

Interspecific Kleptoparasitism

submitted by

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Summary

Although interspecific kleptoparasitism is widespread, theoretical models of kleptoparasitism focus on the intraspecific case. In this project a game-theoretic model of the behavioural decisions of a host species exploited by a kleptoparasite is developed. The case where the host species can choose to fight to retain its food or immediately surrender its food is considered and the model is used to determine the optimal host strategy for different ecological conditions. This model is a modification of published intraspecific models, in particular that of Ruxton & Moody (1997). We extend our basic model in various ways to make it more biologically plausible. One such extension is to include parasite strategies and then find the optimal host strategy when the parasite can choose to kleptoparasitise or not. We find the optimal strategies for different combinations of parameter values.

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Chapter 1

Introduction

Kleptoparasitism is a foraging tactic where an individual (the kleptoparasite) attempts to steal food which has been discovered and captured by another individual (the host). Kleptoparasitism occurs obligatorily or opportunistically throughout the animal kingdom in both intra- and interspecific interactions (Ridley & Child, 2009). There are several benefits associated with kleptoparasitism; including a greater food intake rate and acquiring otherwise unobtainable food items, and several costs; including the time and energy spent trying to steal food and the risk of a physical injury. In this chapter I will mention some of the studies which have been made into kleptoparasitism, I will then discuss some of the influences on the evolution of kleptoparasitism and finally I will review some of the work which has been done on modelling intraspecific kleptoparasitism.

1.1 Studies of Kleptoparasitism in Birds

Observations of kleptoparasitism have been reported in many species (Iyengar, 2008) and for some of these there have been detailed studies of the costs and benefits associated with using this foraging technique (Luther & Broom, 2004). Kleptoparasitism is particularly well studied in avian species and in particular seabirds (Brochman & Barnard, 1979; Le Corre & Jouventin, 1997). Seabird species such as skuas (*Stercorariidae*) and sheathbills (*Chionididae*) are considered to be obligate kleptoparasites, and species such as frigatebirds (*Fregatidae*), gulls and terns may practise kleptoparasitism opportunistically (Shealer *et al*, 2004). Such cost/benefit studies have been made (amongst others) into the fitness benefits of opportunistic kleptoparasitism (e.g. Shealer *et al*, 2004); the impact of kleptoparasitism on the host species and its avoidance responses (e.g. Le Corre & Jouventin, 1997 and Vickery & Brooke, 1994);

the trade-off between looking for kleptoparasitic opportunities and looking for food (e.g. Smith *et al*, 2002); tactics to reduce the costs of kleptoparasitism (e.g. Ridley & Child, 2009); and also the reasons why kleptoparasitism occurs in some species, or sometimes in some individuals of a species, but it is not used by every individual (Morand-Ferron *et al*, 2007).

1.1.1 *Sterna dougallii*

Habitual food stealing by individual parent roseate terns (*Sterna dougallii*) is associated with enhanced fitness, which is measured by the growth and survival to fledging in their offspring. In a study of a colony site by Shealer *et al* (2004) it was found that the roseate terns which regularly stole food from other terns to feed their own chicks were expected to produce about 45% more fledglings. Despite this, kleptoparasitism was only practised by a small number of terns in the colony. It was suggested that some mechanism (e.g. a high cost or a phenotypic constraint) prevents most individuals from stealing food.

1.1.2 Frigatebirds

Red-footed boobies (*Sula sula*) have been able to develop avoidance responses to kleptoparasitic attacks. Le Corre & Jouventin (1997) studied the behaviour of red-footed boobies in an environment where they were at risk of kleptoparasitism by frigatebirds. They compared this behaviour to that demonstrated in an area where the risk of kleptoparasitic attack was much lower. Their results showed that in the risky environment 1% of the boobies lost their food by kleptoparasitism, and it was observed that there was less chance of frigatebirds chasing boobies which flew in a group >50m high or after dusk. It was also found that birds were more nocturnal and better able to resist chases in the risky environment than in the safer one, suggesting that they have developed avoidance responses.

Vickery & Brooke (1994) evaluated the importance of kleptoparasitic behaviour towards Masked boobies (*Sula dactylatra*) in satisfying the energy needs of the frigatebird. They found that the frequency of kleptoparasitic attacks increased towards dusk, which is the time that the masked boobies return to the roost site. Similarly to Le Corre & Jouventin (1997) they found that there was more likelihood that a masked booby returning to the roost at a low altitude (<30m) or by itself would be chased. They found that approximately 40% of daily energy expenditure of an individual frigatebird may be secured through kleptoparasitism, but frigatebirds on average met under 5% of their daily energy demands by this feeding method. The

avoidance responses of the masked boobies could mean that the kleptoparasitic attack was too costly (e.g. by chases launched on high or distant targets). It was suggested that frigatebirds could assess the profitability of targets carrying food because the presence of food could affect flight. In this case frigatebirds could chase for a fixed time and then give up if no food was obtained, or employ a strategy where they would chase for a fixed time to assess profitability and then decide whether it was worth pursuing the chase or not.

1.1.3 *Dicrurus adsimilis*

Ridley & Child (2009) show that the kleptoparasitic fork-tailed drongo (*Dicrurus adsimilis*) specifically targets juveniles when following pied babblers (*Turdoides bicolor*). Drongos give alarm calls if they see a predator, when they do this pied babblers become startled and as a result often drop any food they are carrying. Drongos can exploit this behaviour by giving false alarm calls and then stealing dropped food items. Drongos have been able to increase their efficiency of kleptoparasitism by differentiating between different ages of babblers and then targeting juveniles (who have a longer handling time and respond to alarm calls by moving to cover rather than looking up). Drongos benefit from obtaining food by kleptoparasitism because it gives them access to subterranean foods which have a higher energy content than aerial prey, and provides them with an alternative foraging technique (Ridley *et al*, 2007). Thus they suggest that it is important that drongos do not over exploit the babblers to the extent that they become tolerant of false alarm calls.

1.2 Influences on the Evolution of Interspecific Kleptoparasitism

Hence, we have seen that within kleptoparasitic species there is evidence of a trade-off of whether to steal food or not, and the associated costs and benefits have been studied. However the reasons why food stealing occurs in some taxa but not in others is still unclear. The main hypotheses which could influence the evolution of interspecific kleptoparasitism are summarised below; these were discussed and tested by Morand-Ferron *et al* (2007) who based their theories on field studies of interspecific kleptoparasitic birds.

1. *The brawn hypothesis*; kleptoparasites should be characterised by a larger body mass, because larger means more chance of winning fights and reduces the

chances of the host aggressively defending its prey. Also, larger eyes means an increased detection of kleptoparasitic opportunities.

2. *The brain hypothesis*; kleptoparasites should have larger brain sizes because this means higher cognitive abilities which allows for better tactics (these include selection of appropriate hosts, attack from suitable angles and distance, using appropriate timing, predicting the behaviour of the host so as to avoid detection).
3. *The vertebrate prey hypothesis*; vertebrate prey are often of high energetic value and require long handling times, factors which increase the probability and/or profitability of kleptoparasitic attacks. Thus birds including vertebrate prey in their diet might encounter profitable kleptoparasitic opportunities more often and hence have more chance of evolving kleptoparasitism.
4. *The group-foraging hypothesis*; there are more opportunities for kleptoparasitism in multispecific groups of foragers because of the increase in the probability of encountering and/or pursuing successful foragers.
5. *The habitat-openness hypothesis*; the type of habitat might affect the evolution of kleptoparasitism, e.g. open habitats have high visibility and hence there is an increased probability of detecting hosts.

Morand-Ferron *et al* (2007) found that the probability of kleptoparasitism foraging strategies occurring was positively associated with brain residual size, habitat openness and the presence of vertebrate prey in the diet, but showed no association with body size or participation in mixed-species foraging groups. The conclusion that kleptoparasitism is associated more closely with cognition than with aggression is further supported by the fact that kleptoparasites have a larger residual brain size than their respective hosts, while their body size is not significantly larger.

However, it is suggested by Iyengar (2008) that studies into the evolution of kleptoparasitism that only focus on avian species are not generalisable. This is because these studies are unable to differentiate between the selective pressures and evolutionary responses of general kleptoparasites and those that are restricted to certain groups.

1.3 The Ideal Free Distribution

There have been several studies of the distribution of kleptoparasitic individuals by looking at the ideal free distribution of foragers among patches of different quality (usually measured by food density) (e.g Parker & Sutherland (1986); Korona (1989); Holmgren (1995)). Holmgren (1995) constructed a simulation model based on a behavioural model of the processes of foraging and kleptoparasitism to investigate the spatial distribution of individuals which differ in foraging ability. He found that when predators were all assumed to be different from one another then those which were more dominant in winning fights for food or more efficient at prey handling would only occur in the high prey density patches, and less dominant/efficient predators would be mixed across patches. He also found that predators which were less efficient at searching would be found in the high prey density patches.

Ruxton & Moody (1997) took the specific case of the Holmgren (1995) model where all the individuals have identical foraging ability. They found the ideal free distribution by finding the distribution of foragers across patches which gives all individuals the same uptake rate (as at the ideal free distribution the intake rates for all individuals will be identical in the occupied patches, as no individual can increase its uptake rate by moving).

They set F as the population density of food items and v_F and v_H as the area an individual can search per unit time for food and handlers respectively. They assumed that individuals search for food items (and find them at a rate of v_FF) and when found a finite amount of handling time is required to process the item before ingestion (this time is assumed to be drawn from an exponential distribution with mean t_h). During this time, if another individual encounters the handler (which happens at a rate of v_HH) then there is a contest for the prey item which takes a finite amount of time (this time is taken from an exponential distribution with mean t_k) and either participant is equally likely to win the fight. The winner of the contest gets the entire food item and begins to handle it, and the loser goes back to searching for food again. It is assumed that the previous amount of handling has no effect on the post-contest handling time.

Ruxton & Moody (1997) looked at the forager distribution on two patches where the food population on one patch is F_1 and on the other F_2 , similarly the forager population on the two patches is P_1 and P_2 (and $P_1 + P_2 = P_T$). By setting the uptake rate in each patch as equal they found P_1 as a function of F_1 . They used this result to investigate the relation between the proportion of food on one patch and the number of foragers predicted on this patch (they also do this for three or more

patches). They found that increasing forager density will increase the use of lower quality patches. They predicted that foraging efficiency will decrease with forager density if kleptoparasitism occurs, so foragers may move into lower quality patches as a way of minimising kleptoparasitic attacks. Figure 1-1 shows that as t_h increases (and thus the likelihood of being encountered by a kleptoparasite rises) individuals will more readily move to the poorer patch. When t_h is very large however, this effect is cancelled by the fact that the time spent searching be also decrease (hence reducing the strength of kleptoparasitism).

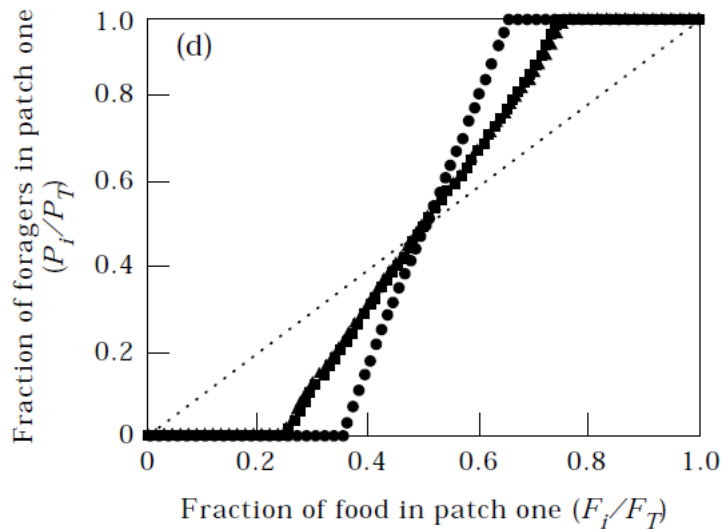


Figure 1-1: The proportion of foragers in patch one as a function of the proportion of food in that patch. Circles: $t_h = 0.1$, squares: $t_h = 1$, triangles: $t_h = 10$. Other parameter values are taken as $P_T = 10$, $F_T = 100$, $t_k = 1$, $v_F = v_H = 0.1$. Taken from Ruxton & Moody (1997).

1.4 A Game-Theoretic Model for Intraspecific Kleptoparasitism

As discussed earlier, kleptoparasitism is shown to have several benefits, which include a greater food intake rate and acquiring food which is otherwise unavailable by self foraging. For example the size of the prey items that fork-tailed drongos capture via kleptoparasitism are on average three times larger than those captured during self-foraging (Ridley & Child, 2009). There are also costs associated with challenging other individuals for their food; these include the time and energy spent trying to

steal food and the risk of physical injury when a host decides to defend a challenge. Hence attempting to steal food from another individual may not always be an efficient strategy. This trade-off has spurred attempts to construct a game-theoretic model to find which strategy is appropriate for any combination of parameter values (Beddington, 1975; Ruxton *et al*, 1992; Sirot, 2000; and developments of the model by Ruxton & Moody, 1997). These models generally focus on intraspecific kleptoparasitism and how it affects the food uptake rate (the functional response) of an individual. This information can be used to assess the pay-offs of different possible strategies and explore how ecological conditions can affect the evolutionarily stable strategies. [An evolutionarily stable strategy (ESS) is reached when no mutant strategy can invade a population in which all individuals are playing the ESS (Maynard Smith, 1974).]

Most of the game-theoretic work on kleptoparasitism has been based on the model described earlier by Ruxton & Moody (1997), and its refinement in Broom & Ruxton (1998) (the Broom-Ruxton model) where the structure of the states were modified and strategic choice was introduced. Further developments of this model (e.g. Ruxton & Broom, 1999; Broom & Ruxton, 2003; Broom *et al*, 2004, 2008; Luther *et al*, 2007; Broom & Rychtář, 2007, 2009) have added complexity and biological realism, as they often relax previous assumptions. In these models the functional response of an individual (a function of food density and competition from other foragers) and the evolutionarily stable strategy which maximises it are found. In a model by Sirot (2000) (which is based on a hawk-dove model) the pay-offs of different strategies are found using the rate of energy gain by an individual. These models are deterministic and thus effectively assume a large population size, however it is sometimes the case that kleptoparasitic populations are small and hence would be better modelled stochastically. A stochastic model for kleptoparasitism has been developed by Yates & Broom (2007) and later extended by Broom *et al* (2010). Also, the models assume that mixed strategy solutions are not possible; this assumption was relaxed by Broom & Rychtář (2007) where they consider the evolution of kleptoparasitism under adaptive dynamics.

1.4.1 The Broom-Ruxton model

Some of the assumptions in the Ruxton and Moody (1997) model were unrealistic and the results suggested that individuals would act in ways that were not always the most efficient, therefore Broom and Ruxton (1998) extended the model in two ways to allow the individual to act optimally.

One extension was to allow individuals to pass up opportunities to kleptoparasitise when detecting a handler, and the other way was to assume that individuals have to split their searching capacity between searching for food and searching for opportunities to steal food (although in some circumstances this does not hold, see Smith *et al* (2002)). They investigated what circumstances made it beneficial for an individual to challenge a handler.

They considered a population of constant population density, P , which is divided into three subpopulations of searchers (with density S), handlers (with density H) and those involved in aggressive interaction (with density A). These activities are mutually exclusive so $S + H + A = P$. The probability that an individual meeting a handler will enter into a potential fight is a constant, p . For convenience, the aggressive interaction was set to last for a time drawn from an exponential distribution with mean $t_a/2$. Hence, they constructed the following set of equations describing the rates of movement between the three subpopulations:

$$\frac{dS}{dt} = \frac{H}{t_h} - v_f S f - p v_H S H + \frac{A}{t_a}, \quad (1.1)$$

$$\frac{dH}{dt} = -\frac{H}{t_h} + v_f S f - p v_H S H + \frac{A}{t_a}, \quad (1.2)$$

$$\frac{dA}{dt} = 2p v_H S H - \frac{2A}{t_a}. \quad (1.3)$$

They then assumed that the population was at dynamic equilibrium to find that:

$$\frac{H}{P} = \frac{-(C+1) \pm \sqrt{(C+1)^2 + 4pCD}}{2pD}. \quad (1.4)$$

where $C = t_h f v_f$ and $D = t_a P v_H$. An individual's uptake rate (the functional response) is the rate at which it makes the transition from handler back to searcher, i.e. the rate at which it gains food items. They took this rate to be

$$\gamma = \frac{H}{t_h P}, \quad (1.5)$$

which is equal to the population per capita rate of food items consumed because all individuals are intrinsically identical. They then found the optimal value of p which maximises γ for different parameter values. To do this they found the value of p which minimises the mean time taken for a searcher that has just encountered a

handler to begin handling a food item itself, this is

$$\tau = \frac{1}{fv_f} + p \frac{t_a f v_f - 1}{fv_f}. \quad (1.6)$$

Hence if $t_a f v_f > 1$ then the optimal strategy is to play $p = 0$, i.e. never try to steal food. Similarly, if $t_a f v_f < 1$ then the optimal strategy is to play $p = 1$, i.e. always take opportunities to steal food. If $t_a f v_f = 1$ then any value of p adopted will be equally effective. Hence, when the optimal strategy is $p = 0$ then $H/P = C/(C + 1)$ and substituting this into (1.5) gives

$$\gamma = \frac{(\frac{1}{t_h})f}{f + \frac{1}{v_f t_h}}. \quad (1.7)$$

When the optimal strategy is $p = 1$ and in the limit $(C + 1)^2 \gg 4CD$ (which might occur when P is very low (Ruxton & Moody, 1997)) they argue that γ can be well approximated by

$$\gamma t_h = \frac{(\frac{1}{t_h})f}{f + \frac{1}{v_f t_h} + \frac{t_a f v_H P}{t_h f v_f + 1}}. \quad (1.8)$$

Hence they predict that as food becomes more difficult to find (or equivalently fights for food take less time) there will be a dramatic step change in both behaviour and uptake rate. This result can be seen in Figure 1-2, taken from their paper. It shows that the uptake rate increases with food density, and at $f = 20$ the population changes it's strategy from always kleptoparasitising to never kleptoparasitising with increasing food density. This behaviour change results in a step change in the uptake rate because when the population swaps to never kleptoparasitising then all effort goes into finding new food items from the environment, as opposed to only finding new food items when there are no kleptoparasitic opportunities.

The other extension to the Ruxton & Moody (1997) paper was to assume that v_H can only be increased at the expense of decreasing v_f , i.e. that the rates are not independent. This was expressed in the form:

$$\frac{v_f}{\beta_1} + \frac{v_H}{\beta_2} = 1. \quad (1.9)$$

Hence, they defined an individuals strategy by $\{v_f, p\}$. They defined "insular" individuals as those who maximise their prey-finding ability, hence when $v_H = 0$ and thus $v_f = \beta_1$. In this case handlers would never be detected and so the value of p chosen would be irrelevant. "Aggressive" individuals are defined as those which look

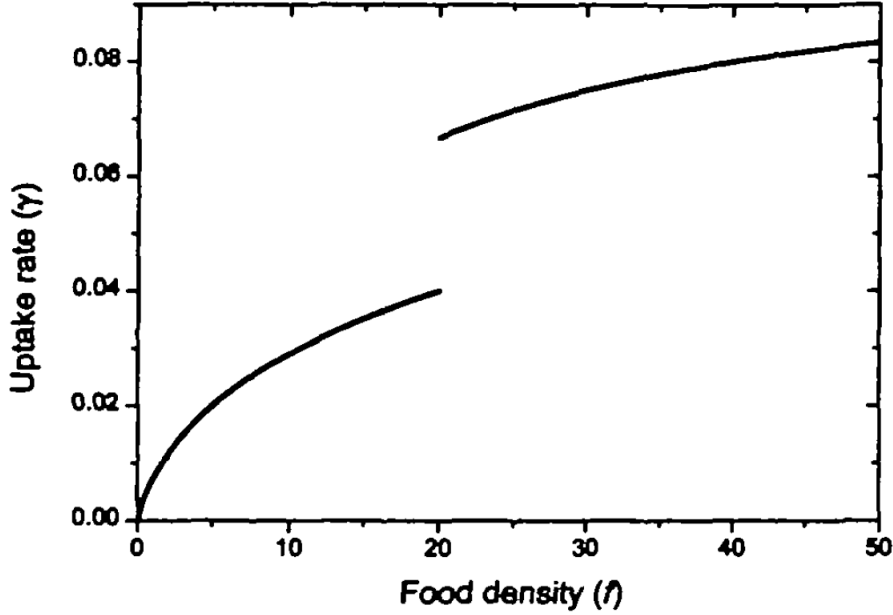


Figure 1-2: Graph of the food uptake rate, γ , as a function of food density, f , taken from Broom & Ruxton (1998). For $f < 20$ kleptoparasitism occurs at every opportunity, and for $f > 20$ kleptoparasitism never occurs. Other parameter values are $P = 20$, $t_a = 5$, $t_h = 10$, $v_f = 0.01$ and $v_H = 0.05$.

for kleptoparasitic opportunities, i.e. $v_H > 0$, and hence $v_f < \beta_1$. In this case it would not be sensible to search for handlers but then never attempt to steal their food (i.e. by playing $p = 0$), so it is assumed that aggressive individuals will always play $p = 1$. They then found the evolutionarily stable strategies by considering a fixed population density and looking at the circumstances for which all individuals should play either $\{v_f = \beta_1\}$ or $\{v_f < \beta_1\}$, and which value of v_f should be played.

When $t_a f v_f > 1$ holds, hence when it is optimal never to kleptoparasitise, then it would not make sense to spend time searching for handlers. Thus when

$$t_a f \beta_1 > 1 \tag{1.10}$$

then $\{v_f = \beta_1, p = 0\}$ is the only ESS. When handlers are scarce or hard to find then it can still be optimal to play $\{v_f = \beta_1\}$ even though (1.10) does not hold, this was shown to be true when

$$P < \frac{2(1 + t_h f \beta_1)}{\beta_2 t_h (1 - t_a f \beta_1)}. \tag{1.11}$$

When neither (1.10) nor (1.11) hold then the unique ESS was found to be $v_f =$

$\beta_1/(1 + F)$ where

$$F = \left(\frac{1 - t_a f \beta_1}{2(1 + t_a f \beta_1)}\right)(\beta_2 P t_h (1 - t_a f \beta_1) - 2(1 + t_a f \beta_1)). \quad (1.12)$$

Hence increasing any of β_2 , P or t_h (which all make handlers easier to find) cause a decrease in v_f .

Although never kleptoparasitising increases the uptake rates for a group of individuals, in certain conditions this is not evolutionarily stable as if there was an individual which kleptoparasitised, then this individual would do better than the others. Hence from their model, Broom and Ruxton found that to always or never challenge others are generally the best strategies to maximise the uptake rate, and these occur respectively when food density is low or high (or equivalently when the fight time is small or large). From this they predicted that small changes in ecological conditions can sometimes cause a dramatic change in the aggressive behaviour of individuals, this can be seen in Figure 1-2. They found the evolutionarily stable strategy for investment in searching for food and searching for handlers in terms of the ecological parameters of the model. An equilibrium distribution of individuals in each of the activity states was found and the population was assumed to be in this equilibrium; this was proved to be a stable equilibrium in a paper by Luther & Broom (2004).

1.4.2 Contests as a “War of Attrition”

Ruxton & Broom (1999) extended the Broom-Ruxton model further by dropping the assumption that contests over resource items are of a fixed duration. They suggest that the winner of a contest will be the individual who is prepared or able to fight for the longer time, i.e. the contest is modelled by a “war of attrition” (formally described by Maynard Smith (1974)). However, individuals which contest for a long time may win but at the cost of investing a large amount of time when encountering a stubborn individual. For this model the evolutionary stable strategy will be a combination of the probability of challenging a handler (p) and the distribution of the lengths of time an individual is prepared to compete for, $g(t)$.

They show that if two individuals compete for a resource of value V then the expected net payoff to an individual which selects time m_1 in contests where the

opponent selects time m_2 , $E[m_1, m_2]$, is equivalent to

$$E[m_1, m_2] = \begin{cases} \frac{V}{k} - m_2, & m_1 > m_2 \\ \frac{V}{2k} - m_2, & m_1 = m_2 \\ -m_1, & m_1 < m_2 \end{cases} \quad (1.13)$$

Where k is a constant which converts time invested in a contest to the same currency as the reward. The ESS of this game was previously shown (by Bishop & Cannings (1976)) to be to play for a time which is selected (independently for each contest) from an exponential distribution with mean time $\frac{V}{k}$,

They let the cost of stealing a food item be the value of the food that could have been found in a time t , i.e. $fv_f Vt$, and thus $k = fv_f V$. They find that the optimal strategy is one for which $\frac{t_a}{2} = \frac{1}{2fv_f}$, i.e. when $t_a fv_f = 1$. Hence they find that contests will last on average the same amount of time as it takes on average for an individual to find a food item. This optimal strategy corresponds to the point where the uptake rate is independent of whether the individual kleptoparasitises or not.

They then consider when the two searching types are not mutually exclusive, i.e. when equation (1.9) holds, so the individuals strategy is defined by $\{v_f, p, g(t)\}$. For this extension they expect that kleptoparasitism will not be observed as it is optimal for individuals to maximise their searching effort for food.

1.4.3 The Apple and the Orange Model

The assumption that the distribution of handling times is exponential is relaxed in Broom & Ruxton (2003). In this paper they consider two scenarios where handling time takes a fixed interval, t_h , and then either at the end of this handling time the whole value of the food it obtained (the ‘‘orange’’ model), or the reward from the food item is extracted continuously (at a constant rate) throughout the handling time (the ‘‘apple’’ model). Hence, in these models an individuals decision to enter into a contest is based on how much handling the food item has already received (thus a key assumption is that individuals are able to assess this amount). They predict that in the orange model kleptoparasitic attacks will be focused on prey items near the end of their handling period and decrease with forager density. Whereas they predict in the apple model these attacks will be biased towards newly discovered items and increase with forager density.

Broom & Rychtář (2009) later developed the Broom & Ruxton (2003) apple model in order to look at the scenario where the defender knows how much handling

a food item has received but the challenger does not. This produced mixed strategies because of the different values of the food items at the time that a defensive choice is made. They found that this situation often favours the challenger; this is because handlers often give up small items and thus provide free food to the challenger.

1.4.4 Varying α and Allowing Resistance Choice

Broom *et al* (2004) then extended the Broom-Ruxton model in two more ways. One extension was to let the probability, α , of the challenger winning vary (this is a general case of the assumption in Ruxton & Broom (1999)), and the other extension was to allow the handler to resist the challenger. In the first part of their paper they considered the optimal strategies for a searcher who has just encountered a handler who always resists.

They set t_s as the time taken to acquire food after a failed attack, so if the attacker does not challenge (which happens with probability $1-p$) then it is effectively foraging and thus the average time to acquire food is just $t_s = (v_f f)^{-1}$. Thus it is advantageous to challenge if the expected time to gain a food item by always challenging is less than when an individual never challenges, i.e. if $t_a/2 + (1-\alpha)t_s < (v_f f)^{-1}$. They found that

$$t_s = \frac{1 + v_h t_a H/2}{v_f f + \alpha v_h H}, \quad (1.14)$$

thus challenging is advantageous if

$$v_f f < \frac{2\alpha}{t_a}. \quad (1.15)$$

The mean time taken, t_e , for a searcher that has just encountered a handler to begin handling was found to be

$$t_e = \frac{1-p}{v_f f} + p\left(\frac{t_a}{2} + (1-\alpha)\left(\frac{1}{v_f f + v_h H} + \frac{v_h H t_e}{v_f f + v_h H}\right)\right). \quad (1.16)$$

They then solved this and found that when $t_a/2 - \alpha/v_f > 0$ then t_e will have its minimum value when $p = 0$, and when $t_a/2 - \alpha/v_f < 0$ then t_e will have its minimum value when $p = 1$. This result assumes that handlers will always resist, but if handlers do not resist challenges then it will always be optimal to challenge.

They then considered what the optimal resistance strategies were for a handler that had just been challenged. Here it is optimal to always resist if the expected time to begin handling again after resisting a challenge is less than the expected time taken to find another food item after surrendering food, i.e. when $0.5t_a + \alpha t_s < t_s$.

By using (1.14) they found that the condition for resisting to be optimal in a population when others are also resisting is

$$v_f f < \frac{2(1-\alpha)}{t_a} + (1-2\alpha)v_h P h_r, \quad (1.17)$$

where $h_r = H/P$ is the handling ratio. When the rest of the population is not resisting then $t_s = \frac{1}{v_f f + v_h H}$, so for this case the condition for resistance to be optimal is

$$v_f f < \frac{2(1-\alpha)}{t_a} - \frac{v_h P v_f f t_h}{v_f f t_h + 1}. \quad (1.18)$$

They also found that if the majority of the population were not making challenges but a handler may be challenged by a mutant aggressor then $t_s = 1/(v_f f)$ and the condition for resistance is

$$v_f f < \frac{2(1-\alpha)}{t_a}. \quad (1.19)$$

For general α they find three ESSs to challenge and resist (the hawk strategy), this is an ESS if (1.15) and (1.17) are satisfied; to challenge but not resist (the marauder strategy), this is an ESS if (1.18) is not satisfied; and to resist but not challenge (the retaliator strategy), this is an ESS if (1.15) is not satisfied but (1.19) is. They also predict that for a given contest time, increasing chance of success for the challenger always results in the same sequence of ESSs.

1.4.5 Sirot, 2000

Another game-theoretic model of intraspecific kleptoparasitism was made by Sirot (2000). He assumed that individuals can choose to kleptoparasitise (as in the Broom-Ruxton model), but also that if an individual is challenged by a kleptoparasite they can either choose to enter the contest (which takes time and energy) or immediately surrender their food (as in the Broom *et al* (2004) extension). The aim of his model was to predict the proportion of time each animal should be aggressive and the proportion of time it should avoid confrontation, taking into account ecological conditions such as food availability and density of competitors.

It was assumed that conflicts always involve only two animals and the two strategies which can be played are:

1. The Hawk Strategy: Challenge and resist the challenges of others;
2. The Dove Strategy: Neither challenge nor resist the challenges of others.

He lets V be the energy gain from a food item, T be the average conflict duration for two hawks and C be the energy loss per time unit in a conflict between two hawks. Thus the average payoff in energy is, $V/2 - CT$ for a conflict between two hawks; V for a hawk encountering a dove; 0 for a dove encountering a hawk; and $V/2$ for a confrontation between two doves.

His model predicts that the level of aggressiveness will progressively increase with group density and it also predicts that aggressiveness should strongly vary with ecological conditions, which are predictions consistent with field observations.

1.4.6 Mixed Strategies

Broom & Rychtářs (2007) used adaptive dynamics to investigate individuals which are allowed to have mixed strategies (i.e. being able to play more than one strategy), rather than the pure strategies which were studied in previous models. Their model follows on from that of Broom *et al* (2004). Their extension allows more flexible and complex behaviour amongst a population to be considered, where the population strategy changes to maximise fitness. They denote an individuals strategy as a combination of, p , the probability to attack a handler and the probability to retaliate when attacked by a searcher, r . They assume all individuals in the population play the same strategy, but this may change if a mutation occurs where a few individuals in the population adopt a strategy which is close to the original strategy. If this mutant strategy gives a higher feeding rate then it has an advantage over the original strategy, and it will eventually take over as the population strategy.

Another follow-on to the 2004 Broom *et al* model was made by Luther *et al* (2007), in this they considered a population of foragers which can have one of two types of behaviour, those that forage and steal and those that only forage. It is assumed the latter have a better foraging rate, which relaxes the Broom *et al* (2004) assumption that searching for kleptoparasitic opportunities has no cost (this is more realistic, see Shealer *et al* (2004)). They find that there are ESSs based on the overall population density; if it is low there is an ESS consisting of only foragers, when it is high then there is an ESS consisting of only kleptoparasites and if it is in-between then there is an ESS consisting of both pure foragers and stealers.

They found that it is theoretically possible for obligate kleptoparasites (which abandon their ability to find food themselves) to persist providing that the population also contains pure foragers to actually find food items. However, there are no known populations in which a significant fraction are obligate kleptoparasites, Luther *et al*

(2007) suggest that this may be because there is no set of ecological circumstances in which obligate kleptoparasites would evolve.

1.4.7 A Stochastic Model

The models discussed so far have been deterministic and hence assume that the population is large. However, in small populations individual movements between the subpopulations have a larger effect on transition rates than in larger populations and can often give quite different results in the expected proportion of the population on each site. Yates & Broom (2007) adapted the Broom-Ruxton model where individuals are not allowed decisions, to find a stochastic model which was able to deal with small populations exhibiting kleptoparasitism. They compared this to the original deterministic model and also considered a normal approximation to the stochastic model. Broom *et al* (2010) later solved the stochastic model explicitly to find the distribution of the population over the states.

1.5 Modelling Interspecific Kleptoparasitism

Although interspecific kleptoparasitism is widespread, theoretical models of kleptoparasitism focus on the intraspecific case. In this project we will develop a game-theoretic model of the behavioural decisions of a host species exploited by a kleptoparasite exerting a constant parasitism pressure, defined to be the rate at which hosts with food are challenged by the parasite. The model will be a modification of the published intraspecific models discussed earlier and will be used to determine the optimal host strategy/strategies for different combinations of parameters. We will consider the case when the host species can choose to fight to retain its food or immediately surrender its food (as in Broom *et al* (2004) and Sirot (2000)). As in the intraspecific case there will be possible extensions to be made which may make the model more realistic.

In order to account for a different type of food item we will consider the apple model (as described in Broom & Ruxton (2003)) and see what affect this would have on the hosts decision to defend food. As suggested in the study by Vickery & Brooke (1994) there is an energy cost in the avoidance responses of flying at a higher altitude, thus another extension will be to consider the affects of the host using an avoidance response. Further, we will consider the optimal strategies for the parasite when it has the choice of kleptoparasitising or not (which could be influenced by avoidance

responses of the host). We can make this extension more realistic by assuming that the parasite has a finite searching capacity, as in Broom & Ruxton (1998).

Chapter 2

A Basic Model for Interspecific Kleptoparasitism

In this chapter we will develop a basic game-theoretic model of the behavioural decisions of a host species which is exploited by a kleptoparasitic species. We will use the model to determine the optimal host strategies for different ecological conditions. The pay-off for a host strategy, q , will depend upon the cost of being in a contest, the cost of finding food items and the parasitic pressure (which is defined to be the rate at which hosts with food are challenged by the parasite). We will think of costs in terms of energy loss, which will be proportional to time expenditure. We will assume that if one strategy has a higher pay-off than another, then this will translate into a fitness advantage for the genes that code for this strategy.

2.1 The Model

We will consider a large population of hosts and parasites, the hosts and parasites have constant population densities of N and P respectively. The hosts are split into three subpopulations according to their activity: a density searching for food items S , a density handling food items H and a density involved in a contest with a parasite A . It is assumed that there is an excess of parasites. Hosts searching find food items at a rate of $v_f f$, where f is the population density of food items. After a food item is found the host begins to handle the food and this takes a time taken from an exponential distribution with mean t_h . In this handling time the host is vulnerable for a parasite to try and steal the food item. It is also assumed that the parasite will always try to steal food if it encounters a host handling food; therefore the parasitic pressure is just the rate at which the parasite encounters handlers,

which is taken as $v_h H$. When a parasite encounters a host the host can decide (with probability q) to resist the attack and thus be in a contest for a fixed time taken from an exponential distribution with mean t_a , or immediately surrender its food item. After a contest there is a clear winner who takes the entire food item. An illustration of the transitions between the three different subpopulations of hosts can be seen in Figure 2-1.

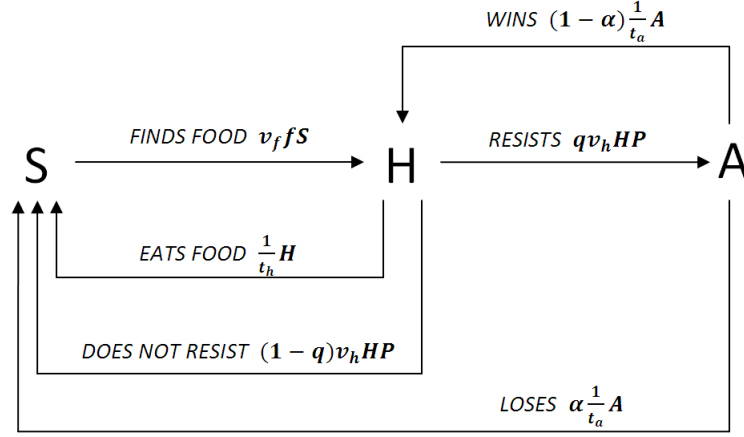


Figure 2-1: Transitions between the three subpopulations of searchers, handlers and those involved in an aggressive encounter. Transition rates are in bold.

As in the extension to the intraspecific Broom-Ruxton model by Broom *et al* (2004), we have allowed the probability of the host winning to vary, i.e. $(1 - \alpha) \in [0, 1]$. In the intraspecific case Broom *et al* (2004) suggest the handler may be at a disadvantage because it has to fight whilst holding on to the food item and also because the parasite may be able to surprise the handler; on the other hand the handler may be at an advantage because the time taken for the parasite to approach the handler might give it a chance to escape, or else make the parasite use more energy trying to catch the handler.

Therefore we have:

$$\frac{dS}{dt} = \frac{H}{t_h} - v_f f S + (1 - q) v_h H P + \alpha \frac{A}{t_a}, \quad (2.1)$$

$$\frac{dH}{dt} = -\frac{H}{t_h} + v_f f S - v_h H P + (1 - \alpha) \frac{A}{t_a}, \quad (2.2)$$

$$\frac{dA}{dt} = q v_h H P - \frac{A}{t_a}, \quad (2.3)$$

$$N = S + H + A. \quad (2.4)$$

Parameter	Units	Default Value	Value Range
N	hosts/hectare	20	1 – 100
P	predators/hectare	20	1 – 100
f	prey/hectare	10	1 – 100
v_f	hectare/seconds	0.01	0.001 – 1
v_h	hectare/seconds	0.05	0.001 – 1
t_h	seconds	10	1 – 100
t_a	seconds	5	1 – 100

Table 1: Default parameter values and their range within which values are chosen.

Hence at equilibrium (justification for later assuming that the population is at this equilibrium state is given in Appendix A) we have

$$S^* = \frac{N(1 + v_h P t_h - v_h P t_h q + q v_h P t_h \alpha)}{1 + v_f f t_h t_a q v_h P + v_f f t_h + v_h P t_h - v_h P t_h q + q v_h P t_h \alpha}, \quad (2.5)$$

$$H^* = \frac{v_f f t_h N}{1 + v_f f t_h t_a q v_h P + v_f f t_h + v_h P t_h - v_h P t_h q + q v_h P t_h \alpha}, \quad (2.6)$$

$$A^* = \frac{v_f f t_h t_a q v_h P N}{1 + v_f f t_h t_a q v_h P + v_f f t_h + v_h P t_h - v_h P t_h q + q v_h P t_h \alpha}. \quad (2.7)$$

2.2 Parameter Values

By considering the parameter values chosen in Holmgren (1995), Ruxton & Moody (1997) and Broom & Ruxton (1998), we will use the default parameter values and their ranges given in Table 1. These values were more or less arbitrarily chosen by Holmgren (1995), where no units were given and little biological interpretation was given. We will use the units given by Luther & Broom (2004). Note: Here we have chosen t_h and t_a to be measured in seconds, but perhaps in different circumstances (e.g. for larger prey items) then these should be measured in minutes.

In Figure 2-2 (a)–(d) we have used these parameters to show how the population densities of each subpopulation change with time. We have set the initial population densities for each subpopulation to be $S_0 = 20$, $H_0 = 0$ and $A_0 = 0$ (we will assume that initially none of the host population have found any food). We have let $q = 0$ and $\alpha = 1/2$ in Figure 2-2 (a) and $q = 1$ and $\alpha = 1/2$ in Figure 2-2 (b). It can be seen that when the host never resists there will be a much higher searcher density than handler density, this is because the hosts are being encountered (and surrendering their food item) at a higher rate than they find food. If we were to increase v_f then we would find that the handler density would increase, and the searcher density decrease, and

for high enough v_f the handler density would be higher than the searcher density. When the host always resists then the number of aggressive individuals increases and the number of searchers decreases, but because the probability of winning is $1/2$ then there are still more searchers than handlers at equilibrium. The steady state solution when $\alpha = 1/2$ and the default parameters are used is $S^* = 10$, $H^* = 1\frac{2}{3}$, $A^* = 8\frac{1}{3}$ when $q = 1$, and $S^* = 18\frac{1}{3}$, $H^* = 1\frac{2}{3}$, $A = 0$ when $q = 0$. In Figure 2-2 (c) we have looked at when the host always resists and always loses, and in Figure 2-2 (d) when the host always resists and always wins. When hosts always win contests we find that the number of handlers is the same as the number of searchers at equilibrium.

2.3 The Uptake Rate

To consider the pay-off for a strategy we can find the uptake rate, γ , this is the rate at which an individual makes the transition from a handler back to a searcher. This rate is effectively the same as the host population per capita rate of food items consumed (as in Broom & Ruxton (1998)), i.e. $\gamma = \frac{H^*}{t_h N}$. Therefore the optimal strategy, q , is the one which maximises γ . As in Broom & Ruxton (1998) we will assume that the system has reached dynamic equilibrium.

Thus, from equation (2.6) we find that the uptake rate as a function of the host strategy, q , is

$$\gamma = \frac{v_f f}{1 + v_f f t_h + v_h P t_h (v_f f q t_a + 1 - q(1 - \alpha))}. \quad (2.8)$$

Thus, in order to maximise γ we need to minimise $v_f f q t_a + 1 - q(1 - \alpha)$, hence the optimal strategy depends upon the values of v_f , f , α and t_a . We will now examine what affect individual parameters have on maximising γ .

Although handling hosts are more likely to be encountered when the number of parasites is very high, their pay-off when encountered is not dependent on how many other parasites there are, and so the value of P has no impact on the optimal strategy. This also makes sense even if there are no parasites because hosts are never encountered so their decision to defend food or not is irrelevant. Similarly, for changes in t_h or v_h it does not matter what choice of q is made, as the optimal strategy only depends upon $v_f f t_a$. This makes sense because if the handling time or the rate parasites encounter handlers are low then there wont be opportunities for kleptoparasitism so it wont matter whether the host defends its food or not.

We can consider what effect the average time spent in an aggressive encounter has on the choice of strategy. When $t_a > (1 - \alpha)/v_f f$ then the optimal strategy is $q = 0$, i.e. if the time in an aggressive encounter is long then it is optimal for an

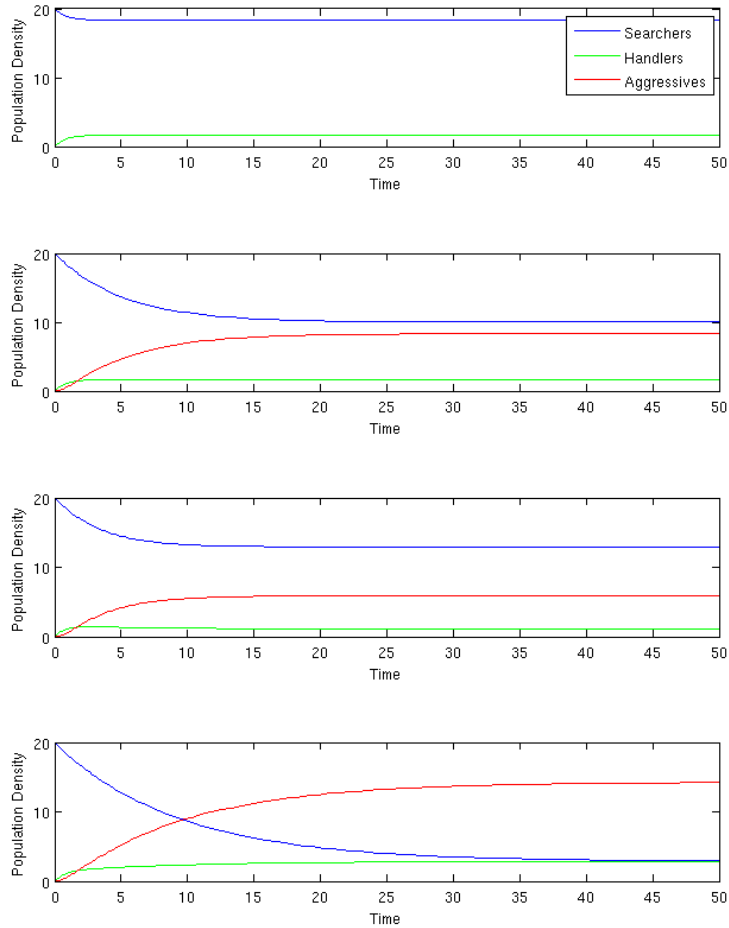


Figure 2-2: Plots of the population density of searchers (blue), handlers (green) and those involved in aggressive interaction (red) as a function of time. (a) Setting $q = 0$, $\alpha = 1/2$; (b) $q = 1$, $\alpha = 1/2$; (c) $q = 1$, $\alpha = 1$; (d) $q = 1$, $\alpha = 0$. The initial population densities for each subpopulation are $S_0 = 20$, $H_0 = 0$ and $A_0 = 0$. Other parameter values are taken as the default values $f = 10$, $P = 20$, $v_f = 0.01$, $v_h = 0.05$, $t_h = 10$, $t_a = 5$.

individual to surrender its food. Alternatively if $t_a < (1 - \alpha)/v_f f$ it is optimal when $q = 1$, i.e. when the time in an aggressive encounter is very small then it is optimal to always resist in a fight. These results are illustrated in Figure 2-3, where it is clear that γ is maximised at either $q = 0$ or $q = 1$. We can see at a threshold value of $t_a = (1 - \alpha)/v_f f$ any value of q gives the same value for γ .

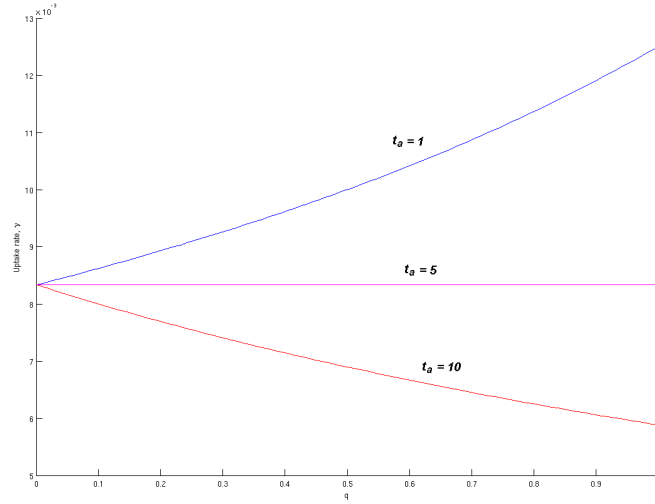


Figure 2-3: Plot of the uptake rate, γ , as a function of q with different values for the time spent in an aggressive encounter. $t_a = 1$ (blue), $t_a = 5$ (magenta) and $t_a = 10$ (red). Other parameter values are taken as $P = 20$, $f = 10$, $v_f = 0.01$, $v_h = 0.05$, $t_h = 10$, $\alpha = 1/2$.

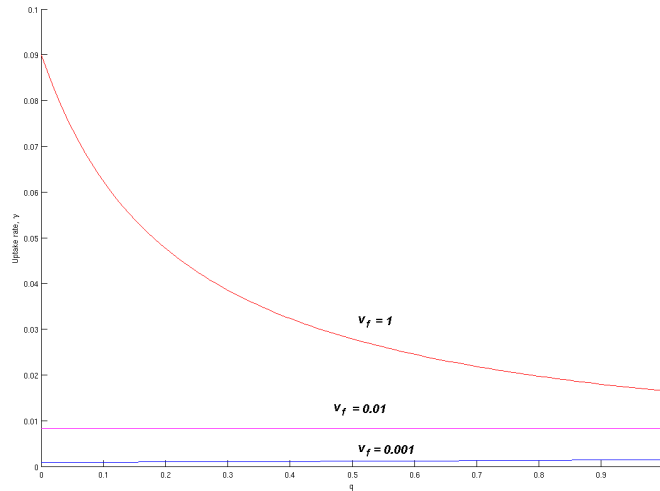


Figure 2-4: Plot of uptake rate, γ , as a function of q with different values for the rate a searcher looks for food items. $v_f = 0.001$ (blue), $v_f = 0.01$ (magenta) and $v_f = 1$ (red). Other parameter values are taken as $P = 20$, $f = 10$, $v_h = 0.05$, $t_h = 10$, $t_a = 5$, $\alpha = 1/2$.

We can also consider what affect the rate at which hosts encounter food items

has in the choice of strategy. If $v_f f < (1 - \alpha)/t_a$ then $q = 1$ is optimal. This makes sense because if there is a low rate of finding food items (because of either a low searching for food rate or a low food density), then an individual which has secured a food item should want to resist a parasite trying to steal its food. Alternatively if $v_f f > (1 - \alpha)/t_a$ then the optimal strategy is $q = 0$. This makes sense because the time cost of finding food items is likely to be smaller than the time cost of being in a contest, hence it would be sensible to avoid contests. These results are illustrated in Figure 2-4 and Figure 2-5.

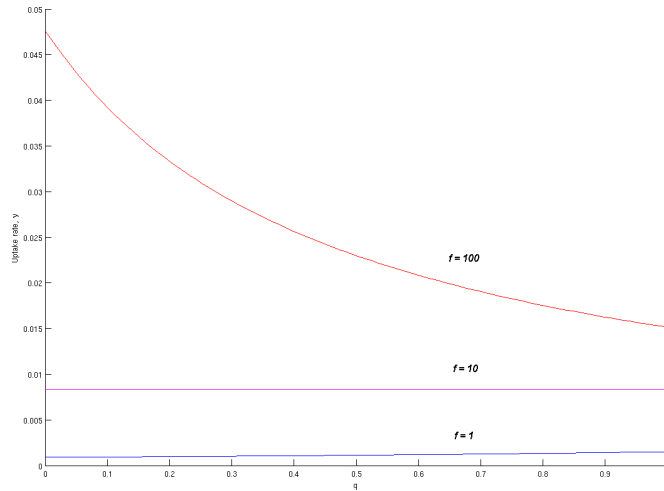


Figure 2-5: Plot of uptake rate, γ , as a function of q with different values for the density of food items. $f = 1$ (blue), $f = 10$ (magenta) and $f = 100$ (red). Other parameter values are taken as $P = 20$, $v_f = 0.01$, $v_h = 0.05$, $t_h = 10$, $t_a = 5$, $\alpha = 1/2$.

2.4 Minimising the Time Expenditure

We will now consider the different options for a handler that has just been challenged by a parasite and the time expenditure for each option. The optimal strategy will be the one which minimises time expenditure, which translates into energy use.

One option for an encountered handler is to immediately surrender its food (with probability $1 - q$) and return to searching for another food item, where the expected time to find another food item is $\frac{1}{v_f f}$. Alternatively the individual could resist the challenge (with probability q) and enter into a contest lasting for an average time of t_a . After this contest the individual could win (with probability $1 - \alpha$) and straight away go back to handling the food item, or it could lose and then go back to searching

and then find food at an expected time of $\frac{1}{v_f f}$. These different sequences of events are shown in Figure 2-6.

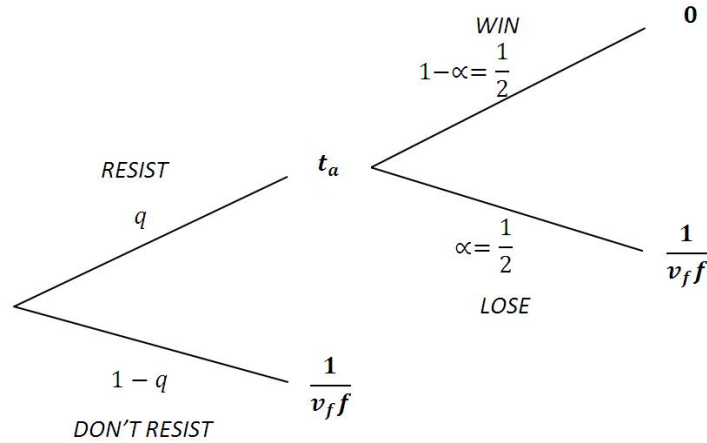


Figure 2-6: Probability tree for a handler who has been encountered by a parasite; showing contest time and the times to become a handler again, (times in bold), and the probabilities of resisting and winning a contest.

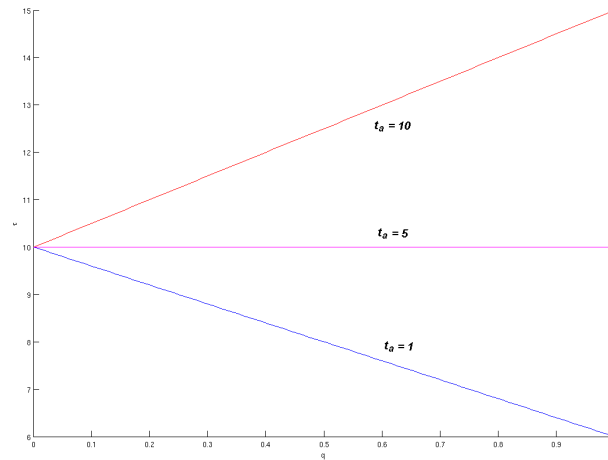


Figure 2-7: Plot of the mean time for an encountered individual to begin handling again, τ , as a function of q with different values for the lengths of contests. $t_a = 1$ (blue), this corresponds to when $v_f f t_a < 1 - \alpha$; $t_a = 5$ (magenta), this corresponds to when $v_f f t_a = 1 - \alpha$; $t_a = 10$ (red), this corresponds to when $v_f f t_a > 1 - \alpha$. Other parameter values are taken as $P = 20$, $f = 10$, $v_f = 0.01$, $v_h = 0.05$, $t_h = 10$, $\alpha = 1/2$.

Therefore the mean time, τ , taken for a handler that has just been encountered

by a parasite to begin handling again is

$$\tau = (1 - q) \frac{1}{v_f f} + q \left(t_a + \alpha \frac{1}{v_f f} \right) = \frac{1}{v_f f} + q \left(t_a - \frac{1 - \alpha}{v_f f} \right). \quad (2.9)$$

Thus there is a linear relationship between q and τ , hence to find the value of q which minimises τ we just need to know the sign of the gradient, i.e. the sign of $t_a - \frac{1 - \alpha}{v_f f}$, this is illustrated in Figure 2-7. If $v_f f t_a > 1 - \alpha$ (which corresponds to the gradient being positive) then it is optimal to play $q = 0$ in order to minimise τ , i.e. never resist. If $v_f f t_a < 1 - \alpha$ then it is optimal to play $q = 1$, i.e. always resist. When $v_f f t_a = 1 - \alpha$ then any value of q chosen gives the same τ value.

These results agree with those found in the previous section. Before we found that $q = 0$ is the optimal strategy when $t_a \rightarrow \infty$ or $v_f f \rightarrow \infty$ (in either case $v_f f t_a > 1 - \alpha$), and $q = 1$ is the optimal strategy when $t_a \rightarrow 0$ or $v_f f \rightarrow 0$ (in either case $v_f f t_a < 1 - \alpha$). We can also see that the choice of q does not matter when the default parameters are used, as using these gives $v_f f t_a = 1 - \alpha$.

2.5 Implications for the Uptake Rate

When $v_f f t_a > 1 - \alpha$ then the optimal strategy is $q = 0$, and so the maximum uptake rate is

$$\gamma_1 = \frac{v_f f}{1 + v_f f t_h + v_h P t_h}, \quad (2.10)$$

hence for this condition it does not matter what the value of α is.

Similarly when $v_f f t_a < 1 - \alpha$ then the optimal strategy is $q = 1$, and so the maximum value for the uptake rate is

$$\gamma_2 = \frac{v_f f}{1 + v_f f t_h + v_h P t_h (v_f f t_a + \alpha)}. \quad (2.11)$$

Note that these are Holling Type II functional responses with extra terms in their denominator. Hence, the uptake rate decelerates due to saturation when the food density is high. This is realistic because we would expect the host to reach a processing food limit when there is a lot of food available.

Hence when $v_f f t_a < 1 - \alpha$ hosts should always resist a kleptoparasitic attack because either the rate at which they find food is low and/or the time in an aggressive encounter is low enough for the contest to not be too much of a cost. On the other hand, when it is very easy for the host to find more food and/or the cost of an aggressive encounter is high then hosts should always surrender their food in a kleptoparasitic attack. From Figure 2-8 we can see that the gradient of the line

chances slightly around the threshold value of $f = 20(1 - \alpha)$, when food density is low ($f < 20(1 - \alpha)$) then the uptake rate decelerates more rapidly as food becomes more plentiful than it does when food density is high ($f > 20(1 - \alpha)$). We can also see that there is no change in the value of the uptake rate as the optimal strategy moves from $q = 1$ to $q = 0$. Thus, around $f = 20(1 - \alpha)$ the choice of strategy doesn't make very much impact to the host's uptake rate. Perhaps for food densities close to this threshold food density it could be observed that there was a mix of behaviours in the host population, as one type of behaviour would only be very slightly more advantageous than the other.

This result is quite different from that found in the intraspecific case by Broom & Ruxton (1998) where they predicted that there would be a dramatic step change in both behaviour and uptake rate as food becomes more difficult to find. This is because in the intraspecific case changing strategy to never kleptoparasitising will mean that the whole population is now only finding new food items, rather than only doing this when there are no kleptoparasitic opportunities, thus there will be a significant change in uptake rate. In our interspecific case, the amount of new food items the host finds from the environment will not depend on whether they resist or not. Hence for food densities around $f = 20(1 - \alpha)$, the threshold between $q = 1$ being an optimal strategy and $q = 0$ being the optimal strategy, the uptake rate will not change.

Figure 2-9 shows the uptake rate as a function of food density for the case when $\alpha = 0$ (the host always wins), again we can see that there is no change in uptake rate as the optimal strategy moves from $q = 1$ to $q = 0$. Although in this case the change in curvature is slightly different. In the plot where $q = 1$, the uptake rate sharply increases with food density and then decelerates. In this case the hosts are always resisting challenges and then always winning them, and so there will be a high proportion of handlers in the population. Hence, it makes sense that increasing the density of food makes less of a difference to the uptake rate than in does in the case where $\alpha = 1/2$.

Hence, for different ecological conditions the optimal strategies are either $\{q = 0\}$ or $\{q = 1\}$. When the chance of a host winning a contest is low then it is only for very low food densities when resisting a contest is a good strategy. On the other hand, even if the host always wins contests then there is still a threshold food density when it is no longer optimal to always resist challenges. Figure 2-10 shows how the uptake rate changes with α and f .

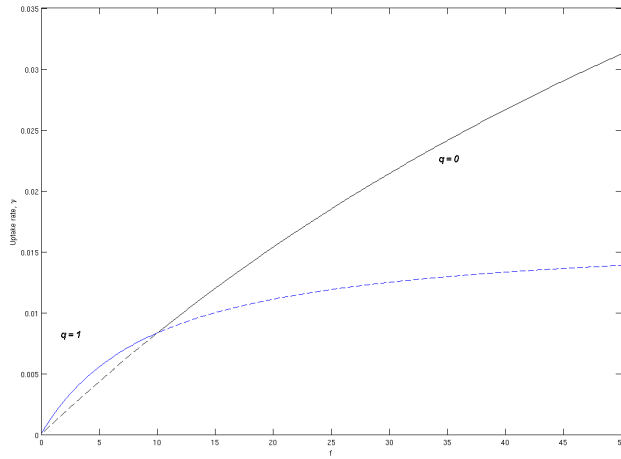


Figure 2-8: Plot of the uptake rate, γ , as a function of food density, f . The blue line is where $q = 1$ and the black where $q = 0$. For $f > 10$, $v_f f t_a > 1 - \alpha$ and handlers should never resist a contest, $q = 0$. For $f < 10$, $v_f f t_a < 1 - \alpha$ and handlers should always resist a contest, $q = 1$. The optimal strategy for each food density is represented by a smooth line. Parameter values are taken as $P = 20$, $v_f = 0.01$, $v_h = 0.05$, $t_h = 10$, $t_a = 5$, $\alpha = 1/2$.

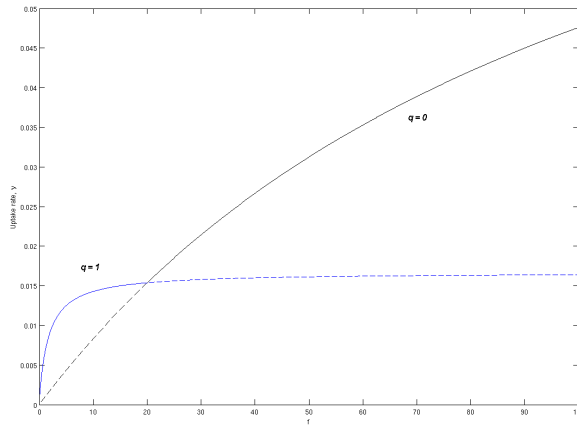


Figure 2-9: Plot of the uptake rate, γ , as a function of food density, f , when the host species always win contests. The blue line is where $q = 1$ and the black where $q = 0$. For $f > 20$, $v_f f t_a > 1 - \alpha$ and handlers should never resist a contest, $q = 0$. For $f < 20$, $v_f f t_a < 1 - \alpha$ and handlers should always resist a contest, $q = 1$, here we have also set $\alpha = 0$. The optimal strategy for each food density is represented by a smooth line. Parameter values are taken as $P = 20$, $v_f = 0.01$, $v_h = 0.05$, $t_h = 10$, $t_a = 5$.

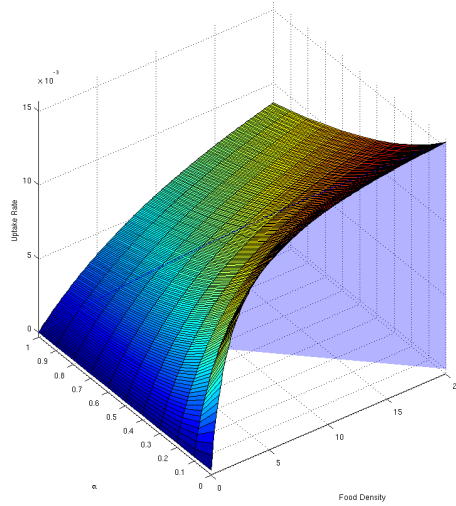


Figure 2-10: Plot of the uptake rate, γ , as a function of food density, f , and the probability of the parasite winning α . We have taken $q = 1$ so we need to look at the non-shaded area of the graph (which is where $v_f f t_a < 1 - \alpha$ holds). Parameter values are taken as $P = 20$, $v_f = 0.01$, $v_h = 0.05$, $t_h = 10$, $t_a = 5$.

2.6 Evolutionarily Stable Strategies.

Maynard Smith & Price (1973) define an Evolutionarily Stable Strategy (ESS) as a strategy such that if most individuals in a population adopt it, then there is no 'mutant' strategy that would give a higher reproductive fitness. We have found unique optimal strategies for different environmental conditions, $q = 0$ and $q = 1$, hence these are the ESS's for their respective conditions. In more detail, if $v_f f t_a > 1 - \alpha$ then the ESS is $q = 0$, because if there was an individual playing another value of q (a 'mutant' strategy) then this individual would have a lower uptake rate and τ would be higher. Thus natural selection would not act on increasing the frequency of alleles for the mutant strategy, so it could never take over a population of individuals playing $q = 0$. The same argument holds to show that $q = 1$ is the ESS when $v_f f t_a < 1 - \alpha$.

In the following chapters we will relax some of the assumptions of the basic model to make it more biologically plausible.

Chapter 3

A Different Food Type

In this chapter we will drop the assumption that handling prey items takes a time randomly drawn from an exponential distribution with mean t_h , and then all the food value is obtained. Here we will consider the case when the amount of previous handling a food item has received has implications on how much food value will be obtained.

As in Broom & Ruxton (2003) we will look at the “apple” food item and find the conditions for which resistance is optimal. The “apple” food item is one for which handling takes a fixed time t_h and the reward from the food item is extracted continuously (and at a constant rate) throughout handling. Our notation and approach will be similar to that in Broom & Ruxton (2003). We will take $h(x)$ as the population density of handlers that are handling a food item that still requires a further handling time, x . Thus when a searcher encounters a food item it enters $h(t_h)$. We also have

$$H = \int_{x=0}^{t_h} h(x) dx. \quad (3.1)$$

If a handler is encountered by a searching parasite (which to begin with we will assume will always try and steal the food item) then the probability that the host will resist the attack is $q(x)$. We will define $a(x)$ as the population density of hosts in aggressive interaction over a food item that still requires a further handling time, x . Hence, like for H we have

$$A = \int_{x=0}^{t_h} a(x) dx. \quad (3.2)$$

We will also take

$$q = \frac{1}{t_h} \int_{x=0}^{t_h} q(x) dx. \quad (3.3)$$

Hence from (2.8) we have

$$\frac{H}{N} = \frac{v_f f t_h}{1 + v_f f t_h + v_h P t_h (v_f f q t_a + 1 - (1 - \alpha) q)} \quad (3.4)$$

where q satisfies (3.3).

3.1 The Apple Model

For this model we should have that when the remaining handling time tends to zero, then $q(x)$ should also tend towards zero. If most of the food value has been obtained, then if challenged it would be sensible to surrender the remaining item and not waste time fighting. We also have that if $q(t_h) = 0$ is an optimal strategy, then $q(x) = 0 \forall x \in [0, t_h]$ is an optimal strategy (as if not resisting a fight over a whole food item is optimal, it will never be optimal to resist over a partial food item). By a similar argument if resisting is ever a good strategy then $q(t_h) = 1$.

We will take X_a as the critical amount of time remaining between playing $q(x) = 0$ (which is optimal when $x < X_a$) and $q(x) = 1$ (which is optimal when $x > X_a$). If $X_a > t_h$ then the optimal strategy is always $q = 0$. Hence we have

$$\int_{x=0}^{t_h} q(x) dx = \int_{x=0}^{X_a} 0 dx + \int_{X_a}^{t_h} 1 dx = t_h - X_a. \quad (3.5)$$

We can consider when a handler of type $h(X_a)$ is encountered by a host, hence resisting or not have equal results. If we look at the case when the individual decides to resist, then it can win with probability $1 - \alpha$ and go back to handling the food. If it gets challenged again then we will assume that now $x < X_a$, so it will surrender the food. If we find the ratio of the expected reward to the expected time to obtain this reward, this will be the long-term average reward rate for challenging in these circumstances, this is

$$\frac{(1 - \alpha) X_a}{t_a + (1 - \alpha) X_a}. \quad (3.6)$$

Hence we have that the long-term rate of food uptake for $0 < X_a < t_h$ as

$$\frac{H}{N} = \frac{(1 - \alpha) X_a}{t_a + (1 - \alpha) X_a}. \quad (3.7)$$

Hence for $0 < X_a < t_h$, using (3.4), (3.5) and (3.7), we have

$$\frac{(1 - \alpha)X_a}{t_a + (1 - \alpha)X_a} = \frac{v_f f t_h}{1 + v_f f t_h + v_h P t_h ((1 - X_a/t_h)(v_f f t_a + \alpha - 1) + 1)}, \quad (3.8)$$

which gives

$$(1 - \alpha)v_h P(1 - \alpha - v_f f t_a)X_a^2 + (1 - \alpha)v_h P\left(\frac{1}{v_h P} + t_h(v_f f t_a + \alpha)\right)X_a - v_f f t_h t_a = 0. \quad (3.9)$$

Which can be solved in Maple to find (when $\alpha = 1/2$)

$$X_a = \frac{1}{2v_h P(2v_f f t_a - 1)} \left(2 + 2v_h P t_h v_f f t_a + v_h P t_h \pm \sqrt{4 + v_h P t_h (4 + 4v_f^2 f^2 t_a^2 (v_h P t_h - 8) + 4v_f f t_a (6 + v_h P t_h) + v_h P t_h)} \right). \quad (3.10)$$

We can see that when $2v_f f t_a - 1 = 0$ there will be a discontinuity, this corresponds to the point in our basic model where the choice of q has no impact on the uptake rate.

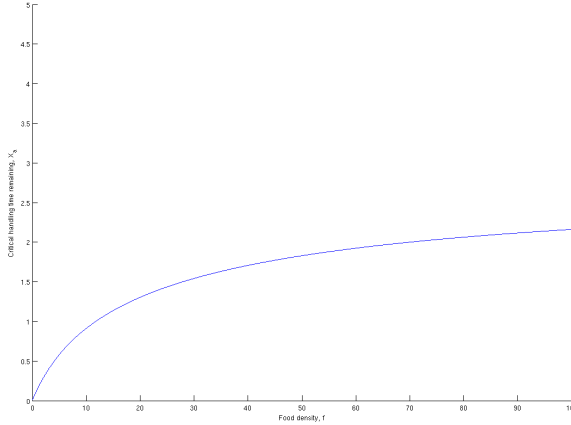


Figure 3-1: Plot of the critical handling time remaining, X_a , as a function of food density. Other parameter values are taken as $P = 20$, $v_f = 0.01$, $v_h = 0.05$, $t_h = 10$, $t_a = 5$, $\alpha = 1/2$.

Figure 3-1 shows a plot of the critical handling time remaining as a function of food density. At the ESS, if a handler is encountered it resists if its food item has more than X_a handling time remaining, and surrenders the food item if the time

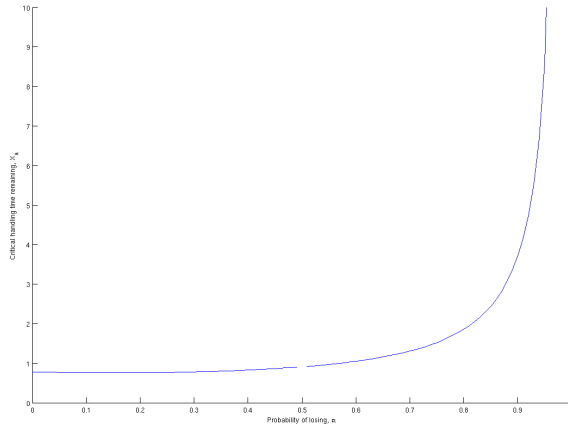


Figure 3-2: Plot of the critical handling time remaining, X_a , as a function of α . Other parameter values are taken as $f = 10$, $P = 20$, $v_f = 0.01$, $v_h = 0.05$, $t_h = 10$, $t_a = 5$.

remaining is less than X_a . We can see that when food density increases X_a also increases, so resisting contests becomes less frequent. This makes sense because if there is more food around then individuals should be more inclined to surrender their food item and look for another. We can see from the graph that X_a is always significantly less than its upper limit of $t_h = 10$, and in fact for $f \in [0, 100]$, $X_a < 3$, hence there is a larger range of handling time remaining for which resisting a contest over a food item is optimal. Thus if it is equally likely that a parasite will challenge a host handling a food item of any handling time remaining, then resisting attacks will be more frequent in the population than surrendering attacks.

Figure 3-2 shows how the critical handling time remaining changes with the probability of the host losing the contest, α increases, with our default parameters. We can see that X_a exponentially increases with α . Hence, when the probability of winning is likely ($\alpha < 1/2$), then hosts will resist contests, even if the food item has a very small handling time remaining. When the probability of winning is unlikely ($\alpha > 1/2$) then it becomes optimal to only resist for food items with large handling times remaining. When $\alpha = 0.953$ it is optimal to never resist kleptoparasitic attacks. Thus we have a similar change in behaviour as in our basic model, except in this case the behaviour change is not as clear cut; when $v_f f t_a < 1 - \alpha$ it is almost always optimal to always resist kleptoparasitic attacks, and when $v_f f t_a > 1 - \alpha$ it gradually becomes less and less optimal to resist kleptoparasitic attacks.

If we look at Figure 3-3 we can see when $P = 5$ there is only one value for X_a for any food density. As the parasite density increases there becomes points where there

are two values for $X_a \leq 10$ for each food density value. For $P = 10$, for example, we have a similar situation to in Broom & Ruxton (2003), where for the lower part of the graph X_a increases and resistance becomes less common as food density increases. The upper part of the graph starts at $X_a = t_h$ and then decreases with increasing food density. At a critical food density the upper and lower parts of the graphs meet.

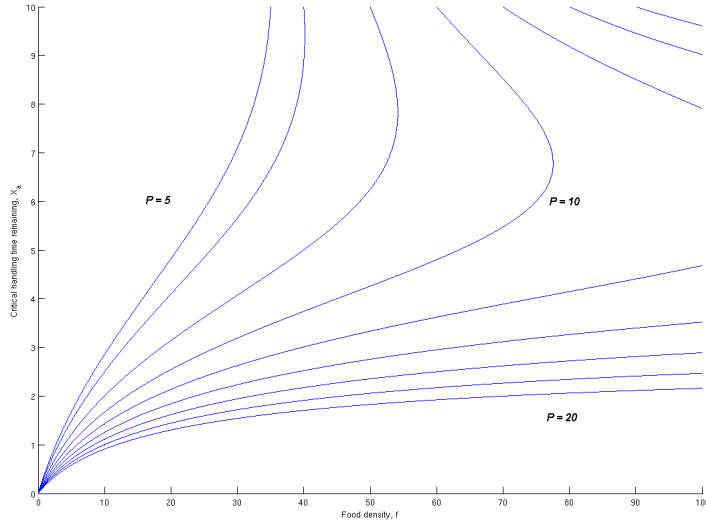


Figure 3-3: Plot of the critical handling time remaining, X_a , as a function of food density for different parasite density values ranging from 5 to 20. Other parameter values are taken as $v_f = 0.01$, $v_h = 0.05$, $t_h = 10$, $t_a = 5$.

Chapter 4

Including an Avoidance Response

Avoidance responses are known to exist in nature, as mentioned in the introduction. The use of an avoidance response by the host will have an energy cost, which could also mean a decreased chance of winning a contest. The benefits to the host of using an avoidance response could include a decreased rate of being encountered by parasites while handling food, and possibly an increase in the chance of the host winning the contest.

For example, boobies are known to fly at a higher altitude on their way back to the roost as a way to avoid kleptoparasitism by frigatebirds (Vickery & Brooke, 1994; Le Corre & Jouventin, 1997). Using this avoidance response may make their journey take longer and also the increased use of energy may make them less efficient if they do become attacked by a frigatebird. However, by flying high the rate at which boobies encounter frigatebirds may decrease. Also, flying high may increase the boobies' chance of winning if a contest does occur because frigatebirds may have used a lot of energy chasing further away Boobies and thus be less efficient in a contest.

Hence, in this chapter we will consider another host strategy, r , which will be the probability of a host using an avoidance response when handling a food item. When a host is not using an avoidance response we will still set the rate of encountering handlers, the probability of the parasite winning a contest and the time taken to handle food items as $v_h H$, α and t_h respectively.

4.1 The Model

We will assume that when an avoidance response is used the rate at which hosts handling food items encounter parasites decreases, thus we will now take this rate to be $(1 - \lambda)v_h P$, where $\lambda \in (0, 1]$ is some constant. We will also assume that the probability of a parasite winning a contest (previously α) will be affected by the use of an avoidance response. When an avoidance response is used this probability is increased (by a factor of a) because of the loss of efficiency by the host and decreased (by a factor of b) because of the loss of efficiency by the parasite, as explained above, hence this probability is now $(1 + a - b)\alpha$. However, for simplicity we will assume that these two effects are equal and so $a = b$. Hence the probability that a parasite will win a contest is just α . A further assumption will be that the use of an avoidance response increases the time taken for a host to handle a food item (e.g. boobies flying higher have a longer flight path as the journey is not as direct). Hence we will now take this time to be $(1 + s)t_h$, where $s > 0$ is some constant.

It should be noted that if the use of an avoidance response increases the handling time for the host then this will give the parasite more chance of encountering the handling host, even though the use of an avoidance response should also decrease this chance. However, we will assume that this decrease in chance of encounter is much higher than its increase and thus treat λ and s as independent of one another.

The transitions between the subpopulations are summarised in Figure 4-1; we have now divided the handling subpopulation into those using an avoidance response, H_2 , and those not, H_1 . Hence, by including the possibility of using an avoidance response we have the system of equations;

$$\frac{dS}{dt} = \frac{2\alpha}{t_a}A - v_f f S + ((1 - q)v_h P + \frac{1}{t_h})H_1 + ((1 - q)(1 - \lambda)v_h P + \frac{1}{t_h(1 + s)})H_2, \quad (4.1)$$

$$\frac{dH_1}{dt} = (1 - r)v_f f S - (v_h P + \frac{1}{t_h})H_1 + \frac{1 - \alpha}{t_a}A, \quad (4.2)$$

$$\frac{dH_2}{dt} = r v_f f S - ((1 - \lambda)v_h P + \frac{1}{(1 + s)t_h})H_2 + \frac{1 - \alpha}{t_a}A, \quad (4.3)$$

$$\frac{dA}{dt} = q v_h P H_1 + q(1 - \lambda)v_h P H_2 - \frac{2}{t_a}A. \quad (4.4)$$

We can look at the case when the whole population uses an avoidance response.

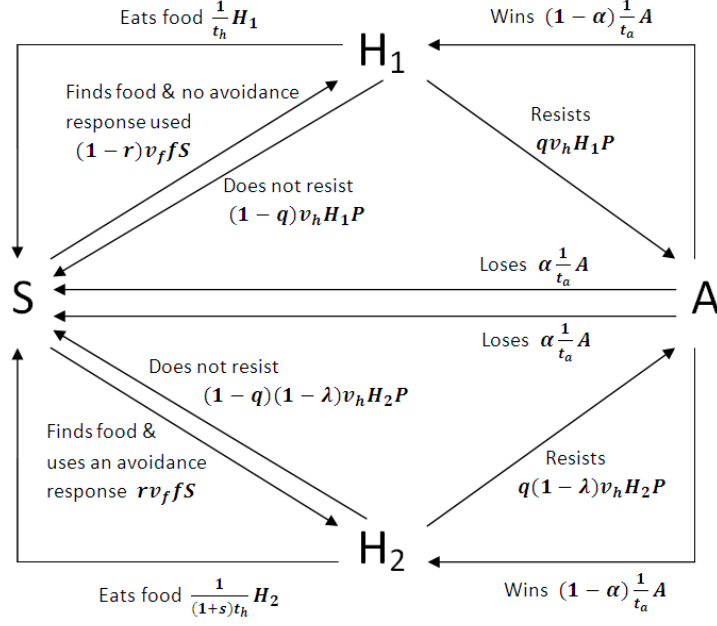


Figure 4-1: Transitions between the subpopulations of searchers, handlers using an avoidance response, handlers not using an avoidance response and those involved in an aggressive encounter. Transition rates are in bold.

In this case we have

$$\frac{dS}{dt} = \frac{\alpha}{t_a} A - v_f f S + ((1-q)(1-\lambda)v_h P + \frac{1}{t_h(1+s)})H_2, \quad (4.5)$$

$$\frac{dH_2}{dt} = v_f f S - ((1-\lambda)v_h P + \frac{1}{(1+s)t_h})H_2 + \frac{1-\alpha}{t_a} A, \quad (4.6)$$

$$\frac{dA}{dt} = q(1-\lambda)v_h P H_2 - \frac{1}{t_a} A, \quad (4.7)$$

$$S + H_2 + A = N. \quad (4.8)$$

4.2 Optimal Strategies

We can find the uptake rate for this population of hosts using an avoidance response at steady state, which will now be $H_2^*/N(1+s)t_h$.

$$(4.7) : \quad A^* = t_a q(1-\lambda)v_h P H_2^*, \quad (4.9)$$

$$(4.8) : \quad S^* = N - (1 + t_a q(1-\lambda)v_h P)H_2^*, \quad (4.10)$$

$$(4.5) - (4.6) : \quad -2v_f f S^* + ((2 - q)(1 - \lambda)v_h P + \frac{2}{(1 + s)t_h})H_2^* + (2\alpha - 1)\frac{1}{t_a}A^* = 0, \quad (4.11)$$

$$\implies \quad \gamma = \frac{H_2^*}{N(1 + s)t_h} = \frac{v_f f}{1 + (1 + s)t_h(v_f f + (1 - \lambda)v_h P(1 + q(v_f f t_a + \alpha - 1)))}. \quad (4.12)$$

As before, to maximise this uptake rate we need to also minimise the time expenditure. We will assume that an individual will always use an avoidance response. Thus the average time taken for an encountered individual to begin handling again will be the same as in the previous chapter (because using an avoidance response has no effect on the probability that the host will win a contest, the time taken for it to find food, or the time taken in an aggressive encounter), i.e.

$$\tau = \frac{1}{v_f f} + q(t_a + \frac{\alpha - 1}{v_f f}). \quad (4.13)$$

Therefore, as before it is optimal never to resist, $q = 0$, when $v_f f t_a > 1 - \alpha$ and always to resist, $q = 1$, when $v_f f t_a < 1 - \alpha$. Hence when $v_f f t_a > 1 - \alpha$ holds the uptake rate is

$$\gamma_1 = \frac{v_f f}{1 + (1 + s)t_h(v_f f + (1 - \lambda)v_h P)}. \quad (4.14)$$

and when $v_f f t_a < 1 - \alpha$ holds the it is

$$\gamma_2 = \frac{v_f f}{1 + (1 + s)t_h(v_f f + (1 - \lambda)v_h P(v_f f t_a + \alpha))}. \quad (4.15)$$

The plot of the uptake rate as a function of food density when an avoidance response is used and when one is not is shown in Figure 4-2 for a few different combinations of λ and s values. When we consider a “bad” avoidance response, i.e. one for which the handling time is greatly increased and the encounter rate isn’t decreased by much, for example when $s = 2$, $\lambda = 0.5$, we can see that the uptake rate is never higher than when not using an avoidance response. On the other hand when we consider a “good” avoidance response, i.e. one where the handling time is slightly increased and the encounter rate is heavily decreased, for example when $s = 0.1$, $\lambda = 0.9$, we find that the uptake rate is always higher than in the case where an avoidance response is not used.

We can now look at the conditions for which the value of the uptake rate when using an avoidance response is higher than when one is not used, i.e. the conditions for which $r = 1$ is the optimal strategy. When $q = 0$ the value of the uptake rate when using an avoidance response is higher than its value when one is not used, (2.10)

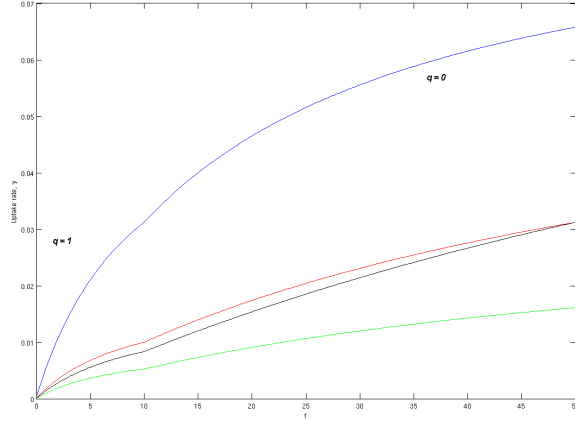


Figure 4-2: Plot of the uptake rate, γ , as a function of food density, f . When an avoidance response is never used (black line) and when one is always used (green, red and blue lines) for different values of s and λ . Green line: $s = 2$, $\lambda = 0.5$; Blue line: $s = 0.1$, $\lambda = 0.9$; Red line: $s = \lambda = 0.5$. When $f > 10$, $q = 0$. When $f < 10$, $q = 1$. Other parameter values are taken as $P = 20$, $v_f = 0.01$, $v_h = 0.05$, $t_h = 10$, $t_a = 5$, $\alpha = 1/2$.

< (4.14), when

$$1 + t_h(v_f f + v_h P) > 1 + (1 + s)t_h(v_f f + (1 - \lambda)v_h P). \quad (4.16)$$

Hence, when

$$s < \frac{\lambda v_h P}{v_f f + (1 - \lambda)v_h P} \quad \text{and} \quad v_f f t_a > 1 - \alpha \quad (4.17)$$

the optimal strategy is $\{q = 0, r = 1\}$, but when

$$s > \frac{\lambda v_h P}{v_f f + (1 - \lambda)v_h P} \quad \text{and} \quad v_f f t_a > 1 - \alpha \quad (4.18)$$

the optimal strategy is $\{q = 0, r = 0\}$.

Similarly when $q = 1$ the uptake rate when using an avoidance response is higher than its value when an avoidance response is not used, (2.11) < (4.15), when

$$1 + t_h v_f f + t_h v_h P(v_f f t_a + \alpha) > 1 + (1 + s)t_h(v_f f + (1 - \lambda)v_h P(v_f f t_a + \alpha)). \quad (4.19)$$

Hence, when

$$s < \frac{\lambda v_h P(v_f f t_a + \alpha)}{v_f f + (1 - \lambda)v_h P(v_f f t_a + \alpha)} \quad \text{and} \quad v_f f t_a < 1 - \alpha \quad (4.20)$$

the optimal strategy is $\{q = 1, r = 1\}$, but when

$$s > \frac{\lambda v_h P(v_f f t_a + \alpha)}{v_f f + (1 - \lambda)v_h P(v_f f t_a + \alpha)} \quad \text{and} \quad v_f f t_a < 1 - \alpha \quad (4.21)$$

the optimal strategy is $\{q = 1, r = 0\}$.

The area where the use of an avoidance response is optimal in the cases where the host population never and always resists are shown in Figures 4-3 and 4-4 respectively, for these we have taken $\alpha = 1/2$. We can see that when $q = 1$ using an avoidance response is optimal when the food density is low and the value of λ is high (corresponding to a low rate of parasites encountering handling hosts). When $q = 0$ there is larger range of food densities and values of λ for which using an avoidance response is optimal.

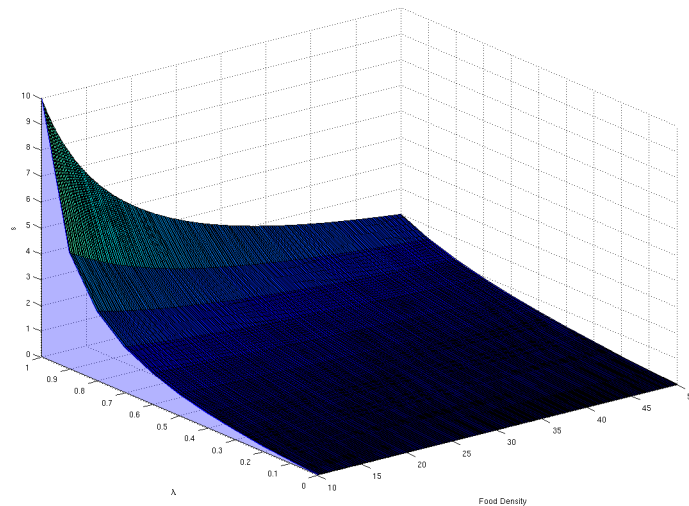


Figure 4-3: Plot of the region within the parameters λ , f and s where the use of an avoidance response maximises the uptake rate (shaded). In this case individuals never resist, $q = 0$, and $v_f f t_a > 1 - \alpha$. Other parameter values are taken as $P = 20$, $v_f = 0.01$, $v_h = 0.05$, $t_h = 10$, $t_a = 5$, $\alpha = 1/2$.

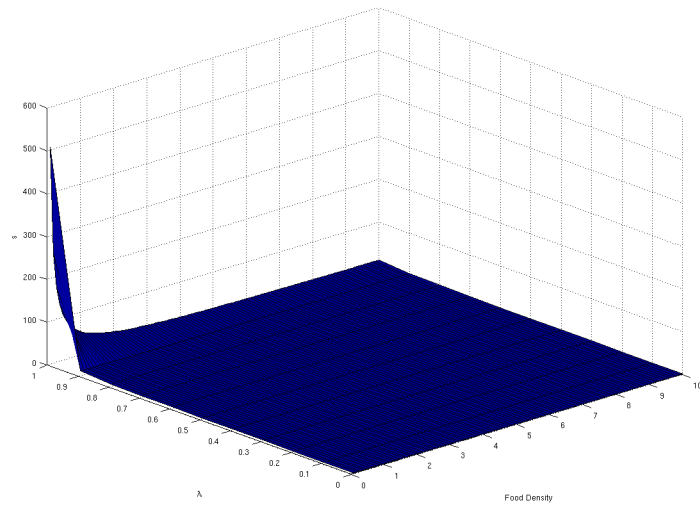


Figure 4-4: Plot of the region within the parameters λ , f and s where the use of an avoidance response maximises the uptake rate (shaded). In this case individuals always resist, $q = 1$, and $v_f f t_a < 1 - \alpha$. Other parameter values are taken as $P = 20$, $v_f = 0.01$, $v_h = 0.05$, $t_h = 10$, $t_a = 5$, $\alpha = 1/2$.

Chapter 5

Including Parasite Strategies

In the intraspecific case Broom & Ruxton (1998) considered the optimal p strategy, which was the probability that an individual will choose to kleptoparasitise. In the previous sections we were setting $p = 1$, i.e. if a parasite encountered a handling host it would always try and steal the food, and found the optimal q value. In this section we will look at the optimal parasitic strategies for different environmental conditions. Since when hosts never resist contests it will always be beneficial for the parasite to kleptoparasitise, we will just consider the case where the host always resists ($q = 1$) and the parasite can choose to kleptoparasitise (with probability p) or not.

5.1 The Model

We will assume that the searching parasites only kleptoparasitise the host species, and the parasitic population is split up into searchers (S_P), handlers (H_P) and those in an aggressive contest (A_P), hence $S_P + H_P + A_P = P$. We will now refer to the subpopulations of hosts as S_H , H_H and A_H . Note that the subscript “H” denotes that a subpopulation of hosts, and the subscript “h” denotes a property associated with handling. We will also assume that the parasites eat the same food items as the hosts, and that they both encounter these food items at the same rate (i.e. $v_f f$). Another assumption is that the average time taken to handle a food item is the same for both the hosts and the parasites (i.e. t_h). These assumptions are for simplicity, although they are probably not very realistic. The transition rates between the subpopulations of both the host and the parasite are shown in Figure 5-1.

Hence, for the hosts we have

$$\frac{dS_H}{dt} = \frac{1}{t_h} H_H + \alpha \frac{1}{t_a} A_H - v_f f S_H, \quad (5.1)$$

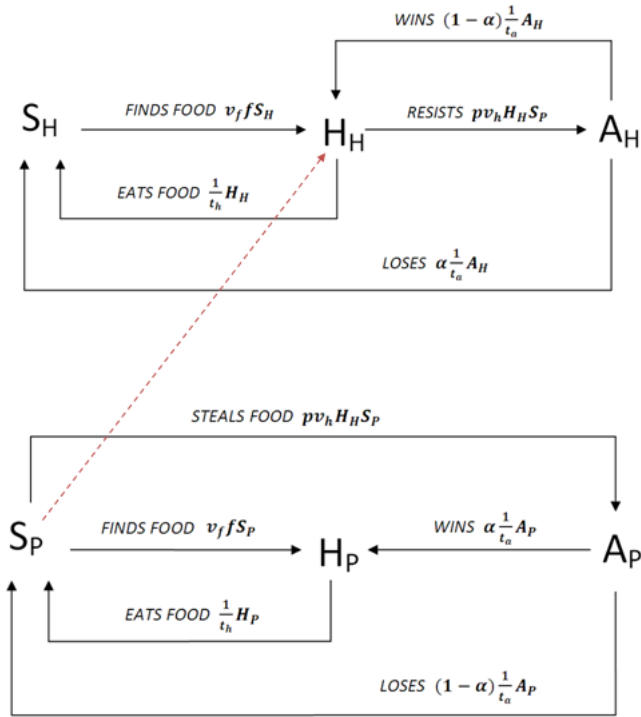


Figure 5-1: Transitions between the subpopulations of searchers, handlers and those involved in an aggressive encounter for both host and parasite populations. Here hosts always resist contests and parasites can choose to kleptoparasitise with probability, p . Transition rates are in bold. The dashed red line represents where kleptoparasitism occurs.

$$\frac{dH_H}{dt} = v_f f S_H - \frac{1}{t_h} H_H + (1 - \alpha) \frac{1}{t_a} A_H - p v_h H_H S_P, \quad (5.2)$$

$$\frac{dA_H}{dt} = p v_h H_H S_P - \frac{1}{t_a} A_H, \quad (5.3)$$

and for the parasites we have

$$\frac{dS_P}{dt} = \frac{1}{t_h} H_P + (1 - \alpha) \frac{1}{t_a} A_P - p v_h H_H S_P - v_f f S_P, \quad (5.4)$$

$$\frac{dH_P}{dt} = -\frac{1}{t_h} H_P + \alpha \frac{1}{t_a} A_P + v_f f S_P, \quad (5.5)$$

$$\frac{dA_P}{dt} = p v_h H_H S_P - \frac{1}{t_a} A_P. \quad (5.6)$$

5.2 Optimal Parasite Strategies

Thus we can consider what value of p is optimal for the parasites when the hosts are always resisting contests. To do this, as before, we can look at maximising the uptake rate, $\gamma_P = \frac{H_P^*}{P t_h}$, of the parasites. We must first find an expression for H_H^* , using Maple, at dynamic equilibrium we find

$$H_H^* = \frac{v_f f N}{v_f f + \frac{1}{t_h} + S_P^* p v_h (v_f f t_a + \alpha)}, \quad (5.7)$$

we can see that if the number of searching parasites which always kleptoparasitise tends to infinity then the number of handling hosts will tend towards zero.

For the parasitic system of equations at dynamic equilibrium we have:

$$(5.6) : \quad A_P^* = t_a p v_h H_H^* S_P^*, \quad (5.8)$$

$$(P = S_P^* + H_P^* + A_P^*) : \quad S_P^* = P - H_P^* - t_a p v_h H_H^* S_P^* \implies S_P^* = \frac{P - H_P^*}{1 + t_a p v_h H_H^*}, \quad (5.9)$$

$$(5.4) - (5.5) : \quad \frac{2}{t_h} H_P^* + (1 - 2\alpha) \frac{1}{t_a} A_P^* - (p v_h H_H^* + 2 v_f f) S_P^* = 0, \quad (5.10)$$

$$(5.8) : \quad \frac{2}{t_h} H_P^* - 2\alpha p v_h H_H^* S_P^* - 2 v_f f S_P^* = 0. \quad (5.11)$$

From Figure 5-2 we can see that the average time taken for a parasite which has just encountered a host handling food to begin handling again (in an environment where hosts always resist challenges) is

$$t_o = (1 - p) t_s + p(t_a + (1 - \alpha) t_s), \quad (5.12)$$

where t_s is the average time taken for a searching parasite to begin handling again. This is

$$t_s = \frac{1}{v_f f + v_h H_H^*} + \frac{v_h H_H^*}{v_f f + v_h H_H^*} t_o. \quad (5.13)$$

Hence, we can find the average time taken for a parasite which has just started handling a food item to begin handling again, this is

$$T_P = t_h + t_s = t_h + \frac{1 + p v_h H_H^* t_a}{v_f f + p \alpha v_h H_H^*}. \quad (5.14)$$

Which is more complicated than before because we have a H_H term, and this is also dependent on p , in the equation. However, we can show numerically that $p H_H$

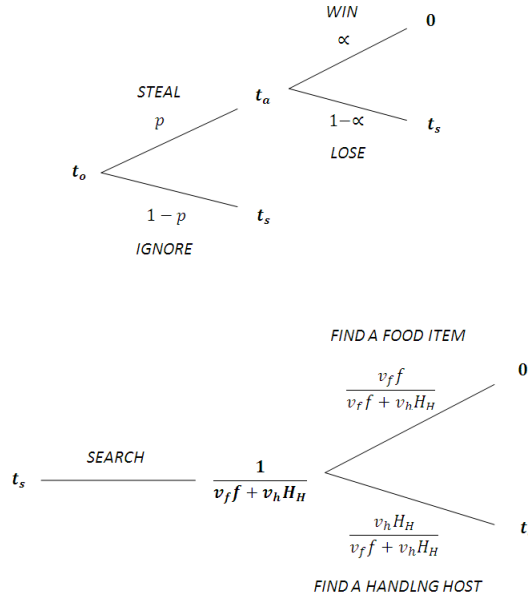


Figure 5-2: Probability trees for a parasite which has just had the opportunity to steal food off a handling host (upper) and a parasite which has just started searching for food (lower). Showing contest time and the time to find food, (times in bold), and the probabilities of stealing food, winning contests, and finding a handling host or a food item when searching for food.

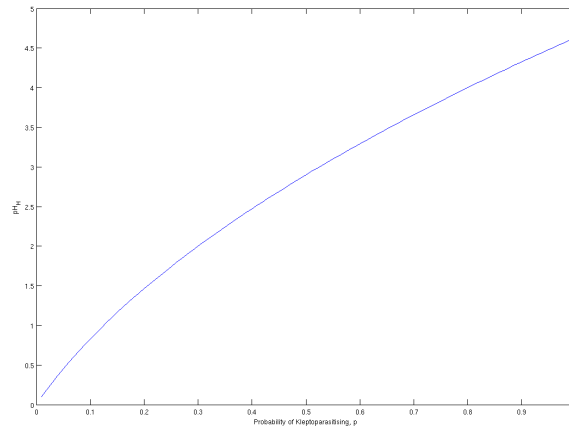


Figure 5-3: pH_H against p . Parameter values are taken as $P = 20$, $N = 20$, $f = 10$, $v_f = 0.01$, $v_h = 0.05$, $t_h = 10$, $t_a = 5$ and $\alpha = 1/2$.

increases when p increases for our default parameters (Figure 5-3). Thus to find the

conditions for which T_P is minimised we can effectively ignore the H_H^* term, as the same inequalities will hold. Hence $p = 0$ is the optimal strategy if

$$\frac{1}{v_f f} < \frac{1 + v_h t_a}{v_f f + \alpha v_h} \quad (5.15)$$

which corresponds to $v_f f t_a > \alpha$. On the other hand $p = 1$ is the optimal strategy if

$$\frac{1}{v_f f} > \frac{1 + v_h t_a}{v_f f + \alpha v_h} \quad (5.16)$$

which corresponds to $v_f f t_a < \alpha$.

Hence, when $v_f f t_a > \alpha$ we have that

$$H_H^* = \frac{v_f f N}{v_f f + 1/t_h} \quad \text{and} \quad S_P^* = P - H_P^*, \quad (5.17)$$

$$(5.11) : \quad \frac{1}{t_h} H_P^* - v_f f (P - H_P^*) = 0. \quad (5.18)$$

Thus the uptake rate for this condition is

$$\gamma_{P,1} = \frac{H_P^*}{P t_h} = \frac{v_f f}{1 + t_h v_f f}. \quad (5.19)$$

We can solve (5.7), (5.9) and (5.11) in Maple to find an expression for the uptake rate for any p . Figures 5-4 (a)–(c) show how the uptake rate is affected by various parameters.

Using default parameters and $\alpha = 1/2$, we can find an expression in Maple for the uptake rate when $p = 1$ as a function of f . This is plotted, along with the $p = 0$ case, in Figure 5-5.

In the Broom & Ruxton (1998) paper they find the same uptake rate value for when $v_f f t_a > \alpha$ holds (note: in their paper they use $t_a/2$ as the mean contest time). In their paper then they are also looking at the optimal parasite strategy $\{p\}$ and assume that the hosts that they are challenging will always resist. Thus it makes sense that when kleptoparasitism never occurs the uptake rate for the parasite should be the same for both the inter- and intraspecific case. When kleptoparasitism always occurs and $v_f f t_a < \alpha$ Broom & Ruxton (1998) find in the intraspecific case that the uptake rate for the parasite is

$$\gamma_{th} = \frac{-(C + 1) + \sqrt{(C + 1)^2 + 4CD}}{2D}, \quad (5.20)$$

where $C = t_h f v_f$ and $D = 2t_a P v_h$ (because they use $t_a/2$).

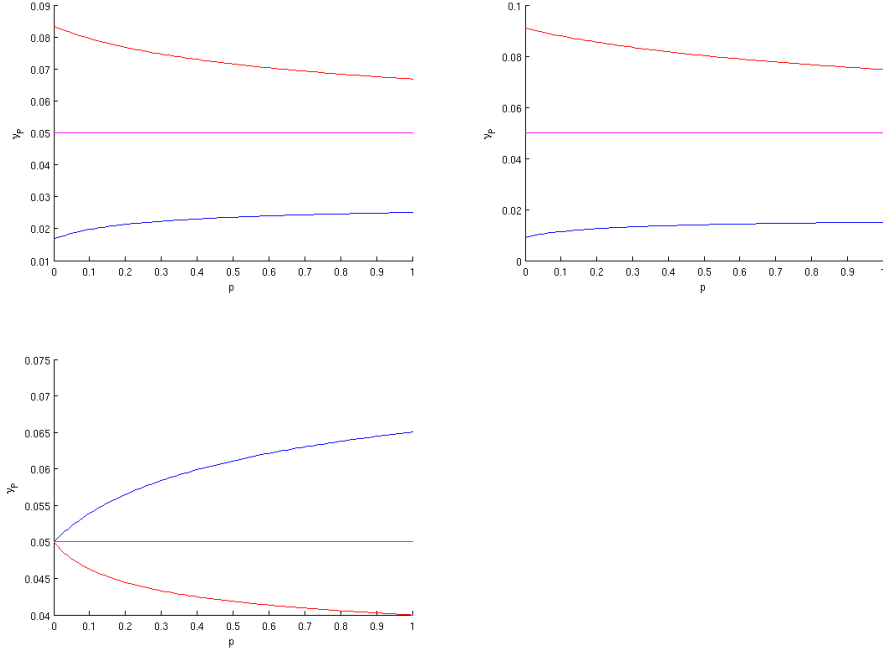


Figure 5-4: The uptake rate for the parasite against p , varying different parameters. (a) Varying food density, blue: $f = 2$, magenta: $f = 10$, red: $f = 50$. (b) Varying v_f , blue: $v_f = 0.001$, magenta: $v_f = 0.01$, red: $v_f = 0.1$. (c) Varying t_a , blue: $t_a = 1$, magenta: $t_a = 5$, red: $t_a = 10$. Other parameter values are taken as $P = 20$, $N = 20$, $f = 10$, $v_f = 0.01$, $v_h = 0.05$, $t_h = 10$, $t_a = 5$ and $\alpha = 1/2$.

5.3 Including an avoidance response

In this section we will consider the case where the host population can use an avoidance response or not and is also able to resist or not. The transitions between subpopulations for both the hosts and the parasites can be seen in Figure 5-6. When an avoidance response is not used then we can just set $s = \lambda = 0$.

Hence we have

$$\frac{dS_H}{dt} = \frac{1}{(1+s)t_h} H_H + p(1-q)(1-\lambda)v_h H_H S_P + \alpha \frac{1}{t_a} A_H - v_f f S_H, \quad (5.21)$$

$$\frac{dH_H}{dt} = v_f f S_H - \frac{1}{(1+s)t_h} H_H - p(1-\lambda)v_h H_H S_P + (1-\alpha) \frac{1}{t_a} A_H, \quad (5.22)$$

$$\frac{dA_H}{dt} = pq(1-\lambda)v_h H_H S_P - \frac{1}{t_a} A_H, \quad (5.23)$$

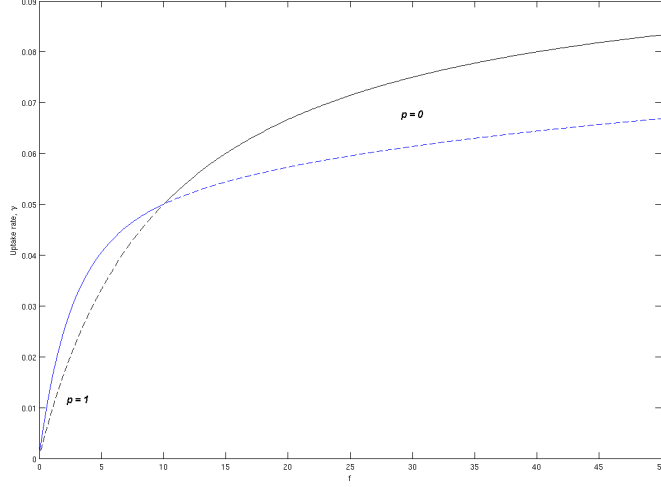


Figure 5-5: Plot of the uptake rate, γ , as a function of food density, f . The blue line is where $q = 1$ and the black where $q = 0$. For $f > 10$, $v_f f t_a > \alpha$ and parasites should never kleptoparasitise, $p = 0$. For $f < 10$, $v_f f t_a < \alpha$ and parasites should always kleptoparasitise, $p = 1$. Hosts always resist contests. The optimal strategy for each food density is represented by a smooth line. Parameter values are taken as $P = 20$, $N = 20$, $v_f = 0.01$, $v_h = 0.05$, $t_h = 10$, $t_a = 5$ and $\alpha = 1/2$.

$$\frac{dS_P}{dt} = \frac{1}{t_h} H_P - p(1 - \lambda)v_h H_H S_P + (1 - \alpha)\frac{1}{t_a} A_P - v_f f S_P, \quad (5.24)$$

$$\frac{dH_P}{dt} = -\frac{1}{t_h} H_P + p(1 - q)(1 - \lambda)v_h H_H S_P + \alpha\frac{1}{t_a} A_P + v_f f S_P, \quad (5.25)$$

$$\frac{dA_P}{dt} = pq(1 - \lambda)v_h H_H S_P - \frac{1}{t_a} A_P. \quad (5.26)$$

At dynamic equilibrium we find that:

$$(5.23) : \quad A_H^* = t_a p q (1 - \lambda) v_h H_H^* S_P^*, \quad (5.27)$$

$$(N = S_H^* + H_H^* + A_H^*) \implies \quad S_H^* = N - (1 + t_a p q (1 - \lambda) v_h S_P^*) H_H^*, \quad (5.28)$$

$$(5.21)-(5.22) : \quad \frac{2}{(1+s)t_h} H_H^* + p(2-q)(1-\lambda)v_h H_H^* S_P^* + (2\alpha-1)\frac{1}{t_a} A_H^* - 2v_f f S_H^* = 0, \quad (5.29)$$

$$\implies \quad H_H^* = \frac{v_f f N}{\left(\frac{1}{(1+s)t_h} + v_f f + p(1-\lambda)v_h S_P^*(1+q(\alpha-1+v_f f t_a))\right)}. \quad (5.30)$$

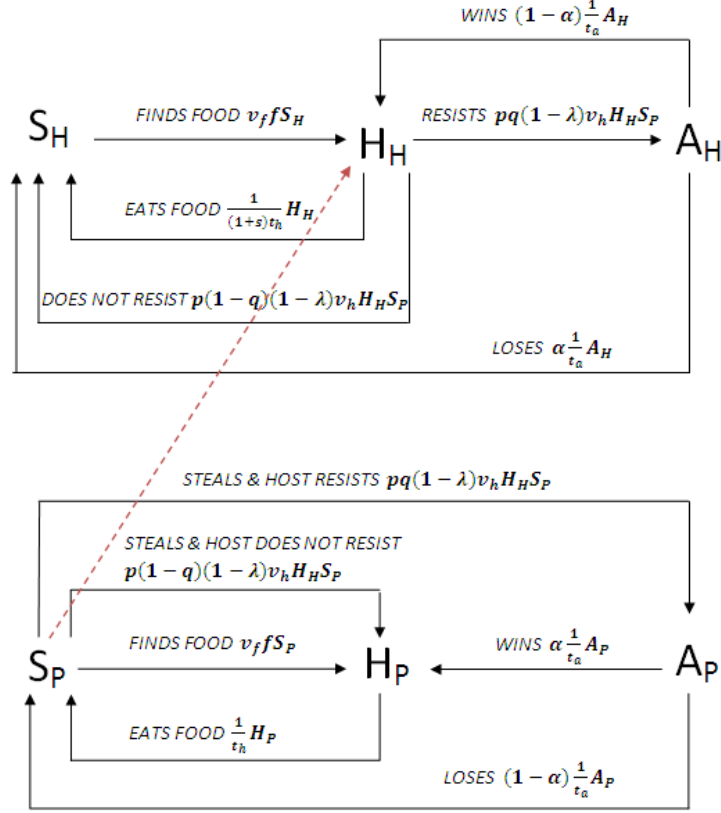


Figure 5-6: Transitions between the subpopulations of searchers, handlers and those involved in an aggressive encounter for both host and parasite populations. Here hosts always use an avoidance response. Transition rates are in bold. The dashed red line represents where kleptoparasitism occurs.

From the equations for the parasite population we have

$$(5.26) : \quad A_P^* = t_a p q (1 - \lambda) v_h H_H^* S_P^*, \quad (5.31)$$

$$(P = S_P^* + H_P^* + A_P^*) \implies \quad S_P^* = \frac{P - H_P^*}{1 + t_a p q (1 - \lambda) v_h H_H^*}, \quad (5.32)$$

$$(5.24) - (5.25) : \quad \frac{2}{t_h} H_P^* - (2 - q) p (1 - \lambda) v_h H_H^* S_P^* + (1 - 2\alpha) \frac{1}{t_a} A_P^* - 2v_f f S_P^* = 0, \quad (5.33)$$

$$\implies \quad \frac{2}{t_h} H_P^* + 2p(1 - \lambda) v_h H_H^* S_P^* (-1 + q - \alpha q) - 2v_f f S_P^* = 0, \quad (5.34)$$

$$H_P^* = \frac{-t_h P (2p(1 - \lambda) v_h H_H^* (-1 + q - \alpha q) - 2v_f f)}{2 + 2p(1 - \lambda) v_h H_H^* (t_a q - t_h (-1 + q - \alpha q)) + 2t_h v_f f}. \quad (5.35)$$

Hence, when parasites never kleptoparasitise, $p = 0$, we find the uptake rate for

the host and the parasites respectively as

$$\gamma_H = \frac{H_H^*}{N(1+s)t_h} = \frac{v_f f}{1 + (1+s)t_h v_f f}, \quad (5.36)$$

$$\gamma_P = \frac{H_P^*}{P t_h} = \frac{v_f f}{1 + t_h v_f f}. \quad (5.37)$$

To find the uptake rates when parasites always kleptoparasitise we will need to use Maple to solve (5.30), (5.32) and (5.34).

In this section we will not be considering the conditions for minimising the time expenditure, we will just be looking at maximising the uptake rate.

Plots of the uptake rate for the parasites and hosts with varying α can be seen in Figures 5-7 –5-9. In Figures 5-7 and 5-8 we have used a low food density value of $f = 1$. In Figures 5-9 (a) and (b) we have looked at at high food density value of $f = 100$. We have also assumed hat if an avoidance response is used by a host then it will be a “good” one, i.e. one for which $s = 0.1$ and $\lambda = 0.9$.

5.3.1 Optimal strategies for the parasite for low food densities.

We can see from Figure 5-7 that the best scenario for the parasite (in terms of maximising its uptake rate) is when the host never resists contests and does not use an avoidance response, and the parasite always kleptoparasitises (the red line), which is an obvious conclusion for low food densities.

We can also see that when the probability of winning is greater than a value α_1 , then it is always optimal to kleptoparasitise. If $p = 1$ and $q = 0$ then the uptake rate for the parasite is independent of α (because contests never even occur) and is always lower when the host uses an avoidance response than when it doesn’t. This result makes sense because the parasite will not be encountering hosts as frequently so there won’t be as many handling parasites.

We also observe that when the host always resists and $\alpha < \alpha_1$ then it is optimal for the parasite to never kleptoparasitise. When the parasite does steal food however, the parasite has a higher uptake rate when the host uses an avoidance response than it does when the host doesn’t use an avoidance response. If α is low then there will be more handling hosts in the population because they are more likely to win the contests, and thus if $p = 1$ then there will be more hosts for the parasites to exploit. Hence this could increase the number of handling parasites (and thus γ_P) because there will be more contests. We can see that when $p = q = 1$ and $\alpha \rightarrow 0$ in (5.35) then H_P is greater when $s, \lambda \neq 0$, i.e. when an avoidance response is used.

We can also see that when $\alpha < \alpha_2$ other than when $p = 1, q = 0$ and $r = 0$, the parasites uptake rate is greatest when $p = 1, q = 0$ and $r = 1$, however when $\alpha > \alpha_2$ this is greatest when $p = 1, q = 1$ and $r = 0$. Thus, when a parasite is likely to win a contest then it benefits from the host resisting but not using an avoidance response, because in this case it will probably win and also encounter hosts at a higher rate. When the parasite is less likely to win a contest ($\alpha < \alpha_2$) then it is best for the parasite to never be resisted. We can find that $\alpha_1 = 0.05$ and $\alpha_2 = 0.26$.

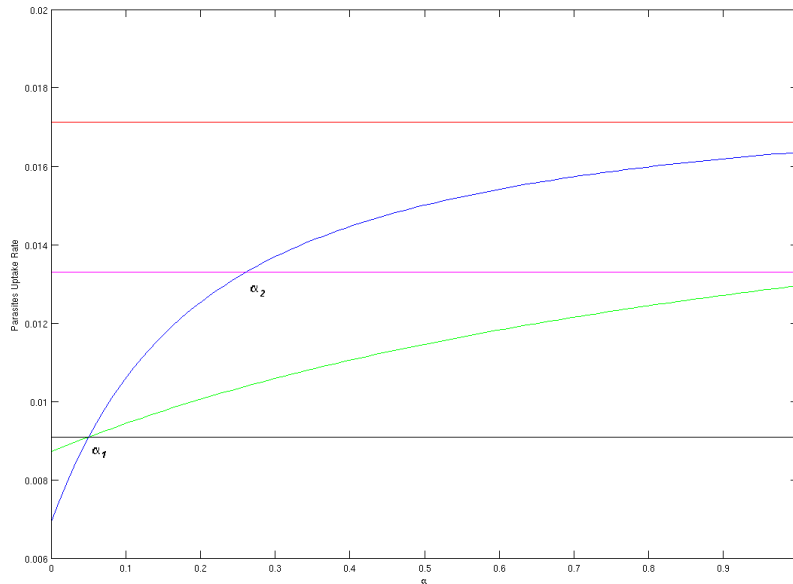


Figure 5-7: Uptake rates for the parasite when the probability of it winning, α , is varied. When an avoidance response is used ($r = 1$) we take $s = 0.1$ and $\lambda = 0.9$, we have also set $f = 1$. Black line: $p = 0$ (this gives the same uptake rate regardless of the value of q or r); red line: $p = 1, q = 0, r = 0$; magenta line: $p = 1, q = 0, r = 1$; blue line: $p = 1, q = 1, r = 0$; green line: $p = 1, q = 1, r = 1$. Other parameter values are taken as $P = 20, N = 20, v_f = 0.01, v_h = 0.05, t_h = 10$ and $t_a = 5$

5.3.2 Optimal strategies for the host for low food densities.

For the host population the best scenario is obviously when the parasite never kleptoparasitises and when no avoidance response is used (using one would have no benefits if $p = 0$). For $p = 1$ we can see from Figure 5-8 that when an avoidance response is used (the magenta and green lines) and $\alpha > \alpha_3$ then the uptake rate for the host is always higher than when one is not used (the blue and red lines). When $\alpha < \alpha_3$

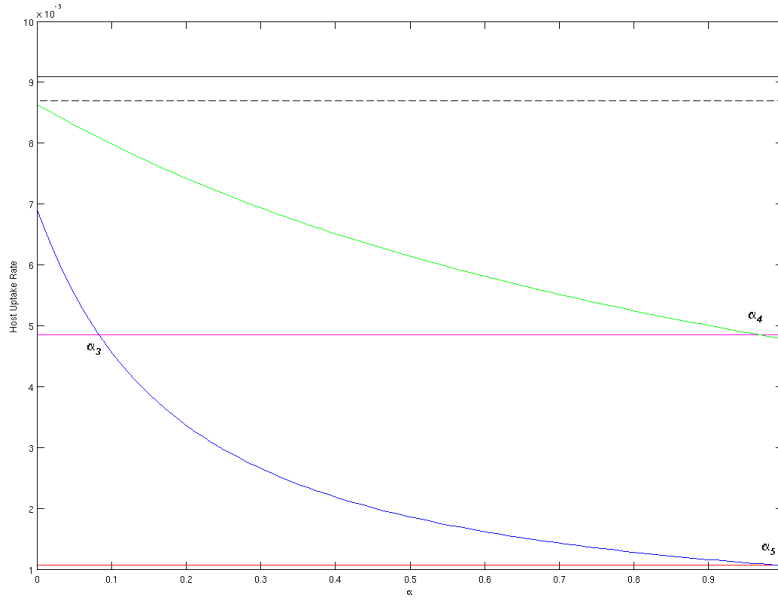


Figure 5-8: Uptake rates for the host when the probability of it winning, $1 - \alpha$, is varied. When an avoidance response is used ($r = 1$) we take $s = 0.1$ and $\lambda = 0.9$, we have also set $f = 1$. Black line: $p = 0, r = 0$; black dashed line: $p = 0, r = 1$; red line: $p = 1, q = 0, r = 0$; magenta line: $p = 1, q = 0, r = 1$; blue line: $p = 1, q = 1, r = 0$; green line: $p = 1, q = 1, r = 1$. Other parameter values are taken as $P = 20, N = 20, v_f = 0.01, v_h = 0.05, t_h = 10$ and $t_a = 5$.

and $p = 1$ then the uptake rate is higher when the host always resists.

When $p = 1$ and $r = 1$ and $\alpha < \alpha_4$ it is best for the host to always resist contests, but when the chance of the host winning is very low ($\alpha > \alpha_4$) it becomes optimal for the host to never resist contests.

When $p = 1$ and $r = 0$ the same thing happens, but this time the threshold α value between always and never resisting, α_5 , is slightly higher. Hence when an avoidance response is not used it is only for very low probabilities of winning that a host should decide not to resist contests anymore. We find $\alpha_3 = 0.08, \alpha_4 = 0.97$ and $\alpha_5 = 0.99$.

5.3.3 Optimal strategies for the parasite for high food densities.

When we look at high food densities we can see from Figure 5-9 (a) that it is best for the parasite to kleptoparasitise when the host never resists (obviously). Otherwise it is always optimal not to steal food.

When the parasite does steal food however we can see that that the uptake rate is higher when the host always resists and uses an avoidance response (the green line) than when the host always resists and never uses an avoidance response (the blue line). This could be accounted for because of the fact that when there is a high food density then obtaining food from foraging would be more profitable than from stealing it. So when a host uses an avoidance response the parasite has a decreased chance of encountering kleptoparasitic opportunities, and thus it will mostly forage for its own food, and hence the parasites uptake rate will be higher than when the host does not use an avoidance response and thus gets in to costly contests more often.

5.3.4 Optimal strategies for the host for high food densities.

From Figure 5-9 (b) we can see that for $p = 1$, $q = 1$ and $r = 0$ (the blue line) the uptake rate of the host actually increases as their probability of winning decreases for high food density. However for $p = 1$, $q = 1$ and $r = 1$ (the green line) the uptake rate of the host decreases (very slightly) as its probability of winning decreases. Perhaps this is because when α is high then the parasite has a good chance of winning and becoming a handler (and thus meaning less searching parasites in the population), and also because there is a high food density then the rate of finding food and thus moving from S_P to H_P will also be higher. Hence, handling hosts will have less attacks by kleptoparasites and also because there is high food densities there will be a high transition rate between S_H and H_H .

On the other hand when the probability of the parasite winning is low and no avoidance response is used then the parasite population in the S_P subgroup will be high so there will be a higher threat from kleptoparasites and the uptake rate will be less. When an avoidance response is used (and $p = 1$ and $q = 1$) then the uptake rate of the host decreases with it's probability of winning. This could be because there will be less aggressive encounters happening in the first place (which accounts for the uptake rate changing only slightly with α), so although food is found at a high rate because food density is high, there are more S_P in the population than there would be if an avoidance response was not used.

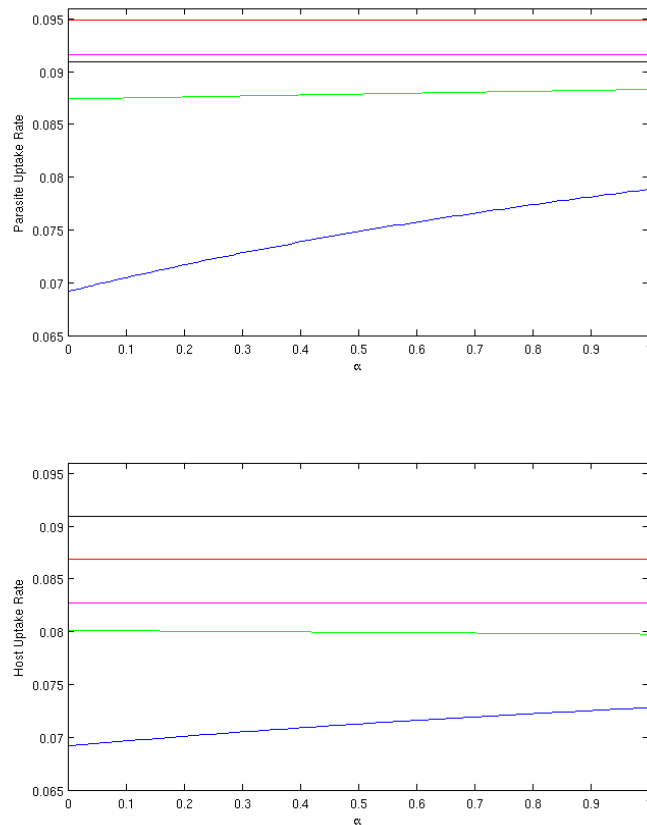


Figure 5-9: Uptake rate as a function of probability of winning. When an avoidance response is used ($r = 1$) we take $s = 0.1$ and $\lambda = 0.9$, here we have set $f = 100$. (a) The parasites uptake rate; (b) the hosts uptake rate. Black line: $p = 0, r = 0$; black dashed line: $p = 0, r = 1$; red line: $p = 1, q = 0, r = 0$; magenta line: $p = 1, q = 0, r = 1$; blue line: $p = 1, q = 1, r = 0$; green line: $p = 1, q = 1, r = 1$. Other parameter values are taken as $P = 20, N = 20, v_f = 0.01, v_h = 0.05, t_h = 10$ and $t_a = 5$. Note: in graph (b) the green line also represents the black dashed line.

5.4 Optimising Searching

We will now drop the assumption that parasites have a fixed rate of encountering handling hosts. We will now assume that the parasites have a finite capacity for searching which they need to divide between searching for food items and searching for handling hosts. Broom & Ruxton (1998) describe how in certain wading birds this is more realistic since detecting prey items involves looking down, but observing other species involves looking sideways, thus there is a trade-off between effectiveness

in these two activities. As in Broom & Ruxton (1998) we will express the relationship between searching for food items and searching for handling hosts by

$$\frac{v_{fP}}{\beta_1} + \frac{v_h}{\beta_2} = 1 \quad (5.38)$$

(note that before the rate of searching for food items was the same in both the parasite and the host populations, this rate is now v_{fP} for parasites and v_{fH} hosts). Hence the parasites strategy is now defined by $\{v_{fP}, p\}$. We will define “insular” parasites as ones which only look for food items, hence $v_h = 0$ and thus $v_{fP} = \beta_1$. Insular parasites would never encounter handlers, thus the value of p chosen would be irrelevant. “Aggressive” parasites are defined as those which look for kleptoparasitic opportunities (and hence play $p = 1$), so $v_H > 0$, and thus $v_{fP} < \beta_1$.

As in Broom & Ruxton (1998) we will now find the ESSs by considering a fixed population density and looking at the circumstances for which all parasites will either be Aggressive or Insular.

When $t_a f v_{fP} > 1 - \alpha$ holds we previously found that the parasite should play $p = 0$, thus for this condition the parasite should not waste any time searching for handling hosts, and hence the only ESS is $\{v_{fP} = \beta_1, p = 0\}$.

When $t_a f v_{fP} < 1 - \alpha$ holds then we found that the parasite should play $p = 1$, we show in Appendix B that for this case $\{v_{fP} = \beta_1\}$ can still be an ESS when the following hold

$$f > -\frac{2(5q\beta_2 - 10\beta_2 + \beta_1)}{\beta_1(1 + 100q\beta_2)}, \quad (5.39)$$

(where $\beta_1 \leq 10\beta_2$ since $f \geq 0$) or (in an alternative form)

$$q < -\frac{\beta_1 f - 20\beta_2 + 2\beta_1}{10\beta_2(10\beta_1 f + 1)}, \quad (5.40)$$

(where $\beta_1 < \frac{20\beta_2}{f+2}$ since $0 \leq q$).

Thus we have seen the conditions for which insular parasitism is an ESS. When $t_a f v_{fP} < 1 - \alpha$ holds and (5.39) does not hold, then the optimal strategy is $\{v_{fP} < \beta_1, p = 1\}$. However it becomes very difficult to find the conditions for which aggressive parasitism is an ESS, and thus we have left this out.

Chapter 6

Discussion

6.1 Conclusions

In the basic model, where if a parasite encounters a handling host it will always challenge it, we found that a host should always resist kleptoparasitic attacks when $v_f f t_a < 1 - \alpha$, and should never resist kleptoparasitic attacks when $v_f f t_a > 1 - \alpha$. When $v_f f t_a = 1 - \alpha$ then it will take an encountered host the same average amount of time to begin handling again regardless of whether it resists the challenge or not. Hence, behaviour change for the host solely relies on the ratio of time in an aggressive encounter to the time taken to find food items. If food is easy to find or fight time is long, then the host should never resist attacks; when food is hard to find and fight times are short, then the host should always resist kleptoparasitic challenges. We have shown that when a host changes between always and never resisting kleptoparasitic attacks, then there is no change in the uptake rate. We find that the uptake rate is maximised when $p = 1$ if $v_f f t_a < 1 - \alpha$, and maximised when $p = 0$ if $v_f f t_a > 1 - \alpha$, and for these conditions the average time to become a handler after being encountered is also minimised. In other words, the strategy which optimises individual pay-off, for any of the environmental conditions considered, also optimises the uptake rate for the population. This makes sense since in our model the choice of strategy by an individual host should make no difference to the other hosts. In Broom & Ruxtons (1998) work on intraspecific kleptoparasitism, however, they find that the uptake rate is higher when no kleptoparasitism occurs, but when $v_f f t_a < \alpha$ it is evolutionarily stable to always kleptoparasitise. This is because if one individual in a population of non kleptoparasites switched to kleptoparasitism then the others in the population would be worse off.

We then looked at when the amount of previous handling a food item has already

received has implications on how much food value will be obtained. We considered when handling takes a fixed time, t_h , and the reward is extracted continuously throughout its handling. This is different from in our basic model where handling took a fixed time and then the whole food value was obtained, and adds another factor to the hosts' decision of whether it is optimal to resist a kleptoparasitic attack or not. We found that if a handler is challenged over a food item which still requires a further amount of handling time, x , then if $x < X_a$, where

$$X_a = \frac{1}{2v_h P(2v_f f t_a - 1)} (2 + 2v_h P t_h v_f f t_a + v_h P t_h \pm \sqrt{4 + v_h P t_h (4 + 4v_f^2 f^2 t_a^2 (v_h P t_h - 8) + 4v_f f t_a (6 + v_h P t_h) + v_h P t_h)}). \quad (6.1)$$

then it is optimal for the host to surrender the food item. Alternatively, if $x > X_a$ (with X_a as above) then it is optimal for the host to resist the challenge. We found that when $v_f f t_a < 1 - \alpha$ then for most values of x it is optimal to resist contests. When $v_f f t_a > 1 - \alpha$ then there becomes less values of x for which it is optimal to resist contests. We found that when the probability of the host winning in low ($\alpha \geq 0.953$) then it is never optimal to resist contests for any value of x . Thus the conditions for always resisting contests or never resisting contests to be optimal, are generally the same even when considering a different type of food item to in our basic model.

We have also included the possibility of the host using an avoidance response. We found that if the host always surrenders kleptoparasitic attacks then it should use an avoidance response if $s < s_s$, and not use one if $s > s_s$, where

$$s_s = \frac{\lambda v_h P}{v_f f + (1 - \lambda) v_h P}. \quad (6.2)$$

On the other hand, if the host always resists kleptoparasitic attacks then it should use an avoidance response if $s < s_r$, and not use one if $s > s_r$, where

$$s_r = \frac{\lambda v_h P (v_f f t_a + \alpha)}{v_f f + (1 - \lambda) v_h P (v_f f t_a + \alpha)}. \quad (6.3)$$

We then allowed the parasite to choose whether to kleptoparasitise or not, and found the optimal strategies for the parasite when the host always resists attacks (when the host never resists attacks it will always be optimal for the parasite to kleptoparasitise). We found when $v_f f t_a > \alpha$ it is optimal for the parasite to never kleptoparasitise, and when $v_f f t_a < \alpha$ it is optimal for the parasite to always klep-

toparasitise. These are the same conditions as found in the intraspecific case by Broom & Ruxton (1998), this makes sense since the only difference that we have is that the parasite is not kleptoparasitised by other parasites, and hence the pay-offs of stealing food or not should not be affected.

We then looked at the optimal strategies for the host and parasite when the host was able to resist or not *and* use an avoidance response or not and the parasite was able to kleptoparasitise or not. Using our default parameters, we found that for the parasite in an environment with low food density ($f = 1$) the optimal strategy is $p = 1$ when $q = 0$. On the other hand, when the host always resists, if $\alpha < 0.05$ then the optimal parasite strategy is $p = 0$, and if $\alpha > 0.05$ then the optimal parasite strategy is $p = 1$. In high food densities ($f = 100$) if $q = 0$ then the optimal parasite strategy is $p = 1$ for any value of α , but if $q = 1$ then it is $p = 0$ for any value of α . Hence these results agree with the conditions for $p = 0$ or $p = 1$ to be optimal as found in the previous section.

Hence when there is no parasitic pressure then it is optimal for the host to never use an avoidance response, we can see that this keeps with our earlier findings of when $s > s_s$ or $s > s_r$ then is it optimal never to use an avoidance response. These hold since when there is no parasitic pressure then $v_h P = 0$ and hence $s_r, s_s = 0$. It makes sense that a host shouldn't waste energy using an avoidance response when there is no parasitic threat. Using our default parameters, we found that low food densities when $p = 1$ and $\alpha < 0.97$ then the optimal host strategy is $\{q = 1, r = 1\}$, for these conditions we find that $s < s_r$ holds. When $\alpha > 0.97$ then the optimal host strategy switches to $\{q = 0, r = 1\}$, and here we find $s < s_s$ holds. In our basic model we found that $q = 1$ should be the optimal host strategy when $v_f f t_a < 1 - \alpha$, which for these conditions is equivalent to $\alpha < 0.95$, and likewise $q = 0$ is the optimal host strategy when $\alpha > 0.95$. Hence it could be estimated that the same conditions as in the basic model are needed for determining whether resisting contests or not is optimal. For high food densities we find that $\{q = 0\}$ is the optimal host strategy when $p = 1$ whether an avoidance response is used or not, for these conditions $s > s_s$ holds, and we also find that $v_f f t_a > 1 - \alpha$ and hence this also agrees with our basic model.

We have also considered when parasites have a finite capacity for searching, and looked at the conditions for which dedicating all efforts to searching for new food items is an ESS, when $t_a f v_f P < 1 - \alpha$ holds. This is when

$$q < -\frac{\beta_1 f - 20\beta_2 + 2\beta_1}{10\beta_2(10\beta_1 f + 1)}, \quad (6.4)$$

(where $\beta_1 < \frac{20\beta_2}{f+2}$ since $0 \leq q$).

6.2 Extensions and Limitations

Our model assumes that all individuals are intrinsically identical, however this may not always be an accurate assumption. Individuals could vary in their ability to find food, their ability in a contest (and therefore their probability of winning and the time taken in a contest) and the time they take to handle food items, thus strategies could vary depending on the individual. For example a juvenile host may do better to always surrender food even if food densities are low, because it may be a lot weaker than the parasite and have no chance in winning in a contest. Also, from the study by Ridley & Child (2009) where juvenile pied babblers were observed to be more frequently attacked by kleptoparasites, we could also assume that the encounter rate should be different for individual hosts. Perhaps parameters could be seen as functions of age, with very young or very old hosts having lower rates of finding food, a lower probability of winning in a contest and longer handling times.

As mentioned earlier, our analysis in the later chapters has assumed that when a host uses an avoidance response then it will be a “good” one. This is probably quite unrealistic and could be extended to look for the conditions needed for host and parasite strategies to be optimal for a whole range of different types of avoidance response. We also didn’t consider what the effect of using an avoidance response would have on other hosts not using an avoidance response. It would be of interest to see what the conditions were for $r = 0$ being an ESS. It might be expected that if the whole population played $r = 0$, and a rare mutant plays $r = 1$, then the mutant strategy could actually take over the resident strategy because kleptoparasites would be more likely to encounter individuals playing $r = 0$.

An extension of this interspecific model for kleptoparasitism would be to look at a structured population model for the hosts, as it could be expected that certain host species forage and handle food in groups. Group handling could be an avoidance response as observed in boobies by Le Corre & Jouventin (1997) and also Vickery & Brooke (1994), which would mean that if a group was small in size, or if a host handled alone then it would have an increased risk of kleptoparasitism (and a possible decrease in risk for the other groups). Also, for larger groups there would be more intraspecific competition for resources within the group. Thus it might be expected that hosts have very different intake rates of food depending on the size of their group, and hence it would be unrealistic to take this rate as equal for the whole host population as we did before.

In our basic model we found the optimal strategies as ones which minimise the time taken for a handler which has just been encountered by a kleptoparasite to start handling food again. Perhaps as an extension we could allow contests to also have a cost associated with physical harm to the host (due to injury), and look for optimal strategies which minimise this too.

Finally, since the parameter values used here were taken from a paper that gave no empirical evidence to suggest that they or the units used are correct, it would be worth finding experimental values for various species. It also might be interesting to compare results for different pairs of host and parasitic species. Our assumption that v_f and t_h are the same for hosts and parasites will probably be inaccurate, since we are considering different species which will have different foraging and handling abilities. Hence it would be worth checking with real data how inaccurate this assumption is, and changing the analysis accordingly.

Appendix

A. Checking Equilibrium state

In our previous models we have assumed that the population has an equilibrium state and when analysing we have assumed that the population is at this state. Luther & Broom (2004) point out that if we are considering a bird population at the beginning of the day (when they are all searchers), then we need to know whether the equilibrium will have been reached by the end of the day, i.e. do the population spend most of the day in this state or are they still converging towards it when they return to their nests at night? In this section we will check whether the equilibrium state found in Chapter 2 is stable, and whether the population converges to this equilibrium quickly.

If we consider a small perturbation of the population from the equilibrium (where * denotes the subpopulation at equilibrium), so that

$$S = S^* + \epsilon s, \quad (6.1)$$

$$H = H^* + \epsilon h, \quad (6.2)$$

$$A = A^* - \epsilon h - \epsilon s. \quad (6.3)$$

we can see whether or not the equilibrium state is stable by seeing if these disturbances of the population when it is in its equilibrium state decay to zero.

Substituting these into our basic model equations (2.1)-(2.4) we have

$$\frac{ds}{dt} = \frac{1}{\epsilon} \left(\frac{dS}{dt} - \frac{dS^*}{dt} \right) = \left(\frac{1}{t_h} + (1-q)v_h P - \frac{\alpha}{t_a} \right) h + \left(-v_f f - \frac{\alpha}{t_a} \right) s = as + bh, \quad (6.4)$$

$$\frac{dh}{dt} = \frac{1}{\epsilon} \left(\frac{dH}{dt} - \frac{dH^*}{dt} \right) = \left(-\frac{1}{t_h} - v_h P - \frac{1-\alpha}{t_a} \right) h + \left(v_f f - \frac{1-\alpha}{t_a} \right) s = cs + dh. \quad (6.5)$$

Hence we have the Jacobian matrix

$$J = \begin{bmatrix} -v_f f - \frac{\alpha}{t_a} & \frac{1}{t_h} + (1-q)v_h P - \frac{\alpha}{t_a} \\ v_f f - \frac{1-\alpha}{t_a} & -\frac{1}{t_h} - v_h P - \frac{1-\alpha}{t_a} \end{bmatrix}, \quad (6.6)$$

where $tr(J) = -v_f f - \frac{\alpha}{t_a} - \frac{1}{t_h} - v_h P - \frac{1-\alpha}{t_a} < 0$ and $det(J) = \frac{1}{t_a}(1/t_h + v_f f v_h P + q v_h P(\alpha - 1 + v_f f t_a)) > 0$. Hence the equilibrium state is stable.

We can see from the Figures 2-2 that the equilibrium population densities are reached relatively quickly (they take about 40 seconds), and this would change very slightly for different sets of parameter values.

B. When is $\{v_{fP} = \beta_1\}$ an ESS?

We will look at a mixed population of parasites playing two different strategies for v_{fP} , and find the conditions for when a large population of parasites (of density P_1) playing $\{v_{fP}\}$ cannot be invaded by another initially rare population of parasites (of density P_2) playing $\{u_{fP}\}$, for any possible u_{fP} . We have $S_{P,1} + H_{P,1} + A_{P,1} = P_1$, $S_{P,2} + H_{P,2} + A_{P,2} = P_2$ and $P = P_1 + P_2$. From (5.21)–(5.23) and because $P_1 \gg P_2$

$$\begin{aligned} \frac{dS_H}{dt} &= \frac{1}{(1+s)t_h} H_H + p(1-q)(1-\lambda)v_{hP}H_H S_{P,1} + p(1-q)(1-\lambda)u_{hP}H_H S_{P,2} + \alpha \frac{1}{t_a} A_H - v_{fH}fS_H \\ &\approx \frac{1}{(1+s)t_h} H_H + p(1-q)(1-\lambda)v_{hP}H_H S_{P,1} + \alpha \frac{1}{t_a} A_H - v_{fH}fS_H, \end{aligned} \quad (6.1)$$

$$\begin{aligned} \frac{dH_H}{dt} &= v_{fH}fS_H - \frac{1}{(1+s)t_h} H_H - p(1-\lambda)v_{hP}H_H S_{P,1} - p(1-\lambda)u_{hP}H_H S_{P,2} + (1-\alpha)\frac{1}{t_a} A_H \\ &\approx v_{fH}fS_H - \frac{1}{(1+s)t_h} H_H - p(1-\lambda)v_{hP}H_H S_{P,1} + (1-\alpha)\frac{1}{t_a} A_H, \end{aligned} \quad (6.2)$$

$$\begin{aligned} \frac{dA_H}{dt} &= pq(1-\lambda)v_{hP}H_H S_{P,1} + pq(1-\lambda)u_{hP}H_H S_{P,2} - \frac{1}{t_a} A_H \\ &\approx pq(1-\lambda)v_{hP}H_H S_{P,1} - \frac{1}{t_a} A_H. \end{aligned} \quad (6.3)$$

Hence from (5.30) we have

$$H_H = \frac{v_{fH}fN}{\frac{1}{(1+s)t_h} + v_{fH}f + p(1-\lambda)v_{hP}S_{P,1}(1 + q(\alpha - 1 + v_{fH}ft_a))}. \quad (6.4)$$

Since (5.24)–(5.26) will be the same for the two parasite populations (with their respective encounter rates) (5.32) becomes

$$S_{P,1} = \frac{P_1 - H_{P,1}}{1 + t_a pq(1-\lambda)v_{hP}H_H}, \quad S_{P,2} = \frac{P_2 - H_{P,2}}{1 + t_a pq(1-\lambda)u_{hP}H_H}, \quad (6.5)$$

and (5.34) becomes

$$\frac{2}{t_h} H_{P,1} + 2p(1-\lambda)v_{hP}H_H S_{P,1}(-1 + q - \alpha q) - 2v_{fP}fS_{P,1} = 0, \quad (6.6)$$

$$\frac{2}{t_h}H_{P,2} + 2p(1 - \lambda)u_{hP}H_H S_{P,2}(-1 + q - \alpha q) - 2u_{fP}fS_{P,2} = 0. \quad (6.7)$$

If strategy v_{fP} is better than strategy u_{fP} , then P_1 will have a higher proportion of handlers than in P_2 , i.e. when $H_{P,1}/P_1 > H_{P,2}/P_2$. Taking $p = 1$, we can solve equations (6.4)–(6.7) using Maple to find that this occurs when

$$\frac{\beta_1}{10\beta_1 f + 1} > \frac{u_{fP}f + 20u_{hP} + 2u_{fP} - 10qu_{hP}}{f + 2 + 200u_{hP}f + 10u_{fP}f^2 + 20u_{fP}f}. \quad (6.8)$$

Where we have taken $r = 0$, $\alpha = 1/2$, $v_{fH} = 0.05$, $t_a = 5$, $t_h = 10$ and $N = 20$ for simplicity. We have also taken the case when $v_{fP} = \beta_1$, i.e. the P_1 population of parasites is insular, and thus we have also taken $v_{hP} = 0$. Hence from (6.8) we find that insular parasites are using a better strategy than aggressive parasites when

$$f > -\frac{2(5qu_{hP} - 10u_{hP} - u_{fP} + \beta_1)}{\beta_1 - u_{fP} + 100qu_{hP}\beta_1} = -\frac{2(5q\beta_2 - 10\beta_2 + \beta_1)}{\beta_1(1 + 100q\beta_2)}, \quad (6.9)$$

or (in an alternative form)

$$q < \frac{-\beta_1 f - 2\beta_1 + u_{fP}f + 20u_{hP} + 2u_{fP}}{10u_{hP}(10\beta_1 f + 1)} = -\frac{\beta_1 f - 20\beta_2 + 2\beta_1}{10\beta_2(10\beta_1 f + 1)}, \quad (6.10)$$

where we have also substituted $u_{hP} = \beta_2(1 - u_{fP}/\beta_1)$.

Since $f \geq 0$

$$-\frac{2(5q\beta_2 - 10\beta_2 + \beta_1)}{\beta_1(1 + 100q\beta_2)} \leq 0, \quad (6.11)$$

must also hold. Hence $\beta_1 \leq \beta_2(10 - 5q) \leq 10\beta_2$. Furthermore, since $0 \leq q$ we must also have

$$0 < -\frac{\beta_1 f - 20\beta_2 + 2\beta_1}{10\beta_2(10\beta_1 f + 1)}, \quad (6.12)$$

which holds when $\beta_1 < \frac{20\beta_2}{f+2}$.

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