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The stochastic modelling of kleptoparasitism using a Markov process

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Abstract

Kleptoparasitism, the stealing of food items from other animals, is a common behaviour observed across a huge variety of species, and has been subjected to significant modelling effort. Most such modelling has been deterministic, effectively assuming an infinite population, although recently some important stochastic models have been developed. In particular the model of Yates and Broom (*Stochastic models of kleptoparasitism.* J. Theor. Biol. **248** (2007), 480–489) introduced a stochastic version following the original model of Ruxton and Moody (*The ideal free distribution with kleptoparasitism.* J. Theor. Biol. **186** (1997), 449–458.), and whilst they generated results of interest, they did not solve the model explicitly. In this paper, building on methods used already by J. van der Meer and I. M. Smallegange (*A stochastic version of the Beddington-DeAngelis functional response: Modelling interference for a finite number of predators.* J. Animal Ecol. **78** (2009) 134–142.) we give an exact solution to the distribution of the population over the states for the Yates and Broom model and investigate the effects of some key biological parameters, especially for small populations where stochastic models can be expected to differ most from their deterministic equivalents.

Key words: Stealing, Finite population, Uptake rate, Interference, Detailed balance

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1. Introduction

The stealing of food by one animal from another, kleptoparasitism, is common in nature, occurring over a wide variety of taxa. Recent examples of this behavior have been observed in large carnivorous mammals (Carbone et al., 2005), seabirds (Dies and Dies, 2005), scavenging bird guilds (Bertran and Margalia, 2004), insects (Reader, 2003), fish (Hamilton and Dill, 2003), lizards (Cooper and Perez-Mellado, 2003), snails (Iyengar, 2002) and spiders (Agnarsson, 2002; Kerr, 2005; Vollrath, 1979; Watson, 1993). Iyengar (2008) provides an excellent review on kleptoparasitism.

When considering kleptoparasitism we must ask, why would an individual evolve this behavior? From an evolutionary standpoint the answer to this is quite logical: in order for a behavior to evolve in a population through natural selection, the individuals who follow this behavior must experiece greater reproductive success (higher fitness) compared to others in the population, and this trait must be passed on to their future offspring. Since not all species that seem capable of kleptoparasitism show it, and since there is strong variation between and within species in the extent to which this tactic is used, there is a need for a predictive theoretical basis to explain this variation. Hence there has been a considerable body of theory aimed at predicting the evolutionarily stable use of kleptoparasitism in different ecological circumstances. The majority of kleptoparasitic behavior is facultative, in that the individual or species exhibiting the behavior have alternative methods of obtaining the desired item. There are some general conditions that predict when kleptoparasitism should evolve including: the net gain of kleptoparasitism is higher than when the individual gains the item independently, the item must be obtainable, the item must be of use to the kleptoparasite, and the host and the kleptoparasites habitat must overlap in some manner (Iyengar, 2008).

Why do some species exhibit kleptoparasitism and not others? There is strong variation between and within species as to the extent, and manner, of kleptoparasitism and it is important to understand the evolutionary rationale for this behavior. Kleptoparasitism has been the subject of significant modelling since the mid-90s, early examples being Holmgren (1995) and Stillman et al. (1997). A mechanistic model was developed in Ruxton and Moody (1997) where individuals moved between a number of states including searching for a food item, handling a food item, winning a contest over a food item and losing a contest over a food item, the fight over a food item resulting when a searcher found a handler.

The model of Ruxton and Moody (1997) was refined by Broom and Ruxton (1998) by modifying the structure of the states of the population and introducing strategic choice for the individuals (to steal or not to steal), looking at when stealing was evolutionarily stable. The model of Broom and Ruxton (1998) provides the foundation for the majority of subsequent papers, such as Broom et at. (2008); Broom et al. (2004); Broom and Ruxton (2003); Broom and Rychtář (2007, in press); Luther and Broom (2004); Ruxton and Broom (1999). The related behavior of interference, where individuals slow consumption of food by neighbours due to their proximity, without actually stealing items has been modelled in a similar way (Beddington, 1975; DeAngelis et al., 1975; Ruxton et al., 1992; Smallegange and Van der Meer, 2009; Van der Meer and Ens, 1997). Note that although the kleptoparasitism models and interference models are different, the simple mechanistic kleptoparasitism model of Ruxton and Moody (1997) has no strategic element unlike later models, and the equations that result are a special case of those that come from the interference model of Smallegange and Van der Meer (2009).

The vast majority of kleptoparasitism models are currently deterministic, based upon a system of ordinary differential equations (ODEs), and thus effectively assume a very large population size. However, as the recorded incidences of kleptoparasitism increase and include previously unknown taxa such as crabs, sea stars (Morissette and Himmelman, 2000) and molluscs (Iyengar, 2004), it is often the case that real populations exhibiting kleptoparasitism have relatively small and limited mobile populations and it is thus important to model kleptoparasitism in a different way. A stochastic version of the state-based mechanistic models, in particular the modified Ruxton and Moody model from Broom and Ruxton (1998), was first developed in Yates and Broom (2007) and further investigated in Crowe et al. (2009) (a stochastic version of the interference models was developed in Van der Meer and Smallegange (2009)). Yates and Broom (2007) introduced a new model, and some approximation methods, but the authors did not get an explicit solution for the probability of the population occupying any particular state, and they focused on situations for medium population sizes, where their approximations were valid. Crowe et al. (2009) investigated this model for smaller populations and found situations where the stochastic model gave significantly different results to the deterministic equivalent (in Yates and Broom (2007) stochastic results generally matched the deterministic results well). In this paper we use an analytical approach to obtain an explicit solution to the Yates and Broom (2007) model using the idea of detailed balance, that was applied by Van der Meer and Smallegange (2009) to find solutions for the similar (and richer) interference system. Van der Meer and Smallegange (2009) used detailed balance to demonstrate a general method for finding solutions to their system, and proved that their solutions were correct for small populations. The main novelty of the current paper is the formal approach and proof of the general solutions in an explicit functional form for any population size.

2. Dynamics in finite populations

We assume the standard food model as introduced in Broom and Ruxton (1998). Each of the n animals can be in one of the following states

- searching for a food item or a handler,
- handling the food item,
- fighting over the food item with another animal.

Once a food item is found (which happens with an average speed $\nu_f f$ where f is the food density), the animal starts to handle it, i.e. preparing to eat it. The handling time is exponentially distributed, with mean T_h. Once the item is properly handled, the item is eaten instantly and the animal returns to searching. If a searcher encounters a handler (which happens at the rate $\nu_h b$, where b is the number of handlers), these two animals engage in a fight over the food item. The fight time is exponentially distributed with mean T_c. At the end of the fight, one animal emerges as a winner and starts handling the item, the other animal becoming a searcher.

We are interested in how much time an average animal spends handling, since this has been shown to be proportional to the uptake rate, Broom and Ruxton (1998).

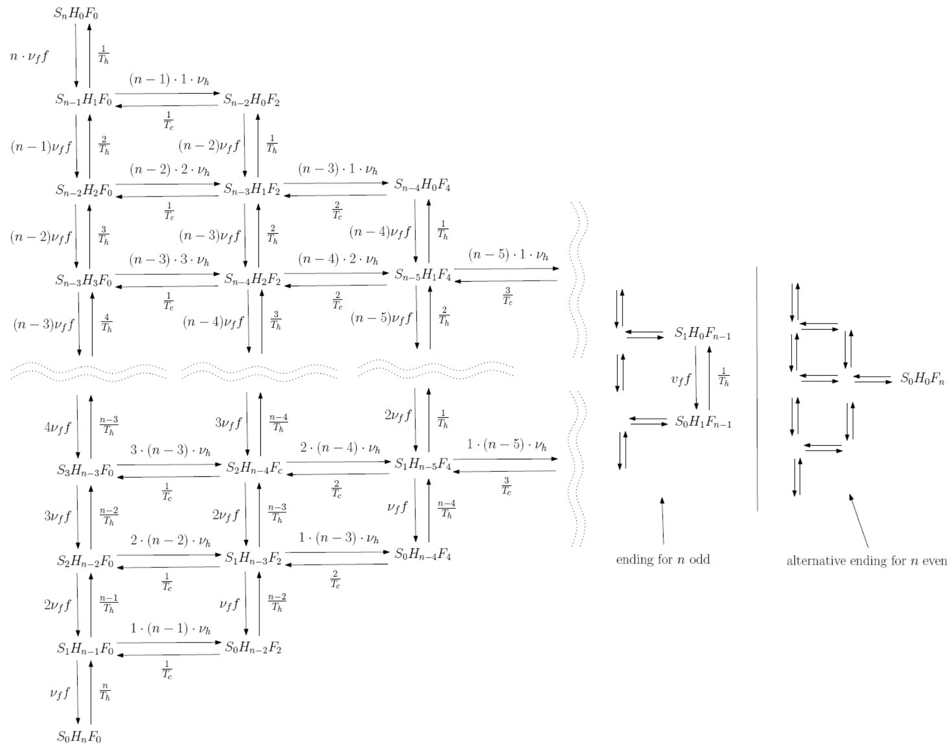

Fig. 1. The continuous time Markov chain model for a population of n individuals. The possible transitions from one state to another are shown by an arrow from the original state to the new state, accompanied by the transition rate. For all non-boundary states there are four possible transitions to and from the state. The exact shape of the scheme on the right end depends on the parity of the population size; both possible ends are shown.

We model the dynamics as a continuous time Markov chain. The state of the population is described by the number of individuals in each of the behavior types $S_aH_bF_{n-(a+b)}$, where a is the number of searchers and b is the number of handlers and since there are n animals in total, the number of animals engaged in the fight is given by $n-(a+b)$. Thus the state $S_aH_bF_{n-(a+b)}$ can be written more succinctly by the pair (a,b), and we use this reduced form throughout, except for in the diagramatic representations in Figures 1, and 2. We denote the probability that the dynamics is in the state (a,b) by $P_{a,b}$. Only states with $0 \leq a, b, (a+b) \leq n$, and $n-(a+b)$ even are admissible states of the dynamics. The scheme of the dynamics with all of the transition rates is given in Figure 1.

The probability distributions follows the following set of Kolmogorov equations:

$$\begin{aligned}\frac{\mathrm{d}}{\mathrm{d}t}P_{a,b} = &-P_{a,b}\left(\frac{b}{T_h}+ab\nu_h+a\nu_f f+\frac{n-(a+b)}{2T_c}\right)\\ &+P_{a+1,b-1}(a+1)\nu_f f+P_{a-1,b-1}\frac{n+2-(a+b)}{2T_c}\\ &+P_{a-1,b+1}\frac{b+1}{T_h}+P_{a+1,b+1}(a+1)(b+1)\nu_h \end{aligned} \tag{2.1}$$

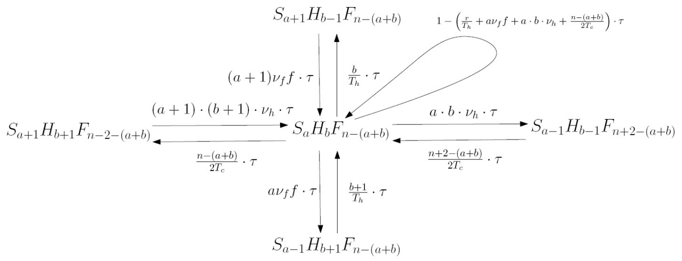

Fig. 2. Transitions from a focal state of the discrete Markov chain. The possible transitions to and from the focal state $S_aH_bF_{n-(a+b)}$ (alternatively labeled (a,b)) are shown by the appropriate arrows, accompanied by the transition probabilities.

with the boundary conditions given by

$$P_{a,b}=0,$$

whenever $a, b, n-(a+b)\notin\{0,1,\dots,n\}$, and $n-(a+b)$ not even.

The above system (2.1) is a system of linear differential equations; in an equilibrium, the time derivatives are 0 and we get the following system of linear equations.

$$\begin{aligned}0=&-P_{a,b}\left(\frac{b}{T_h}+ab\nu_h+a\nu_f f+\frac{n-(a+b)}{2T_c}\right)\\&+P_{a+1,b-1}(a+1)\nu_f f+P_{a-1,b-1}\frac{n+2-(a+b)}{2T_c}\\&+P_{a-1,b+1}\frac{b+1}{T_h}+P_{a+1,b+1}(a+1)(b+1)\nu_h\end{aligned}\tag{2.2}$$

with the same boundary conditions as above. That it is sufficient to consider such an equilibrium was shown for the corresponding deterministic case in Luther and Broom (2004). The system (2.2) is too large to deal with explicitly (it has approximately $n^2/4$ equations since the dynamics is described by the triangular shape that is exactly one half of a square with side $n/\sqrt{2}$). However, it can be solved with the help of the detailed balance conditions (see Van der Meer and Smallegange (2009) for a similar application).

The Markov chain system is said to be in detailed balance, if for any two pairs of states S_1, S_2,

$$P_{S_1}v_{12}=P_{S_2}v_{21},\tag{2.3}$$

where v_{ij} is the transition rate from the state S_i to the state S_j.

Theorem 1 *In the equilibrium, the Markov chain described by (2.1) is in detailed balance. Moreover, the solution of (2.2) is unique and the probability distributions are given by*

$$P_{a,b}=\frac{\frac{n!}{a!b!\left(\frac{n-(a+b)}{2}\right)!}\cdot(\nu_f f\cdot T_h)^{\frac{n+b-a}{2}}\cdot(\nu_h\cdot T_c)^{\frac{n-b-a}{2}}}{\sum_{B=0}^{n}\sum_{C=0}^{\lfloor\frac{n-B}{2}\rfloor}\frac{n!}{(n-B-2C)!B!C!}\cdot(\nu_f f\cdot T_h)^{B+C}\cdot(\nu_h\cdot T_c)^{C}}\tag{2.4}$$

We note that though the form of $P_{a,b}$ is succinct, it does not reduce to well-known distributions and is still a little awkward to work with. In particular the distribution of the number of fighting pairs is the complicating factor. Conditional on the number of such pairs, the distribution of the remaining individuals (those searching or handling) is simple however, with the number of searchers distributed binomially with parameters the number of non-fighting individuals and $1/(1+\nu_f f T_h)$.

Proof of the Theorem. We note that a distribution is a stationary distribution of our Markov process iff it is a solution of the system (2.2). To show that the solution of (2.2) is unique, we will construct a new, discrete time, irreducible and aperiodic Markov process and show that a distribution is a stationary distribution of this new Markov process iff it is a solution of the system equivalent to (2.2). Since any irreducible and aperiodic Markov process has a unique stationary distribution, the system (2.2) has a unique solution and thus the original continuous time Markov process has also a unique stationary distribution.

We will now construct the discrete-time Markov process as follows. The states are the same as the original continuous time Markov process on Figure 1 and if $v_{(a,b;a',b')}$ is the transition rate from state (a,b) to state $(a',b') \neq (a,b)$ of the continuous-time Markov chain, then the transition probability from state (a,b) to state (a',b') in the discrete-time Markov process is given by

$$\phi_{(a,b;a',b')} = v_{(a,b;a',b')}\tau, \qquad (a',b') \neq (a,b) \tag{2.5}$$

$$\phi_{(a,b;a,b)} = 1 - \sum_{(a',b')\neq(a,b)} v_{(a,b;a',b')}\tau, \tag{2.6}$$

where $\tau > 0$ is a parameter small enough so that $\phi_{(a,b;a,b)} > 0$ for all states (a,b). Details of a general state and transition probabilities of the new discrete time Markov process is shown on Figure 2. It is clear that the constructed Markov process is irreducible and aperiodic, and thus it has a unique stationary distribution $\pi = (\pi_{a,b})$. The stationary distribution $\pi = (\pi_{a,b})$ solves

$$\begin{aligned}\pi_{a,b} &= \sum_{(a',b')} \pi_{a',b'}\phi_{(a',b';a,b)} \\ &= \pi_{a,b}\left(1 - \sum_{(a',b')\neq(a,b)} v_{(a,b;a',b')}\tau\right) + \sum_{(a',b')\neq(a,b)} \pi_{a',b'} v_{(a',b';a,b)}\tau. \end{aligned} \tag{2.7}$$

Subtracting $\pi_{a,b}$ from both sides of (2.7) and then dividing by τ shows that (2.7) is equivalent to (2.2). Consequently, (2.2) has a unique solution (and $P_{a,b} = \pi_{a,b}$).

Now, we will proceed to the solution of the system (2.2). Knowing that the solution is unique, it is enough to use any method and assumption to find a solution; in particular, we can assume the Markov process is in detailed balance. As we will see this assumption leads us to a solution (satisfying the detailed balance condition); and since the solution is unique, the Markov process indeed is in detailed balance.

Let us group the states by the number of handlers. This corresponds to partitioning the states into the diagonals going from top right to left down on Figure 1.

Letting c be the number of fighting pairs, so that $a+b+2c = n$, we first consider states $(n-2c, 0)$ for $c = 0, \dots, \lfloor \frac{n}{2} \rfloor$. One can go to $(n-2,0)$ from $(n,0)$ via $(n-1,1)$ and using the detailed balance condition we get

$$P_{n-2,0} = n\nu_f f \cdot (n-1)\nu_h \cdot T_c \cdot T_h \cdot P_{n,0}. \tag{2.8}$$

Similarly, one can go from $(n-2,0)$ to $(n-4,0)$ via $(n-3,1)$ and using the detailed balance conditions one gets

$$P_{n-4,0} = (n-2)\nu_f f \cdot (n-3)\nu_h \cdot \frac{T_c}{2} \cdot T_h \cdot P_{n-2,0} \tag{2.9}$$

$$= \frac{n(n-1)(n-2)(n-3)}{2}(\nu_f f T_h)^2(\nu_h T_c)^2 \cdot P_{n,0}. \tag{2.10}$$

Repeating the above argument yields, for $c = 0, \ldots, \lfloor \frac{n}{2} \rfloor$,

$$P_{n-2c,0} = \frac{n!}{(n-2c)!c!}(\nu_f f T_h)^c(\nu_h T_c)^c P_{n,0}, \tag{2.11}$$

and

$$P_{n-2c,b} = \frac{(n-b)!}{(n-b-2c)!c!}(\nu_f f T_h)^c(\nu_h T_c)^c P_{n-b,b}, \tag{2.12}$$

for $b = 0, \ldots n$, $c = 0, \ldots, \lfloor \frac{n-b}{2} \rfloor$.

It remains to express $P_{n-b,b}$, for $b = 1, \ldots, n$ in terms of $P_{n,0}$. Working in the left part of the dynamics diagram, using the detailed balance conditions, we get

$$P_{n-b,b} = \frac{n!}{(n-b)!b!}(\nu_f f T_h)^b P_{n,0}. \tag{2.13}$$

Putting (2.12) and (2.13) together yields

$$P_{n-b-2c,b} = \frac{n!}{(n-b-2c)!c!b!}(\nu_f f T_h)^{c+b}(\nu_h T_c)^c P_{n,0}, \tag{2.14}$$

and thus

$$P_{a,b} = \frac{n!}{a!b!\left(\frac{n-(a+b)}{2}\right)!}(\nu_f f T_h)^{\frac{n+b-a}{2}}(\nu_h T_c)^{\frac{n-b-a}{2}} P_{n,0}. \tag{2.15}$$

Since

$$\sum_B \sum_C P_{N-B-2C,B} = 1 \tag{2.16}$$

one gets

$$P_{n,0} = \frac{1}{\sum_{B=0}^{n} \sum_{C=0}^{\lfloor \frac{n-B}{2} \rfloor} \frac{n!}{(n-b-2C)!B!C!}(\nu_f f T_h)^{B+C}(\nu_h T_c)^C} \tag{2.17}$$

Finally, (2.17) and (2.14) together yield (2.4) as required. This ends the proof of the Theorem.

3. Uptake rate

Since the uptake rate is proportional to the fraction of handlers in the population, we are interested in the behavior of the function

$$f(n) = \frac{1}{n}\sum_{b=0}^{n} b \cdot \sum_a P_{a,b}$$

$$= \frac{\sum_{b=0}^{n} b \cdot \sum_{c=0}^{\lfloor \frac{n-b}{2} \rfloor} \frac{n!}{(n-b-2c)!b!c!} (\nu_f f T_h)^{b+c} (\nu_h T_c)^c}{n \cdot \sum_{b=0}^{n} \sum_{c=0}^{\lfloor \frac{n-b}{2} \rfloor} \frac{n!}{(n-b-2c)!b!c!} (\nu_f f T_h)^{b+c} (\nu_h T_c)^c} \tag{3.1}$$

The function $f(n)$ measures the uptake rate in the population of n animals. Notice that the function depends on the following 3 factors only
– the size of the population,
– the product $(\nu_f f T_h)$,
– the product $(\nu_h T_c)$.
The second factor corresponds to up-down movement in the diagram on Figure 1 (searching for food and eating), the third factor corresponds to left right movement on the diagram (looking for a handler and the fighting).

Note that by fixing ν_h and allowing the population size to vary the interactions between individuals will always increase with n and inevitable ever more fights will result. Hence, if we are interested in the dependence of the uptake rate on the population size, it is better to consider the parameter $\mu_h = \nu_h / n$ instead of ν_h, as in Yates and Broom (2007), and the density-adjusted uptake rate function

$$\widetilde{f}(n) = \frac{\sum_{b=0}^{n} b \cdot \sum_{c=0}^{\lfloor \frac{n-b}{2} \rfloor} \frac{n!}{(n-b-2c)!b!c!} (\nu_f f T_h)^{b+c} \left(\frac{\nu_h}{n} T_c\right)^c}{n \cdot \sum_{b=0}^{n} \sum_{c=0}^{\lfloor \frac{n-b}{2} \rfloor} \frac{n!}{(n-b-2c)!b!c!} (\nu_f f T_h)^{b+c} \left(\frac{\nu_h}{n} T_c\right)^c} \tag{3.2}$$

By fixing $\mu_h n = \nu_h$ we keep the overall rate of finding handlers for any searching individual as effectively constant no matter the population size.

For each value of ν_h there is initial variation in $\widetilde{f}(n)$ for small values of n, followed by convergence to a constant density-adjusted uptake rate h_r, where

$$h_r = \frac{-(1 + \nu_f f T_h) + \sqrt{(1 + \nu_f f T_h)^2 + 8 T_c \nu_h \nu_f f T_h}}{2 \nu_h T_c} \tag{3.3}$$

as n increases. The formula (3.3) could be derived from (3.2) by using Stirling's formula, noting that in the limit, the probability $P_{a,b}$ is maximised when $b/n = h_r$ and that b/n converges in probability to h_r, so that the population handling ratio is very close to this maximising value almost always. The constant h_r from (3.3) is a classical uptake rate in fighting populations and it has appeared in all of the previous deterministic models such as Broom and Ruxton (1998); Broom et at. (2008) and others.

When ν_h is small, i.e. $\nu_h \approx 0$, then the population stays only in the left part of the diagram on Figure 1. Hence, $P_{a,b} \neq 0$ only if $0 \leq a = n - b \leq n$. Consequently, by (2.13),

$$P_{n-b,b} = \frac{\frac{n!}{(n-b)!b!} (\nu_f f T_h)^b}{\sum_{b=0}^{n} \frac{n!}{(n-b)!b!} (\nu_f f T_h)^b} = \frac{\frac{n!}{(n-b)!b!} (\nu_f f T_h)^b}{(1 + \nu_f f T_h)^n}. \tag{3.4}$$

It follows that

$$f(n) \approx \widetilde{f}(n) \approx \frac{1}{n} \sum_{b=0}^{n} b \cdot P_{n-b,b} \tag{3.5}$$

$$= \frac{1}{n(1 + \nu_f f T_h)^n} \sum_{b=0}^{n} b \frac{n!}{(n-b)!b!} (\nu_f f T_h)^b \tag{3.6}$$

$$= \frac{\nu_f f T_h}{(1 + \nu_f f T_h)}. \tag{3.7}$$

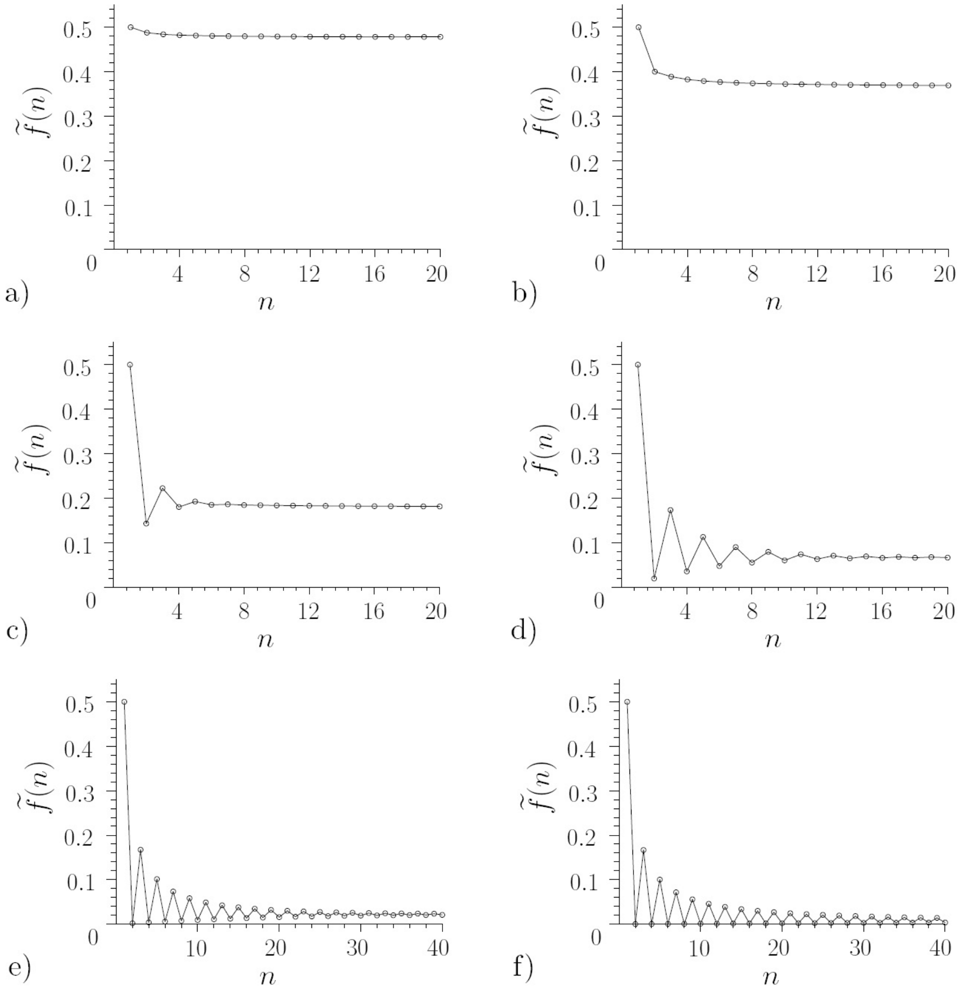

Fig. 3. Uptake rates for kleptoparasitic populations. a) $\nu_h = 0.1$, b) $\nu_h = 1$, c) $\nu_h = 10$, d) $\nu_h = 100$, e) $\nu_h = 1000$, f) $\nu_h = 10000$. Other parameter values are $\nu_f f = 1, T_h = 1, T_c = 1$.

The above is actually an uptake rate for the population with no fights originating from the classical work of Holling (1959).

Notice at Figure 3 that with increasing value of ν_h, the density-adjusted uptake rate $\widetilde{f}(n)$ becomes ever more sensitive to the population size being odd or even. When ν_h is relatively small, then there is little sensitivity, and $\widetilde{f}$ converges quickly to h_r, but for large values the odd numbers converges down to the equilibrium level and the even numbers converge up to that level, but convergence is slow and happens at quite large values of n, with the size adjusted uptake rate of all odd populations higher that all even ones.

When ν_h gets really large (and n is relatively small), there is a significant dependence of $\widetilde{f}$ on the parity of the population size. This is caused by the fact that, for large ν_h, the dynamics is pushed towards the right hand side of the scheme of the dynamics and as demonstrated on Figure 1 the exact shape of the right side depends on the parity of the population size.

Clearly, when n is even and ν_h is large, the population is almost always in the state $(0,0)$, i.e. all animals are fighting. This means that the uptake rate is approximately 0, and is thus not a realistic description of any real population if this occurs over a long period. When n is odd and ν_h large, the population is either in $(1,0)$ or in $(0,1)$, i.e. $n-1$ animals are engaged in fights and the remaining one is either searching or handling. Using the detailed balance condition we get

$$P_{0,1} = \nu_f f \cdot T_h \cdot P_{0,1} \tag{3.8}$$

and since $P_{0,1} + P_{1,0} = 1$ we get

$$f(n) \approx \widetilde{f}(n) \approx \begin{cases} \dfrac{\nu_f f T_h}{n(1+\nu_f f T_h)}, & n \text{ is odd,} \\ 0, & \text{otherwise.} \end{cases} \tag{3.9}$$

This could be derived directly from (3.1) and (3.2) since the maximal degree of ν_h at the top of the fraction is $a = \lfloor \frac{n-1}{2} \rfloor$ (achieved for $b = 1$, while the maximal degree of ν_h at the bottom of the fraction is $a = \lfloor \frac{n}{2} \rfloor$, achieved for $b = 0$ (and possibly for $b = 1$ as well - if n is odd).

4. Discussion

There is now a significant literature modelling kleptoparasitic interactions, and these models have been adapted to a number of different scenarios, and have become more sophisticated allowing for more complex behavior. Most of this work has been deterministic, assuming the large population case, rather than stochastic and able to deal with small populations, which occur frequently in situations where kleptoparasitism occurs. Such stochastic models were introduced for the first time in Yates and Broom (2007), adapting the original fundamental model (the refinement of Ruxton and Moody (1997) from Broom and Ruxton (1998)) and then followed up in Crowe et al. (2009). Also, Van der Meer and Smallegange (2009) analysed and experimentally tested a richer stochastic model of interference system in shore crabs.

Various approximations were considered in Yates and Broom (2007) and small populations in Crowe et al. (2009). In this paper, we have analysed the model of Yates and Broom (2007) and found a complete analytical solution to the probability distribution of the population over its possible states for all population sizes, and so both small and large populations can be considered exactly. Stochastic effects are more pronounced for small populations, but we see from Figure 3 that these effects can persist to quite large population sizes under certain conditions. An interesting feature is the distinction between odd and even sized populations, especially when these population sizes are small. Another interesting result is that, conditional on knowing the number of fighting pairs, the remaining individuals are split between the two categories of handler and searcher according to a Binomial distribution.

The creation and refinement of stochastic models will help us examine and predict the outcome of interactions between competitors. Following the results in this paper, it would be of interest to develop similar methodologies to apply to the more advanced later deterministic kleptoparasitic models, in particular allowing a game-theoretic element in the small population stochastic case for the first time. Strategies may depend significantly on what knowledge the individuals have about the rest of the population (e.g. if most others are fighting, this reduces the risk of being kleptoparasitised yourself). As we stated earlier in the paper, we are now becoming aware of more sedentary kleptoparasitic species that may concentrate their behavior in a limited area and with the same individuals on multiple occasions. For example, kangaroo rats kleptoparasitise unguarded seed caches (Daly et al., 1992) so knowing what behavior the burrow owner is engaged in may influence when an individual decides to kleptoparasitize. In sea otters, territorial adult males are more likely to successfully steal food from females and pups (Riedman and Estes, 1988) so knowing what the sex and age distribution of the population may help determine when this behavior is exhibited.

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