_{12}$ ,  $\lambda_{13}$  and  $\lambda_{31}$  are all positive and  $\hat{\mu}_2 \geq 0$ . This means that the equation can be rearranged, to give an expression for  $\hat{\sigma}_1^2$  in terms of  $\hat{\mu}_2$ . Expression (15) is the partial fraction expansion of this.

Similarly, substituting the expressions for  $\hat{\mu}_1$  and  $\hat{\sigma}_{12}$  into Equation (22) gives

$$\begin{aligned}
& -\left(\lambda_{21} + \lambda_{31} + \frac{\lambda_{13}\lambda_{21}}{\lambda_{12}}\hat{\mu}_2\right)\hat{\sigma}_2^2 + \frac{\lambda_{13}\lambda_{21}}{\lambda_{12}}\hat{\mu}_2^3 + \frac{\lambda_{12}\lambda_{31} + 2\lambda_{21}\lambda_{31} - \lambda_{12}\lambda_{21}}{\lambda_{12}}\hat{\mu}_2^2 \\
& - \frac{\lambda_{31}(\lambda_{12}\lambda_{13}(n+1) + \lambda_{12}^2 + \lambda_{12}\lambda_{21} + \lambda_{13}\lambda_{21}) - \lambda_{31}^2(\lambda_{12} + \lambda_{21}) - \lambda_{12}\lambda_{13}\lambda_{21}}{\lambda_{12}\lambda_{13}}\hat{\mu}_2 \\
& + \frac{\lambda_{31}(\lambda_{12} + \lambda_{13} - \lambda_{31})n}{\lambda_{13}} = 0.
\end{aligned}$$

Since all of the  $\lambda_{ij}$ s are positive and  $\hat{\mu}_2 \geq 0$ , this equation can be rearranged to give  $\hat{\sigma}_2^2$  in terms of  $\hat{\mu}_2$ . Expression (16) is the partial fraction expansion of this.

Finally, the quartic equation for  $\hat{\mu}_2$  is obtained by inserting the expressions for  $\hat{\mu}_1$ ,  $\hat{\sigma}_{12}$ ,  $\hat{\sigma}_1^2$  and  $\hat{\sigma}_2^2$  into Equation (21). When all terms on the left hand side of this equation are placed over a common denominator, we have the left hand side of Equation (17) as the numerator and  $\lambda_{12}\lambda_{13}(\lambda_{12} + \lambda_{31} + \lambda_{13}\hat{\mu}_2)(\lambda_{12}\lambda_{21} + \lambda_{12}\lambda_{31} + \lambda_{13}\lambda_{21}\hat{\mu}_2)$  as the denominator. This denominator can be removed, since it is always positive.

## References

Brockmann, H. J. and Barnard, C. J. (1979) Kleptoparasitism in birds. *Animal Behaviour* 27 487–514.

Broom, M., Luther, R.M. and Ruxton, G.D. (2004) Resistance is useless? - extensions to the game theory of kleptoparasitism. *Bulletin of Mathematical Biology* 66 1645–1658.

Broom, M. and Ruxton, G.D. (1998) Evolutionarily stable stealing: game theory applied to kleptoparasitism. *Behavioural Ecology* 9 397–403.

Broom, M. and Ruxton G.D. (2003) Evolutionarily stable kleptoparasitism: consequences of different prey types. *Behavioral Ecology* 14 23–33.

Durrett, R., Granovsky, B.L. and Gueron, S. (1999) The equilibrium behaviour of reversible coagulation-fragmentation processes. *Journal of Theoretical Probability* 12 447–474.

Durrett, R., Granovsky, B.L. and Gueron, S. (1998) The steady-state distributions of coagulation-fragmentation processes. *Journal of Mathematical Biology* 37 1–27.

Fretwell, S. D. and Lucas, J. H. J. (1970) On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development., *Acta Biotheoretica* 19 16–36.

Hamilton, I.M. (2002) Kleptoparasitism and the distribution of unequal competitors. *Behavioral Ecology* 13 260–267.

Homer, O.P., Wachter, B., East, M.L. and Hofer, H. (2002) The response of spotted hyaenas to long-term changes in prey populations: functional response and interspecific kleptoparasitism. *Journal of Animal Ecology* 71 236–246.

Houston, A. I. and McNamara, J. M. (1988) The Ideal Free Distribution when competitive abilities differ - an approach based on statistical-mechanics. *Animal Behaviour* 36 166–174.

Hugie, D. M. and Grand, T. C. (1998) Movement between patches, unequal competitors and the ideal free distribution. *Evolutionary Ecology* 12 1–19.

Jackson, A.L., Humphries, S. and Ruxton, G.D. (2004) Resolving the departures of observed results from the Ideal Free Distribution with simple random movements. *Journal of Animal Ecology* 73 612–622.

Kryscio, R.J. and Lefèvre, C. (1989) On the Extinction of the SIS Stochastic Logistic Epidemic. *Journal of Applied Probability* 27 685 - 694.

Luther, R.M. and Broom, M. (2004) Rapid convergence to an equilibrium state in kleptoparasitic populations. *Journal of Mathematical Biology* 48 325–339.

Nasell, I. (1996) The Quasi-Stationary Distribution of the Closed Endemic SIS Model. *Advances in Applied Probability* 28 895–932.

Nasell, I. (1999) On the Quasi-Stationary Distribution of the Stochastic Logistic Epi-



demic. *Mathematical Biosciences* 156 21-40.

Nasell, I. (2003) Moment closure and the stochastic logistic model. *Theoretical Population Biology* 62 159-168.

Ruxton, G.D. and Humphries, S. (2003) Multiple ideal free distributions of unequal competitors. *Evolutionary Ecology Research* 1 635–640.

Ruxton, G.D. and A.L. Moody (1997) The Ideal Free Distribution with kleptoparasitism. *Journal of Theoretical Biology* 186 449–458.

Vollrath, F. (1979) Behaviour of the kleptoparasitic spider *argyrodes elevatus* (araneae, theridiidae). *Animal Behaviour* 27 515–521,

Weiss, G.H. and Dishon, M. (1971) On the asymptotic behavior of the stochastic and deterministic models of an epidemic. *Mathematical Biosciences* 11 261 – 265.

Whittle, P. (1957) On the use of the normal approximation in the treatment of stochastic processes. *Journal of the Royal Statistical Society, Series B*, 19 268–281.

Yates, G.E. and Broom, M. (2005) A stochastic model of the distribution of unequal competitors between resource patches. *Journal of Theoretical Biology* 237 227–237.