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Stochastic models of kleptoparasitism

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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.

Keywords: Food stealing; Equilibrium distribution; Cumulant generating function; Markov process; Parasitism

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 Lefèvre, 1989). The deterministic and stochastic models in this case give very different results. The deterministic model either converges to a stable mixture of infective and susceptible individuals, or the disease becomes extinct, depending upon parameter values. For the stochastic model the stationary distribution is always the trivial one where the disease is extinct. Extinction may take a long time to happen, and we

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may be interested in interim behaviour, so that the quasi-stationary distribution (conditional on non-extinction) is considered.

(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, 1999) and their references. The long-term behaviour of these processes again differs between the deterministic and stochastic cases, but the deterministic model is generally a better approximation to the stochastic one than in the SIS epidemic.

(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; Ruxton and Humphries, 2003; Yates and Broom, 2005). Deterministic models predict the optimal distribution of individuals between patches of different quality. Stochastic models generally predict undermatching (a lower proportion of individuals on the higher quality site than predicted by the deterministic model) and this is often what is observed in real populations, see for example Kennedy and Gray (1993). It should be noted that Hamilton (2002) combined the concept of the ideal free distribution and food stealing, and modelled individuals moving between two food patches where stealing was also possible.

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 et al., 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 v_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 $\lambda_{12} = v_f f$. 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 v_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 $\lambda_{13} = v_h$ 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 Fig. 1.

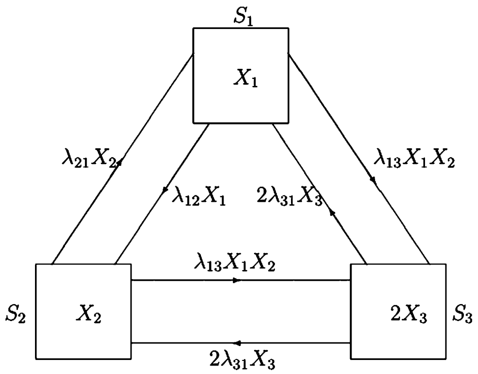

Fig. 1. The stochastic kleptoparasitism model. The sites are indicated by the boxes, transition rates are given on the arc with the arrow in the appropriate direction between the states. Both rates into S_3 are identical, as are those leaving S_3. Individuals enter state S_3 in pairs, one each from S_1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