Information, Game Theory and Patch Defence in the Parasitic Wasp *Trissolcus Basalis Wollaston* *(Hymenoptera:Scelionidae)*

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Signed Statement

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

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Summary

The subject of this dissertation is game-theoretic models of patch defence in the quasi-gregarious parasitoid *Trissolcus Basalis Wollaston (Hymenoptera:Scelionidae)* and the relation of the Evolutionary Stable Strategies derived to the information exchanges between opponents.

Chapter 1 reviews game-theoretic modelling in Behavioural Ecology, with an emphasis on parasitoid behaviour, information exchange and strategies used by owners or intruders of some resource. A discussion of the biology and behaviour of *T. basalis* follows, emphasising pairwise patch competition. Modelling approaches are then discussed.

Competition for patch residency is the subject of Chapter 2. Models of resource allocation, given the outcome of competition as resident or intruder, are constructed. We then present a model of patch competition with perfect information exchange of the opponent's investment. This model is contrasted with models of patch competition in which each player is aware of it's own investment and a distribution of possible opponent's investments.

Chapter 3 focuses on the transition of the resident from a host searching strategy to patch pure defence and the transition of the intruder from attempting to "steal" ovipositions to playing the waiting game. Models of optimal intruder patch return rate are constructed, under the assumption that the patch is least defendable whilst the resident is itself ovipositing. Given an intruder optimal return rate, the resident's switch from searching to guarding is then calculated. We then consider a stochastic dynamic programme of multiple intruder returns where the intruder

decides whether to return or to play the waiting game, based on it's past successes and failures in ovipositing on return to the patch.

The waiting game is the topic of Chapter 4. Constant payoffs from superparasitism and no information exchange to the intruder about the resident's leaving time form the assumptions in this chapter. If there is no resident departure information exchange, we prove that no ESS exists. The dynamics of resident/intruder stratgies are simulated next. Finally, we consider mixed strategies, these being shown to be at best, neutrally stable.

We change two assumptions in the previous analysis of the waiting game, non constant superparasitism payoffs and partial information exchange of the resident's departure time passed to the intruder in Chapter ??. Here we show that as the intruder always returns to superparasitise, this gives the resident the information advantage to leave the patch at a time that takes the intruder's imminent return into account. Patch leaving strategies will therefore form a Stackelberg equilibria. A model of partial resident departure information transfer is then presented.

A discussion of further topics of research and a general conclusion follows in Chapter 6.

Chapter 1

Introduction and Overview

1.1 Adaptationism and Behavioural Ecology

This dissertation focuses on models of patch competition and defence in the parasitoid *Trissolcus basalis (Hymenoptera:Scelionidae)* through an adaptationist perspective (Alcock,[1]). The adaptationist approach views behaviour, not as a series of random acts, but rather as a sequence of actions undertaken to maximise individual fitness (Stephens and Krebs,[77]). Though the adaptationist approach has been the subject of criticism and debate, without viewing behaviour as a series of actions to increase fitness, either directly or indirectly, it would be difficult to understand the underlying causal mechanisms of behaviour common within and across species (Dennett,[14]). The study of how behaviour has evolved and is influenced through interactions of individuals with conspecifics and the external environment is the study of Behavioural Ecology (Hamilton,[29]).

1.1.1 Optimisation: Rate and State based Models

One of the first examples of the application of the adaptationist approach to studying behaviour came with work on predator selection of prey type when foraging

(Stephens and Krebs,[77]). Under the assumption that the long term rate of energy intake determines evolutionary fitness, this prey selection model assigned a simple accept/reject rule to prey types, based on energy returns and encounter rate associated with the considered prey type (Stephens and Krebs, [77]). With the same theme of maximising long term energy intake, Charnov modelled optimal patch leaving times employed by foragers encountering patches whose marginal rate of energy return decreased over the course of patch exploitation (Charnov,[6]). The intuitive insight of this approach can be seen from the simple rule that foragers should leave the patch, when the rate of intake in a patch drops below that of the average intake rate from the habitat (Charnov, [6]).

Though the rate maximising models of early optimal foraging theory appealed because of simplicity of construction and prediction, the link between energy rate maximisation and evolutionary fitness was not clear (Mangel and Ludwig,[51]). Foraging for food is not the only activity animals are engaged in, with decisions such as the apportionment of time between looking for mates and foraging for food clearly affecting fitness (Mangel and Clark,[50]). Before any progress in understanding the forces affecting behavioural decisions could be made, models that mapped behavioural decisions directly to fitness consequences needed to be considered (Stephens and Krebs,[77]). Another important, but overlooked, assumption of simple rate maximisation models was that decisions were made independent of the internal physiology and experience of the animal (Mangel and Clarke,[50]). Empirical studies of parasitoids indicated that both egg load and age influence behaviour (Godfray, [26]). Similarly, some species of parasitoids are known to exhibit associative learning, thus ultimately, experiential states influence fitness related decisions (Wardle and Bowden,[84]).

Having realized that behavioural models should take into account both physiological and experiential variability, as well as modelling decisions that directly influence fitness, Iwasa applied the technique of stochastic dynamic programming (SDP) to model oviposition decisions in parasitoids with different egg loads and mortality levels (Iwasa, Suzuki and Hiroyuki,[38]). Common to all SDP approaches, the state of the parasitoid, the set of possible actions taken by the parasitoid within that state and a transition function, which specifies the subsequent state, once a decision is enacted must be specified. Given these three ingredients, optimal state dependent decisions can be calculated using the dynamic programming algorithm (Filar and Vrieze,[23]). In comparison to rate maximisation models, for example, parasitoids are predicted to accept lower quality hosts for an internal state of large egg load and old age (Iwasa, Suzuki and Hiroyuki,[38], Mangel,[45]).

State dependent models have been used to determine the conditions under which post-oviposition host marking is advantageous (Roitberg and Mangel,[68]). These models consider the spread of a "double-mutant", an individual that can both mark hosts and detect marked hosts. One of the conclusions of this work was that mutants that can mark hosts have a considerable advantage when hosts are distributed in a spatially aggregated manner. Marking mutants will not waste time in superparasitism when unparasitised, higher quality hosts can be readily detected within a patch, due to the level of aggregation (Roitberg and Mangel, [68]).

If an organism lives in a unpredictable changing habitat then fitness will be influenced by the ability to obtain information from the environment and use this information adaptively (McNamara and Houston,[58]). When patches of hosts or food vary in quality, the question of how often foragers should sample each patch type is of fundamental importance, and involves estimating or learning information about the current state of the environment (Stephens and Krebs,[77]). A related problem known as the "two-armed bandit" problem asks when you should give up sampling one of two resources in order to maximise energy returns, given only the variance in per-sample payoff of the two resources is known, not the mean per-sample energy payoff (Holland,[34]).

One way of tracking a highly variable environment comes by apportioning importance to current estimates of a parameter versus past estimates of this parameter (McNamara and Houston,[58]). The so called linear operator model is the simplest implementation of this idea (McNamara and Houston, [57]). An estimate of a parameter at time t, $\hat{\mu_t}$, is found by taking a convex combination of the current sampled value μ, and the previous parameter estimate at $t-1$, $\hat{\mu_{t-1}}$, so $\hat{\mu_t} = \alpha\mu + (1-\alpha)\hat{\mu_{t-1}}$. The parameter $\alpha \in [0,1]$ determines weighting of the past compared to the present and it is this past/present updating that is the common theme of most learning algorithms, such as the Bayesian Method (McNamara and Houston,[57]) and the Sliding Window method (Mangel and Roitberg,[52])). Models of learning have been applied both within the static and dynamic state dependent context. For example, the Bayesian method was applied to model a prey's estimation of the presence of predator, given only partial information as to the presence of the predator at any given time (Sih,[73]). Within a dynamic context, a host acceptance model of a tephritid fruit fly incorporated an information state as one of the dynamic variables (Mangel and Roitberg,[52]). At each time t, the last 5 encounters with either clean or marked fruit were recorded, this information being used to estimate the probability of future encounters with unmarked, acceptable fruit (Mangel and Roitberg, [52]).

1.1.2 Game-Theoretic Approaches.

Well before the advent of the neo-Darwinian Synthesis (Futuyma,[25]), many scholars of natural history recognised that intra-specific competition generated as much, if not more selective forces in the evolution of a species (Darwin,[13]). Geneticists coined the term "frequency dependent selection" (Futuyma,[25]) when viewing the evolution of a trait whose fitness depended on the frequency of other individuals in the population with that same trait. Frequency dependent selection is most clearly seen when studying sex allocation in plants and animals (Charnov,[7],Godfray,[26]). The statistician and biologist R.A. Fisher used frequency dependent arguments to explain why most homogeneously mating populations should have a sex ratio of approximately 50% males and 50% females (Charnov,[7]). When studying sex allocation in parasitoids, W. Hamilton noted many gregarious species mated locally, at the emergence site, with mated females dispersing, to find new patches (Hamilton, [28]). Through population genetic simulations, an "unbeatable sex ratio", that is a ratio of males to females in the population, under which no individual could obtain a selective advantage in applying another sex ratio to its siblings (Hamilton,[28]).

Following the development of game theory in the application of economics (von Neumann and Morgenstein,[81]), a simple model of animal conflict was developed by Maynard-Smith and Price to relate the costs and benefits of either passive or aggressive displays to an optimal frequency of aggressive display. This model was called the Hawk-Dove game (Maynard-Smith, [54]), comparing aggressive "hawk" strategist with a passive dove strategist. At the optimal frequency of aggressive display, no individual can increase its fitness by adopting another aggressive display frequency, thus the optimal frequency was termed "uninvadable" by some mutant individual, and the frequency is an "evolutionarily stable strategy" (ESS) (Maynard-Smith, [54]). To the mathematical biologist, a more succinct expression of the criterion of uninvadability comes from viewing the expected fitness of an individual, as a function of some strategy parameter (such as the frequency of aggressiveness) u, and the strategy parameter adopted by conspecifics in the population u_{pop} denoted $E(u, u_{pop})$. An ESS u^* must satisfy the criterion of best expected returns against any opponent, when adopted by all members of a population,

$$E(u^*, u^*) > E(u, u^*), \tag{1.1.1}$$

and the strategy must spread, when introduced by some mutant (Mesterson-Gibbons, [61]), that is

$$E(u^*, u) > E(u, u). \tag{1.1.2}$$

The second criterion may be replaced by an entrenchment condition: strategies different to u^* cannot spread if introduced, once u^* is established. Thus, for an alternative strategy v, if in small frequency q within the population, so the overall population strategy is $P = qv + (1-q)u^*$ then

$$E(u^*, P) > E(v, P). \tag{1.1.3}$$

Criterion one is termed the Nash Equilbrium condition (Fudenberg and Tirole,[24]) and criteria two and three are stability criteria, guaranteeing that the ESS, once established, will stay dominant in the population.

The Hawk-Dove game's importance came not from any attempt to find a realistic biological model of animal conflict, but in directing both experimental and theoretical biologists towards analysis of conflict and interference competition through cost based, individual fitness benefit decisions (Maynard-Smith,[54]).

Central to finding an ESS, the Bishop-Cannings Theorem (Bishop and Cannings, [3]) states the requirement of any strategy, before it can be considered part of the evolutionary stable strategy set. The theorem states that for any set of strategies $I_1, I_2, .., I_n$ applied in the ESS I, expected payoffs from adopting any of these strategies against I are equal,

$$E(I_1, I) = E(I_2, I) =, \ldots, = E(I_n, I) = E(I, I).$$

The expectation of the ESS I against itself, $E(I, I)$ is called the value of the game (Fudenberg and Tirole, [24]). In symmetric zero sum games, this value will always be precisely zero.

Paths of ESS research have followed similar lines to that of classical optimisation research, with initial static models of interference and conflict extending to the dynamic, state dependent context (Houston and McNamara,[37]).

An example of a static model comes from a model of ESS patch leaving rules, under interference competition (Yamamura,[88]). In this model, animals compete for patches that supply energy, with only one individual allowed on the patch at any one time. Once a patch has been exploited, it is removed from the environment. The problem is to find the ESS patch leaving time, given a constant supply of unused patches, and a number of conspecifics, as to maximise the long-term individual rate of energy gain. An optimal patch leaving time was determined, with the property that the larger the ratio of competitors to patches, termed the *competitive intensity,* the longer a player stayed on to exploit diminishing returns from the patch (Yamamura,[88]). To contrast this model with that of Charnov's, the competitive intensity replaces rate of encounter of patches, as the most important criteria when making decisions as to patch leaving times (Yamamura,[88]).

Including dynamism into game theoretic models introduces a vast increase in the complexity of mathematics required to find either explicit or numerical ESS strategies (Mangel and Clarke, [50]). Such difficulty arises from the observation that by introducing time and state dependency into the model implies that a player must estimate both the state and age of the opponent, when calculating state dependent best response to an opponent's strategy (Mangel,[50], McNamara and Houston, [59]).

Dynamic state dependent games have been applied to understanding such behaviours as the tradeoff between singing to attract a mate and foraging to find food (Houston and McNamara,[37]), scanning to find predators (Kaitala et al,[40]), parent-offspring conflict in feeding and fledging (Clark and Ydenberg,[9]), habitat selection (Mangel, [47]) and superparasitism (Mangel,[50],Visser,[80], van der Hoeven and Hemerik,[78]). The model of van der Hoeven and Hemerik addressed when should a female parasitoid superparasitise the host, given knowledge of the number of eggs present in the host, and the number of searching conspecifics present. As with the study of competitive patch leaving times, the ESS level of superparasitism depends on the ratio of competitors in the patch to hosts present, as well as the remaining eggs of the individual (van der Hoeven and Hemerik,[78]) .

Game theoretic models in Behavioural Ecology may be partitioned into models where the individual plays against "the field", such as the sex ratio games, or where the individual directly competes against another individual (Maynard Smith,[54]). Conflict models may be further partitioned into two classes, the first class being games of timing, where no information about the resource value or costs is exchanged during the contest, but is reflected in the contest outcome. The second class, state dependent sequential assessment games involves the assessment of the relative fighting strength of each player during the contest (Bishop and Cannings,[3],Enquist and Leimar,[16]).

Games of timing approaches involve continuous time models of conflict, where players "fight" for a resource with some specified value to each player. Fighting refers to the mechanism by which one player wins over another. A winning individual could either be the player that persists longest in display, the so called war of attrition, or the player that persists longest in display or the player last to be injured, the graduated risks game (Bishop and Cannings,[3]). In either game, indefinite persistence will have fitness consequences, since there is an associated time cost in fighting, assumed in most models, to be an energetic cost (Marden and Wagge,[53]). Two classes of persistence solution arise, depending on the assumption of what information players have about the opponents reward from winning and cost of persistence (Mesterson-Gibbons,[63]). If players have perfect information and equality in costs and rewards, then the evolutionary stable persistence time is determined by a probability distribution over a set of persistence times (Bishop and Cannings,[3], Sjerps and Haccou,[76]). For example, in the war of attrition with equal reward V and per unit time linear cost C, the optimal persistence time is drawn from the exponential probability density $p(t) = \frac{C}{V}\exp(-\frac{C}{V}t)$.

Imperfect information as to the opponents rewards and costs of fighting form another class of timing games, with more realistic assumptions, increased mathematical difficulty and richer predictions (Bishop, Cannings and Maynard-Smith,[4], Hammerstein and Parker,[31]). Games with variation of rewards are called wars of attrition with random rewards (Bishop, Cannings and Maynard-Smith,[4]). Variation in rewards results in altering the set of ESS persistence times, that is the set of times where the ESS density is non-zero, adopted by each player (Hammerstein and Parker,[31]). Given a set of relative player rewards in fighting, $V_1, V_2, ..., V_n$, where $V_1 \leq V_2 \leq, .., \leq V_n$, this partitions the set of persistence times into disjoint intervals $[t_{a1}, t_{b1}], [t_{a2}, t_{b2}], ..., [t_{an}, t_{bn}]$, with persistence interval $[t_{aj}, t_{bj}]$ associated with the player having reward value V_j. The persistence intervals reflect the rewards to be won, since if two players, labelled j and k have $V_j \leq V_k$ then $t_{bj} \leq t_{ak}$ (Bishop,Cannings and Maynard Smith,[4]). In the limit of continuous variation in rewards for winning the contest, with the reward V drawn from some continuous probability distribution, the ESS is a pure strategy "persist till time t_V" where t_V is some monotonically increasing function of the reward V (Mesterson-Gibbons, Marden and Dugatkin,[64], Enquist and Leimar,[16]).

State variables such as energy reserves have been incorporated into war of attrition models (McNamara and Houston,[59]). The exponential distribution persistence strategy was shown not to be an ESS, with alternative strategies able to invade, though the general state dependent persistence distribution is yet to be found under a range of realistic biological assumptions (McNamara and Houston,[59]).

Of current interest is the extension of the games of timing approach to n-person wars of attrition (Haigh and Cannings,[27], Sjerps and Haccou,[75]) and the application of such models to dispersive behaviour (Sjerps and Haccou,[75]). Observations of the dispersal behaviour of various insect larvae indicate there are tradeoffs in maximising both food intake and survival at the pupal stage (Sjerps and Haccou,[76], Blackwell, [5]). In order to avoid starvation, some larvae must migrate to another patch as resources from the host plant are scarce because competitors also consume the resource. Migration, however, incurs a large potential mortality cost. When two of more individuals remain on the host plant, persistence strategies can be modelled as a G generalised war of attrition. If $V(t)$ is the payoff to the player with the earliest migration time t, and $W(t)$ the payoff to the remaining player, then the ESS migration strategy is to leave with hazard $\lambda(t) = \frac{-V'(t)}{W(t)-V(t)}$ (Sjerps and Haccou, [76]). If players are related, possibly through females laying clusters of eggs on the host plant, this has the effect of altering the migration tendency to $\lambda(t) = \frac{-V'(t)-rW'(t)}{(1-r)\big(W(t)-V(t)\big)}$ where r is the relatedness coefficient between individuals.

In contrast to the games of timing approach, individuals that assess the relative fighting ability of the opponent through a series of escalated bouts are termed sequential assessment games (Enquist and Leimar,[16, 17]). Opponents, labelled players one and two in the sequential assessment game attempt to assess relative fighting costs, here defined to be the relative cost to player one, against player two, $\theta_{12} = \ln(c_2/c_1)$, where $c_j, j = 1, 2$ is the fighting cost imposed by player j against the opponent. In a series of bouts each player samples θ, plus some observational error. Let the ith sample of the relative fighting cost be denoted by X_i. A strategy is specified by a sequence of numbers $\{S_1, S_2, ...\}$ and the persistence rule "give up after step n" if $X_1 > S_1, X_2 > S_2, ..., X_{n-1} > S_{n-1}, X_n \leq S_n$. Through the application of dynamic programming, the ESS is found to be a sequence $S_n, n = 0, 1, ...$ with properties dependent on the sampling error of the relative fighting ability and bout number. Sampled relative fighting estimates constitute a walk through a "causal factor space", and when the sampled value crosses a critical threshold, individuals desist. In accord with biological intuition, animals with the same fighting costs, $\theta_{12} = \theta_{21} = 0$, are predicted to persist the longest in fighting, though through sampling errors, a stronger player may ocassionally desist before the weaker individual. As the relative fighting ability becomes increasingly skewed, fights become shorter with less assessment errors from the stronger player (Enquist and Leimar,[16, 17]).

1.1.3 Sensitivity of Games Models to Information Exchange

Predicted strategies at the evolutionary stable state depend critically on the assumptions of information exchange between opponents (Fundenberg and Tirole,[24]). This is best illustrated by considering an important theorem, relating the set of possible stable strategies, given contestants can perceive asymmetries, such as role or height, between one another. The theorem states that if two contestants have any perceived asymmetry, even if this asymmetry is not related to any fitness outcome, then an ESS cannot be a mixed strategy (Selten,[72]). Though this theorem is difficult to prove, the result can intuitively be seen by an argument developed in (Maynard-Smith,[54]). Suppose animals can adopt two sorts of roles, owner and intruder, with an ESS consisting of playing strategy I in role one, and playing strategy J in role two. Furthermore, suppose the strategy I is mixed, adopting strategy A with probability p and strategy B with probability $(1-p)$. By the Bishop-Cannings theorem, for I to be an ESS, the expected payoffs in role one must be equal, $E(A,J) = E(B,J) = E(I,J)$. For I to be an ESS in role one then $E(I,A) > E(A,A)$ and $E(I,B) > E(B,B)$. Decomposing strategy $I = pA + (1-p)B$, then the identities $E(B,A) > E(A,A)$ and $E(A,B) > E(B,B)$ must be proved to satisfy the ESS criterion. If players can assess roles, then a player in role one will never meet another player in role one, thus the quantities $E(A,A)$ and $E(B,B)$ cannot be calculated, thus we cannot check the ESS criterion. Mixed strategies in asymmetric games can be neutrally stable, in that the mixed strategy will do equally well against a set of pure strategies, but any mixed strategy will not invade a population against pure strategy alternatives in assymetric games.

Errors in role perception can lead to ESS mixed strategies. The most important example of this occurs in the assymetric war of attrition, (Hammerstein and Parker,[31]) where roles A and B are distinguished by the persistence payoffs and attrition costs. In this approach, rewards and costs of a player in role A against a player in role B are denoted by V_{AB}, C_{AB} respectively. With errors in the perception of roles, two players, both in role A may contest, with persistence payoffs and costs V_{AA}, C_{AA}. Hammerstein and Parker established bounds on the probabilities of both players occupying the same role, under which mixed strategies can be an ESS. If p_{AB} is the probability that player one is in role A and player two is in role B, then the asymmetry conditions $p_{AB}V_{AB} > p_{BB}V_{BB}$ and $p_{BA}C_{BA} > w_{AA}C_{AA}$ are required for the existance of ESS mixed strategies, provided role A is favoured in payoffs, that is $\frac{V_{AB}}{C_{AB}} > \frac{V_{BA}}{C_{BA}}$. Derived ESS mixed strategy densities for roles A and B do not overlap, with players having favoured payoffs, that is players in role A, persisting longest (Hammerstein and Parker,[31]).

Studies of the war of attrition in which players either have perfect information and identical states (Bishop and Cannings,[4]), imperfect but partial information about two states (Hammerstein and Parker,[31] Bishop,Cannings and Maynard Smith,[4]), or no information about the opponents state (Mesterson-Gibbons,[63]) show a continuum from entirely mixed strategies to pure strategies with mixed strategies forming the ESS when opponents possess some probability of being in the same state as the opponent.

Information can alter, not only the type of stable strategy, pure or mixed, but also form of equilibria (Sjerps and Haccou,[74], Fundenberg and Tirole,[24]). Central to the definition of the ESS is that strategies must form a Nash equilibria. The process by which a Nash equilibria is attained can be explained with the notion of the best response strategy. Suppose players in a population adopt strategy u_{pop} and a mutant adopts strategy u_{mut}, to maximise its lifetime fitness when competing with u_{pop} strategists. The strategy u_{mut} is termed the best response to the the population strategy. If Br is defined to be the best response function, then

$$u_{mut} = Br(u_{pop}).$$

A Nash equilibrium strategy u^* satisfies the fixed point equation

$$u^* = Br(u^*).$$

The Nash equilibria occurs when neither player has any advantageous information about the opponents strategy before the commencement of the game, this being seen by a general examination of the types of Nash equilibrium strategies derived, when players have identical or distinct states. When players are in identical states, the Nash equilibria are mixed strategies, these being pre-emptively unpredictable to the opponent. If players have different rewards and costs associated with direct conflict, players adopt pure strategies. Though the pure strategies depend on the associated rewards and costs, they cannot be pre-emptively assessed by the opponent, as rewards and costs are internal states of the opponent.

Suppose instead, that a player can preempt the strategy used by the opponent, due to the respective roles of each player. Such preemption permits optimisation of payoffs, in light of the opponents strategy (Sjerps and Haccou,[74]). Thus, given the constrained player adopts some strategy u_c, then the preemptive player will choose u_p^* to maximise expected payoff,

$$u_p^* = \arg\max_u E(u, u_c).$$

The preemptive player has essentially the final round in the best response iteration. If both players cannot do any better, given the preemptive player has the last optimisation round, then the equilibrium generated is called a *Stackelberg* equilibria (Fundenberg and Tirole, [24], Sjerps and Haccou, [74]).

1.1.4 Owners and Intruders

ESS's associated with ownership of a resource have been the subject of both theoretical and experimental study, from the commencement of the application of game theory to animal behaviour (Maynard-Smith,[54]). Maynard-Smith and Parker studied ownership with the Hawk-Dove-Bourgeois game (Maynard-Smith and Parker,[55]). Aggressive competition was the strategy of the Hawk player. Passive competition, always defeated by a Hawk, was the strategy of the Dove. Finally, a Bourgeois strategist will play Hawk of an owner of some territory and Dove if an intruder to an occupied territory. Assuming V is the value of the resource, C is the cost of injury and half of the conflicts are as owner and half as intruder, the following matrix describes the strategic form

	Hawk	Dove	Bourgeois
Hawk	$\frac{1}{2}(V-C)$	V	$\frac{3}{4}V - \frac{1}{4}C$
Dove	0	$\frac{1}{2}V$	$\frac{1}{4}V$
Bourgeois	$\frac{1}{4}(V-C)$	$\frac{3}{4}V$	$\frac{1}{2}V$

Thus, for example, the expected payoff of a Hawk strategist against a Bourgeois is $E(H,B) = \frac{1}{2}E(H,H) + \frac{1}{2}E(H,D) = \frac{3}{4}V - \frac{1}{4}C$. If only pure strategies are considered, when $V > C$ the ESS is to play Hawk. When $V < C$ however, the Bourgeois strategy is the ESS.

The Hawk-Dove-Bourgeois model provided the first theoretical basis for observed patterns of behaviour in ownership across many species (Hammerstein and Riechart [32]). There are some exceptions, including the behaviour of the spider *Oecobius civitas* in which the intruder always displaces the owner (Mesterson-Gibbons,[62]). To understand how different strategies may be favoured under different ecological conditions, a model in which players compete in a sequence of games, either as an owner or as an intruder was analysed under different "ecotypes" or combinations of competitive intensity, probability of injury and expected lifetimes (Mesterson-Gibbons,[62])). Also included was the anti-Bourgeois strategy of playing Dove when an owner and Hawk when intruder. Though the Hawk strategy was the ESS for most ecotypes, both the Bourgeois and anti-Bourgeois strategies were found to be evolutionary stable under certain ecotypes, especially large resource values and long life times (Mesterson-Gibbons,[62]).

1.2 Behavioural Ecology of Trissolcus basalis

The species *Trissolcus Basalis Wollaston (Hymenoptera:Scelionidae),* in Australia, is an quasi-gregarious synovigenic egg parasitoid of the species *Agonoscelis rutila (Hemiptera:Pentatomidae)* commonly known as the horehound bug. In the United States and South Amercia *T. Basalis* also parasitises other pentatomid species, such as *Nezara viridula (Hemiptera: Pentatomidae),* also known as the green vegetable bug, a common agricultural pest (Noble,[66]). *A. rutila* typically lays rafts of between 10 to 30 eggs held together by secreted adhesive (Noble,[66]).

Australian strains of *T. basalis* females have an approximate fecundity of 90-140 eggs, and are attracted to host patches through secretions from the host metathoric gland (Field,[19]). Upon arrival to the patch, the parasitoid commences searching for suitable hosts, this being achieved through an antennated search of individual eggs (Wilson,[86]). Antennae of *T. basalis* have various chemosensillae that function to recognise suitable hosts. Once antennation has focussed on a single host, this host may be accepted for parasitisation, and a sterotypical oviposition sequence commences (Wilson,[86]). Upon finding a suitable host, the parasitoid begins the behavioural sequence that commences with the preliminary probing of the host egg, presumably to find a suitable site for injection of its needle-like ovipositor. Following the probing behaviour, parasitoids commence the sequence of drilling, oviposition and finally host marking. Hosts are marked by running the ovipositor across the surface of the egg in a figure "8" (Wilson,[86]). Host marking enables searching parasitoids to discriminate between unparasitised and parasitised hosts, this restricts the patch search to unparasitised hosts and is thought to have adaptive significance (Roitberg and Mangel,[68]). If a host egg is superparasitised, first instar larvae compete within the host, this competition resulting in complete elimination, commonly of one larvae, and occassionally both larvae (Salt,[70]). First instar larvae develop piercing mandibules that are used in combat. Larval fights are thought to be fatal because only one parasitoid can develop within the egg, thus the total lifetime fitness to the loser of a fight will be precisely zero. If the expected future fitness of a losing player is zero, then it has been shown that the ESS is to fight to the death (Enquist and Leimar,[18]).

If two or more females co-exploit a patch then competition for resources will ensue. Competition for ovipositions is fundamentally different to that of competition between predators for prey. Prey items are consumed by the predators, removing the energy source from the environment, whereas parasitised hosts remain to be superparasitised (Field and Calbert,[20]). The evolutionary mechanisms that induce intra-specific patch defence in gregarious and quasi-gregarious parasitoids, in particular the family Scelionidae, have been studied by comparing the relative host patch sizes, across species in the family Scelionidae (Wagge,[83]). Species with average host patch sizes of less than 50 eggs tended not to fight, whereas smaller patch sizes were shown have fighting parasitoids. The author argued that small host patch sizes can be defended from superparasitism, whereas ovipositions can easily be "stolen" from competitors attempting to defend a larger patch (Wagge,[83]). Patch size is not the only important factor determining defence behaviour. Given that the average host patch of *A. rutila* consists of approximately 20 eggs, in the Australian strain of *T. basalis* a patch will represent a minimum of approximately 10 % of an individuals lifetime success. Add to this mortality of the parasitoid, high ratios of competitors to patches, superparasitism and hyperparasitism then the percentage lifetime contribution to fitness of this patch will increase substantially (Field,[19], Ayal and Green,[2]).

T. basalis is notable in the high expected payoff to the superparasitising female, when the time difference between the first and second ovipositions is small (Field, Keller and Calbert,[22]). In an experiment to determine the probability of superparasitism success, an Adelaide strain of *T. basalis* and a strain from Darwin, distinguished by an enzyme polymorphism, were identified. A female from the second strain oviposited some time after the first strain oviposition. Emerging progeny were thus identified through enzyme analysis. Given progeny success could be recorded as binary data, with 0 for the success of a first strain female, and 1 for the success of a second, analysis of factors such such as order of oviposition, and time difference between ovipositions were done through a statistical technique called logistic regression (McCullagh and Nedler,[56]). Though the order of oviposition, strain one first and strain two second or vice versa was important, the overall conclusion was that the superparasitising female possessed a *greater* than 50 % chance of success in the emergence of its progeny (Field, Keller and Calbert,[22]). As expected, the success of superparasitism gradually decreased over a period of 15 hours from the first oviposition, as can be seen from the results of the fitted logistic model (Figure 1.2.1).

In summary, the evolutionary mechanisms that govern defence behaviour in *T. basalis* include

- defendability of patches from superparasitism,

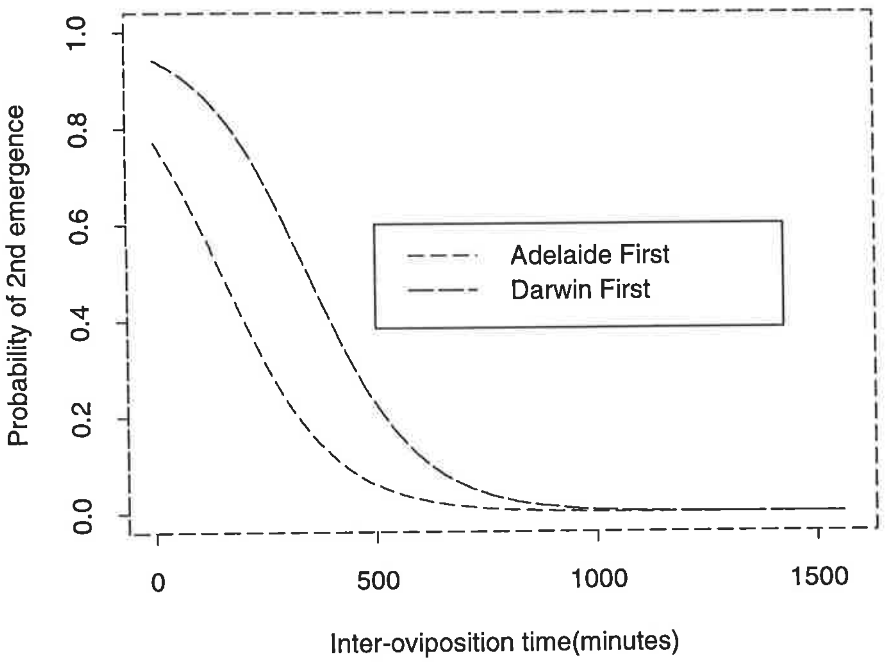

Figure 1.2.1: The probability of emergence of the superparasitising female. Data from an emergence experiment (Field, [19]), fitted with a logistic model. Note the estimated probability of emergence of the superparasitising female is greater than 0.5, for time differences of up to 3 hours, no matter which strain oviposits first.

- large ratios of competitors to patches,
- high payoff from superparasitism and
- a significant percentage of lifetime reproductive potential from a single patch.

1.2.1 Structure of Pairwise Patch Contests

Though there is considerable variation in the behaviour of competing conspecifics, agonistic competition between two *T. basalis* females can be divided into three broad phases. Phase one commences with the arrival of both players to the patch.

During this stage of competition, both females begin antennation of the patch for suitable hosts. Depending on the skewness of the relative patch investments of both players, and the number of remaining eggs to be parasitised, agonistic competition ranges from complete tolerance to extended conflict (Cumber, [12]). When the patch approaches full parasitisation, extended fighting yields a dominant player that can usurp the opponent from the patch. The dominant player takes possession of the patch, though take-overs have been observed. In this dissertation, the dominant player is called the *resident* and the opponent is called the *intruder* (Field,[19]). It is important to note that the notion of a resident is different to that of an owner. We have used the term resident, as the patch may be superparasitised in the future whereas the owner of a food resource may consume the item without need to future defend this food resource (Field, [19]).

The factors that influence the onset of competition in pairwise patch competition have been studied through an experiment in which the second player is released onto the patch, after the first has parasitised some fraction of the patch. As player one will either become resident or intruder, outcomes are binary valued, thus the factors that influence residency can again be modelled with logistic regression (McCullagh and Nelder,[56]). Body weight was not shown to be an important factor determining contest outcomes (Field,[19]). The relative investment of both players was shown to determine which player achieved residency (Field,[19]). During a series of escalated contests, the player that won the previous contest also had the highest probability of winning the current contest (Field,[19]). Once residency was established, takeovers though observed, were rare, occurring in only 3 % of contests (Field,[19]).

Once residency has been established, phase two of competition commences. During this stage, an intruder will not fight the resident, but retreat to the patch periphery if approached. A resident is observed to search for remaining parasitised eggs, while the intruder returns from the patch edge to search for unparasitised hosts, or to superparasitise (Field,Calbert and Keller,[21]). If the resident observes, or comes in contact with the intruder, it is once again removed, either by retreating or by resident force, to the patch periphery. The return frequency of the intruder decreases, depending on the number of times it is removed from the patch and whether the resident ceases to find further unparasitised hosts and commences guarding.

The final stage of patch competition, termed the *waiting game,* commences when the resident ceases searching for remaining unparasitised hosts, and the intruder ceases to return periodically. The resident is observed to wait, motionless, at the center of the patch. There is anecdotal evidence that *T. basalis* has poor vision of stationary objects, but is sensitive to movement (Field,[19],Land,[42]), thus the stationarity of the resident is thought to have adaptive significance, maximising the prospect of detecting a returning intruder (Field,Calbert and Keller,[21]). After a period of time, ranging from 30 minutes to 6 hours, the resident commences a series of excursions around the patch. Each excursion ends with the return of the resident to the patch, followed by another excursion, with larger travel radius, till eventually the resident leaves (Wilson,[86],Field,[19]). Leaving time distributions for patch sizes of 12 and 24 eggs are shown in the following figure.

Rarely does the intruder leave the patch, instead it is found "waiting" in the near periphery. While a resident sits motionless on the patch, an intruder is observed to make occasional partial patch returns and this is hypothesised to increase the intruder's estimate of the resident's presence (Cumber,[12],Field,[19]). Subsequent to the resident leaving, the intruder returns to superparasitise the undefended patch. The time interval between the resident leaving, and the intruder's return may be up to two hours. Both the resident leaving time and intruder return time are influenced by the number of host eggs and the skewness of competitor investment (Field, [19]).

To summarise observations of pairwise patch competition in *T. basalis,*

- Phase one: initially tolerate a conspecifics presence, though as the number of unparasitised eggs diminishes, agonistic competition increases, resulting in the establishment of resident/intruder roles.

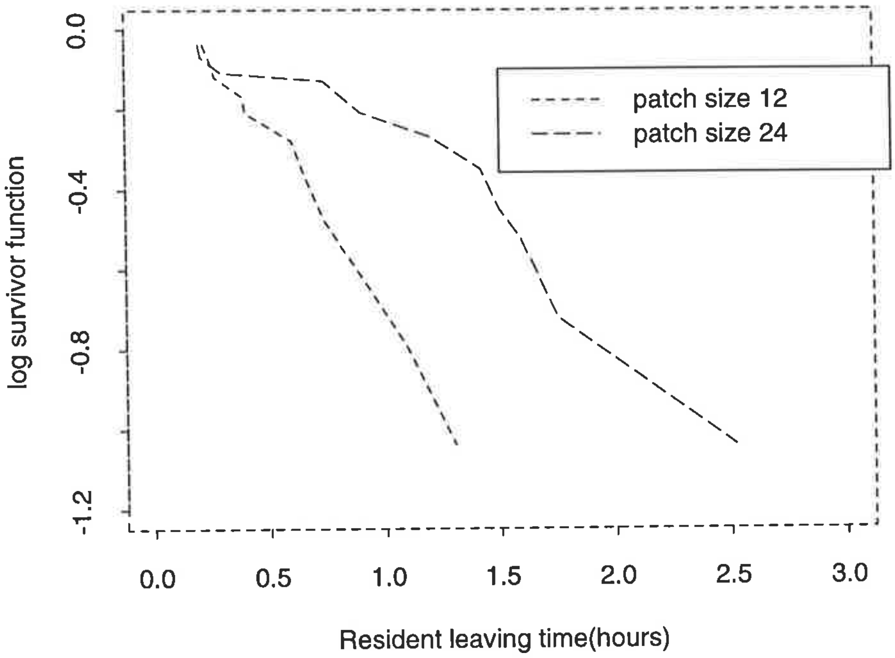

Figure 1.2.2: Graph of the logarithm of the estimated survivor function taken from resident leaving times. Leaving times are recorded from the commencement of the stationary guarding period of the resident. Data is presented for patches with 12 and 24 eggs respectively.

- Phase two: an intruder returns from the patch periphery to search for remaining unparasitised hosts or to superparasitise. The resident searches for remaining unparasitised eggs. An intruder is immediately removed off the patch upon encounter with a resident.

- Phase three: resident ceases searching, but remains stationary on the patch, presumably to maximise motion detection. The intruder waits at the patch edge. After some time, dependent on investment skewness and patch size, the resident leaves and the intruder returns to superparasitise.

1.2.2 Simplifying Complex Behaviours

Eleven behavioural catagories exhibited by *T. Basalis* have been described (Field,[19], pgs 33-34). These behaviours can further be classified into three groups, those associated with search/oviposition, those behaviours associated with patch defence and general behaviour, as are listed below.

Search/Oviposition

- Walk-antennate-host: walking over the egg mass, antennae vibrating and sweeping over the exposed surface of the egg mass.
- Turn: turning on top of a particular host egg.
- Probe: examination of a host egg, probing the egg surface with the ovipositor, ending with insertion of the ovipositor.
- Pump: repeated pumping movements of the head and flexing of the wings during oviposition.
- Rock: entire body vibrating, infrequent head pumping.
- Mark: ovipositor swept over the surface of the egg, in a figure "8".

Guarding

- Stationary: body motionless, antennae vibrating.
- Patrol: repeated bursts of running, from one side of the egg mass to the other.

General

- Walk-antennate substrate: as for walk-antennate-host, but on any general surface.
- Groom: cleaning of body.
- Feed: consumption of honey/water mixture.

Because of this natural classification of behaviours into three catagories, models of patch competition will assume the three behavioural catagories of "search", "oviposit" and "guard". It will be assumed that during oviposition, the parasitoid will not be able to prevent a conspecific from searching for hosts. Furthermore, the patch is assumed to be the most susceptable to conspecific parasitism when the parasitoid is ovipositing.

1.3 Approaches to Modelling Patch Competition

Models of intra-specific patch competition, ideally, should satisfy some minimal requirements to be considered as contributions to understanding the Behavioural Ecology of *T. basalis*. Criteria used to judge a model, or series of models, should include the following.

- Do the assumptions behind such models reflect biological reality ?
- Can such models yield either implicit or computationally tractable results ?
- Do the results reflect the diversity of behaviour, as observed through experiments ?
- Can testable predictions be made from the models ?

It is the balance between tractability and the incorporation of biological detail, that is the challenge to any student of Mathematical Biology (Godfray,[26]). To justify the modelling approach used in this dissertation, some comparisons between various mathematical techniques used in Behavioural Ecology are noted.

One possible approach to modelling *T. basalis* behaviour would be to study behavioural decisions taken over an individual's lifetime and to use state dependent, dynamic games (Mangel,[50, 49], McNamara and Houston,[36]). This method has the advantage that both physiological and experiential factors can be incorporated as state variables. To build a comprehensive model of patch defence behaviour, state variables such as age, egg load, patch size and current number of ovipositions should be incorporated. Furthermore, an information state that included the number of past patch encounters where residency was obtained may serve as important within the model. Minimally the age, egg load and current percentage patch parasitism would have to be included. However, any state dependent, life-history approach will suffer from two problems. Firstly, even with the minimal three states mentioned, dynamic games rapidly become computationally intractable (Houston and McNamara,[36]). Further to this, different time frames are associated with different decisions. For example, the time frame in which fighting decisions are made may be too fine grained, if compared to the time frame of resident leaving, intruder return decisions. For these reasons, life-history models, though initially attempted, are not undertaken in this dissertation.

What if we restrict attention to single patch competition? Attempts at applying the state dependent dynamic games approach are not suitable because of the following reasons. Most dynamic games assume that individuals make decisions against"the field" (Houston and McNamara,[36]). In this case, an individual's optimal strategy will be a function of its internal state variables, and the averaged populations internal state (Mangel and Clark,[50]). This is no longer appropriate when individuals play against one another, as it is no longer sufficient to assume that players choose strategies against some "averaged" player. The sequential assessment games of Leimar and Enquist avoided such problems, as there is only one internal state variable, relative fighting cost, which does not change over the course of the game (Enquist and Leimar,[17],). Furthermore, the decision set of each individual changes over the course of the game, making a formulation of the stages of pairwise competition within *T. basalis* very difficult.

To avoid the forementioned problems, each phase of pairwise competition in *T. basalis* is modelled separately, and each model has a set of assumptions regarding the information exchanged between opponents. No physiological state variables are included in the models, because of the complexity of single patch interactions.

Phase one, in which patch parasitism proceeds and fighting decides residency is modelled using a war of attrition, with individual variation in patch investment. In this phase, players are assumed to be aware of their self-investment and a distribution of possible investments of the opponent. This is similar to the war of attrition with random rewards, with patch investment replacing rewards of winning (Bishop,Cannings and Maynard Smith,[4]). As it was difficult to determine by experiment the exact mechanism of contest resolution (Field,[19]), two hypotheses, addressing different ways of winning an extended fight are modelled. The first mechanism of contest resolution assumes that both players continuously accrue injuries as the fight proceeds, and the winner is the individual to persist the longest (Chapter 2). The second model, called the graduated risks model, is well known in Behavioural Ecology literature, with the loser being either the first player to be injured, or the first player to desist fighting (Bishop and Cannings,[3] and Chapter 2).

Phase two, with residency decided, models the return rate of the intruder, as the resident proceeds to search for remaining unparasitised eggs. Underlying such models is a central assumption regarding the vulnerability of the patch to intruder parasitism and superparasitism. It is assumed that the patch is most vulnerable to an intruder oviposition, if the intruder returns while the resident is itself ovipositing. In some sense, the intruder's best strategy is to return with the same frequency as the resident's oviposition times. The resident, as a response to an intruder's return, chooses to either search for further hosts or cease searching and adopt a purely defensive role. Both players are assumed to possess limited information as to the opponent's actions, with the intruder assumed to have an estimate of the resident's oviposition rate, and the resident, an estimate of the intruder's return frequency (Chapter 3). The hypothesis that patch vulnerability is maximal when the resident is itself ovipositing is not the only hypothesis explored. We also consider an intruder centered stochastic dynamic programme, in which the intruder chooses to return or to play the waiting game, based on the past successes and failures in finding an oviposition on return to the patch (Chapter 3).

Finally, phase three, the waiting game is analysed with different biological and information exchange assumptions and different modelling approaches. Initial modelling approaches assume that the payoffs from superparasitism, over the course of the waiting game are approximately constant. From this basis, models are constructed to calculate the ESS resident leaving time and intruder return time. In Chapter 4 we prove that the waiting game has no ESS if there is no information exchanged to the intruder about the resident's leaving time. If there is a small probability that the opponent may be *absent,* through injury or predation, leaving time densities and return time densities are derived that yield constant payoffs, but are shown to be at best neutrally stable(Chapter 4).

Motivated by the failure to find an ESS under the previous assumptions of information exchange, a new set of models is proposed. Two biological observations underlie this new approach. Firstly, the payoff from superparasitism decreases over the course of the waiting game, in agreement with experimental observations. Second, intruders have *partial* information as to the presence or absence of the resident. Finally, in accord with experimental observations, an intruder is assumed to return only after the resident leaves the patch. The resident, in turn, optimises its leaving decision in light of the intruder's impending return (Chapter 5).

At this point, it should be emphasised that though the work on the waiting game without information exchange of the resident's leaving time failed to find an ESS, the conclusions helped to form a new set of assumptions, with which appropriate ESS leave/return times could be derived. Hence this work, while not suitable for publication, is included in the thesis to highlight the model building process.

In developing the modelling approaches in pairwise *T. basalis* competition, only a limited set of models were explored, due to time and work constraints. Further avenues of research, including spatial foraging issues and $\epsilon-$perfect strategies are explored in the general conclusion (Chapter 6).

Chapter 2

Competition for Residency

Perfect and Imperfect Information of the conspecific's investment.

2.1 Introduction

There are few general rules regarding strategies used in resource competition. One general observation of organisms that compete for a resource is that competition will take place for that resource, if the ratio of competitors to resource patches is sufficiently high (Mangel,[47]). In some species of spiders, for example, failure to secure a territory will imply zero future reproductive success, which implies the only ESS is to fight to the death (Hammerstein and Riechart,[32], Enquist and Leimar,[18]).

The effect on future reproductive success of a resource is not the only criterion in deciding to fight for resource possession. The resource patch should be of such size, that it is economical to defend (Cockburn,[10]). In a seminal study comparing patch size with competition for resources within the parasitoid family Scelionidae, hosts laying small egg rafts were found to have their eggs parasitised by species that fought for the patch, through intra-specific competition. In those host species where large rafts of eggs were laid, intra-specific competition was less prevalent or nonexistant (Wagge,[83]).

By comparisional dissection of developed *T. basalis* that were yet to parasitise a host, embryo counts revealed an estimate of approximately 90-140 embryos available for future investment (Field, [19]). With the host patch size ranging from approximately 10 to 30 eggs, successful parasitism of a patch of say 20 eggs will represent a major proportion of a parasitoid's maximum future reproductive success. With mortality due to superparasitism, host defences and hyperparasitism, this percentage will only increase. This coupled with the fact that during mid-summer, counts of the ratio of parasitoids to patches is extremely high (Hood,[35]), provide both the evolutionary and proximate mechanisms underlying resource competition and patch defence in the species *T. basalis.*

In studying the intensity of competition for resources, both the effects of internal physiological variables such as egg load, competition experience and age as well as the external factors such as the size of the patch, number of competitors and current investment in the patch should be factored into decisions of competition. Statistical models of patch competition within *T. basalis* have been analysed, to determine which factors determine the the onset of fighting for patch possession (Field and Calbert,[20]). Factors such as current oviposition rate, number of total ovipositions and outcomes of previous fighting bouts were deemed to be statistically significant (Field and Calbert,[20]). Ideally, internal variables such as the aformentioned egg load, should be statistically assessed for significance, but for purposes of focusing on the dynamic variables that influence competition resolution, only the external variables, such as number of ovipositions were studied. Modelling patch competition with the emphasis on patch investment and patch fitness value will also be the approach taken in this chapter.

Before constructing an evolutionary model of patch fighting, some broad observations regarding the nature of contest resolution should be taken into account. Firstly, fighting occurs with considerable variability in agonistic intensity (Field,[19], Cumber,[12]). When two conspecifics initially encounter one another, serious escalations are rare, with fights building in intensity as the level of remaining unparasitised hosts diminishes (Field,[19]). As well as this general observation of fighting intensity, the outcomes of fights are normally determined by comparison of the skewness of investment between players. Given two conspecifics compete for the patch, if one player arrives considerably earlier to the patch than the opponent, inevitably this player will attain eventual residency (Field and Calbert,[20]). Furthermore, players that arrive at approximately the same time, will fight with the most intensity when competing for residency (Field, [19]). In this situation, there can be a considerable number of takeovers in which the current resident is forcably removed from this status by an aggressive opponent(Field,[19]).

With these broad observations, some models of patch competition are constructed in this chapter. As a starting point, the level of current self-investment in the patch must be included as a variable determining contest outcomes. Should it be assumed that players are aware of the opponent's current patch investment? Studying the process by which females search for unparasitised eggs provide clues for modelling relative investment information between opponents.

Upon arrival to the patch, females cycle through the behavioural sequence of antennation, oviposition and host marking, as they search the patch for future investments (Field,[19]). This searching strategy, in contrast to a strategy of full patch assessment before oviposition, is a *local information strategy.* Thus another ingredient for a model of patch competition will assume knowledge of self investment and only knowledge of the *distribution* of patch investments of the opponent (Mesterson-Gibbons, Marden and Dugatkin,[64]). In addition, the local searching strategy implies that it should not be assumed that players have knowledge of the fitness value of the patch, rather a distribution of possible fitness returns.

Because of the size of individuals observed, and the pace of movement, contests did not clearly indicate the exact mechanism by which contestants resolved a competition. Thus, in this chapter, two mechanisms of contest resolution are studied, the continuous risks and graduated risks models. In the continuous risks model, as players fight, they are assumed to continuously accrue injuries during the course of the fight, the winner being the individual that persists in competition the longest. The second mechanism of contest resolution, the graduated risks model, has been studied before within the context of wars of attrition (Maynard Smith and Parker,[55], Bishop and Cannings,[3]). Rather than choose an escalation time, players in the graduated risks game choose an escalation level, reflected in the probability that either player will be injured. The winner in the game is either the last player to desist from fighting, or the player that escaped injury.

Before commencing the next section, an overview of the current chapter is given. Section 2.1.1 discusses a model of fitness returns for a player that invests x eggs in a patch of fitness value E. Given a particular percentage investment in a patch, both the returns from current investments and the returns from potential future investments must be considered in the decision as to whether to fight for the patch and at what intensity. Following discourse of patch investment issues, Section 2.2 looks at a simple model of patch competition, in which players have perfect knowledge of self and opponent patch investment and as well as patch size. Expanding the assumptions toward biological realism, through restriction of the information of an opponent's investment and patch size is the focus of the following two sections. The continuous risks model is the first fighting mechanism to be modelled, in Section 2.3.1, followed by the graduated risks model, Section 2.3.2. For both sections, ESS fighting strategies, dependent on current patch investment and expected future returns are derived, and parameter sensitivity studied. A discussion of alternative approaches to modelling patch conflict, with differing biological assumptions and alternative mathematical techniques is included in the Discussion/Conclusion (Section 2.4). Finally in the Appendix (Section 2.5) to this chapter we derive the equations for the calculation of the ESS for the continuous and graduated risks models.

2.1.1 A simple model of Patch Investment

Given that two parasitoids simultaneously host search on a patch, suppose the investment of the first player is x eggs and the second player y eggs. After competition for possession of the patch, the fitness of each player will depend on the role, resident or intruder of each player subsequent to competition, the number of remaining eggs to be parasitised and importantly the *vulnerability* of the patch to intruder parasitism or superparsitism, given a particular proportion of the patch has been already parasitised.

Let the fitness of player one, be denoted by $R(x, y)$, if residency is achieved and $I(x, y)$ if player one loses residency and becomes the intruder. It is assumed that the patch contribution of fitness in both roles can be decomposed into two components, that of fitness accrued from previous parasitism and the expected fitness obtained from future eggs yet to parasitised. In other words

$$\begin{aligned}\text{Fitness} &= \text{Contributions from current investment}\\ &+ \text{Contributions from future.}\end{aligned}$$

To look at the contribution from current investments it is assumed that each player receives a proportion of the opponent's current investment and a proportion of it's own current investment, these proportions dependent on the role of each player after agonistic conflict.

Let $\mathcal{R}$ be the event that the player wins residency, and $\mathcal{I}$ the event that the player loses, becoming an intruder. Then let

$$\alpha = E(\text{proportion of current self investment secured}|\mathcal{R})$$

and

$$\beta = E(\text{proportion of opponent's current investment secured}|\mathcal{R}).$$

Thus, if player one wins residency, then the fitness contribution from total current investments is $\alpha x + \beta y$, and if player two wins residency, it's fitness of current investments is $\alpha y + \beta x$.

As the sum of the current fitness contributions is $x + y$, it follows that the fitness contribution to player one if it becomes an intruder is $(x + y) - (\alpha y + \beta x) = (1 - \alpha)y + (1 - \beta)x$. Though the functions α and β will in general depend on investments x, y of the two players, for simplicity, throughout the remainder of this chapter, they are assumed to be constants.

Since it is assumed that the fitness value of the patch is E, the remaining future patch fitness, $r = E-x-y$, will be distributed amongst each player, this distribution dependent on the role of each player.

We define the remaining resources distributed to the resident and intruder as the *proportion* distributed

$$\gamma(r) = E(\text{proportion of remaining resources secured}|\mathcal{R}, r).$$

Combining current and expected future returns, the expected total fitness of player one, if residency status has been achieved is

$$R(x,y) = \alpha x + \beta y + \gamma(E-x-y)\Big(E-x-y\Big),$$

and if player one becomes an intruder,

$$I(x,y) = (1-\alpha)y + (1-\beta)x + \Big(1-\gamma(E-x-y)\Big)\Big(E-x-y\Big).$$

Functions α, β and γ are measures of the ability of the resident to retain current investment and secure some of the opponent's investment through superparasitism. Generally, the ability of the owner of some patch to secure resources within that patch is known as the *resource holding potential* or RHP (Parker and Rubenstein,[67],Field,[19]), hence α, β and γ embody the RHP.

Decisions such as when to fight for possession of the patch, or when to concede residency should depend on how future self/opponent investment change in proportion to total current investment. This investment dependent patch defendability will be reflected in the possible values of $\gamma(r)$. With no resident advantage in securing future fitness returns, on average each player will secure half of the remaining resources, thus $\gamma(r) = \frac{1}{2}$ for both players. If remaining patch resources become increasingly vulnerable to intruder attempts to "steal" ovipositions, then $\gamma(r)$ will be monotonically decreasing as $r \longrightarrow 0$. In analysis of any model of patch competition,

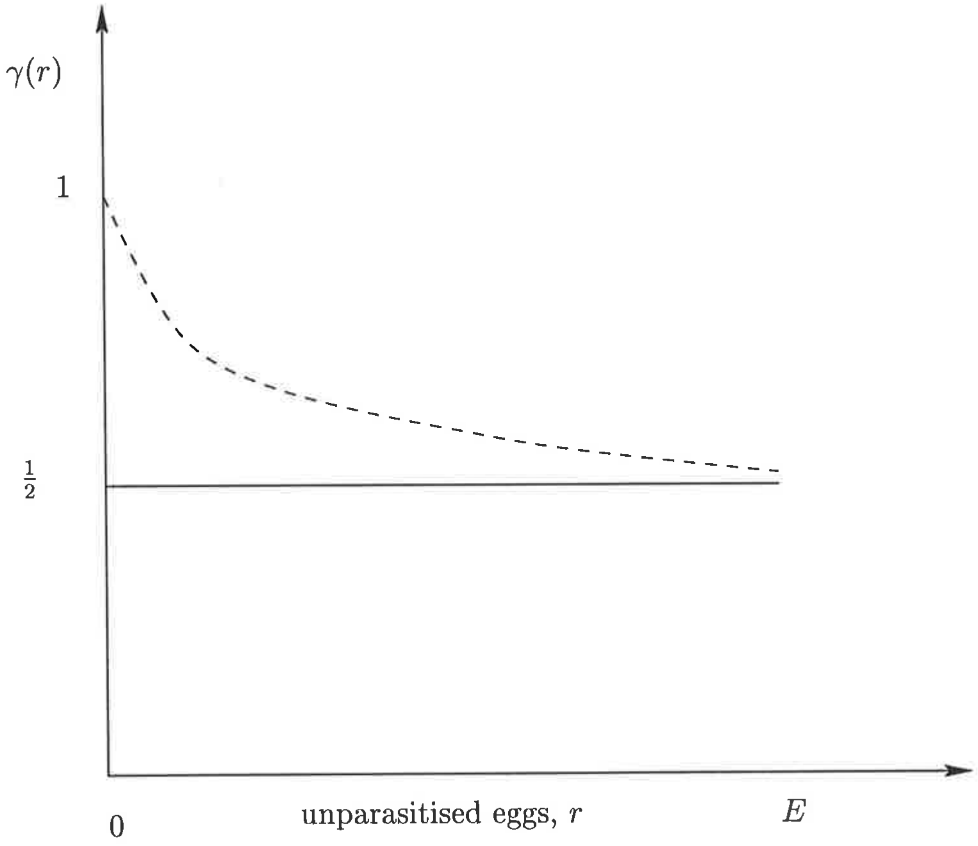

Figure 2.1.1: Hypothesised expected fraction of remaining unparasitised eggs given to the resident, as a function of the remaining fitness value of the patch, $\gamma(r)$, where r ranges from E to 0. The hatched line shows a slow increase in defendability of remaining unparasitised hosts, compared to the dotted line where defendability is independent of investment.

an ESS fighting strategy must depend on changes in resource holding potential over the course of patch parasitism.

2.2 Perfect Knowledge of Opponent's Investment

If competing parasitoids are able to assess the opponent's patch investment, through some cues found while searching, any assymetries between investments of players will be used to settle contests for residency (Maynard Smith and Parker,[55], Hammerstein,[30]). Such an assymmetry will be prominent, when the difference between patch arrival times of players is large, as this gives the earlier arriving player more time to invest in the patch, and more time to assess the total fitness worth of the patch.

To find the ESS adopted by competing players with differing investments, suppose two players, one and two, have respective patch investments x and y, where $x+y \leq E$, the total fitness value of the patch. It is further assumed that players can adopt two strategies, either persistance in fighting or retreat from conflict. If both players have equal fighting ability then the cost of fighting for residency is assumed to be C for both players. Viewing the strategy combinations for each player generates the following payoff matrix or strategic form, with top corner payoffs given to player one, and bottom corner payoffs given to player two,

where $A(x,y) = \big(R(x,y) + I(x,y)\big)/2$ is the expected payoff from competition.

		Player two	
		Fight	Retreat
Player One	Fight	A(x,y)-C A(y,x)-C	R(x,y) I(y,x)
	Retreat	I(x,y) R(y,x)	E/2 E/2

Figure 2.2.2: Payoffs to player one, with investment x and player two, investment y, as determined by the two strategies "Fight" and "Retreat".

If both players adopt the strategy of "retreat" then they are assumed to "share" payoffs from the patch, resulting in $E/2$ given to each.

As the game played is assymetric, only the pure strategy combinations for both players need to be considered as candidates for the ESS (Selten, [72]). A strategy is specified by the pair of actions of each player, either in the role of player one or the role of player two. If it is assumed that a contestant will be in the role of player one or player two with equal probability, let role dependent strategies be denoted by $(S_1, S_2), S_i = F, R$, where the strategy of fighting is denoted by F and retreat by R.

An ESS is found by calculating the best response of players in each role, dependent on the opponent's strategy (Hammerstein,[30]). Starting from a randomly chosen strategy pair, player one's best response to player two's strategy is calculated. In turn, player two finds the best response to player one's strategy. This cycle continues till there is no change in either players best response.

For example, if $I(x,y) < A(x,y) - C$, then starting from the strategy pair (R, F), the best response of player one is to switch from the strategy of retreating to that of persisting. If $I(y,x) > A(y,x) - C$, then the best response, in turn, for player two is to retreat. Now if $R(x,y) > E/2$, then player one will not change strategies in response to player two's strategy of retreating. Thus the the strategy "player one fights, player two retreats" forms a role dependent ESS with the conditions, though not unique, that are listed above. A set of role dependent strategies are graphed for a choice of parameters below.

Consider the region in Figure 2.2.3 where the ESS is the strategy pair (F, R). Within this region, investments satisfy the conditions

$$\{(x,y)|R(x,y) > E/2, R(y,x) < E/2, A(x,y) - C < I(x,y), A(y,x) - C < I(y,x)\}.$$

The diagram of best responses to the opponent's strategy is shown below.

With the parameters $\alpha = 1, \beta = 0$ and $\alpha = \frac{3}{4}$, it is intuitively clear as to why the ESS is to fight with small investments. The resident gets none of the intruder's current ovipositions ($\beta = 0$) and most of the remaining unpapasitised hosts ($\gamma = 3/4$). Under these conditions, there will be no advantage in fighting when the number of unparasitised hosts drops to zero, as residency secures most

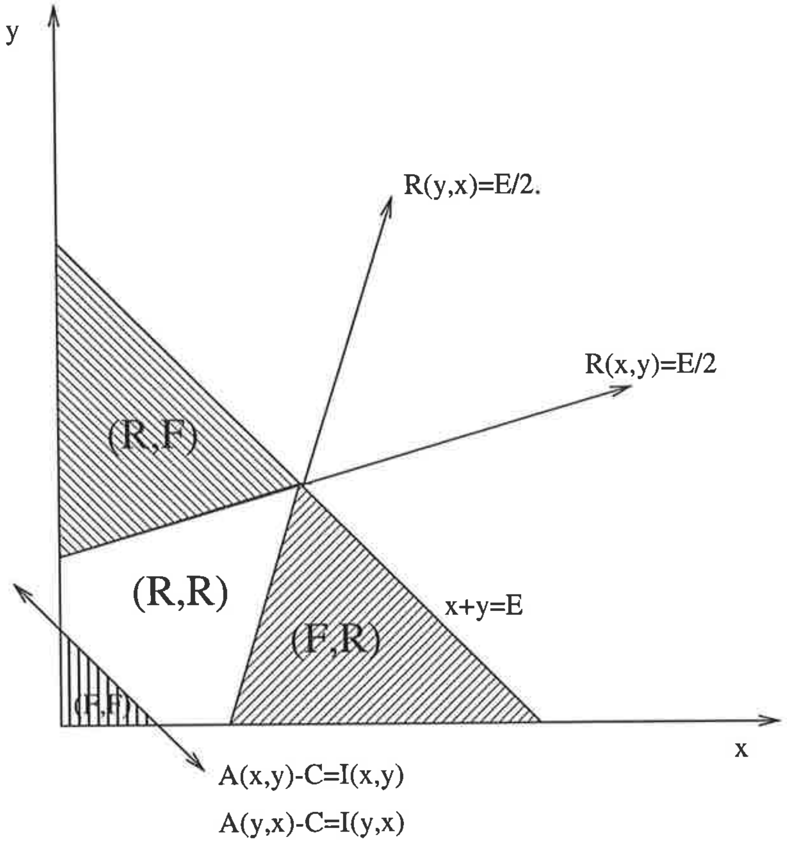

Figure 2.2.3: Role dependent ESS pure strategies, as a function of player one's investment x and player two's investment y. Strategies within a region are denoted by the vector $(S_1, S_2), S_i$ the strategy for player $i = 1, 2$. The parameters chosen are $\alpha = 1, \beta = 0, \gamma = \frac{3}{4}, C = 2$ and $E = 10$.

unparasitised hosts, even when total current patch investment is low.

When the difference between investments is large, the costs of fighting negate the payoffs of residency for the player with the smaller investment. Given this observation, the role dependent ESS for the player with highest investment is to fight for residency while the opponent retreats to the role of intruder, as seen in the sensitivity analysis of Figure 2.2.3.

How does this model compare with general observations of patch competition in *T. basalis*? When the investments of players are skewed, as will most often be the

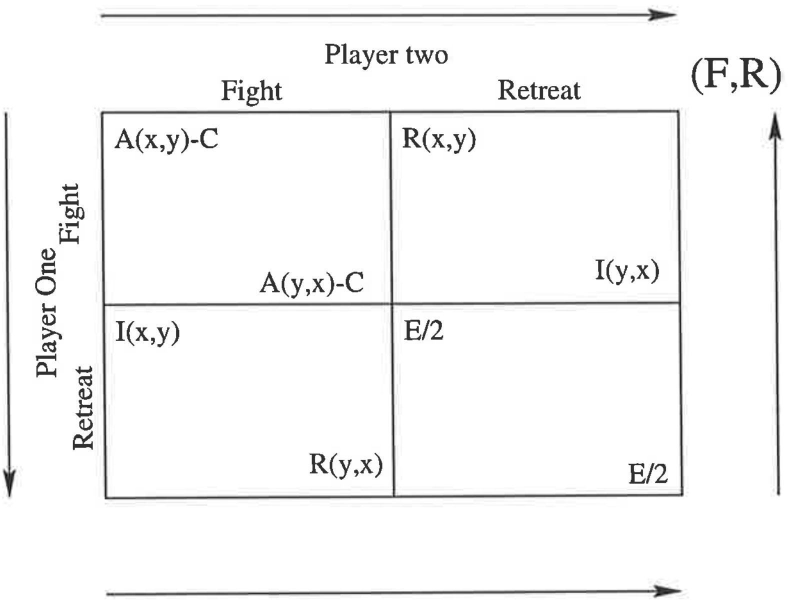

Figure 2.2.4: Role dependent best responses in patch competition of residency, under the conditions listed above. The vertical arrows give the direction of player one's best response, horizontal arrows player two's best response. At an ESS the arrows meet.

case because simultaneous arrivals are rare, the player with the larger investment wins residency, usually with little competition (Field,[19], Cumber,[12]) and this is the result of the analysis of the prefect information model. However, if investments are approximately equal, fighting usually occurs when the *number of unparasitised hosts approaches zero,* thus we would expect the ESS within some neighbourhood of the patch investments $(x, y) = (E/2, E/2)$ to be "both fight." At the investment point $(x, y) = (E/2, E/2)$, the strategy (F, F) cannot be an ESS in the perfect information case, since fighting comes at a cost C, negating the payoffs if both fight.

One reason for the anomaly between observations and the model of patch conflict may come from the assumption of constancy in the parameters α, β and γ and the values of these parameters chosen in our example. As mentioned in Section 2.1.1, the parameter that measures the defendability of future investments, γ will generally be a function of the number of host eggs and the current player investments. For example, if the patch increases in defendability as current investments increase, then γ may take the form $\gamma(x, y) = (1 - \exp(-(E - x - y)))$.

Another more fundamental reason that fighting is an ESS at low investments is the assumption that both players have perfect information, both of the patch size, defendability and the opponent investment. With perfect information, there is no "risk" in making the wrong decision, as a player can exactly specify the costs and benefits of winning residency at any current level of self or opponent investment. If there is uncertainty about an opponent's investment then the best strategy may be to secure as many current investments as possible to guarantee certainty of having the larger investment.

2.3 Imperfect Knowledge of Opponent's Investment

As players adopt a "local" search strategy (see Section 2.1), small inter-arrival times will make information of the opponent's investment inexact. Information about the relative investment of each player may be obtained through extended agonistic competition to win residency (Field and Calbert,[20]). In this section, models of patch competition to achieve residency status are studied, with two models of contest resolution being proposed.

Suppose, as before, that two players compete for the patch. At the time of fighting player one has investment x, player two investment y. Each player is aware of it's own self investment, and a distribution of possible investments of the opponent.

Games in which players are aware of their self-investment and the distribution of an opponent's investment have been studied in the evolutionary game-theoretic context. Using the games of timing approach, variation between players fighting rewards had the effect of altering the set of possible persistance times each player would adopt (Bishop, Cannings and Maynard Smith,[4]). Those players with a higher reward for winning where predicted to persist the longest, and in the limit of continuous variation in fighting reward, the ESS is chosen to be a persistance time pure strategy increasing for increasing rewards for winning the contest (Bishop, Cannings and Maynard Smith,[4]).

An extension of this model comes from contests with continuous variation in the energy reserves of each player (Mesterson-Gibbons, Marden and Dugatkin,[64]). It was shown that the ESS persistance strategy for a player with energy reserve Z, at each time t is of the form

$$\begin{cases} \text{Persist} & \text{if} \quad t < uZ, \\ \text{Retreat} & \text{if} \quad t \geq uZ \end{cases} \tag{2.3.1}$$

Here, u is a scaling factor depending on the population distribution of energy reserves, the fitness gains in winning the fight and the unit time costs in fighting. As the persistance time of each player depends linearly on self-investment, the scaling factor u converts the fitness based currency Z to a temporal based attrition currency uZ.

Further extensions of this work exist, in finding equilibrium concession functions which map an individuals valuation of a resource, v, onto a time of concession, $T(v)$, where T is a monotonically increasing function of the resource value v (Nalebuff and Riley,[65]).

As a simplification, we assume both for the continuous risks and graduated risks models, that this time of concession is linearly dependent on the current patch investment. The scaling factor, $u(\alpha, \beta, \gamma)$, will depend on the fraction of self/opponent investments kept if residency is achieved, and the future returns, determined by the function γ. Analogous work on the war of attrition with a distribution of energy reserves (Mesterson-Gibbons,[63]), here the scaling factor u converts the *current investment number* into a fitness based temporal currency.

There is a fundamental difference in the structure of the opponent's investment distribution, in comparison to wars of attrition with random rewards. Models of fighting with variation in energy reserves assume that the energy distributions of each player, before competition, are independent (Mesterson-Gibbons,[63]). With patch investment models of competition, as there is a finite fitness value for the patch, investments of both players must be conditioned to be less than or equal to the patch fitness value. Thus players are assumed to be aware of the opponent's possible investment distribution, conditioned on the patch not being fully parasitised.

Therefore, the conditioned investment density of player one, for example, takes the form $\Pr(X = x|X + Y \leq E, X \geq 0, Y \geq 0)$, inducing dependency between players investments. Explicitly representing the conditioned density, let

$$U(E) = \{(x, y)|x + y \leq E, x \geq 0, y \geq 0\},$$

this set being the investment space of players one and two. By defining the indicator function

$$I_{U(E)}(x, y) = \begin{cases} 1 & \text{if} \quad (x, y) \in U(E), \\ 0 & \quad\;\; \text{otherwise,} \end{cases}$$

then

$$\begin{aligned} \Pr(X = x|U(E)) &= \frac{\Pr(\{X = x\} \cap U(E))}{\Pr(U(E))} \\ &= \frac{\Pr(X = x) I_{U(E)}(x, y)}{\Pr(U(E))}. \end{aligned}$$

In order to apply the optimisation techniques efforded in Calculus, investments are modelled with the currency of fitness acquired from the patch, rather than the discrete currency, number of ovipositions. Any such fitness distribution must be positive valued and one such candidate is the Gamma distribution, with density

$$p(x) = \frac{b^{-a} x^{a-1} \exp(-x/b)}{\Gamma(a),}$$

which has expectation $E(X) = ab$ and variance $\text{var}(X) = ab^2$. The gamma function is defined to be $\Gamma(z) = \int_0^\infty t^{z-1} e^{-t} dt$. Other postive valued densities, such as the Weibull or Lognormal densities may be considered, but we will focus on the Gamma density for the remainder of this chapter.

2.3.1 A Continuous Risks Model

In this model both players will incur a non-fatal injuries as they fight for patch possession and the last player to desist is the winner of the contest, attaining residency. In order to incorporate in effects of injury when fighting, the following model is assumed.

Suppose two players compete for patch residency, player one having investment x and player two investment y. A simple model of continuous accrual of injuries will assume that the value of the resource after fighting will decrease as the time of fighting increases. Thus, if $V(t)$ is the resource value at time t, then it is assumed that

$$V(t) \longrightarrow 0 \text{ as } t \longrightarrow \infty.$$

If $R(x, y)$ is player one's residency fitness value, then after t minutes of competition, it is assumed that the residency fitness value will be $\lambda^t R(x, y)$, where $\lambda \in [0, 1)$ determines the decay of resource value from fighting. Suppose that t_1 and t_2 are the respective persistance times in fighting for residency. The expected payoff to player one will have the form

$$E(t_1, t_2) = \begin{cases} \lambda^{t_1} I(x, y) & \text{if} \quad t_1 < t_2, \\ \lambda^{t_2} R(x, y) & \text{if} \quad t_1 > t_2. \end{cases}$$

As $\lambda \longrightarrow 0$ extended fights become increasingly costly. The loser in this game is not the first player to be injured, but the first player to give up, as both players may incur injuries during the fight. A modification of this model, in which the first player to be injured is the loser of the fight is constructed in the next section.

Other more general models of continuous accrual of injuries could be included. For example, let the fitness value of the resident, after j injuries be $f(j)R(x, y)$, where $f(j)$ is a monotonically decreasing function of j, such that $f(j) \in [0, 1)$. The expected fitness of a resident, who's opponent fought for time t would then be

$$\sum_{j=0}^{\infty} \Pr(\text{ j injuries after time t}) f(j) R(x, y).$$

However, inclusion of more complicated fitness models will make the equations increasingly parameter rich. The simple model captures the essential feature of continuous risks in that resource value decreases as time spent fighting increases.

Before continuing to find an evolutionary stable persistance times the assumptions behind the continuous risk model are recapped.

- Two players compete for current residency of a patch, player one having investment x in the patch and player two investment y.
- The loser is the first player to give up in fighting.
- Each player's self-investment is known, but only the distribution of the opponent's investment is known. This opponent investment distribution is conditioned on the sum of investments being less than the total fitness value of the patch E. Thus player one knows the distribution $\Pr(Y < y|U(E))$. To keep the mathematical expressions as simple as possible, let the conditioned distribution $P(Y < y|U(E)) = P(y|E)$, with the conditioned density $p(y|U(E)) = p(y|E)$.
- The actual fitness value of the patch is not known to either player, though a total patch fitness density $p(E)$ is known and is assumed to be Gamma distributed, with some mean μ_E and variance σ_E^2.
- Each player chooses a persistance time in proportion to it's current investment. Hence player one chooses persistance time xu_1 and player two chooses persistance time yu_2 with u_1, u_2 representing the scaling factors of player one and two respectively. Player one will win residency if $xu_1 > yu_2$ otherwise it will loose residency. [1]

With these assumptions, the expected fitness of player one using scaling factor u_1 competing against player two using scaling factor u_2 is constructed and denoted by

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[1] As we are considering continuous representations of fitness, the probability that $xu_1 = yu_2$ is precisely zero.

$E(u_1, u_2)$.

First, let S be the set of patch investments of player one and player two such that player one wins current residency and let S' be the set of patch investments of each player such that player one loses.

Recalling the definition of $U(E) = \{(x,y)|x+y \leq E \text{ and } x \geq 0, y \geq 0\}$, and noting that player one will win residency if $xu_1 > yu_2$, then let

$$W = \{(x,y)|x > y\frac{u_2}{u_1}\}.$$

Thus $S = U(E) \cap W$ and $S' = U(E) \cap W^c$. With this the expected fitness of player one, adopting scaling factor u_1, against player two adopting scaling factor u_2 is

$$\begin{aligned} E(u_1, u_2) &= \int_{E=0}^{\infty} \int\int_{S'} \lambda^{xu_1} I(x,y) p(y|E) p(x|E) p(E) dy dx dE \\ &+ \int_{E=0}^{\infty} \int\int_{S} \lambda^{yu_2} R(x,y) p(x|E) p(y|E) p(E) dx dy dE. \end{aligned}$$

The evolutionary stable scaling factor u^* is calculated according to the definition of an ESS, namely that

$$E(u^*, u^*) > E(u, u^*),$$

or, if $E(u^*, u^*) = E(u, u^*)$, then

$$E(u^*, u) > E(u, u).$$

An ESS scaling factor u^* will satisfy $\frac{\partial}{\partial u_1} E(u_1, u_2)_{u_1=u_2=u^*} = 0$ and $\frac{\partial^2}{\partial u_1^2} E(u_1, u_2) \leq 0$ (Mesterson-Gibbons, [63])

In order to differentiate this expectation, Leibniz' Rule, as stated below, is needed,

$$\frac{\partial}{\partial z} \int_0^{f(z)} g(x,z) dx = \int_0^{f(z)} \frac{\partial}{\partial z} g(x,z) dx + g(f(z), z) \frac{\partial f}{\partial z}(z).$$

After differentiation (see the Appendix, Section 2.5) the ESS must be found by finding the fixed point of the equation

$$u = \mathcal{F}_{cr}(u),$$

where $\mathcal{F}_{cr}(u)$ has the following form

$$\mathcal{F}_{cr}(u) = -\frac{\mathcal{A}(u)}{\mathcal{B}(u)},$$

with

$$\mathcal{A}(u) = \int_{E=0}^{\infty}\int_{x=0}^{\frac{E}{2}} \lambda^{xu}(R(x,x) - I(x,x))xp(x|x \leq \frac{E}{2})^2 p(E)dxdE$$

and

$$\mathcal{B}(u) = \int_{E=0}^{\infty}\int_{x=0}^{\frac{E}{2}}\int_{y=x}^{E-x} x\ln(\lambda)\lambda^{xu}I(x,y)p(y|E)p(x|E)p(E)dydxdE.$$

The function $\mathcal{F}_{cr}(u)$ is evaluated using numerical integration. Starting from a random initial point u_0, a sequence is generated using the recurrence relation $u_{n+1} = \mathcal{F}_{cr}(u)$. Calculation of this sequence is halted when $||u_n - u_{n+1}|| \leq \epsilon$, for ϵ a small positive constant.

Observations from sensitivity analysis over the cost of fighting λ, and the expected future returns are in accord with biological intuition. As extended fights increase in cost, players will persist less in proportion to their investments, so as $\lambda \to 0, u \to 0$. As $\lambda \to 1$, costs of attrition decrease thus the scaling factor $u \longrightarrow \infty$ as seen in Figure 2.3.5.

On observation of the following Figure 2.3.6, changes in expected future returns, $\gamma(r)$, seem to have less of an effect, if compared to costs in fighting. As persistance is assumed to be proportional to current investment, the scaling factor will increase for smaller investments, if the proportion of remaining resources given to the resident increases to one. Observation of Figure 2.3.6 shows an approximately linear increase in ESS scaling factor u^* when $\gamma(r) \longrightarrow 1$ as $r \longrightarrow 1$. Decreased relative importance of future investments, if compared to the costs of fighting, may be due to the central assumption of persistance in proportion to the current investment. An optimal persistance time, in proportion to some combination of current and expected future returns is a subject of future research.

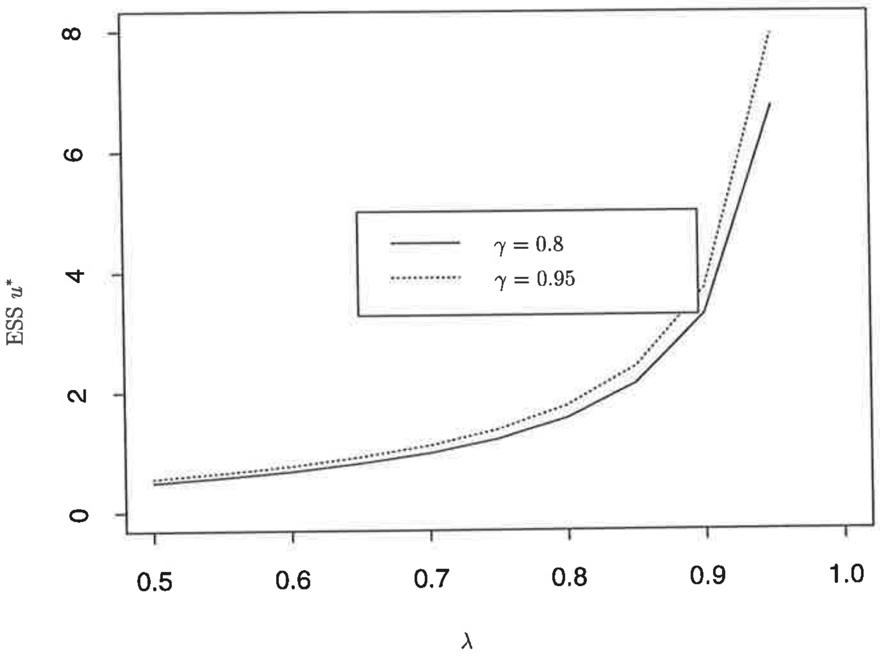

Figure 2.3.5: ESS scaling factor u^* for the continuous risks model, with $\gamma = 0.8, 0.95$. The cost in fighting λ ranges from 0.5(high risk) to 0.95(moderate risk). The other parameters used in this model were $E = 10, \alpha = 3/4, \beta = 1/4$.

2.3.2 A Graduated Risks Model

In this section, a different mechanism of contest resolution is modelled. Previously there was some probability of being injured during the contest for the patch. An injury decreased the expected fitness return to a player, though it did not stop attrition in the contest and thus there was no inherent possibility of a chance win of one of the contestants. Other fighting models such as the sequential assessment games of Enquist and Leimar include the possibility of an accidental victory (Enquist and Leimar, [16]).

For the graduated risks model, players choose some level of escalation, the win-

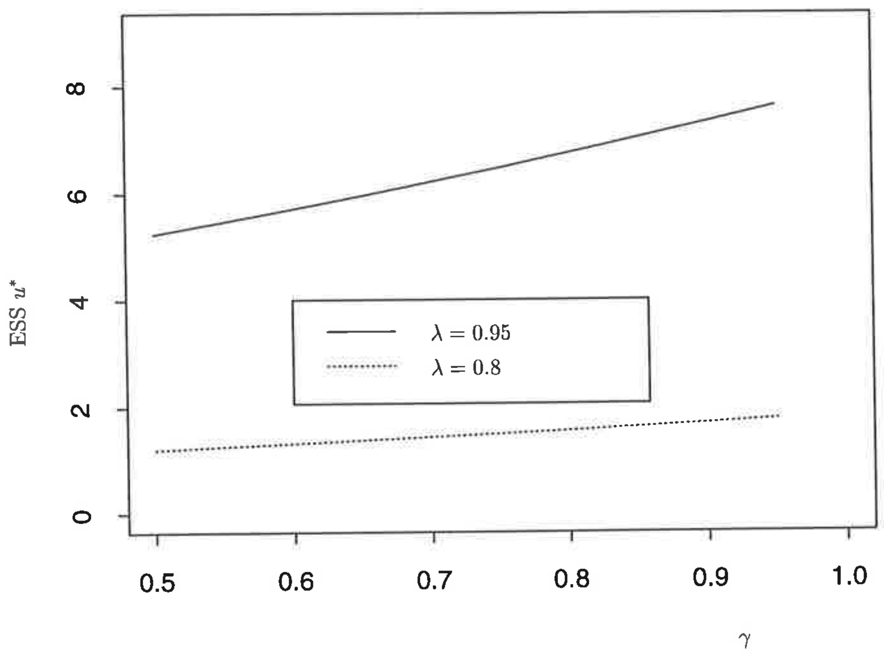

Figure 2.3.6: ESS scaling factor u^* for the continuous risks model. Sensitivity analysis for $\lambda = 0.95$ and $\lambda = 0.8$, as the remaining fraction of patch payoff given to the resident γ ranges from 0.5 to 0.95.

ner of the game being the player that persists the longest or the player to escape being injured during the contest. Thus, there is a possibility that the player with the longest persistance time is injured during the contest, giving the opponent residency.

Let us hightlight the differences in contest resolution mechanisms of the continuous risks and graduated risks models. In the continuous risks model, there is *a continuous decrease* in fitness as the contest progresses. The level of this fitness decrease is measured by the parameter λ. Within the graduated risk model the winner of the game is either the player that escapes injury or the player that chooses the highest escalation level, thus there is no *temporal decrement* in the winners fitness gain for the graduated risks model.

The level of escalation is defined here to be the probability that no player will be injured in the contest (Maynard Smith and Parker,[55]). If it is assured that a player will be seriously injured, then the escalation level is maximal. Thus

$$a = \Pr(\text{no player is injured}).$$

During the contest, the probability that one of the players will be injured, at a cost C, is simply $(1-a)$. Thus, assuming that before residency is decided, both players have equal probabilities of injuring the conspecific, then

$$\begin{aligned}(1-a)/2 &= \Pr(\text{player one is injured }) \\ &= \Pr(\text{player two is injured }).\end{aligned}$$

Thus $(1-a)$, the probability of injury is the associated cost in entering the contest.

An ESS escalation level is assumed to be proportional to the risk associated with entering the contest, that is, the probability of injury. Suppose player one chooses a risk level, or probability of injury $(1-a_1)$ that it is willing to escalate up to. Here, the scaling factor, now denoted by υ, scales the current investment to the probability of injury. Thus, if player one has investment x, then the scaling factor υ_1 will satisfy

$$x\upsilon_1 = (1-a_1).$$

If no injuries occur during competition, the winner is the player willing to escalate to the highest risk level, thus the expected reward to player one, with persistance rule $x\upsilon_1$, against player two with persistance rule $y\upsilon_2$ is

$$E(x,y) = \begin{cases} H(x,y)x\upsilon_1 + I(x,y)(1-x\upsilon_1) & \text{if} \quad x\upsilon_1 \le y\upsilon_2, \\ H(x,y)y\upsilon_2 + R(x,y)(1-y\upsilon_2) & \text{if} \quad x\upsilon_1 > y\upsilon_2. \end{cases}$$

where $H(x,y) = \big(R(x,y) + I(x,y) - C\big)/2$ is the expected gain to each player, if an injury occurs. As the persistance rule is a probability, both $x\upsilon_1 \le 1$ and $y\upsilon_y \le 1$, hence

$$0 \le \upsilon_1, \upsilon_2 \le \frac{1}{E},$$

and also, the patch size must be fixed to fitness value E.

As in the previous model, let S be the set of each player's patch investment such that player one has the highest persistance rule, and S' is the set of patch investments where player two has the highest persistance rule. Integration over the investment distributions of player one and player two determines the fitness of player one adopting scaling factor v_1 against player two adopting scaling factor v_2 with density of investments $p(x|E), p(y|E)$,

$$\begin{aligned} E(v_1, v_2) &= \int_S \int \Big(R(x,y)(1-yv_2) + H(x,y)yv_2\Big)p(x|E)p(y|E)dxdy \\ &+ \int_{S'} \int \Big(I(x,y)(1-xv_1) + H(x,y)xv_1\Big)p(y|E)p(x|E)dydx. \end{aligned}$$

As with the continuous risk model, the ESS scaling factor v^* is found by solving for the fixed point of the equation

$$v = \mathcal{F}_{gr}(v)$$

with

$$\mathcal{F}_{gr}(v) = -\frac{\mathcal{C}(v)}{\mathcal{D}(v)}$$

where

$$\mathcal{C}(v) = \int_{x=0}^{E/2} (R(x,x) - I(x,x))(1-xv)p(x|x \leq E/2)^2 x dx$$

and

$$\mathcal{D}(v) = \int_{x=0}^{E/2} \int_{y=x}^{E-x} \frac{(R(x,y) - I(x,y) - C)}{2} p(y|E)p(x|E)dydx.$$

This fixed point expression is proved in the appendix. Again integration of the function $\mathcal{F}_{gr}(v)$ is done numerically. By choosing a random initial scaling factor v_0 and applying the recurrance relation $v_{n+1} = \mathcal{F}_{gr}(v_n)$, we generate the sequence $v_n, n = 1, 2, \cdots$. Calculation of the sequence is stopped when $||v_n - v_{n-1}|| < \epsilon$ where ϵ is some small positive constant.

The results from iterating the fixed point expression, for the graduated risks model are markedly different to that of the continuous risks model. For this model,

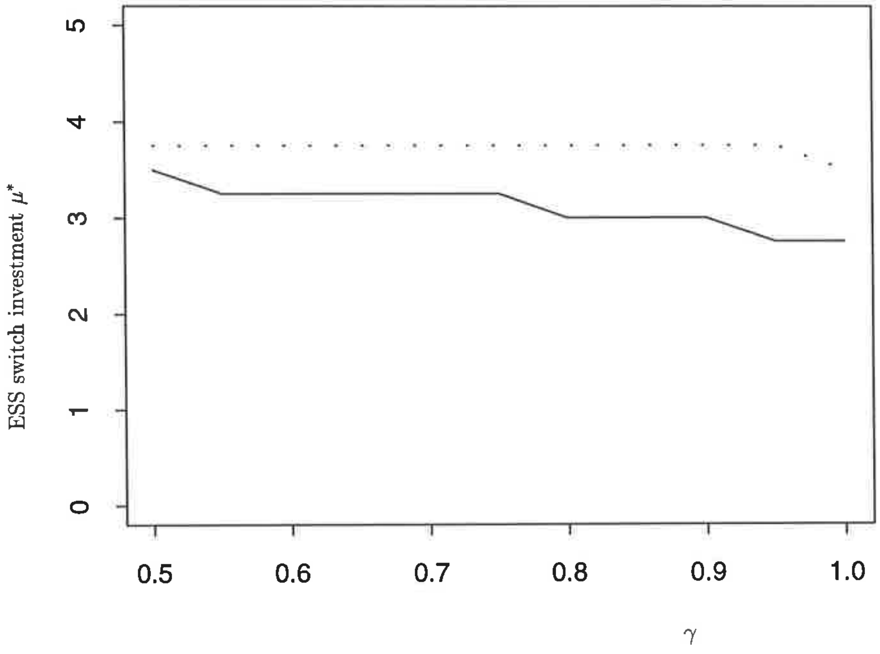

Figure 2.3.7: ESS investments where players switch from no aggression, $v = 0$, to full aggression $v = 1/E$, for the graduated risks model with patch fitness value $E = 10$. The full line is for $C = 10$ and the dashed line for $C = 20$. The ESS scaling factor is determined for the expected fraction of remaining eggs given to the resident $\gamma \in [0.5, 1.0]$.

a transition occurs, from no conflict, $v = 0$, to that of escalation to , $v = \frac{1}{E}$, depending on the expected investment of the opponent, μ, the cost of injury C and the relative returns of a resident over an intruder. The ESS thus takes the form, for self-investment x and expected opponent investment μ,

$$E(t_1, t_2) = \begin{cases} 0 & \text{if} \quad \mu < \mu^*, \\ x/E & \text{if} \quad \mu > \mu^*. \end{cases}$$

where μ^* is the threshold patch investment instigating the switch to aggression. Thus, prior to a critical investment threshold, players are predicted not to fight. If only one player is past this threshold investment, the opponent will not escalate, backing off from conflict. With both players past this threshold investment level and fight will occur with both players escalating till an injury occurs.

Viewing the sensitivity over $\gamma(r)$, the threshold investment over which players switch to high aggression decreases for increasingly guardable future investments. The evolutionary logic of this strategy is clear, since if players risk injury then fighting should occur when potential losses from injury are compensated for by maximal returns from winning residency.

If losing an agonistic bout implies a high cost, then the graduated risks model

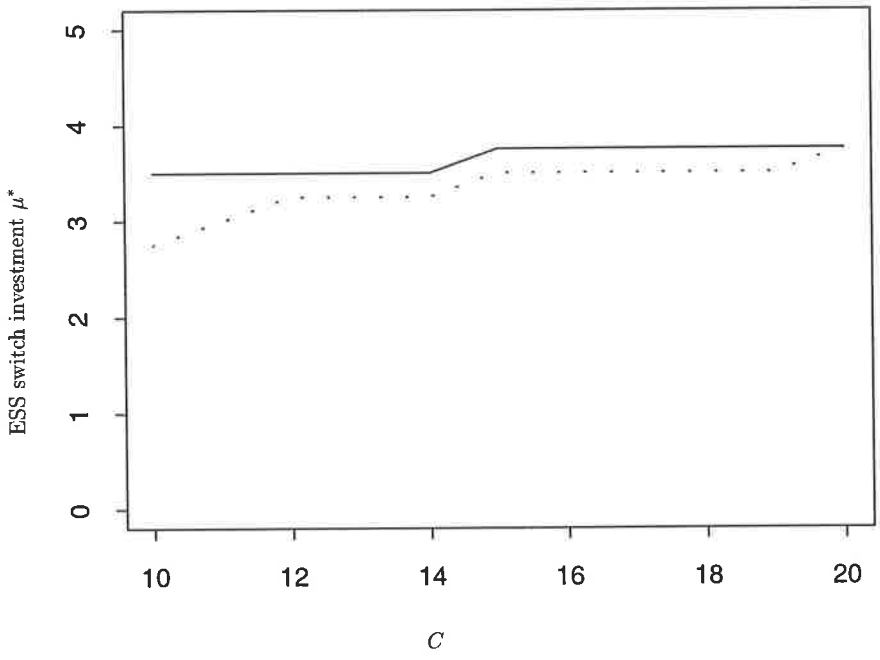

Figure 2.3.8: Sensitivity over costs for ESS investments where players switch from no aggression, $\upsilon = 0$, to full aggression $\upsilon = 1/E$, in the graduated risks model, with patch fitness value $E = 10$. The full line is for $\gamma = 0.5$ and the dashed line for $\gamma = 0.95$. Costs range from 10 to 20.

predicts a later switch to aggression. Here, the strategy is to delay aggression as long as possible, adopting the "safe" foraging option till the benefits gained from past investments equal the risks and costs of fighting.

Fighting, with imperfect information will occur only when *both* players have parasitised a sufficiently large proportion of the patch. This is in contrast to the results of the perfect information analysis (Section 2.2), in which fighting occurs at the start of patch parasitism. With perfect information, about self and opponent investments, winning residency guarantees large payoffs. If there is uncertainty about the number of opponent ovipositions, gaining residency over a patch may not be advantageous enough, thus it is more profitable to fight only when the patch approaches full parasitisation. In a very strong sense, assumptions of information exchange between opponents determine the structure of the ESS as patch parasitism proceeds.

The strategy of switching from tolerance to conflict, within a resource limited patch is analogous to similar ESS results for switching from parasitism to superparasitism in time limited parasitoids (Visser,[80]). In these models, two or more searching females initially accept only unparasitised hosts, but switch to superparasitism at a certain threshold encounter rate with unparasitised hosts (Visser,[80, 79]). Similarily, as the number of unparasitised hosts decreases, female *T. basalis* are predicted to switch from a risk-averse to a risk-prone strategy of competing for the patch.

2.4 Conclusion

One of the principal observations from outcomes in pairwise contests was the player who last "won" a bout for residency seemed to win all of the contests thereafter, and the player that initially arrived on the patch won residency most of the time (Field and Calbert, [20]). Both of these observations can be explained by the simple rule of attrition in proportion to your investment. If investments are correlated with the time on the patch, on average, the early arriver will have the largest investment, thus will secure the patch because of longer attrition. Similarily, if a player has larger investment upon agonistic competition, it will have a higher probability of having a larger investment at the time of the next bout. The experimental observations of contest resolutions motivated this principal assumption of the chapter (Field and Calbert,[20]).

Though the models considered in this chapter assume a single fight for patch possession, in fact, many such competitions may occur, again depending on the skewness of the relative investments. New models of patch residency competition may take into account multiple fights, if one considers updating the distributions of investments to take into account information obtained by the previous contest outcomes. For example, given the information states $\mathcal{W}$ = "Won the last fight" and $\mathcal{L}$ = "Lost the last fight", the new distribution of investments may be updated to take into account this information. Thus, prior to a fight, the distribution of your opponent's investment was $\Pr(x|E)$ and now will be $\Pr(x|E, \mathcal{W})$, if you won previously.

Having considered one possible extension of these fighting models, some of the difficulties associated with construction of the models of patch competition are discussed. Consider the assumptions behind both war of attrition and sequential assessment approaches to contest resolution. Both approaches assume either a static reward V or some distribution of rewards that does not change over the course of the contest (Enquist and Leimar,[16],Bishop and Cannings,[4]). Furthermore, the contest resolution mechanisms are relatively simple, winners being either the player to persist the longest, the player persisting longest or avoiding injury, or the player crossing the line in "causal factor space" as in the sequential assessment game (Leimar and Enquist,[44]). Similarily, the cost structure in fighting is known in these games.

Observations of *T. basalis* do not indicate which approach, attrition or sequential assessment is more appropriate in modelling contests. Similar questions, regarding the mechanisms of contest resolution have been addressed for competition with the

Cichlidae species *Nannacara anomala* (Enquist and Jakobsson,[15]). To illustrate the complexity of possible contest resolution mechanisms, fights may be decided not only by combinations of current investment and potential future investments, but also the spatial status of opposing players, as the contest progresses. An attack from one player, from behind the opponent, may generate an intrinsic advantage that outweights current state variables such as the forementioned current and future investments (Field, personal observation). Furthermore, a player fighting closer to the patch "edge" when compared to the opponent may have an intrinsic disadvantage, since it could be easily "pushed" off the edge. Advantages due to the spatial configurations of the opponent have been observed when an intruder attempts to return from the patch periphery to parasitise, only to be "pushed" to the periphery again by the resident (personal observation).

Coupled with the difficulties in finding the correct contest resolution mechanism are the problems in assessing the fitness value of the patch, given particular patch investments during the fighting phase, as other stages of patch competition, such as intruder returns to "steal" ovipositions and the final return of the intruder (see the following three Chapters) make the map from current investment to total patch fitness return unclear. The question of how fitness returns are correlated with investments is at the very least, difficult to answer. As mentioned in Section 2.1, payoff from superparasitism varies over time, thus patch fitness will depend not only on the number of eggs parasitised/superparasitised but also the order and time interval with which these events take place (Godfray,[26], Field, [19]). Host patches vary not only in size, but also in the quality of individual eggs that make up the patch. As a general rule, eggs near the periphery are of lower quality than eggs in the interior (Hood,[35]). Thus the spatial configuration of ovipositions will also have an effect on fitness outcomes. These problems may be addressed with extensive simulations, but lacking any empirical data as to overall total fitness outcomes from pairwise competition, a simple model of fitness, comparing investment gains kept by the players if either resident or intruder was deemed the best approach in the present course of research.

Finally this discussion will focus on the assumption of *pairwise* competition between players. Though competition between opponents in the laboratory was pairwise, in the field, up to as many as sixteen conspecifics have been recorded, fighting for a single patch, though the mean number, recorded over a season was two (Field,[19]). Further work in modelling patch competition must therefore include multiple competitors, with incomplete information as to the opponent's investment. There has been substantial progress in n-person wars of attrition games (Haigh and Cannings,[27], Blackwell,[5]), but of particular note is the work of patch leaving strategies adopted by multiple foragers on a patch (Sjerps and Haccou,[76]). The authors calculated a probabilistic patch leaving strategy, according to the degree of conspecific interference, the resource intake rate, and the number of remaining competitors on the patch.

Inclusion of both incomplete information of the opponent's state, resource intake or degree of superparasitism and number of opponents are just some of the assumptions to be incorporated in the n-person war of attrition approach (See Section 6).

In summary, this chapter addressed competition for residency in pairwise patch competition. The complete information scenario was briefly studied. Following this, players where assumed to have incomplete information of the opponent's investment and patch size. With the rule "persist in proportion" to your current investment, ESS scaling factors, relating persistance times or injury levels to current investments were found in the continuous risks and graduated risks games. Players persisted according to costs of injury, relative rewards between resident and intruder, as well as the expected *future* patch returns from securing residency. The continuous risks model predicts a "smooth" rise in agonistic conflict, as the level of parasitism increases. A graduated risks approach predicts a switch from tolerance to aggression, once a players investment rises above some threshold. Additional factors leading to contest resolution, such as spatial configuration of players at the point of competition may be important. Further research directions should focus on n-person wars of attrition with incomplete information.

2.5 Appendix

2.5.1 Proof of continuous risk fixed point equation

Here we prove that the ESS scaling factor u^* is found by solving the fixed point equation $u = \mathcal{F}_{cr}(u)$, where $\mathcal{F}_{cr}(u) = -\mathcal{A}(u)/\mathcal{B}(u)$.

If S is the set of patch investments such that player one wins competition then

$$S = \{(x,y)|0 \leq y \leq \Big(\frac{E}{\frac{u_2}{u_1}+1}\Big), \frac{u_2}{u_1}y \leq x \leq E - y\}$$

and the region where player one loses competition

$$S' = \{(x,y)|0 \leq x \leq \Big(E - \frac{E}{\frac{u_2}{u_1}+1}\Big), \frac{u_1}{u_2}x \leq y \leq E - x\}.$$

The union of these two sets $S \cup S' = U(E)$.

With the structure of the sets S and S' and the notation

$$X = \Big(E - \frac{E}{\frac{u_2}{u_1}+1}\Big), Y = \Big(\frac{E}{\frac{u_2}{u_1}+1}\Big)$$

the expected fitness of player one takes the form

$$\begin{aligned} E(u_1, u_2) &= \int_{E=0}^{\infty}\int_{x=0}^{X}\int_{y=\frac{xu_1}{u_2}}^{E-x} \lambda^{xu_1} I(x,y)p(x|E)p(y|E)p(E)dydxdE \quad (2.5.2) \\ &+ \int_{E=0}^{\infty}\int_{y=0}^{Y}\int_{x=\frac{u_1}{u_2}y}^{E-y} \lambda^{yu_2} R(x,y)p(x|E)p(y|E)p(E)dxdydE. \quad (2.5.3) \end{aligned}$$

Due to the complexity of the differentiation, the two integrals are treated separately. Differentiating the first integral

$$\begin{aligned} &\frac{\partial}{\partial u_1}\int_{E=0}^{\infty}\int_{x=0}^{X}\int_{y=\frac{xu_1}{u_2}}^{E-x} \lambda^{xu_1} I(x,y)p(y|E)p(x|E)p(E)dydxdE \\ = &\int_{E=0}^{\infty}\int_{x=0}^{X}\frac{\partial}{\partial u_1}\int_{y=\frac{xu_1}{u_2}}^{E-x} \lambda^{xu_1} I(x,y)p(y|E)p(x|E)p(E)dydxdE \\ + &\int_{E=0}^{\infty}\frac{\partial X}{\partial u_1}\int_{y=\frac{Xu_1}{u_2}}^{E-X} \lambda^{Xu_x} I(X,y)p(X|E)p(y|E)p(E)dydE. \end{aligned}$$

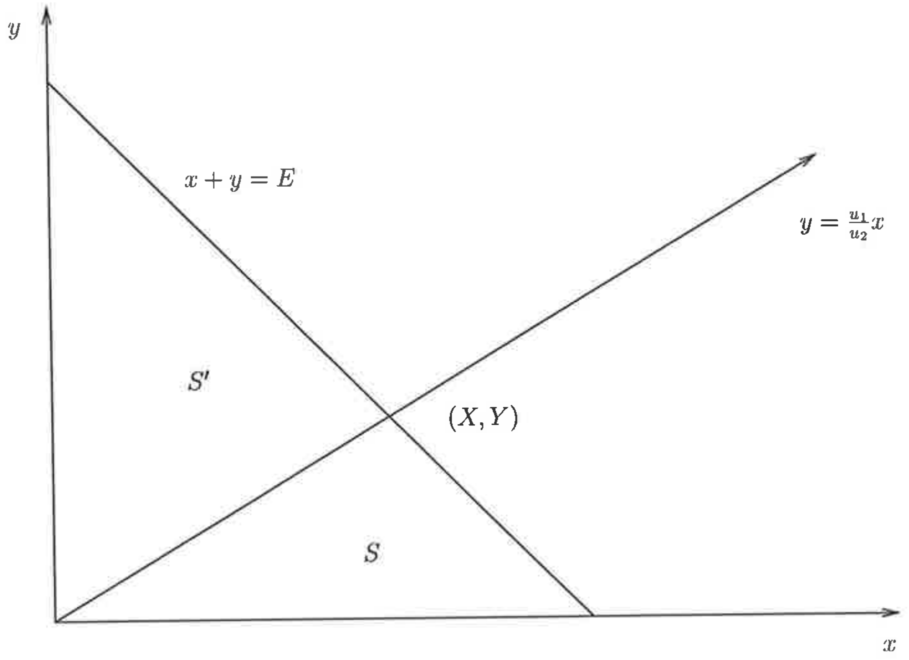

Figure 2.5.9: Region of integration in player one,two patch investments x and y. Set S is the region where player one persists longest and the set S' is the region where player two persists longest.

Leibniz rule must once again be applied to the inner expression

$$\begin{aligned}
&\int_{E=0}^{\infty}\int_{x=0}^{X}\frac{\partial}{\partial u_x}\int_{y=\frac{xu_1}{u_2}}^{E-x}\lambda^{xu_1}I(x,y)p(y|E)p(x|E)p(E)dydxdE\\
=&\int_{E=0}^{\infty}\int_{x=0}^{X}\int_{y=\frac{xu_1}{u_2}}^{E-x}\ln(\lambda^{x})\lambda^{xu_1}I(x,y)p(y|E)p(x|E)p(E)dydxdE\\
-&\int_{E=0}^{\infty}\int_{x=0}^{X}\lambda^{xu_1}I(x,\frac{xu_1}{u_2})p(\frac{xu_1}{u_2}|E)p(x|E)p(E)\frac{\partial}{\partial u_1}(\frac{xu_1}{u_2})dxdE.
\end{aligned}$$

In deriving this expression, the derivative $\frac{\partial}{\partial u_1}\lambda^{xu_2}=\ln(\lambda^{x})\lambda^{xu_1}$, was used.

Now to the differentiation of the second expression

$$\int_{E=0}^{\infty}\int_{y=0}^{Y}\int_{x=\frac{yu_2}{u_1}}^{E-x}\lambda^{yu_2}R(x,y)p(x|E)p(y|E)p(E)dxdydE$$

with application of Leibniz rule, the partial derivative with respect to u_1 is

$$\int_{E=0}^{\infty}\int_{y=0}^{Y}\frac{\partial}{\partial u_1}\int_{x=\frac{yu_2}{u_1}}^{E-y}\lambda^{yu_2}R(x,y)p(x|E)p(y|E)p(E)dxdydE$$

$$+ \int_{E=0}^{\infty} \frac{\partial Y}{\partial u_1} \int_{x=\frac{Yu_2}{u_1}}^{E-Y} \lambda^{Yu_y} R(x,Y)p(Y|E)p(x|E)p(E)dxdE.$$

Evaluating the inner partial derivative

$$\begin{aligned}
&\int_{E=0}^{\infty} \int_{y=0}^{Y} \frac{\partial}{\partial u_1} \int_{x=\frac{yu_2}{u_1}}^{E-y} \lambda^{yu_2} R(x,y)p(x|E)p(y|E)p(E)dxdydE \\
= & -\int_{E=0}^{\infty} \int_{y=0}^{Y} \lambda^{yu_2} R(\frac{yu_2}{u_1}, y)p(y|E)p(\frac{yu_2}{u_1}|E)p(E)\frac{\partial}{\partial u_1}(\frac{yu_2}{u_1})dydE \\
= & \int_{E=0}^{\infty} \int_{y=0}^{Y} \lambda^{yu_2} R(\frac{yu_2}{u_1}, y)p(y|E)p(\frac{yu_2}{u_1}|E)p(E)\frac{yu_2}{u_1^2}dydE.
\end{aligned}$$

Hence the total derivative of the second integral is

$$\begin{aligned}
&\int_{E=0}^{\infty} \int_{y=0}^{Y} \lambda^{yu_2} R(\frac{yu_2}{u_2}, y)p(y|E)p(\frac{yu_2}{u_1}|E)\frac{yu_2}{u_1^2}dydP(E) \\
+ & \int_{E=0}^{\infty} \frac{\partial Y}{\partial u_1} \int_{x=\frac{Yu_2}{u_1}}^{E-Y} \lambda^{Yu_y} R(x,Y)p(Y|E)p(x|E)p(E)dxdE.
\end{aligned}$$

At the ESS $u_1 = u_2 = u$, thus

$$(X,Y) = (E/2, E/2).$$

Thus upon substitution of u, integrals with the limits

$$\begin{aligned}
y &= \frac{u_1}{u_2}X, E - X, \\
x &= \frac{u_2}{u_1}Y, E - Y
\end{aligned}$$

will vanish. Upon substitution of $u_1 = u_2 = u$, the density product

$$\begin{aligned}
p(y|E)p(\frac{yu_2}{u_1}|E) &= p(y|\frac{u_2}{u_1}y + y \leq E)p(\frac{yu_2}{u_1}|\frac{yu_2}{u_1} + y \leq E) \\
&= p(y|2y \leq E)^2 \\
&= p(y|y \leq E/2)^2.
\end{aligned}$$

Thus the substitution $u_1 = u_2 = u$ leaves the following expression for the derivative of the $E(u_1, u_2)$

$$\begin{aligned}
&\frac{1}{u}\int_{E=0}^{\infty} \int_{y=0}^{E/2} \lambda^{yu} yR(y,y)p(y|y \leq E/2)^2 p(E)dydE \\
- & \frac{1}{u}\int_{E=0}^{\infty} \int_{x=0}^{E/2} \lambda^{xu} xI(x,x)p(x|x \leq E/2)^2 p(E)dxdE \\
+ & \int_{E=0}^{\infty} \int_{x=0}^{E/2} \int_{y=x}^{E-x} \ln(\lambda^{x})\lambda^{xu} I(x,y)p(y|E)p(x|E)p(E)dydxdE = 0.
\end{aligned}$$

To simplify this expression, let $y = x$ in the first integral, leaving

$$\begin{aligned} &\frac{1}{u}\int_{E=0}^{\infty}\int_{x=0}^{E/2} \lambda^{xu}x\Big(R(x,x) - I(x,x)\Big)p(x|x \leq E/2)^2 p(E)dxdE \\ + &\int_{E=0}^{\infty}\int_{x=0}^{E/2}\int_{y=x}^{E-x} \ln(\lambda^x)\lambda^{xu}I(x,y)p(y|E)p(x|E)p(E)dydxdE = 0 \end{aligned}$$

this expression being

$$\frac{\mathcal{A}(u)}{u} + \mathcal{B}(u) = 0,$$

which is solved to yield the equation $u = \mathcal{F}_{cr}(u)$.

2.5.2 Proof of graduated risks fixed point equation

Here, the proof that the ESS scaling factor υ^* is found by finding the fixed point to the equation $\upsilon = \mathcal{F}_{gr}(\upsilon)$, where $\mathcal{F}_{gr}(\upsilon) = -\mathcal{C}(\upsilon)/\mathcal{D}(\upsilon)$ is completed. As with the continuous risks model, the region of investments where player one chooses the highest risk is denoted by the set S. Player two chooses the highest risk of injury within the set $S' = U(E)/S$. Integration proceeds in exactly the same manner as the continuous risks model, implying that the expected fitness of player one against player two is

$$\begin{aligned} E(\upsilon_1, \upsilon_2) &= \int_{y=0}^{Y}\int_{x=\frac{y\upsilon_2}{\upsilon_1}}^{E-y} \Big(R(x,y)(1 - y\upsilon_2) + H(x,y)y\upsilon_2\Big)p(x|E)p(y|E)dxdy \\ &+ \int_{x=0}^{X}\int_{y=\frac{x\upsilon_1}{\upsilon_2}}^{E-x} \Big(I(x,y)(1 - x\upsilon_1) + H(x,y)x\upsilon_1\Big)p(y|E)p(x|E)dydx. \end{aligned}$$

and the ESS scaling factor found by differentiating with respect to υ_1 and solving at zero, $\frac{\partial E(\upsilon_1,\upsilon_2)}{\partial \upsilon_1} = 0$.

Differentiating the first integral, the application of Leibniz rule gives

$$\begin{aligned} &\frac{\partial}{\partial \upsilon_1}\int_{y=0}^{Y}\int_{x=\frac{y\upsilon_2}{\upsilon_1}}^{E-y} \Big(R(x,y)(1 - y\upsilon_2) + H(x,y)y\upsilon_2\Big)p(x|E)p(y|E)dxdy \\ = &\int_{y=0}^{Y}\frac{\partial}{\partial \upsilon_1}\int_{x=\frac{y\upsilon_2}{\upsilon_1}}^{E-y} \Big(R(x,y)(1 - y\upsilon_2) + H(x,y)y\upsilon_2\Big)p(x|E)p(y|E)dxdy \\ + &\frac{\partial Y}{\partial \upsilon_1}\int_{x=\frac{Y\upsilon_2}{\upsilon_1}}^{E-Y} \Big(R(x,Y)(1 - \upsilon_2 Y) + H(x,Y)u_2 Y\Big)p(Y|E)p(x|E)dx. \end{aligned}$$

Applying the derivative within the first integral leaves

$$\int_{y=0}^{Y} \Big(R(\frac{yv_2}{v_1}, y)(1 - yv_2) + H(\frac{yv_2}{v_1}, yv_2)\Big)\frac{\partial}{\partial v_1}\big(\frac{yv_2}{v_1}\big)p(\frac{yv_2}{v_1}|E)p(y|E)dy.$$

Now to the derivative of the second integral,

$$\begin{aligned}
& \frac{\partial}{\partial v_1}\int_{x=0}^{X}\int_{y=\frac{xv_1}{v_2}}^{E-x} \Big(I(x,y)(1-v_1x) + H(x,y)v_1x\Big)p(y|E)p(x|E)dydx \\
= \; & \int_{x=0}^{X}\frac{\partial}{\partial v_1}\int_{y=\frac{xv_1}{v_2}}^{E-x} \Big(I(x,y)(1-xv_1) + H(x,y)xv_1\Big)p(y|E)p(x|E)dydx \\
+ \; & \frac{\partial X}{\partial v_1}\int_{\frac{Xv_1}{v_2}}^{E-X} \Big(I(X,y)(1-xv_1) + H(X,y)Xv_1\Big)p(X|E)p(y|E)dy.
\end{aligned}$$

The inner derivative yields

$$\begin{aligned}
- \; & \int_{x=0}^{X} \Big(I(x,\frac{xv_1}{v_2})(1-xv_1) + H(x,\frac{xv_1}{v_2})xv_1\Big)p(\frac{xv_1}{v_2}|E)\frac{\partial}{\partial v_1}\big(\frac{xv_1}{v_2}\big)p(x|E)dx. \\
+ \; & \int_{x=0}^{X}\int_{y=\frac{xv_1}{v_2}}^{E-x} \Big(-I(x,y)x + H(x,y)x\Big)p(y|E)p(x|E)dydx.
\end{aligned}$$

At the ESS $X = Y = E/2$ and as with the graduated risks model, the integral with the limits $y = \frac{Xv_1}{v_2}, E - X$ will vanish, leaving

$$\begin{aligned}
& \int_{y=0}^{E/2} \Big(R(y,y)(1-yv) + H(y,y)yv\Big)\frac{y}{v}p(y|E/2)^2dy \\
- \; & \int_{x=0}^{E/2} \Big(I(x,x)(1-xv) + H(x,x)xv\Big)\frac{x}{v}p(x|E/2)^2dx \\
+ \; & \int_{x=0}^{E/2}\int_{y=x}^{E-x} \big(\frac{R(x,y) - I(x,y) - C}{2}\big)xp(y|E)p(x|E)dydx.
\end{aligned}$$

By substitution of $y = x$ into the first integral, we have

$$\begin{aligned}
& \frac{1}{v}\int_{x=0}^{E/2} \Big(R(x,x) - I(x,x)\Big)(1-xv)p(x|E/2)^2xdx \\
+ \; & \int_{x=0}^{E/2}\int_{y=x}^{E-x} \frac{\Big(R(x,y) - I(x,y) - C\Big)}{2}xp(y|E)p(x|E)dydx = 0.
\end{aligned}$$

This equation is

$$\frac{\mathcal{C}(v)}{v} + \mathcal{D}(v) = 0.$$

Thus, solving for v, the fixed point equation for the graduated risks model $v = \mathcal{F}_{gr}(v)$ is obtained.

Chapter 3

The Intruder's Patch Return.

Two hypotheses about the information governing intruder returns.

3.1 Introduction

This chapter addresses the second stage of patch competition in which the roles of both players, as resident or intruder have been settled through agonistic conflict. Both players still search for unparasitised eggs and conspecific parasitised eggs (Field,[19]). This stage of conflict marks the transition from residency settlement to the waiting game (Field, Calbert and Keller, [21]).

Patches exhibit varying degrees of defendability, depending on the number of eggs laid in the host clutch and the number of conspecifics competing for host eggs (Cumber,[12], Wagge,[83]). Resident females searching for unparasitised eggs at the periphery leave the remainder of the egg clutch exposed to a searching conspecific. For large clutch sizes this makes the patch only partially defendable. This partial defendability is compounded by the fact that once a resident has discovered a suitable host egg, it must temporarily resign from the current role of defending past investment, to gain present fitness returns (Field,[19]).

Given that the past history of agonistic bouts reveal the resident to be the player with the most at stake in defending the resource, one fundamental question must be addressed: how much time on the patch should the defending resident apportion to pure patch defence and how much time should it apportion to searching the patch for further suitable host eggs? This question can be rephrased as the juxtaposition between defence of past investment versus the accrual of future fitness fitness returns by recommencing host search (Field and Calbert,[20]).

Intruding parasitoids face a different class of problems in maximising any fitness returns from the patch. One factor in deciding just when to return to the patch rests on the observation that any initial fitness gains the intruding female has gained before the onset of agonistic competition may be eroded by a resident superparasitising intruder parasitised hosts. The second problem of the timing of patch return is more fundamental and centres on *information asymmetry* between contestants (Field, Calbert and Keller,[21]).

Subsequent to an intruder being forceably removed from the patch, it will have no knowledge as to the location or the current behaviour of the resident. An intruder that possessed knowledge of the location of the resident could decide at what time to attempt to return to find further hosts. For instance, if the resident was on one side of the patch, the intruder could choose to return on the other side, maximising any chance of being intercepted. Similarly, an intruder that would know the resident was in the act of oviposition, having found a suitable host, could judge when best to return. It is most likely that none of this information is fully available when waiting at the side of the patch, as there is evidence that *T. basalis* females have limited scope in vision (Field,[19], Land,[42]). In the field, *T. basalis* females, searching for a patch are seen to pass near an egg mass. The close location of the patch does not seem to have an effect on the parasitoid as it passes. (personal observation).

In this chapter we consider two hypotheses about the information that the intruder uses to judge when and if it is best to return, in order to find further hosts.

The first hypothesis is constructed by assuming that the lack of information on the behaviour or position of the resident forces an intruder instead to rely on broad characteristics of the resident's behaviour to make optimality decisions. One such characteristic is the resident's current rate of encounter with suitable hosts and the time taken from insertion of the ovipositor to the withdrawal time, otherwise known as the handling or oviposition time (Godfray,[26]). While the resident is ovipositing, it temporarily suspends defending the patch. If the intruder can estimate the rate at which the resident oviposits, then it can ascertain a patch return rate which maximises the chances of arriving on a patch while the resident is itself ovipositing, increasing it's chances of finding a suitable host before being intercepted by the resident. In turn, if the resident can estimate the intruder's return rate, it can decide whether to search for remaining unparasitised hosts or whether to guard. If the resident chooses to guard, by patrolling the boundary of the patch, it increases the chances of intercepting the intruder before it has time to superparasitise (Field,[19]).

The intruder must also decide *whether* to return while the resident is present or to wait for the resident to leave before returning (see Chapters 4 and **??**). This decision must be based on estimates of the probability of success in finding further suitable hosts and the costs associated with resident interception. If the intruder has returned a number of times before, then it's interception cost estimates may be based on the past successes and failures in finding ovipositions before being intercepted and removed by the resident.

The nature of the two types of information exchanged to the intruder, either resident oviposition rates or interception costs, is completely different. If resident oviposition rate information is exchanged, this will determine *when* the intruder should return. If interception cost information is exchanged, this will determine *whether* the intruder will return.

At present, it is not clear as to which information the intruder uses to base it's return decisions. The intruder may use both information about resident oviposition rates and the costs of being intercepted. By evaluation of the merits and failures of both hypotheses, some progress can be made in understanding the adaptive tactics of intruder returns.

Models of intruder return decisions and the adaptive responses of the resident are presented in this chapter. We first consider a model of an optimal intruder return frequency, given that the patch is temporarily undefended while the resident oviposits (Section 3.2). Following an analysis of the optimal return rate as a function of patch defendability, we consider a model in which the resident chooses to defend for some random time, before re-commencing host search (Section 3.2.4). The result of this analysis is the proof that a mixed strategy does not exist and the resident should choose to either guard or host search, depending on the the host encounter rate and the relative costs of opponent superparasitism (Section 3.2.7). We then consider a model in which the intruder decides whether to return at all, based on an assessment of past successes and failures when returning to superparasitise (Section 3.3). The probability of being intercepted is calculated by the application of Bayes' Theorem and this probability is used to estimate the expected payoff from returning to the patch versus the payoff of returning after the resident leaves the patch altogether (Section 3.3.2). Finally, we consider multiple intruder returns through a stochastic dynamic programme, with past successes and failures in patch return as the available information that govern the decision whether to return or to commence the next phase of patch competition (Section 3.3.3).

3.2 Information exchange of the Resident's Oviposition Rate

The question of when an intruding conspecific should return to a patch in order to attempt searching for unparasitised eggs and to superparasitise the resident's egg investment is the subject of this section.

Prior to the commencement of this game, the resident has usurped the intruder from the patch. Given that the resident is the superior competitor, as assessed from previous bouts for possession of the patch, the tradeoffs for a return to the patch for the intruding parasitoid need to be addressed. On return to the patch the behaviour of the resident is the crucial determinant of intruder oviposition success.

Rather than constructing a game of return rate and patch guarding between the intruder and resident, it is assumed that the resident initially has not commenced patch occupancy from a purely defensive role, but instead is still attempting to search for further suitable hosts after temporarily removing the intruder from the patch. Given that the resident is not guarding, the vulnerability of the patch to intruder superparasitism still fluctuates over time. Whether the resident has found a suitable host and is committed to oviposition may determine when the patch is maximally subject to intruder success in parasitism or superparasitism.

Once a suitable host egg is found by the resident, it begins the sequence of acts typical of an oviposition event, beginning with the insertion of it's ovipositor into the egg. During the act of host parasitism, a resident must sit motionless over the host, and is no longer able to respond in defence to an intruder searching over the patch, unless oviposition has just begun, in which case the resident can withdraw it's ovipositor and usurp the intruder from the patch (Field,[19], Cumber,[12]). If the resident is still foraging for hosts once the intruder has returned, an encounter between the players will result in the intruder once again being forced off the patch, inducing the intruder to await yet another return in an attempt to superparasitise or find undiscovered unparasitised host eggs (Field,[19]).

Thus, in making a decision as to *when* to return to the patch, the intruder must take into account the costs of returning, which critically depend on the rate at which the resident encounters eggs suitable for parasitism and also the time it takes for the resident to complete a successful oviposition.

Rather than derive the structure of a return time distribution for the intruder, a constant tendency to return is assumed, dependent on the resident oviposition rate, the host handling time and the relative costs of resident ovipositions on intruder investments. This restricts the return time to be drawn from an exponential distribution, which is agreement with experimental observations (Field,[19]). Assuming a constant return tendancy also has the advantage of tractable expressions in the calculation of intruder fitness equations. In this chapter, we make extensive use of

Renewal Theory (Cox,[11]) to calculate quantities such as the probability of resident oviposition over time, given some baseline rate of finding suitable hosts.

3.2.1 Assumptions

Assumptions behind the model of return, based on information of the resident's oviposition rate are listed here.

- Only two players compete for fitness returns on the patch.
- The status of each player has been estabished through previous bouts or escalated conflicts. One player has the role of resident on the patch, the other the role of an intruding parasitoid.
- The game commences immediately after the player roles have been estabished and the intruding female is jostled off the edge of the patch or when an intruder has been removed after a prior return.
- Termination of competition is marked by the forced removal of the intruder to the periphery after the return, that is only one return to find suitable eggs rather than multiple returns is considered (see Section 3.3 for analysis of multiple returns).
- The fitness payoffs have the following general form: suppose player 1 oviposits in a eggs and player 2 oviposits in b eggs during the course of patch competition. Further suppose that the cost to player 1 from the opponent's b ovipositions is $C_1(b)$, then the fitness gain of player 1, $f_1(a, b)$ is defined to be

  $$f_1(a, b) = a - C_1(b).$$

  Similarily, the fitness return to player 2, $f_2(a, b)$ with cost imposed by player 1,$C_2(a)$ is $f_2(a, b) = b - C_2(a)$.
- Once the resident commences oviposition, both the rate of encounter with suitable hosts and the handling or oviposition time are assumed to be constant.

- Fitness payoffs to the resident depend on the current oviposition rate and handling time, as well as the time between commencement of host searching and the return time of the intruder.
- Payoffs to the intruder, from returning, depend on the behaviour of the resident on the patch. On return to the patch, an intruder is hypothesised to accumulate the highest fitness returns whilst the resident is ovipositing, compared to the gains when the resident is searching for acceptable hosts.

3.2.2 Intruder's Fitness Equation

It is assumed that the resident oviposits with a constant tendancy λ_o and the time from the commencement to completion of an oviposition event, the handling time, is k time units. The end of an oviposition defines a renewal epoch and this is followed by another search phase for suitable hosts, provided the intruder has not been encountered yet. We can therefore infer that subject to the intruder not arriving on the patch, the time from the commencement of searching to the end of the oviposition phase, known as the inter-renewal time, satisfies the following time distribution

$$F_1(t) = \begin{cases} 0 & \text{for} \quad 0 \leq t \leq k, \\ 1 - \exp(-\lambda_o(t-k)) & \text{for} \quad t > k. \end{cases}$$

The subscript of one indicates that this is the distribution of the first inter-oviposition time.

Given that inter-oviposition times are independent and identically distributed, we can calculate the distribution of times to the end of the j^{th} oviposition, defined as $F_j(t)$, using the notion of the convolution of distributions. Suppose the times T_a, T_b for two particular events have distribution functions given by $F_a(t), F_b(t)$ with the corresponding density functions given by $p_a(t)$ and $p_b(t)$. Then the distribution of the sum of the times $T_a + T_b, \Pr(T_a + T_b \leq t)$ is given by the convolution

$$F_a \star F_b(t) = \int\int_{x+y\leq t} p_a(x) p_b(y) dx dy$$

$$= \int_0^t F_a(t-x)dF_b(x).$$

From basic probability theory the distribution $F_j(t)$, is simply j convolutions of the distribution $F_1(t)$, that is

$$F_j(t) = \underbrace{F_1 \star F_1 \star \ldots \star F_1}_{\text{j times}}(t).$$

Let T_I denote the time of return of the intruder. If we define $N_o(t)$ to be the expected number of ovipositions in time t of the resident, conditioned on the intruder not returning by time t,

$$N_o(t) = E(\text{number of resident ovipositions} \mid T_I > t),$$

then a fundamental result of renewal theory (Cox,[11]) relates the distribution of times till the end of the j^{th} oviposition to the expected number of ovipositions.

Lemma 1

$$N_o(t) = \sum_{j=1}^{\infty} F_j(t).$$

We will use this result (Cox, [11], Ross,[69]) in calculating the expected fitness of the intruder adopting some return tendancy.

The fitness gains of the intruder are assumed to be only dependent on the state, either searching or ovipositing, of the resident when returning to the patch. Let T_o indicate the commencement of an oviposition event for the resident. Fitness gains of the intruder conditioned on the resident searching or ovipositing are defined as

$$A_o = \Pr(\text{ intruder oviposits on return} \mid \text{resident is ovipositing})$$

and

$$A_s = \Pr(\text{intruder oviposits on return} \mid \text{resident is searching}).$$

Because the probability of the intruder finding a suitable host is assumed to be highest if returning while the resident is ovipositing then

$$A_s < A_o.$$

One possible measure of the resident's effectiveness in patch defence is the ratio of the probabilities of intruder oviposition, whilst the resident searches or oviposits, $\frac{A_s}{A_o}$. As $\frac{A_s}{A_o} \to 1$, the patch becomes decreasingly defendable to intruder attempts to steal ovipositions.

With these expressions, we can calculate the expected intruder fitness at return time T_I, conditioned on the commencement time of oviposition T_o. It is assumed that no more than one suitable host can be found by the intruder, so conditioned on the intruder returning while the resident is ovipositing, the expected intruder fitness gain $E(I \mid \text{resident is ovipositing})$ is just

$$E(I \mid \text{resident is ovipositing}) = 1A_o + 0(1 - A_o) = A_o.$$

For time of oviposition T_o, the expected fitness gain of the intruder, $E(I|T_I, T_o)$, satisfies

$$E(I|T_I,T_o) = \begin{cases} A_s & \text{for} \quad 0 \leq T_I \leq T_o, \\ A_o & \text{for} \quad T_o < T_I < T_o + k, \\ A_s & \text{for} \quad T_I \geq T_o + k. \end{cases}$$

Now the expected fitness of the intruder, adopting a specific return distribution can be derived assuming the fitness of the intruder is the difference between the expected number of ovipositions and the resident's total ovipositions weighted by the per oviposition cost C_I.

Suppose that we define the following probability distributions

$$G_I(t) = \Pr(\text{intruder returns at time} \leq t)$$

and

$$G_o(t) = \Pr(\text{resident is ovipositing at time } \leq t).$$

The corresponding density of the intruder return time is simply $p_I(t) = \lambda_I \exp(-\lambda_I t)$. Before calculating the expected fitness of the intruder, we must calculate $p_o(t)$.

Lemma 2

$$p_o(t) = N_o(t + k) - N_o(t).$$

Proof

$$\begin{aligned} p_o(t) &= \int_t^{t+k} \Pr(\text{renewal at time}[\tau, \tau+\Delta\tau])d\tau \\ &= \int_t^{t+k} \sum_{j=1}^{\infty} \Pr(\text{ jth renewal at time } \tau)d\tau \\ &= \int_t^{t+k} \sum_{j=1}^{\infty} \frac{d}{d\tau} F_j(\tau)d\tau \\ &= \sum_{j=1}^{\infty} \int_t^{t+k} \frac{d}{d\tau} F_j(\tau)d\tau \\ &= \sum_{j=1}^{\infty} F_j(t+k) - F_j(t). \end{aligned}$$

Therefore

$$p_o(t) = N_o(t+k) - N_o(t).$$

□

Recalling the assumptions listed in Section 3.2.1, the expected fitness of the intruder $E(I \mid \lambda_I, \lambda_o)$, given that the resident oviposits at a rate λ_o and the intruder returns with rate λ_I, will therefore satisfy

$$E(I \mid \lambda_I, \lambda_o) = \int_0^{\infty} p_I(t)\Big(p_o(t)(A_o - C_I N_o(t)) + (1 - p_o(t))(A_s - C_I N_o(t))\Big)dt,$$

where C_I is the relative cost to the intruder of a resident's oviposition.

With the restriction of the intruder adopting an exponential distribution on return, we can find an explicit expression for this fitness integral using some standard results in Renewal Theory (Cox,[11]). The fundamental result that is applied here relates the expected number of ovipositions in some time t, with it's Laplace transform.

The Laplace transform with respect to s, of some continuous bounded function $f(t)$, is defined as

$$\int_o^{\infty} f(t)\exp(-st)dt.$$

Let $\mathcal{L}(f(t), s) = f^*(t)$ denote the Laplace transform of some function $f(t)$, with respect to the variable s, then the Laplace transform of the convolution of two functions $f_a(t), f_b(t), \mathcal{L}(f_a \star f_b(t), s) = f_a^*(s) f_b^*(s)$. Suppose the distribution of time to the first resident oviposition $F_1(t)$ has density $f_1(t)$, with Laplace transform with respect to $s, f_1^*(s)$. Using this property of convolutions and using the fact (proved by integration by parts)

$$\mathcal{L}(F_j(t), s) = \frac{1}{s}\mathcal{L}(f_j(t), s),$$

we can show that the Laplace transform of the expected number of ovipositions with respect to variable s has the form

$$\begin{aligned} \mathcal{L}(N_o(t), s) &= \mathcal{L}(\sum_{j=1}^{\infty} F_j(t), s) \\ &= \frac{1}{s}\sum_{j=1}^{\infty} (f_1^*(s))^j. \end{aligned}$$

As $\sum_{j=1}^{\infty} x^j = \frac{x}{1-x}$, the Laplace transform of the number of ovipositions, $N_o(t)$ reduces to

$$\mathcal{L}(N_o(t), s) = \frac{f_1^*(s)}{s(1 - f_1^*(s))}.$$

To complete the calculation, we must evaluate the Laplace transform of the density of the time between ovipositions. The density of the time between ovipositions, $f_1(t)$ may be written as

$$f_1(t) = \lambda_o \exp(-\lambda_o(t-k))h(t-k)$$

where the Heaviside step function is defined as

$$h(t) = \begin{cases} 0 & \text{for} \quad t \le 0, \\ 1 & \text{for} \quad t > 0. \end{cases}$$

Using an elementary result of Laplace transforms known as the shifting lemma, stating that

$$\mathcal{L}(f(t-a)h(t-a), s) = \exp(-as)f^*(s),$$

we have that

$$\mathcal{L}(f_1(t), s) = \exp(-ks)\frac{\lambda_o}{\lambda_o + s},$$

thus

$$\frac{f_1^*(s)}{s(1-f_1^*(s))} = \frac{\lambda_o \exp(-ks)}{s(s+\lambda_o-\exp(-ks)\lambda_o)}.$$

Consider the expected fitness of the intruder, returning in an exponentially distributed manner with rate λ_I,

$$\begin{aligned} E(I|\lambda_I,\lambda_o) &= \lambda_I \int_0^\infty \exp(-\lambda_I t)\Big(\Big(A_o(N_o(t+k)-N_o(t))\Big) \\ &+ \Big(A_s(1-N_o(t+k)+N_o(t))\Big) - C_I N_o(t)\Big)dt \\ &= \lambda_I \mathcal{L}\Big(A_o(N_o(t+k)-N_o(t)) \\ &+ A_s(1-N_o(t+k)+N_o(t)) - C_I N_o(t), \lambda_I\Big). \end{aligned}$$

Once again, by direct calculation or application of the shifting lemma of Laplace transforms, we calculate

$$\begin{aligned} \mathcal{L}(N_o(t+k),\lambda_I) &= \mathcal{L}(N_o(t+k)h(t+k),\lambda_I) \\ &= \exp(k\lambda_I)\mathcal{L}(N_o(t),\lambda_I). \end{aligned}$$

With this we can evaluate the intruder's expected fitness

$$\begin{aligned} E(I \mid \lambda_I,\lambda_o) &= \lambda_I\{A_s\mathcal{L}(N_o(t),\lambda_I)(\exp(k\lambda_I)-1) + A_s\mathcal{L}(1,\lambda_I) \\ &+ A_s\mathcal{L}(N_o(t),\lambda_I)(1-\exp(k\lambda_I)) - C_I\mathcal{L}(N_o(t),\lambda_I)\} \\ &= A_s + \lambda_I\mathcal{L}(N_o(t),\lambda_I)\Big((A_o-A_s)(\exp(k\lambda_I)-1) - C_I\Big) \\ &= A_s + \frac{\lambda_o\exp(-k\lambda_I)\Big((A_o-A_s)(\exp(k\lambda_I)-1)-C_I\Big)}{\lambda_o+\lambda_I-\lambda_o\exp(-k\lambda_I)}. \end{aligned}$$

This expectation has a well defined maximum, as shown by comparing $E(I \mid \lambda_I,\lambda_o)$ against values of λ_I in Figure 3.2.1.

3.2.3 Optimal Return Rate to Superparasitise

Many methods exist to calculate the optimum rate of return λ_I^*, all of these must satisfy

$$\frac{\partial E(I \mid \lambda_I^*,\lambda_o)}{\partial \lambda_I} = 0 \text{ and } \frac{\partial^2 E(I \mid \lambda_I^*,\lambda_o)}{\partial \lambda_I^2} < 0.$$

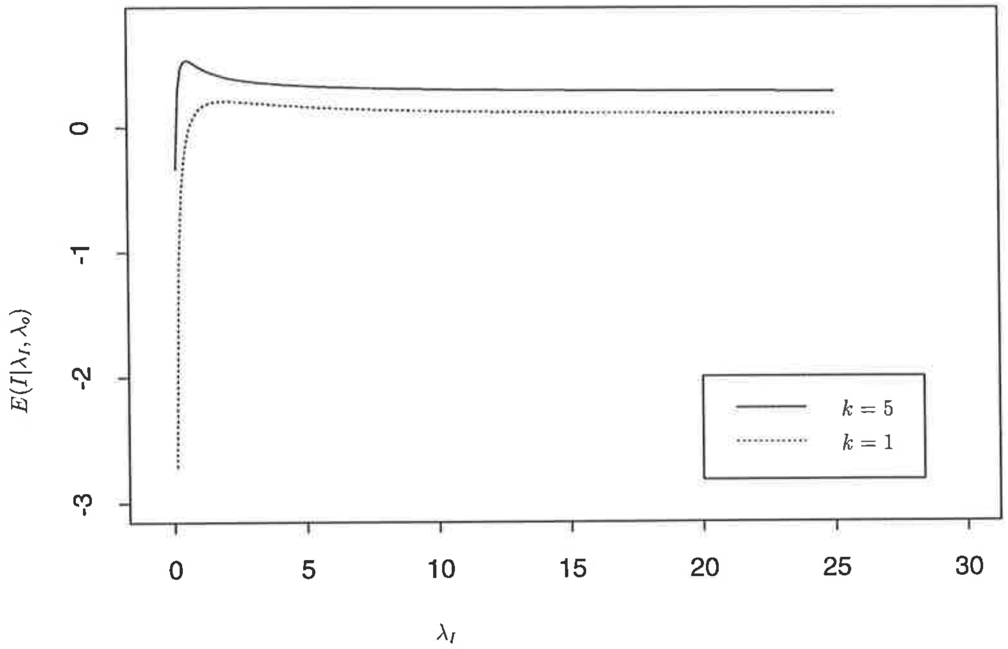

Figure 3.2.1: The expected intruder's fitness $E(I \mid \lambda_I, \lambda_o)$ against intruder return rate λ_I. Parameters used in this figure $A_o = 0.9, \lambda_o = 0.5, C_I = 1$, with lines drawn for $k = 5, \frac{A_s}{A_o} = 0.3$ and $k = 1, \frac{A_s}{A_o} = 0.1$.

Differentiating the intruder's fitness expression with respect to λ_I, we are left with the following implicit expression for λ_I^*

$$\begin{aligned} &\Big((A_o - A_s)k\exp(-k\lambda_I^*) + C_I k\exp(-k\lambda_I^*)\Big)\{\lambda_o + \lambda_I^* - \lambda_o\exp(-k\lambda_I^*)\} \\ - &\Big(1 + \lambda_o k\exp(-k\lambda_I^*)\Big)\{(A_o - A_s)(1 - \exp(-k\lambda_I^*)) - C_I\exp(-k\lambda_I^*) = 0 \end{aligned}$$

There is no closed form solution to this equation, therefore a numerical approach is required. This is done by first guessing the solution then, iterating the equation to find a fixed point. Defining $\lambda_I[0] := a$ (the initial guess) and

$$\lambda_I[n+1] := \frac{1}{k}\ln\left(\frac{D_1[n]}{D_2[n]}\right),$$

Iteration number:n	$\lambda_I[n]$	$\lambda_I[n]$
0	2.00	4.00
1	2.303	2.773
2	2.389	2.511
3	2.413	2.445
4	2.419	2.428
5	2.421	2.423
6	2.422	2.422
7	2.422	2.422

Table 3.2.1: Table of the values $\lambda_I[n]$, for different initial conditions $\lambda_I[0] = 2.00, 4.00$. The parameters used in this table are $\lambda_o = 0.50, k = 1.00, A_o = 0.5, \frac{A_s}{A_o} = 0.1$ and $C_I = 1$.

where

$$D_1[n] := \Big((A_o - A_s)k + C_I k)(\lambda_o + \lambda_I[n] - \lambda_o \exp(-k\lambda_I[n])\Big)$$

and

$$D_2[n] := -\Big(C_I \exp(-k\lambda_I[n]) - (A_o - A_s)(1 - \exp(-k\lambda_I[n])))(1 + \lambda_o k \exp(-k\lambda_I[n])\Big).$$

for $n = 1, 2, \cdots$, we iterate this equation till the difference between successive approximations converges to some small arbitrary constant ϵ, that is till $\mid \lambda_I[n+1] - \lambda_I[n] \mid < \epsilon$.

Computations show that $\lambda_I[n] \longrightarrow \lambda_I^*$, for small values of n, under different initial conditions $\lambda_I[0]$, as seen in the Table 3.2.1.

Plots of the optimal return frequency λ_I against λ_o show that as the resident's rate of encounter with suitable host eggs increases, so does the rate of return to the patch for the intruder (Figure 3.2.2). This increase in return rate is to be expected since an intruder will increase the return tendancy whilst the resident is more often predisposed to oviposition at high values for λ_o.

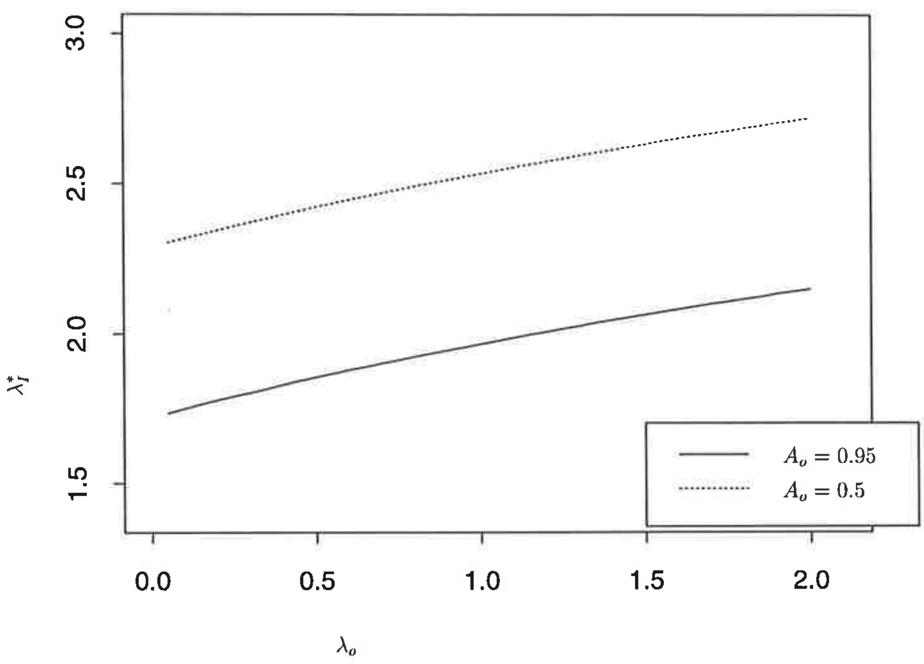

Figure 3.2.2: Graph of the optimal intruder return rate λ_I^* versus the resident's current rate of oviposition λ_o using the iteration formula for $\lambda_I[n]$. Iterations ceased when $\mid \lambda_I[n+1] - \lambda_I[n] \mid < \epsilon$.

As the ratio of payoffs from returning while the resident is searching or ovipositing approaches one, $\frac{A_s}{A_o} \longrightarrow 1$, the cost of returning to the patch decreases, as there is no gain for the intruder in waiting for the resident to oviposit, therefore the optimal return frequency must increase. Viewing the equation for λ_I^*, as $\frac{A_s}{A_o} \longrightarrow 1$, $\lambda_I^* \longrightarrow \infty$ and the graph in Figure 3.2.3 of the optimal return frequency λ_I^* confirms this.

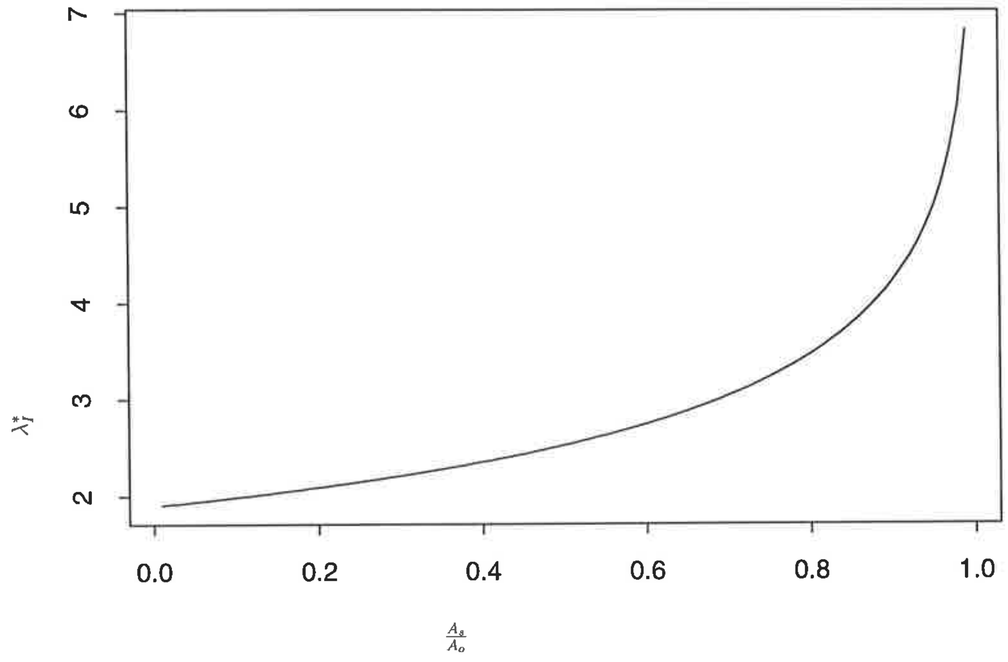

Figure 3.2.3: Graph of the Optimal Intruder Return Rate λ_I^* against $\frac{A_s}{A_o}$ as $\frac{A_s}{A_o} \longrightarrow 1$. This graph assumes the parameters $A_o = 0.9, k = 1.0, \lambda_o = 0.5$.

3.2.4 Resident's Best Response to the Intruder's Return

The resident's response to the intruder's strategy is considered in this section. Behavioural observations of *T. basalis* contests indicate considerable variation in the actions of a resident on an intruder's patch return (Field,[19]). This behaviour can range from pure patch defence in which the resident must sit motionless, awaiting any peripheral movement, to active forgaging for acceptable hosts (Field, Calbert and Keller,[21]). If we observe typical resident behaviour over the course of multiple intruder returns, there seems to be a change from partial to total exclusion of the intruder from the patch (Field, Calbert and Keller,[21], Field,[19]).

In order to incorporate some component of pure patch defence in this model, it is assumed that once a resident has usurped an intruder from the patch a new game commences. Initially, the resident guards for some time specified by an exponential distribution then switches to a search/oviposit phase. Lower fitness returns are accrued to the intruder if it returns while the resident is guarding, as compared to the fitness returns while the resident searches/oviposits. This game is assymetric in both player role and costs, therefore we expect to find only pure strategies for the resident, that is either guard or oviposit, but not both within the course of a game. Crucial to the decision of the resident to guard are the relative costs in defending the patch, versus the potential fitness gains in ovipositing (Field, Calbert and Keller,[21]).

If the intruder arrives on the patch once a large proportion of the eggs have been parasitised by the resident, then intruder superparasitism will evoke a higher cost to the resident. Thus, in choosing to defend the patch, a resident will face a trade off between defending past patch investment versus future fitness gains from oviposition (Field,[19]). Therefore, to understand the nature of patch competition, it is reasonable to ask at what superparasitism cost should the resident switch from search/oviposition to pure patch defence.

3.2.5 Payoffs to the Resident and Intruder

Before construction of the fitness equations for each player in patch competition, the following terms must be defined. Let C_R be the expected per oviposition cost to the resident each time the intruder oviposits in a random egg. Similarily, C_I is the per resident oviposition cost to the intruder. Costs are relative, since the fitness gain of a player is defined to be the total number of self ovipositions minus the cost of the opponent ovipositions, with the relative cost of self-superparasitism not taken into account. These costs are assumed to be constant over the course of a single intruder return. As it is assumed that the player with the largest investment is the resident. Therefore, if the intruder superparasitises a random egg it will most likely be a resident parasitised egg, thus the relative superparasitism costs will be greater for the resident, $C_R > C_I$. As in the previous model, we must define the payoffs to the intruder from returning to the patch, conditional on the resident either guarding,searching or ovipositing. Here

$$\begin{aligned} A_g &= E(\text{payoff to the intruder} \mid \text{resident is guarding}), \\ A_o &= E(\text{payoff to the intruder} \mid \text{resident is ovipositing}), \\ A_s &= E(\text{payoff to the intruder} \mid \text{resident is searching}). \end{aligned}$$

These definitions are made on the assumption that the following inequality holds

$$A_g < A_s < A_o.$$

As would be biologically expected, the smallest expected payoff to the intruder comes from returning to the patch while the resident is guarding. If we let $T_{s/o}$ denote the time at which the resident ceases guarding and starts the search/oviposit phase and T_I be the return time of the intruder then the number of ovipositions of the resident is

$$E(\text{number of ovipositions by the resident } \mid T_{s/o} = t, T_I = \tau, \tau > t) = N_o(\tau - t),$$

where $N_o(t)$ is the expected number of ovipositions for the resident, with host encounter rate λ_o and handling time k. With these definitions we can calculate the expected payoff to both players. An intruder's expected payoff, conditional on $T_{s/o} = t$ and $T_I = \tau$ is seen as

$$E(I \mid T_{s/o} = t, T_I = \tau) = \begin{cases} A_g & \text{if } \tau \leq t, \\ A_o - C_I N_o(\tau - t) & \text{if } \tau > t \text{ and } T_o \leq \tau < T_o + k, \\ A_s - C_I N_o(\tau - t) & \text{otherwise.} \end{cases}$$

The resident's expected payoff, under the same conditioning assumptions is given by

$$E(R \mid T_{s/o} = t, T_I = \tau) = \begin{cases} -C_R A_g & \text{if } \tau \leq t, \\ N_o(\tau - t) - C_R A_o & \text{if } \tau > t \text{ and } T_o \leq \tau < T_o + k, \\ N_o(\tau - t) - C_R A_s & \text{otherwise.} \end{cases}$$

3.2.6 Approximating Fitness Expressions

Expected payoffs for this game can be calculated by integrating over all possible times when the resident ceases guarding and times when the intruder returns to the patch. Given that $p_o(t)$ is again the probability that the resident is ovipositing at time t and $p_I(t), p_{s/o}(t)$ are the respective densities for $T_I, T_{S/O}$ then

$$p_I(t) = \lambda_I \exp(-\lambda_I t), p_{s/o}(t) = \lambda_{s/o} \exp(-\lambda_{s/o} t),$$

then the intruder's expected payoff $E(I, R)$ is

$$\begin{aligned} E(I,R) &= \int_0^\infty p_{s/o}(t)\Big(\int_0^t A_g p_I(\tau)d\tau\Big)dt \\ &+ \int_0^\infty p_{s/o}(t)\Big(\int_t^\infty \{p_o(\tau-t)(A_o - C_I N_o(\tau-t)) \\ &+ (1-p_o(\tau-t))(A_s - C_I N_o(\tau-t))\}p_I(\tau)d\tau\Big)dt. \end{aligned}$$

Expected payoff for the resident is given by

$$\begin{aligned} E(R,I) &= \int_0^\infty p_{s/o}(t)\Big(\int_0^t -C_R A_g p_I(\tau)d\tau\Big)dt \\ &+ \int_0^\infty p_{s/o}(t)\Big(\int_t^\infty \{p_o(\tau-t)(N_o(\tau-t) - C_R A_o) \\ &+ (1-p_o(\tau-t))(N_o(\tau-t) - C_R A_s)\}p_I(\tau)d\tau\Big)dt. \end{aligned}$$

Even with the restriction that the guarding times and the return times are drawn from exponential distributions, some approximations need to be made in evaluating these integrals. The main difficulty lies in the integration of the probability of oviposition

$$p_o(\tau - t) = N_o(\tau - t + k) - N_o(\tau - t).$$

Instead we will apply a *Tauberian* approximation to this probability of oviposition (Cox,[11]). The Tauberian Theorem gives us an approximation for the number of ovipositions $N_o(t)$, for large times t and in turn a time independent approximation for the probability of oviposition $p_o(t)$. Firstly the Tauberian Theorem is stated formally (Ross,[69])

Theorem 1 (Tauberian Theorem) *Suppose a continuous and bounded function* $f(t)$, *has Laplace transform with respect to variable* s *given by*

$$\mathcal{L}(f(t), s) = f^*(s)$$

and let $0 < \rho < \infty$. *Then*

$$\lim_{t \longrightarrow \infty} \frac{f(t)\Gamma(\rho+1)}{t^\rho} = 1 \Longleftrightarrow \lim_{s \longrightarrow 0} f^*(s)s^{\rho+1} = 1.$$

Where $\Gamma(\rho) = \int_0^\infty \exp(-x)x^{\rho-1}dx$. *If* ρ *is an integer, then* $\Gamma(\rho) = (\rho - 1)!$.

Informally this theorem states that the function $f(t)$ for large times t, can be approximated by the Laplace transform $f^*(s)$ of $f(t)$, with respect to variable s near $s = 0$. If $\mathcal{L}(f(t), s)$ can be expanded in the form

$$\mathcal{L}(f(t), s) \approx \frac{l}{s^2}$$

then

$$f(t) \approx lt.$$

The coefficient l is then calculated as

$$\lim_{s \longrightarrow 0} f^*(s)s^2 = l.$$

This theorem is now applied to an approximation of the number of ovipositions $N_o(t)$ and it's Laplace transform with respect to variable λ_I. For large times, $N_o(t)$ can be linearly approximated (Cox, [11]),

$$N_o(t) \approx R_o t.$$

Applying the Tauberian theorem (Cox,[11]) to find the coefficient R_o, we have

$$\begin{aligned} R_o &= \lim_{\lambda_I \longrightarrow 0} \lambda_I^2 \mathcal{L}(N_o(t), \lambda_I) \\ &= \lim_{\lambda_I \longrightarrow 0} \lambda_I^2 \frac{\lambda_o \exp(-k\lambda_I)}{\lambda_I(\lambda_I + \lambda_o - \lambda_o \exp(-k\lambda_I))}. \end{aligned}$$

The denominator and numerator are both zero when applying this limit, hence L'Hopital's rule may be applied, thus

$$\begin{aligned}
R_o &= \lim_{\lambda_I \longrightarrow 0} \lambda_I^2 \frac{\lambda_o \exp(-k\lambda_I)}{\lambda_I(\lambda_I + \lambda_o - \lambda_o \exp(-k\lambda_I))} \\
&= \lim_{\lambda_I \longrightarrow 0} \frac{\lambda_o \exp(-k\lambda_I) - \lambda_o k \lambda_I \exp(-k\lambda_I)}{1 + \lambda_o k \exp(-k\lambda_I)} \\
&= \frac{\lambda_0}{1 + \lambda_o k}.
\end{aligned}$$

Conditioned on the intruder not returning at time t, the number of ovipositions of the resident is therefore approximated as

$$N_o(t) \approx \frac{\lambda_o t}{1 + \lambda_o k}.$$

With this approximation, the probability of oviposition is calculated as

$$\begin{aligned}
p_o(\tau - t) &= N_o(\tau - t + k) - N_o(\tau - t) \\
&\approx \frac{\lambda_o(\tau - t + k)}{1 + \lambda_o k} - \frac{\lambda_o(\tau - t)}{1 + \lambda_o k} \\
&= \frac{\lambda_o k}{1 + \lambda_o k.}
\end{aligned}$$

Some properties of the linear approximation are evident, since dividing the denominator and numerator by λ_o we have

$$\begin{aligned}
R_o &= \frac{1}{\frac{1}{\lambda_o} + k} \\
&= \frac{1}{E(\text{time to find host}) + (\text{handling time})}.
\end{aligned}$$

This is just Hollings Disc Equation (Stephens and Krebs,[77]) for the rate of parasitism, with inter-host travel time $\frac{1}{\lambda_o}$ and handling time k. With this result we can now evaluate the resident and intruder fitness equations, to give approximate expressions for the fitness of the intruder and the resident

$$\begin{aligned}
E(I,R) &= \int_0^\infty p_{s/o}(t)\Big(\int_0^t A_g p_I(\tau) d\tau\Big) dt \\
&+ \int_0^\infty p_{s/o}(t)\Big(\int_t^\infty \{p_o(\tau - t)(A_o - C_I N_o(\tau - t))
\end{aligned}$$

$$
\begin{aligned}
&+ \quad (1-p_o(\tau-t))(A_s - C_I N_o(\tau-t))\}p_I(\tau)d\tau\Big)dt \\
&\approx \quad \int_0^\infty p_{s/o}(t)\Big(\int_0^t A_g p_I(\tau)d\tau\Big)dt \\
&+ \quad \int_0^\infty p_{s/o}(t)\Big(\int_t^\infty \frac{\lambda_o k}{1+\lambda_o k}(A_o - C_I N_o(\tau-t)) \\
&+ \quad \frac{1}{1+\lambda_o k}(A_s - C_I N_o(\tau-t))p_I(\tau)d\tau\Big)dt \\
&= \quad A_g\frac{\lambda_I}{\lambda_I+\lambda_{s/o}} + \frac{A_o\lambda_o k + A_s}{1+\lambda_o k}\frac{\lambda_{s/o}}{\lambda_{s/o}+\lambda_I} \\
&+ \quad \int_0^\infty p_{s/o}(t)\int_t^\infty p_I(\tau)N_o(\tau-t)d\tau dt.
\end{aligned}
$$

To evaluate this last integral, we may evoke the Tauberian theorem again

$$
\begin{aligned}
&\int_0^\infty p_{s/o}(t)\int_t^\infty p_I(\tau)N_o(\tau-t)d\tau dt \\
\approx\ &\int_0^\infty p_{s/o}(t)\int_t^\infty p_I(\tau)\frac{\lambda_o(\tau-t)}{1+\lambda_o k}d\tau dt \\
=\ &\frac{\lambda_{s/o}}{\lambda_{s/o}+\lambda_I}\frac{\lambda_o}{1+\lambda_o k}\Big(\frac{1}{\lambda_I}\Big).
\end{aligned}
$$

Thus

$$E(I,R) \approx A_g\frac{\lambda_I}{\lambda_I+\lambda_{s/o}} + \frac{\lambda_{s/o}}{\lambda_I+\lambda_{s/o}}(B - C_I N(\lambda_I)),$$

where $N(\lambda_I)$ is Tauberian approximation of the expected number of ovipositions to the resident, given that the intruder returns at a rate λ_I,

$$N(\lambda_I) = \frac{\lambda_o}{1+\lambda_o k}\Big(\frac{1}{\lambda_I}\Big)$$

and B is the expected number of ovipositions of the intruder, given that the resident has commenced searching/oviposition,

$$B = A_s + (A_o - A_s)\frac{\lambda_o k}{1+\lambda_o k}.$$

By a similar calculation, the resident's fitness equation is

$$E(R,I) \approx -C_R A_g\frac{\lambda_I}{\lambda_I+\lambda_{s/o}} + \frac{\lambda_{s/o}}{\lambda_I+\lambda_{s/o}}(N(\lambda_I) - C_R B).$$

The structure of the equations are easier to recognise if we note that

$$\Pr(T_I < T_{s\emptyset}) = \frac{\lambda_I}{\lambda_I+\lambda_{s/o}},$$

so that the expected payoffs become

$$\begin{aligned} E(I,R) &\approx A_g \Pr(T_I < T_{s/o}) + E(\text{ intruder payoff } \mid T_I > T_{s/o}) \Pr(T_I > T_{s/o}), \\ E(R,I) &\approx -C_R A_g \Pr(T_I < T_{s/o}) + E(\text{ resident payoff } \mid T_I > T_{s/o}) \Pr(T_I > T_{s/o}). \end{aligned}$$

The fitness equations can be rewritten as

$$E(I,R) \approx A_g + \frac{\lambda_{s/o}}{\lambda_{s/o} + \lambda_I}\big(B - A_g - C_I N(\lambda_I)\big)$$

and

$$E(R,I) \approx -C_R A_g + \frac{\lambda_{s/o}}{\lambda_{s/o} + \lambda_I}\big(N(\lambda_i) - C_R B + C_R A_g\big).$$

Furthermore, we must note that the expected return to the resident, conditioned on the intruder returning after search/oviposition has commenced, must increase as $\lambda_I \longrightarrow 0$, thus $N(\lambda_I)$ satisfies

$$\frac{\partial N(\lambda_I)}{\partial \lambda_I} < 0.$$

Now suppose the current population resident and intruder strategies are denoted by $\lambda_{s/o}^{pop}$ and λ_I^{pop} and these are finite in value, $0 < \lambda_I^{pop} < \infty$, $0 < \lambda_{s/o}^{pop} < \infty$. Having rewritten the fitness equations, the best response of an invading mutant resident can be seen from looking at the sign of the terms in parentheses of $E(R,I)$. Since these terms in parentheses are only dependent on the population rate of intruder return, λ_I^{pop}, we will look at the best response of an invading resident. Defining the best response strategy of a mutant resident as

$$B_R(\lambda_I^{pop}) = \arg \sup_{\lambda_{s/o} \in [0,\infty)} E(R,I),$$

then this best response satisfies

$$B_R(\lambda_I^{pop}) = \begin{cases} 0 \text{ (always guard)} & \text{if} \quad \big(N(\lambda_I^{pop}) - C_R(B + A_g)\big) < 0, \\ \text{all strategies} & \text{if} \quad \big(N(\lambda_I^{pop}) - C_R(B + A_g)\big) = 0, \\ \infty \text{ (always search)} & \text{if} \quad \big(N(\lambda_I^{pop}) - C_R(B + A_g)\big) > 0. \end{cases}$$

This analysis implies that when the relative cost of searching is high, the resident's only response is to guard. If the payoffs from oviposition are sufficiently large because many unparasitised hosts remain, then the resident should search for remaining hosts, forgoing the costs of intruder induced superparasitism.

The derivation of the pure strategy best responses of the resident was based on the assumption that the resident chooses to guard before searching for remaining hosts and the Tauberian approximation for the number of ovipositions $N_o(t)$. An exact calculation, comparing fitness payoffs when the resident chooses to search or to guard will yield the criterion under which the resident will switch from ovipositing to guarding.

3.2.7 Resident's Searching to Guarding Switch

If the resident chooses to search for remaining hosts ($\lambda_{s/o} = \infty$) then the expected payoff to the intruder

$$\begin{aligned} E(I \mid \lambda_{s/o} = \infty) &= \int_0^\infty \lambda_I \exp(-\lambda_I t)\Big(A_o(N_o(t+k) - N_o(t)) \\ &+ A_s(1 - N_o(t+k) + N_o(t)) - C_I N_o(t)\Big)dt, \end{aligned}$$

this expression was evaluated in Section 3.2.2. A similar expression exists for the resident's payoff, $E(R \mid \lambda_{s/o} = \infty)$, given the per opponent oviposition cost C_R,

$$\begin{aligned} E(R \mid \lambda_{s/o} = \infty) &= \int_0^\infty \lambda_I \exp(-\lambda_I t)\Bigg(N_o(t) - C_R\Big(A_o(N_o(t+k) - N_o(t)) \\ &+ A_s(1 - N_o(t+k) + N_o(t))\Big)\Bigg)dt. \end{aligned}$$

Once again we can find an expression for the intruder's optimal rate of return by setting $\frac{\partial E(I|\lambda_{s/o}=\infty)}{\partial \lambda_I} = 0$ and solving by numerical iteration (see Section 3.2.2). Let us denote this optimal rate of return by $\lambda_I^*(C_I)$. Once $\lambda_I^*(C_I)$ has been found, then this can be substituted into the payoff expectations of both players to yield

$$\begin{aligned} E(I \mid \lambda_{s/o} = \infty) &= A_s + \frac{\lambda_o \exp(-\lambda_I^*(C_I)k)\Big(\big(\exp(\lambda_I^*(C_I)k) - 1\big)(A_o - A_s) - C_I\Big)}{\lambda_I^*(C_I) + \lambda_o - \lambda_o \exp(-\lambda_I^*(C_I)k),} \\ E(R \mid \lambda_{s/o} = \infty) &= -C_R A_s + \frac{\lambda_o \exp(-\lambda_I^*(C_I)k)\Big(1 - C_R\big(\exp(\lambda_I^*(C_I)k) - 1\big)(A_o - A_s)\Big)}{\lambda_I^*(C_I) + \lambda_o - \lambda_o \exp(-\lambda_I^*(C_I)k).} \end{aligned}$$

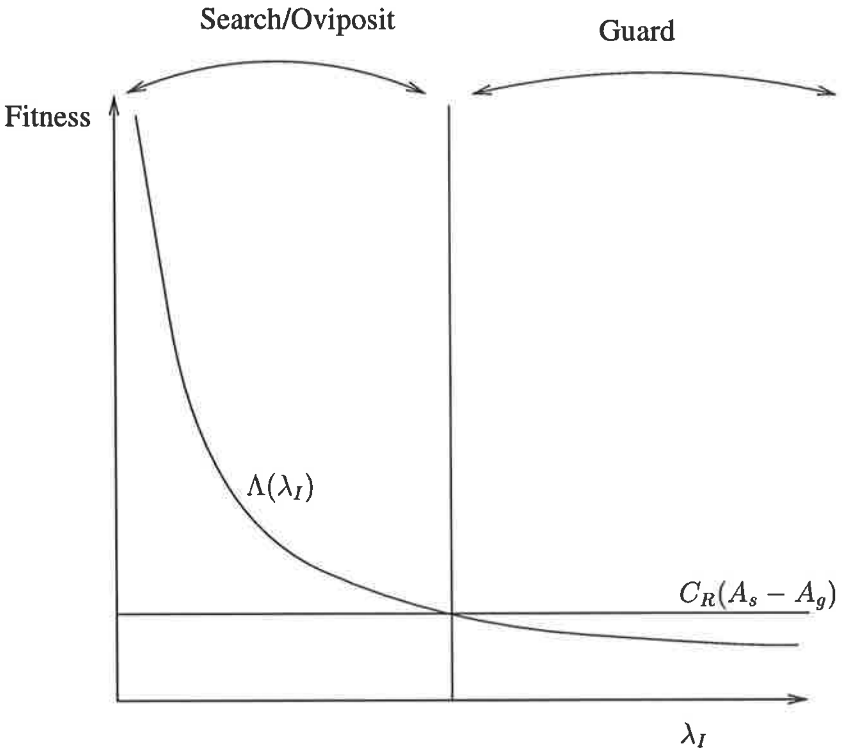

Figure 3.2.4: Diagram illustrating the resident switch from ovipositing to guarding, for λ_I that satisfies $\Lambda(\lambda_I) = C_R(A_g - A_s)$.

If $\lambda_{s/o} = 0$ (always guard), the respective payoffs to the intruder and resident will be

$$\begin{aligned} E(I \mid \lambda_{s/o} = 0) &= A_g, \\ E(R \mid \lambda_{s/o} = 0) &= -C_R A_g. \end{aligned}$$

Hence the optimal strategy to the resident $\lambda^*_{s/o}(C_R)$ will be

$$\lambda^*_{s/o}(C_R) = \begin{cases} \infty & \text{if} \quad E(R \mid \lambda_{s/o} = \infty) > E(R \mid \lambda_{s/o} = 0), \\ 0 & \text{if} \quad E(R \mid \lambda_{s/o} = \infty) < E(R \mid \lambda_{s/o} = 0). \end{cases}$$

For simplicity, let

$$\Lambda(\lambda_I) = \frac{\lambda_o \exp(-\lambda_I k)\big(1 - C_R(\exp(\lambda_I(C_I)k) - 1)(A_o - A_s)\big)}{\lambda_I + \lambda_o - \lambda_o \exp(-\lambda_I k)},$$

this expression being the expected fitness gain of the resident, finding suitable hosts at rate λ_o, before the intruder returns. The set of intruder return rates by which the resident oviposits satisfies

$$\Lambda(\lambda_I) > C_R(A_s - A_g),$$

with $C_R(A_s - A_g)$ being the cost of searching compared to guarding. Since $\Lambda(\lambda_I)$ is monotone decreasing, there will be a return tendency below which the resident should oviposit and above which the resident should guard.

So far, we have considered the resident's oviposition rate, λ_o to be constant in our analysis. The method of calculating the switch from guarding to ovipositing needs to be carried out when the rate of parasitism/superparasitism decreases over time. Simulation of the fitness returns may be the only method by which the switch from guarding to ovipositing may be calculated.

3.3 Assessment of Oviposition Success Through Multiple Returns.

In the previous section, we assumed that the intruder bases its returns to "steal" ovipositions on estimates of the resident's *oviposition rate.* This hypothesis is appealing because of it's adaptive advantage *if* this information is available to the intruder. The decision to return at all, however, must be made before deciding when to return. The available information by which this decision is made must be different to that of the resident's oviposition rate, as other factors such as the size of the egg mass and the overall level of patch parasitism will influence the probability of successful superparasitism (Field, Calbert and Keller, [21]).

Consider the case in which the intruder has returned a number of times, after being removed from the patch, either by resident force or by retreating. Prior to the removal, the intruder may or may not have had success in oviposition. Over a series of returns, the intruder may estimate the chance of successfully ovipositing if it chooses to return again. Furthermore, the intruder may estimate the cost associated with returning. If the resident is nearing the end of it's life or has low egg load, then it may repel the intruder with great ferocity (Field,[19]). Thus the intruder may jointly estimate the chances of successful oviposition and the costs of being intercepted.

The two proposed information states, resident host encounter rates and success in previous returns are not at odds with one another. Both may be used by the intruder to make the optimal decision as to if and when to return. A review of other possible available information follows in Section 3.4.

In this Section, patch return, based on estimates of the probability of success in oviposition are modelled. It is assumed that after being ejected from the patch after the previous return, the intruder makes the single decision of returning in an attempt to "steal" further ovipositions or to commence the final stage of patch competition, returning after the resident abandons the patch (see the next two chapters for a discussion of this). The decision of whether to return or to wait will depend on the relative costs and benefits of each action.

3.3.1 Assumptions

- Both the roles of resident and intruder are established.
- The intruder makes a decision either to return or to wait till the resident has left before returning.
- Let the expected fitness payoff, if the intruder is successful in finding suitable ovipositions on return be A. If it is intercepted before finding a suitable host, then it receives zero payoff.
- If the intruder chooses to wait till the resident has left before returning then the fitness payoff from this strategy is W.

- The probability of not being injured on return is independent of the number of returns and is denoted by π.

- After each return, the intruder estimates the probability of success if it chooses to return once again. For the n^{th} decision point, the probability of success is a random variable denoted by $x \in [0,1]$ and the estimate of the probability of success is the expectation $p_n = E(x|n-1 \text{ previous returns })$. Given an estimate of the subsequent probability of success of the n^{th} return, p_n then the optimal strategy at the n^{th} decision point is found by comparing the sum of the estimated payoff on returning, Ap_n, and the payoffs from future decision points with the payoff from waiting till the resident leaves altogether, W.

Let $F_I(n, p_n)$ be the expected fitness of the intruder at the n^{th} decision point (implying $(n-1)$ previous returns) and the estimate of oviposition success at the n^{th} return, p_n. If choosing to return, then the payoff is decomposed into the immediate payoffs from return, Ap_n and the payoffs from future decision points, $F_I(n+1, p_{n+1})$. At the n^{th} decision point, the choice between returning or waiting is therefore calculated from the simple stochastic dynamic programme (Iwasa, Suzuki and Hiroyuki,[38], Mangel and Clarke,[50])

$$F_I(n, p_n) = \max_{\text{Return,Wait}} \left\{ Ap_n + \pi F_I(n+1, p_{n+1}); W \right\}.$$

Estimation of the probability of success is accomplished through the use of Bayes' theorem (McNamara and Houston,[57]).

3.3.2 Bayesian estimates of Oviposition Success

If the probability of success in oviposition, after n returns, x is drawn from some distribution on the interval $[0,1]$, then Bayes' theorem is a general way of updating this distribution given information about the success or failure of the previous $n-1$ returns.

It is assumed that the probability of success of n returns is drawn from the *beta* distribution (Law and Kelton,[43]). This distribution, determined by two parameters a and b has density

$$f(x) = \begin{cases} \frac{x^{a-1}(1-x)^{b-1}}{B(a,b)} & \text{for } 0 < x < 1, \\ 0 & \text{otherwise,} \end{cases}$$

were $B(a,b) = \int_0^1 t^{a-1}(1-t)^{b-1}dt$. The beta distribution has mean

$$E(X) = \frac{a}{a+b}$$

and variance

$$var(X) = \frac{ab}{(a+b)^2(a+b+1)}.$$

This distribution was chosen because of it's generality, as it can represent a wide variety of distributional forms on the interval $[0,1]$ (Law and Kelton,[43]).

Now suppose, after $n-1$ returns, that the intruder successfully oviposited in j occasions before being ejected. The other $n-j-1$ returns the intruder was ejected before it could oviposit. What will be the estimate of x? Bayes' Theorem gives us a way of updating the density of x, by considering the intruder's past successes and failures in finding ovipostions.

The prior estimate of the oviposition success density, before returning is

$$x_0 \sim beta(a,b).$$

Now suppose that the intruder returns and successfully oviposits, as denoted by event $\mathcal{S}$, then the posterior estimate of the oviposition sucess density is

$$f_1(x) = f_0(x|\mathcal{S}).$$

By Bayes' theorem,

$$\Pr(A|B) = \frac{\Pr(B|A)\Pr(A)}{\Pr(B)},$$

the posterior density

$$\begin{aligned} f_1(x) &= f_0(x|\mathcal{S}) \\ &= \frac{\Pr(\mathcal{S}|x)f_0(x)}{\int_0^1 \Pr(\mathcal{S}|x)f_0(x)dx.} \end{aligned}$$

Now $\Pr(\mathcal{S}|x) = x$. Thus the posterior density takes the form

$$\begin{aligned} f_1(x) &= \frac{\frac{x^a(1-x)^{b-1}}{B(a,b)}}{\int_0^1 \frac{x^a(1-x)^{b-1}}{B(a,b)} dx} \\ &= \frac{x^a(1-x)^{b-1}}{B(a+1,b)}. \end{aligned}$$

If the intruder is successful on return then

$$x \sim beta(a+1,b).$$

Similarily, if the intruder fails to find a suitable host before being intercepted by the resident, as denoted by the complement of the event $\mathcal{S}, \mathcal{S}^c$ then the posterior density

$$\begin{aligned} f_1(x) &= f_0(x|\mathcal{S}^c) \\ &= \frac{x^{a-1}(1-x)^b}{B(a,b+1)}. \end{aligned}$$

Hence, if the intruder has no ovipostion success on return then

$$x \sim beta(a,b+1).$$

To illustrate, consider the the initial distribution of oviposition success on return $x \sim beta(1,1)$. The density

$$f_0(x) = \frac{x^0(1-x)^0}{B(1,1)} = 1,$$

thus our initial choice of distribution is the uniform distribution,

$$beta(1,1) = U(0,1).$$

Consider the sequence of five returns, with success/failure to oviposit on return denoted by $\{\mathcal{S}^c, \mathcal{S}, \mathcal{S}^c, \mathcal{S}^c, \mathcal{S}^c\}$. The estimates of the probability of success in oviposition on return will be

$$p_0 = \frac{1}{2}, p_1 = \frac{1}{3}, p_2 = \frac{1}{2}, p_3 = \frac{1}{3}, p_4 = \frac{1}{4}, p_5 = \frac{1}{5}.$$

The intruder will choose not to return when

$$p_n < \frac{W - \pi F_I(n+1, p_{n+1})}{A},$$

thus if $W = 0.25, A = 1, \pi = 1.0$ and $F_I(n+1, p_{n+1}) = 0$ then the intruder will return only four times before commencing the final stage of patch competition, that of waiting till the resident leaves the patch before making a patch return.

3.3.3 Solving the Stochastic Dynamic Program

Having illustrated the estimation of return ovipostion success through Bayesian updating of the beta distribution, the stochastic dynamic program constructed in Section 3.3 may be constructed to incorporate this estimation. If n is the number of intruder returns, a the number of previous returns where the intruder successfully oviposited before interception and b the number of unsuccessful returns, then the fitness of the intruder, $F_I(a, b, n)$ with available state (a, b, n) will therefore satisfy

$$F_I(a,b,n) =$$
$$\max_{\text{Return,Wait}} \Big\{\frac{a}{a+b}A + \pi(\frac{a}{a+b}F_I(a+1,b,n+1) + \frac{b}{a+b}F_I(a,b+1,n+1)); W\Big\}$$

Before solving this equation, we must impose some constraints on the information state variables and apply boundary conditions (Mangel and Clarke,[50], Mangel,[48]). Clearly, the number of successes and failures must equal the number of past returns, $a + b = n$. For the boundary conditions, we will restrict the number of decision points to a maximum of nineteen, after which the intruder chooses to play the waiting game (see the next two chapters for analysis of the waiting game). Thus, at the twentieth decision point

$$F_I(a, b, 20) = W, \text{ for all } a + b = 20.$$

With these conditions, the dynamic programming algorithm (Filar,[23]) working backwards from the twentieth decision point, starting from the nineteenth decision point and solving the optimal strategy for each $a, b, a+b = 19$, then to the eighteenth decision and so on is implemented. This is possible since

$$F_I(a, b, 19) = \max_{\text{Return,Wait}} \left\{ \frac{a}{a+b}A + \pi\left(\frac{a}{a+b}F_I(a+1, b, 20) + \frac{b}{a+b}F_I(a, b+1, 20)\right); W \right\}$$

and $F_I(a, b, 20)$ is known for each value of a, b. Using the values of $F_I(a, b, 19)$ we can in turn solve for $F_I(a, b, 18)$ and so on, this technique being termed *backward recursion* (Mangel and Clarke, [50]).

Qualitatively, the results show a switch from returning to waiting, depending on the expected return fitness value, A, the probability of injury on return $(1 - \pi)$ and most importantly the past successes, a and failures, b when returning. The following table (Table 3.3.2) illustrates this switch by considering the following question. Given ten previous returns, how many past successes and failures are needed so the intruder switches from returning to waiting at the eleventh decision point, for a particular fitness value A?

As the risk in returning decreases, that is $\pi \longrightarrow 1$ the price sampling the patch for suitable hosts (interception by the resident) decreases, thus the intruder will make a greater number of returns before the switch to the waiting game.

The dynamic programme constructed in this Section may be expanded in a number of state variables from which to make adaptive return decisions. Indeed, the work of *when* to return (Sections 3.2 to 3.2.7) and *if* to return (Sections 3.3 to 3.3.3) may be united by adding another state variable to the dynamic programme, the estimate of the resident's oviposition rate. Bayes' theorem may be used to estimate estimate the oviposition rate of the resident, since if we let the event of intruder oviposition before resident interception be denoted by $\mathcal{A}$ and the events of resident searching and ovipositing by $\mathcal{S}, \mathcal{O}$ respectively then $\Pr(\mathcal{A}) = \Pr(\mathcal{A}|\mathcal{S})\Pr(\mathcal{S}) + \Pr(\mathcal{A}|\mathcal{O})\Pr(\mathcal{O})$. Recalling the definitions listed in Section 3.2.2,

$$\Pr(\mathcal{A}) = A_s + (A_o - A_s)(N_o(t+k) - N_o(t)).$$

A	Successes out of 10 returns before the switch to waiting
0.5	always wait,
1.0	always wait,
1.5	always wait,
2.0	return if $>$ 7 successes, wait otherwise,
2.5	return if $>$ 6 successes, wait otherwise,
3.0	return if $>$ 5 successes, wait otherwise,
3.5	return if $>$ 4 successes, wait otherwise,
4.0	return if $>$ 3 successes, wait otherwise.

Table 3.3.2: A table of the optimal decision at the 11^{th}, to return or to wait, as a function of the past successes and failures in oviposition. Here, the fitness value from waiting $W = 2.0$ and the probability of not being injured, $\pi = 0.99$. The expected fitness value on return, A ranges from 0.5 to 4.0.

This time dependent distribution is a function of the oviposition rate λ_o which may be updated by past return successes and failures through Bayes' Theorem.

3.4 Discussion and Conclusion

A review of the proceeding models and a biological interpretation of the results will be the focus of this discussion.

Under the assumption of information transfer of the resident's oviposition rate, an optimisation model was constructed, to calculate the best return rate of the intruder, under the condition of a foraging resident. A core assumption behind the model concerned the variation in patch vulnerability. While ovipositing, the resident temporarily suspends any possible defence of the patch, increasing the probability of successful intruder superparasitism.

Higher return rates were predicted, as the resident encounter rate with suitable hosts increased. On analysis of the possibility of guarding, for a period of time before commencing search/oviposit behaviour, it was concluded that the resident's best response to a returning intruder could only be drawn from the pure strategy set "always guard" or "always search", as all mixed guarding strategies were inherently unstable.

Though any patch defence is temporarily suspended when the resident oviposits, this is not the only time when the patch is left exposed to potential intruder superparasitism. As the resident must search for remaining unparasitised hosts, it may venture to the boundary of the patch. If the intruder waits on the opposite side, this may leave one half of the patch unguarded and subject to attempts at superparasitism (Field, Calbert and Keller,[21]). The available information transferred to the intruder here will be the position of the resident. As mentioned in Section 3.1 there is some evidence that insects have limited scope in the detection of a stationary object, instead relying on movement. If information is transferred as to a resident's location, this information will most likely be imperfect. The hypothesis about information transfer of the resident's position is both simple and plausible and will be fully explored, through a Bayesian model of imperfect information transfer in Chapter **??**.

The behaviour of the intruder, mimics aspects of male polymorphism in other species of animals. The bird species *Philomachus pugnax* exhibits a sexual dimorphism in the plumage and behaviour of males. Some males establish territories, the so called "independent" males and others do not, the so called "satellite" males (Maynard Smith,[54]). Within this species, the dimorphism is not strict, as about half of the male population will both be independent and satellite males at some stage of their lives. Satellite males are occasionally tolerated when in an independent male's territory and have been shown to be successful in mating, when the independent male is otherwise occupied and cannot drive off the satellite male from it's territory (see also Alcock,[1] for a review of male and female polymorphisms). Further work is required to understand what available information influences resource stealing strategies across dimorphic male species and parasitoids that defend patches.

In summary this chapter explored adaptive hypotheses of intruder returns to "steal" remaining unparasitised hosts and to superparasitise. As is the theme of this thesis, any strategy adopted by the intruder must depend on the nature of information transfer between the resident and intruder. We explored the hypotheses of patch return when the resident is preoccupied with oviposition, leaving the patch undefended. Multiple returns were also considered through a Bayesian analysis of the fitness gains from returning. More work is required to understand what available information the intruder uses to judge it's patch return when attempting to steal ovipositions.

Chapter 4

The Waiting Game

Instability of Strategies without information exchange.

4.1 Introduction and Chapter Overview

The focus of this chapter is the last stage of pairwise competition in *T. basalis,* and the necessary conditions for the existence of an ESS in the final stage of patch competition. When an intruder no longer returns to steal ovipositions (see Chapter 3), a waiting game ensues (Field, Calbert and Keller[21], Wilson,[86]). The resident sits motionless on the centre of the patch, while the intruder waits near the patch periphery. When competition was restricted to pairwise events, all observations pointed to a clear behavioural pattern. After some time, the resident commenced radial searches around the patch, each search increasing in radius, after which it leaves the patch altogether, a patch leaving strategy common amongst many insect parasitoids (Wagge,[82], Godfray,[26]). Some time thereafter, the intruder is observed to return to the unguarded patch, after which it sets forth to superparasitise the patch (Field, Calbert and Keller,[21], Cumber,[12]).

There are sound reasons, based on behavioural observations, to believe that the return strategy of the intruder may be considered as the final return and not just another attempt to covertly superparasitise in the presence of the resident (Field, Calbert and Keller,[21]). Firstly, during this phase of competition, the resident has completely ceased searching for unparasitised hosts and instead adopts a purely defensive role, remaining stationary at the center of the patch to maximise any detection of movement whilst occassionally making excusions to the patch boundary, presumably to find the intruder (Field,[19]). This is in contrast to the second phase of competition, in which roles are established but the resident still searches for remaining hosts, exposing the patch to covert intruder ovipositions (Field,[19] and Chapter 3). Second, the intruder no longer is seen to walk onto the patch, rather it waits near the patch boundary, occasionally moving closer, presumably to obtain information as to the resident's location (Field, Calbert and Keller,[21]). Finally, when the intruder returns to find a resident after a significant period of time waiting it leaves, though these observations are rare (Field, personal communication).

This game, known here as the waiting game (Field, Calbert and Keller,[21]) motivates a series of questions about adaptive significance. Why should the resident leave at the observed time? Does the intruder know when the resident has left? The first question can be answered when viewing patterns of resident leaving times, as a function of the patch size and the resident/intruder assymetries in patch investment. The waiting game lasts longer with large patch sizes and highly skewed investments (Field, [19]). The second question is more difficult to definitively answer. Initially it was thought that the intruder possessed no information about the leaving time of the resident. It is the purpose of this chapter and the next to study the waiting game under differing assumptions of information exchange about the departure time of the resident given to the intruder.

A game of similar structure exists, in the context of interspecific competition, with a predator-prey game between predaceous bullheads, *Cottus gobio* and case making caddis larvae, *Halesus radiatus* (Johansson, [39]). Predators attacked the caddis larvae and surviving individual larvae feigned dead for some time as the bullheads waited for signs of caddis larvae movement. Winners in this game are the individuals that persisted longest in waiting (Johansson, [39]). For the predator, a longer persistance time ensures catching and consuming further larvae, for the prey longer persistance implies safe passage from predation.

Of biological importance was the conclusion that the waiting times of both predator and prey depend on each players estimation of habitat value and information passed between players during the predators' attack of the prey. In the predator-prey game, a key theoretical point was made noting the instability of models based on the assymetric war of attrition (Hammerstein and Parker,[31]) as this approach to a waiting strategy cannot take into account information exchanges between opponents during the commencement or course of the game (Johansson,[39]).

Without information exchange on the leaving time of the resident, the waiting game *is not* a war of attrition, for the following reasons. Firstly, there is an assymmetry in the roles and actions of the resident and intruder, whereas in the war of attrition both players adopt the same action of attrition. Second, in the war of attrition, if either player surrenders, the game ends and the payoff is given to the victor with costs payed by both players. In the waiting game, the resident may leave without the knowledge of the intruder, who percieves the game is still on. A payoff is given to both players, even if the intruder returns to a guarded patch.

If the waiting game without information exchange is not a war of attrition, what strategies should one play? If patch payoffs are given to both players, albeit a lower payoff to the resident if the intruder superparasitises, should the waiting game be played at all? In this Chapter it is proved that no ESS exists if there is no information exchange as to the leaving time of the resident. Two arguments are developed which underlie the proofs. If the intruder returns after the resident, as there is no information exchange about the resident's leaving time given to the intruder, the resident may cheat, leaving at earlier and earlier times. The second argument is the instability of any leaving time if the intruder returns before the resident. If the intruder returns before the resident, as there is no selection on the resident's departure time, leaving it free to drift towards the commencement of the game. This makes the resident's leaving time unstable and an unsuitable candidate for an ESS.

Though rare, ocassionally an intruder is injured during the contest for residency, usually with severed antennae (Field,[19]). This motivated a model of the waiting game in which the intruder may be absent from the contest altogether. With this assumption, there is a tradeoff for the resident, between leaving at the commencement of the game, the best strategy if the intruder is not present, and guarding the patch against an intruder return. Motivated by this tradeoff, mixed strategies may be candidates for an ESS.

Following this introduction, the assumptions behind the waiting game are listed in Section 4.2. We show that a set of leave/return time pure strategies cannot form an ESS, in Section 4.3. The instability of leave/return pure strategies is illustrated through simulation, in Section 4.3.1. Next, we consider strategies when there is uncertainty concerning the presence of the opponent in Section 4.4. Mixed leave/return strategies are derived, but are shown to be evolutionarily unstable, both with certainty and uncertainty in the presence of the opponent. New assumptions and approaches to modelling the waiting game are discussed in the Conclusion, Section 4.5.

4.2 Assumptions

Before commencing the construction of the waiting game, a list of assumptions is stated below

- There are two competitors in this game, a resident female that guards a patch of self and conspecific parasitised eggs and an intruding conspecific that waits at the patch perifery for the resident to leave, in order to superparasitise the patch.
- Both players adopt a strategy to maximise their expected fitness from the commencement of the waiting game to the end of the day. We have chosen the end of day as the boundary time for the model for two reasons.
    1. At the end of the day, surface temperature is reduced, so insects tend to

stop the process of competition (Field,[19]).

2. Fitness gains or losses from the patch will not change from the next day, as the parasitised/superparasitised larvae will be entrenched in the host egg (see Section 1.2 and Figure 1.2.1).

- A resident adopts a time to leave the patch and an intruder chooses a time to return from the patch periphery. The leave/return times may be pure strategies or times drawn from a set of leaving time distributions and return time distributions.

- Either competitor may be absent, due to external factors such as predation, discovery of another patch or competitive factors such as injury caused by agonistic conflict, may be *absent* from competition for the patch.

- If an intruder returns to a guarded patch, then information is exchanged to the intruder about the presence of resident and information is exchanged to the resident about the presence of the intruder. Thus, if t_R is the leaving time of the resident and t_I is the return time of the intruder, information is exchanged if $t_R > t_I$. If $t_R \leq t_I$, no information is exchanged to the intruder about the leaving time of the resident. This assumption, constructed to highlight ESS analysis without information exchange, is altered in the next chapter.

- Suppose a player leaves the patch and returns to the habitat at some time t from the commencement of the game, then the fitness that yet can be realised within this day by a parasitoid abandoning the current patch at time t, defined here to be the post patch habitat payoff $\phi(t)$ is collected where ϕ has the following form

$$\phi(t) = \alpha - C(t).$$

  Here α is the maximal habitat payoff associated with leaving at the commencement of the waiting game, time $t = 0$, and $C(t)$ is the cost associated with leaving some time t thereafter. A simple linear example of a post patch habitat payoff is

$$\phi(t) = \alpha\Big(1 - (\frac{t}{H})\Big),$$

where α is the baseline habitat value and H denotes the time to the end of the day. We note that in general, $\phi(t)$ is assumed to be continuous, differentiable and strictly decreasing.

- Suppose both players are present to compete for the patch. If the intruder returns at time t_I while the resident is still present guarding the patch, then it collects a payoff determined by any previous investment before the waiting game. This payoff is denoted by int_p. As the intruder returns to a guarded patch, it is assumed that it is removed immediately by the resident. As this is assumed to be the final return, the intruder leaves collecting a post patch habitat payoff $\phi(t_I)$. On the intruder's return to the patch at time t_I, if the resident is absent then it collects a payoff determined by previous patch investments as well as the superparasitism of the resident's patch investment. This payoff is denoted by int_{sp}. Subsequent to this the intruder leaves and collects a habitat payoff $\phi(t_I + \mathcal{T})$, where $\mathcal{T}$ is the time taken for the intruder to superparasitise the patch. For the rest of the analysis of the waiting game we will assume that $\mathcal{T}$ is small in comparison to both the resident's guarding time and the intruder's waiting time - thus can be effectively taken to be zero.

- Suppose again that both players are present to compete for the patch. If the resident leaves at time t_R and the intruder has not returned, then the resident collects a patch payoff determined by its previous investment and the intruder's superparasitism of the patch. This is denoted by res_{sp}. Upon leaving the patch a habitat payoff $\phi(t_R)$ is also collected. If the intruder returns at time t_I to an occupied patch, then no superparasitism of the resident's patch investment occurs and the resident collects the payoff res_p and habitat payoff $\phi(t_I)$.

We note here that these assumptions make the game fundamentally different to the war of attrition since in this game the first player to cease competition ends the game.

- If an intruder returns to superparasitise then the patch payoff to this player increases whereas the patch payoff to the resident decreases. Therefore

  $$res_p > res_{sp} \text{ and } int_{sp} > int_p.$$

- Finally we assume that the fitness gain to the intruder by superparasitism is the fitness loss of the resident. Hence if $\Delta res = res_p - res_{sp}$ and $\Delta int = int_{sp} - int_p$, then

  $$\Delta res = \Delta int = \Delta.$$

4.2.1 Expected Payoffs

This section addresses the payoffs to both players. It will be assumed that the game commences at time $t = 0$. Remembering that both players cannot ascertain the presence or absence of the opponent, we have the following definitions of presence to play the game

$$\sigma_R = \Pr(\text{resident plays the waiting game})$$

and

$$\sigma_I = \Pr(\text{intruder plays the waiting game}).$$

It is noted that the probabilities $(1 - \sigma_I), (1 - \sigma_R)$ are leaving atoms of probability at the commencement of the game.

Conditioned on the presence of both competitors, $\sigma_R = \sigma_I = 1$, here denoted by the event $\mathcal{BP}$, suppose the resident chooses a time t_R to leave the patch where $0 \leq t_R \leq H$ and the intruder chooses a time t_I to return to the patch with $0 \leq t_I \leq H$. Let $E(R \mid t_R, t_I, \mathcal{BP})$ be the expected payoff to the resident given times t_R, t_I and both players present, then this expectation satisfies

$$E(R \mid t_R, t_I, \mathcal{BP}) = \begin{cases} res_p + \phi(t_I) & \text{for} \quad t_R > t_I, \\ res_{sp} + \phi(t_R) & \text{for} \quad t_R \leq t_I. \end{cases}$$

Similarily let $E(I \mid t_I, t_R, \mathcal{BP})$ be the intruder's expected payoff conditioned on times t_R, t_I and both being present. It is observed that

$$E(I \mid t_R, t_I, \mathcal{BP}) = \begin{cases} int_{sp} + \phi(t_I) & \text{for} \quad t_I \geq t_R, \\ int_p + \phi(t_I) & \text{for} \quad t_I < t_R. \end{cases}$$

There are a few points to emphasise about the expected payoffs. First, the intruder superparasitises the patch even when the resident's leaving time is the same as the intruder's return time, this assumption being used to highlight information exchange. Second, as it is assumed that this is the final intruder return, when $t_I < t_R$, the payoff to the resident is $res_p + \phi(t_I)$, *not* $res_p + \phi(t_R)$, the payoff from leaving at the time selected at the beginning of the waiting game. If the intruder leaves altogether when intercepted by the resident, then it would not be evolutionarily advantageous for the resident to wait till time t_R to leave, as it would lose $\phi(t_R) - \phi(t_I)$ fitness points.

4.3 Pure Strategies with Certainty in the Presence of the Opponent

The dynamics of resident leaving times and intruder return times are analysed with the previous assumptions under the condition of $\sigma_I = \sigma_R = 1$. In this Section, we restrict our analysis to that of pure strategies. Mixed strategies will be considered both when $\sigma_I < 1, \sigma_R < 1$ and $\sigma_I = \sigma_R = 1$ in Section 4.4.

In the normal definition of an ESS, the roles of each player are identical, thus strategy w^* is an ESS if the expected payoff $E(w^*, w^*) > E(w, w^*)$ for other w belonging to the strategy set defined in the game (Maynard Smith,[54]). When considering a game in which the roles of each player are well defined, making the game assymetric, we must apply a definition of evolutionary stability in which each player finds the best response when that player is in a particular role. This role dependent best response is called an evolutionary stable local strategy (Hammerstein,[30]). First we define an evolutionary stable set of local strategies.

Definition 1 (Evolutionary Stable Local Strategies) *Strategies* R^* *and* I^* *are defined to be evolutionary stable local strategies if for all strategies of the resident* $S_R \neq R^*$ *and all strategies of the intruder* $S_I \neq I^*$*, the expected payoff to the resident adopting strategy* R^* *against the intruder satisfies*

$$E(R|R^*, I^*, \mathcal{BP}) > E(R|S_R, I^*, \mathcal{BP})$$

and the expected payoff to the intruder adopting I^* *satisfies*

$$E(I|R^*, I^*, \mathcal{BP}) > E(I|R^*, S_I, \mathcal{BP}).$$

Now suppose leave/return times are denoted by t_R, t_I where $t_R \geq 0$ and $t_I \geq 0$.

Theorem 2 *There is no Evolutionary Stable set of Local Strategies in the waiting game when the intruder has no information about the leaving time of the resident.*

Proof

We will consider four cases, when $t_R < t_I, t_R > t_I, t_R = t_I = 0$ and when $t_R = t_I > 0$.

Case one: If $t_R < t_I$, then the intruder superparasitises the patch. The intruder however, would increase its payoff by returning earlier to collect a higher habitat payoff since

$$int_{sp} + \phi(t_I) < int_{sp} + \phi(t_I - \epsilon),$$

for an arbitrarily small positive ϵ. Thus

$$E(I|t_R, t_I, \mathcal{BP}) < E(I|t_R, t_I - \epsilon, \mathcal{BP}).$$

Therefore the strategies t_R and t_I cannot be evolutionarily stable when $t_R < t_I$.

Case two: If $t_R > t_I$ then the intruder returns early and is removed by the resident. The resident however would do better by leaving slightly earlier, increasing its habitat payoff since

$$res_{sp} + \phi(t_R) < res_{sp} + \phi(t_R - \epsilon).$$

This implies that

$$E(R|t_R, t_I, \mathcal{BP}) < E(R|t_R - \epsilon, t_I, \mathcal{BP}).$$

Again the strategies t_R and t_I cannot be evolutionarily stable if $t_R > t_I$.

Case three: If $t_R = t_I = 0$ then the intruder superparasitises the patch, since no information was exchanged about the intruder's return time when the resident leaves at the same time (see Section 4.2.1). The resident would do better by leaving at a time arbitrarily larger than zero, since

$$res_{sp} + \phi(0) < res_p + \phi(\epsilon)$$

if ϵ is sufficiently small and positive. Therefore

$$E(R|0, 0\mathcal{BP}) < E(R|\epsilon, 0, \mathcal{BP}).$$

Case four: Finally we consider $t_R = t_I > 0$. Again the patch is superparasitised by the intruder. Here, the resident would do better by leaving earlier to collect a larger habitat payoff, as

$$res_{sp} + \phi(t_R) < res_{sp} + \phi(t_R - \epsilon).$$

Hence

$$E(R|t_R, t_I, \mathcal{BP}) < E(R|t_R - \epsilon, t_I, \mathcal{BP})$$

and t_R, t_I cannot be evolutionarily stable if $t_R = t_I > 0$. This concludes the proof of the instability of the waiting game without information exchange of the leaving time of the resident.

□

The results above rely on the assumptions of information exchange. Without information exchange to the intruder on the leaving time of the resident, there is no *evolutionary incentive* for the resident to guard. Therefore, the resident leaving times will drift towards zero, without intruder estimates of the leaving time of the opponent.

4.3.1 Simulations of Leave/Return times.

The instability of resident/ intruder strategies is best illustrated by studying the evolutionary dynamics of each strategy over the course of time. The following method simply traces the dynamics of strategies, by choosing the best strategy that is a small increment away from the current strategy.

Consider an initial set of leave/return times denoted by $(t_R[0], t_I[0])$. Now suppose we restrict the evolution of strategies to be at most δ away from the current strategy where δ is some small positive constant. Strategies at generations g and $(g+1)$, denoted by $(t_R[g], t_I[g])$ and $(t_R[g+1], t_I[g+1])$ will thus satisfy

$$\begin{aligned} |\ t_R[g] - t_R[g+1]\ | &\leq \delta, \\ |\ t_I[g] - t_I[g+1]\ | &\leq \delta. \end{aligned}$$

Consider the strategies at generation $g, t_R[g]$ and $t_I[g]$. The strategy $t_R[g+1]$ is calculated according to the expected fitness of strategies $t_R[g]-\delta, t_R[g], t_R[g]+\delta$ against $t_I[g]$. If there is a unique maximum then simply

$$t_R[g+1] = \arg\max\left\{E(R|t_R[g]-\delta, t_I[g], \mathcal{BP}), E(R|t_R[g], t_I[g], \mathcal{BP}), E(R|t_R[g]+\delta, t_I[g], \mathcal{BP})\right\}.$$

This unique strategy is called the δ−step best response.

When there are two or three strategies of equal fitness, as is the case when $t_I[g] < t_R[g]$, where all strategies $t_R \in (t_I[g], H]$ yield equal fitness, then the strategy at generation $g+1$ is chosen probabilistically in order to simulate genetic drift

(Futuyma,[25]). Thus, for example, if

$$E(R|t_R[g]-\delta, t_I[g], \mathcal{BP}) = E(R|t_R[g], t_I[g], \mathcal{BP}) = E(R|t_R[g]+\delta, t_I[g], \mathcal{BP}),$$

then

$$t_R[g+1] = \begin{cases} t_R[g]-\delta & \text{with} \quad \text{probability} = 1/3, \\ t_R[g] & \text{with} \quad \text{probability} = 1/3, \\ t_R[g]+\delta & \text{with} \quad \text{probability} = 1/3. \end{cases}$$

Restricting the evolution of strategies to $\delta-$step best responses has the advantage of clearly explicating the evolution of strategies, however this restriction does not fully portray the evolution of strategies when these strategies are allowed to undergo "jumps". In order to illustrate how a jump would occur, we must define the time, denoted by $\widehat{t}$, where the payoff from leaving at the commencement of the game, forfeiting fitness gains from patch defence if resident, equals the fitness gains from defending the patch. Thus $\widehat{t}$ satisfies

$$res_p + \phi(\widehat{t}) = res_{sp} + \phi(0).$$

If the intruder refrains from waiting, forfeiting potential gains from superparasitism, this will similarily yield equal fitness returns from waiting till $\widehat{t}$ since

$$int_{sp} + \phi(\widehat{t}) = int_p + \phi(0).$$

With the definition of $\widehat{t}$ in mind, suppose at some generation $g, t_R[g] > \widehat{t}$ and $t_I[g] = 0$. As the intruder always returns earlier than the resident, the strategy of the resident will not be subject to selection and will therefore drift. Let κ be the first generation after g where the leaving time of the resident drifts below $\widehat{t}$, so

$$\kappa = \inf\{l \text{ such that } t_R[g+l] < \widehat{t}\}.$$

Before generation $g+\kappa$ is reached, there is no fitness advantage for the intruder to make a jump in its return time strategy. The only possible fitness advantage would be to return after the resident has left, at time $t_I[g+k] = t_R[g+k] + \epsilon, 0 \leq k < \kappa$, where ϵ is an arbitrarily small positive constant, to gain fitness from the superparasitism of the patch. However, the fitness accrued from this jump would be less than that of leaving at the commencement of the game since

$$\begin{aligned} int_{sp} + \phi(t_I[g+k]) &= \\ &= int_{sp} + \phi(t_R[g+k] + \epsilon) \\ &< int_{sp} + \phi(\widehat{t}) \\ &= int_p + \phi(0) \\ &= int_p + \phi(0). \end{aligned}$$

When generation $g+\kappa$ is reached, the *best response* of the an intruder is to return after the resident at time $t_I[g+\kappa+1] = t_R[g+\kappa]+\epsilon < \widehat{t}$, since by the definition of $\widehat{t}$, the fitness gain of the intruder from superparasitism outweighs the cost of waiting

$$int_{sp} + \phi(t_I[g+\kappa+1]) > int_p + \phi(t_I[g+\kappa]) = int_p + \phi(0).$$

This jump in return time strategy will not happen when we are restricted to $\delta-$step best responses as the only $\delta-$step best response available to the intruder when $t_I[g+\kappa] = 0$ is to return at time $t_I[g+\kappa+1] = \delta$, which will not increase the intruder's fitness since

$$int_p + \phi(t_I[g+\kappa]) = int_p + \phi(0) > int_p + \phi(t_I[g+\kappa] + \delta),$$

hence no single step will increase the intruder's fitness, thus the intruder's return time strategy will remain at zero, if we restrict our analysis to $\delta-$step best responses.

Though the analysis of leave/return time trajectories does not allow jumps in the evolutionary strategy, if a mutant strategy with increased fitness is introduced into the population, it is unlikely to replace the current population strategy in a single generation (see McNamara, Webb, Collins, Szekely and Houston,[60] for a discussion of the invasion of a population strategy with alternative strategies). Instead, the strategy will spread over a series of generations, implying a continuous change in the strategy over the course of several generations. Thus, $\delta-$step best responses will mimic the slow change in population strategy trajectories.

The trajectories of respective strategies will depend on the initial conditions, and will mimic the strategy responses given in the proofs of the instability of pure strategies (Section 4.3).

Consider Figure 4.3.1, with the initial conditions $t_I[0] = t_R[0] = 20$. As the

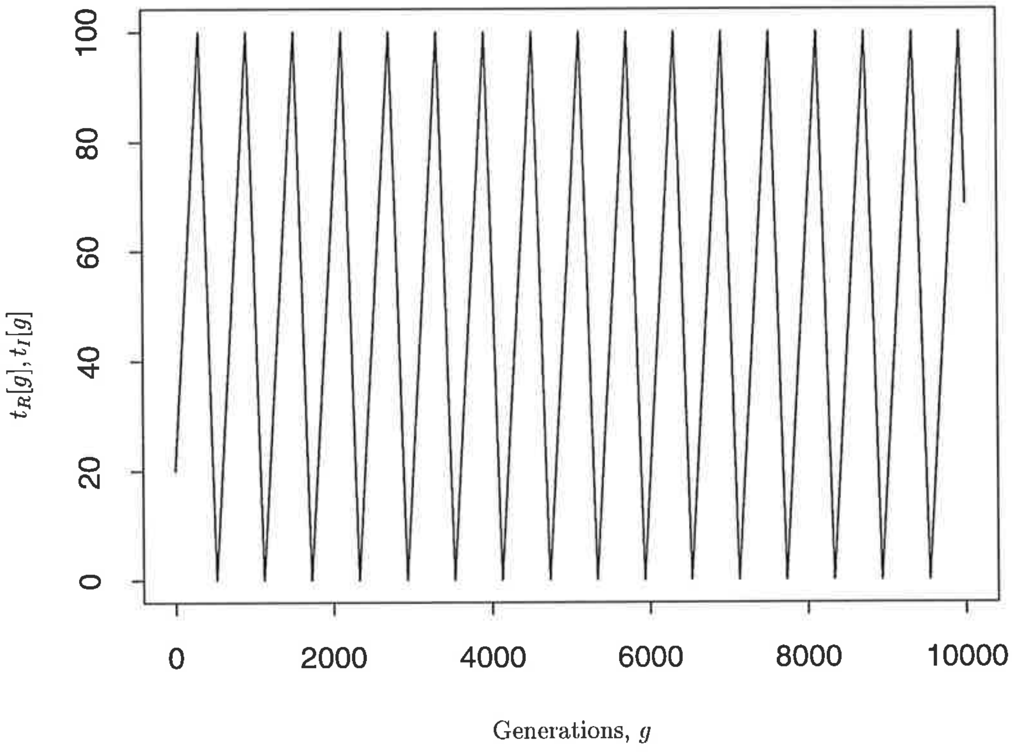

Figure 4.3.1: Cycling of strategies when the initial conditions are equal, $t_I[0] = t_R[0] = 20$. Here parameters are $\alpha = 10, \Delta = 10, res_p = int_{sp} = 20, res_{sp} = int_p = 10, \delta = 0.5, H = 100$.

intruder superparasitises the patch (see the expected payoffs in Section 4.2.1), when the initial conditions are equal, the $\delta-$step best response of the resident is to increase its leaving time to $t_R[0]+\delta$, with an increase in fitness of $res_p+\phi(t_R[0]+\delta)-res_{sp}-\phi(t_R[0])\approx\Delta+\delta\phi'(t_R[0])$ fitness units. In turn, the $\delta-$step best response of the intruder is to return at $t_I[0]+\delta$ to superparasitise the patch. This process is repeated until the leave/return times reach the end of the day, where at some generation $g', t_R[g']=t_I[g']=H$. In generation g' the intruder superparasitises the patch and the only $\delta-$step best response of the resident is to leave at an earlier time, increasing habitat payoff, whilst still exposing the patch to intruder superparasitism. Thus at generation $g'+1, t_R[g'+1]=H-\delta$. The intruder's $\delta-$step best response is to "follow" the resident, increasing its own habitat payoff while still superparasitising the patch. This process continues, instigating the process of strategy cycling seen in Figure 4.3.1.

Figure 4.3.2 considers the evolution of strategies when $t_I[0]<t_R[0]$. As the intruder returns to a guarded patch, its only $\delta-$step best response is to return earlier, increasing habitat payoffs, thus $t_I[1]=t_I[0]-\delta$. There is no incentive for the resident to follow the intruder's strategy in its return time decent to the commencement of the waiting game, since the resident intercepts the intruder at earlier and earlier times, increasing its own habitat payoff as $E(R|t_R,t_I,\mathcal{BP})=res_p+\phi(t_I)$ if $t_I<t_R$. Because there is no selection on the resident's leaving time when $t_I[g]<t_R[g]$, then the leaving time will drift.

When the initial conditions are such that $t_I[0]>t_R[0]$, the leave/return time trajectories mimic those seen when $t_I[0]=t_R[0]$, as in figure 4.3.1. If $t_I[0]>t_R[0]$, the intruder successfully returns to superparasitise. The only resident $\delta-$step best response is to leave earlier, collecting a larger habitat payoff, thus $t_R[1]=t_R[0]-\delta$. Similarily, the intruder's $\delta-$step best response will be to leave earlier, collecting a higher habitat payoff whilst superparasitising the patch. At some generation $\hat{g}$, the resident's strategy evolves to zero and the intruder's return time catches up with the resident's leaving time so $t_R[\hat{g}]=t_I[\hat{g}]=0$. At generation $\hat{g}+1$, a resident will evolve to recoup the fitness gains lost from superparasitism, leaving at $t_R[\hat{g}+1]=\delta$. The intruder's strategy will catch up with the resident's strategy in the next generation,

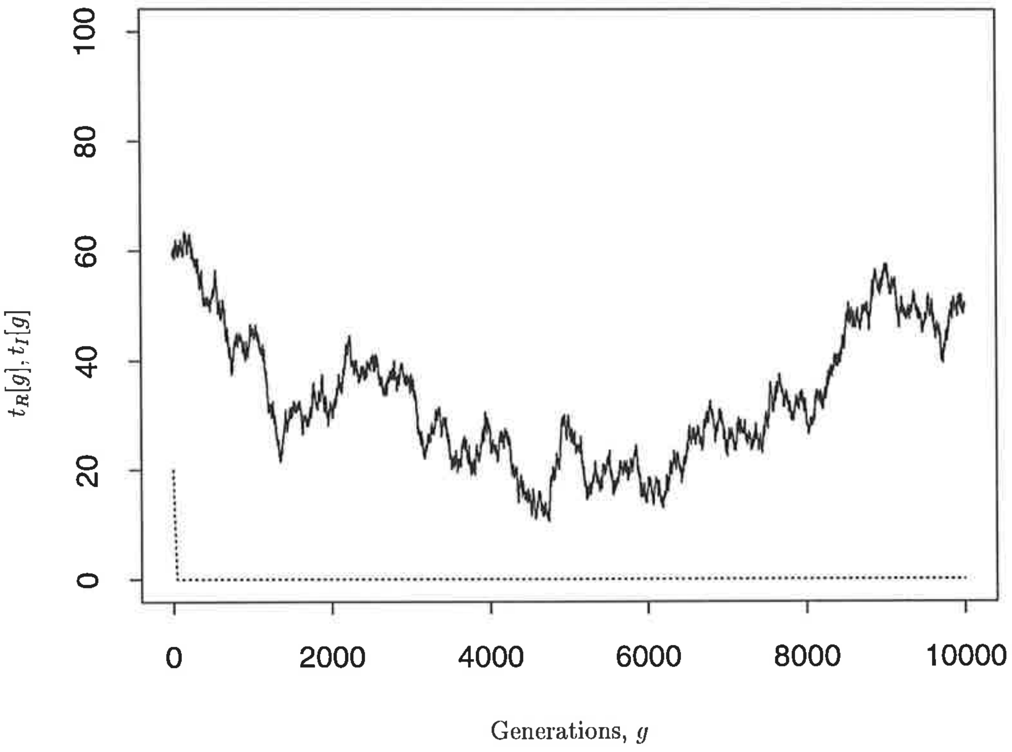

Figure 4.3.2: Drift of the resident's leaving time with the initial conditions $t_I[0] < t_R[0]$. The parameters in this simulation are $t_I[0] = 20, t_R[0] = 60, \alpha = 10, \Delta = 10, res_p = int_{sp} = 20$ and $res_{sp} = int_p = 10, \delta = 0.5, H = 100$.

so the process of evolutionary strategy cycling continues.

4.4 Uncertainty in Opponent Presence: Can a mixed strategy form an ESS?

When there is uncertainty in the presence of the opponent then the resident cannot assume that the intruder will return to superparasitise. Uncertainty in the presence of the opponent was one of the topics of research when attempting to find ESS strategies for the waiting game. The motivation for this direction of research came from the observation of injuries incurred during patch competition (Field,[19]). During one fight, a female had an antennae severed, causing it to leave the patch altogther, though lesser injuries such as bites forced the injured player to become an intruder, adopting the pattern of playing the waiting game (Field, personal observation). In keeping with the theme of this thesis, patch defence models with different information states, we will consider modelling the waiting game, under the assumption that there is a small probability of the opponent being absent during the waiting game.

The inclusion of a small probability of opponent injury changes the possible set of decisions that the resident can make, as there now is the resident's tradeoff between leaving early, to collect maximal habitat returns and waiting for the possible return of the intruder. Because of this tradeoff between leaving early and waiting for the opponent to leave/return, mixed leave/return distributions are sought, using the Bishop-Cannings theorem of constancy of payoffs (Bishop and Cannings,[3], also see Chapter 1).

In deriving a set of mixed leave/return strategies, the set of pure strategies used to define the mixed strategy must be defined.

Definition 2 (Support of a Mixed Strategy) *The support of some strategy S, defined by the probability density $p_S(x)$ or mass $\Pr(x)$ on the interval $x \in [0, \infty)$ is the set*

$$supp(S) = \{x \in [0, \infty) | p_S(x) \neq 0 \text{ or } \Pr(x) \neq 0\}.$$

Having previously defined a local ESS in Section 4.3, a version of the Bishop-Cannings theorem, in which a player may be present or absent is proved. Before doing this, expected payoffs to each player if absent are defined. Suppose the resident is absent, through injury or predation. The probability of absence, as defined in Section 4.2, is $(1 - \sigma_R)$. Here we define the expected payoff to the resident, if absent to be F_R. Similarily, if the intruder is absent, with probability $(1 - \sigma_I)$, then its expected payoff is F_I.

With these definitions, the Bishop-Cannings theorem, with presence/absence uncertainty, can now be proved.

Theorem 3 (Constancy of Expected Payoffs) *Let $\mathcal{RP}$ be the event that the resident is present and $\mathcal{IP}$ be the event that the intruder is present to play the waiting game. Suppose R^*, I^* are the respective local ESS's adopted by the resident and intruder, if present. Then the expected payoff to the resident satisfies*

$$E(R|t_R, I^*, \mathcal{RP}) = E(R|R^*, I^*, \mathcal{RP}) \text{ for all } t_R \in supp(R^*).$$

Similarily for intruder's leaving distribution we require

$$E(I|R^*, t_I, \mathcal{IP}) = E(I|R^*, I^*, \mathcal{IP}) \text{ for all } t_I \in supp(I^*).$$

Proof

This proof follows the same structure as that of (Bishop and Cannings, [3]). If R^*, I^* are the local ESS's for the resident and intruder, then by definition of evolutionary stability, for $t_R \in supp(R^*)$

$$\begin{aligned} \sigma_R(E(R|R^*, I^*, \mathcal{RP})) &+ (1-\sigma_R)(F_R) > \\ \sigma_R(E(R|t_R, I^*, \mathcal{RP})) &+ (1-\sigma_R)(F_R). \end{aligned}$$

Hence, $E(R|R^*, I^*, \mathcal{RP}) > E(R|t_R, I^* \mid \mathcal{RP})$. Now let $\Pr(t_R|\mathcal{RP})$ be the resident's leaving distribution, which may include atoms of probability, conditioned on staying to defend the patch. Then

$$\begin{aligned} E(R|R^*, I^*, \mathcal{RP}) &= \int_{supp(R^*)} E(R|t_R, I^*, \mathcal{RP}) d\Pr(t_R|\mathcal{RP}) \\ &\leq \int_{supp(R^*)} E(R|R^*, I^*, \mathcal{RP}) d\Pr(t_R \mid \mathcal{RP}) \\ &= E(R|R^*, I^*, \mathcal{RP}). \end{aligned}$$

The only way that this inequality can be satisfied is if

$$E(R|t_R, I^*, \mathcal{RP}) = E(R|R^*, I^*, \mathcal{RP}) \text{ for all } t_R \in supp(R^*).$$

The proof of constant payoffs for the intruder follows in precisely the same manner.

□

4.4.1 Strategies with Constant Payoff

Before commencing construction of the leave/return time distributions some comments about the support of both players are made.

Theorem 4 (Equality of Supports) *Suppose R^* and I^* are respective ESS's with supports $supp(R^*)$ and $supp(I^*)$, then $supp(R^*) = supp(I^*)$.*

Proof

Suppose that $a, b \in supp(I^*), a < b$, and the return time distribution of the resident is denoted by $\Pr(t_R)$. By the Bishop-Cannings theorem the difference

$$E(I^*|a, R^*, \mathcal{IP}) - E(I^*|b, R^*, \mathcal{IP}) = 0,$$

if I^* is an ESS. Now

$$\begin{aligned} E(I^*|a, R^*,\mathcal{IP}) - E(I^*|b, R^*,\mathcal{IP}) = \\ & \sigma_R\Big(\Pr(t_R < a)\{int_{sp} + \phi(a) - int_{sp} - \phi(b)\} \\ + & \Pr(a \le t_R < b)\{int_p + \phi(a) - int_{sp} - \phi(b)\} \\ + & \Pr(t_R > b)\{int_p + \phi(a) - int_p - \phi(b)\}\Big) \\ + & (1 - \sigma_R)\{int_{sp} + \phi(a) - int_{sp} - \phi(b)\} \\ = & \sigma_R \Pr(a \le t_R < b)(int_p - int_{sp}) + (\phi(a) - \phi(b)). \end{aligned}$$

As $\phi(a) - \phi(b) > 0$, since ϕ is monotonic decreasing and $int_p - int_{sp} = -\Delta < 0$, this implies that

$$\Pr(a \le t_R < b) > 0,$$

if the Bishop-Cannings theorem is to be satisfied. As $\Pr(a \le t_R < b) > 0$ this implies that $(a, b) \cap supp(R^*) \neq \emptyset$, as this holds for all $a, b \in supp(I^*)$ then

$$supp(I^*) \subseteq supp(R^*).$$

By exactly the same method we can show that $supp(R^*) \subseteq supp(I^*)$, so

$$supp(I^*) = supp(R^*).$$

□

Using the Bishop-Cannings theorem, leave/return densities are now derived, with the resident's leaving density derived first. As the supports of both players must be equal, the derivation of the leaving time density and return time density will be done on an interval in $[0, H]$.

Suppose the intruder adopts return time t_I, the resident's ESS, R^*, is to leave with probability density conditioned on being present to play the game $p_R(t \mid \mathcal{RP})$. The expected payoff to the intruder adopting pure strategy t_I, $E(I|t_I, R^*, \mathcal{IP})$ given that it plays the waiting game and is not injured is

$$\begin{aligned} E(I|t_I, R^*, \mathcal{IP}) &= \sigma_R\Big\{ \int_0^{t_I} p_R(\tau \mid \mathcal{RP})(int_{sp} + \phi(t_I))d\tau \\ &+ \int_{t_I}^{H} p_R(\tau \mid \mathcal{RP})(int_p + \phi(t_I))d\tau\Big\} \\ &+ (1 - \sigma_R)\{int_{sp} + \phi(t_I)\}. \end{aligned}$$

For constancy of payoffs, the derivative with respect to pure strategy t_I must be zero, that is,

$$\frac{\partial}{\partial t_I} E(I|t_I, R^*, \mathcal{IP}) = 0.$$

Before differentiating, let $t_I = t$ for convenience. The derivative then takes the form

$$\begin{aligned} &\sigma_R\Big\{int_{sp} p_R(t \mid \mathcal{RP}) + \phi(t) p_R(t \mid \mathcal{RP}) + \phi'(t) \int_0^t p_R(\tau \mid \mathcal{RP})d\tau \\ &- \ int_p p_R(t \mid \mathcal{RP}) - \phi(t) p_R(t \mid \mathcal{RP}) + \phi'(t) \int_t^H p_R(\tau \mid \mathcal{RP})d\tau\Big\} \\ &+ \ (1 - \sigma_R)\phi'(t) = 0. \end{aligned}$$

Grouping terms and noting the normalisation condition $\int_0^H p_R(\tau \mid \mathcal{RP})d\tau = 1$, this expression simplifies to

$$\sigma_R\Big\{\Delta p_R(t \mid \mathcal{RP}) + \phi'(t)\Big\} + (1 - \sigma_R)\phi'(t) = 0$$

hence

$$\sigma_R \Delta p_R(t \mid \mathcal{RP}) + \phi'(t) = 0.$$

Therefore, if a leaving density is a candidate ESS, then

$$p_R(t \mid \mathcal{RP}) = -\frac{\phi'(t)}{\sigma_R \Delta}.$$

Now to the intruder's return density. The expected payoff $E(R|t_R, I^*, \mathcal{RP})$ to the resident adopting pure strategy t_R, against an intruder that adopts the strategy I^*, with density $p_I(\tau \mid \mathcal{IP})$ has the form

$$\begin{aligned} E(R|t_R, I^*, \mathcal{RP}) &= \sigma_I\Big\{\int_0^{t_R} p_I(\tau \mid \mathcal{IP})(res_p + \phi(\tau))d\tau \\ &+ \int_{t_R}^{H} p_I(\tau \mid \mathcal{IP})(res_{sp} + \phi(t_R))d\tau\Big\} \\ &+ (1-\sigma_I)(res_p + \phi(t_R)). \end{aligned}$$

Again the constancy condition is applied $\frac{\partial}{\partial t_R}E(R|t_R, I^*, \mathcal{RP}) = 0$. Differentiating and setting $t_R = t$

$$\sigma_I\Big\{res_p p_I(t \mid \mathcal{IP}) + \phi(t)p_I(t \mid \mathcal{IP}) - res_{sp}p_I(t \mid \mathcal{IP}) - \phi(t)p_I(t \mid \mathcal{IP})$$
$$+\phi'(t)\int_t^H p_I(\tau \mid \mathcal{IP})d\tau\Big\} + (1-\sigma_I)\phi'(t) = 0,$$

or

$$\sigma_I\{\Delta p_I(t \mid \mathcal{IP}) + \phi'(t)\int_t^H p_I(\tau \mid \mathcal{IP})d\tau\} + (1-\sigma_I)\phi'(t) = 0$$

This expression can for solved for $p_I(t \mid \mathcal{IP})$ by setting $S(t) = \int_t^H p_I(\tau \mid \mathcal{IP})d\tau$ so $S'(t) = -p_I(t \mid \mathcal{IP})$. The function $S(t)$ satisfies the differential equation

$$\sigma_I\Big\{-\Delta\frac{\partial}{\partial t}S(t) + \phi'(t)S(t)\Big\} + (1-\sigma_I)\phi'(t) = 0$$

This is a first order linear differential equation, with solution up to a constant ς,

$$S(t) = \varsigma \exp\left(\frac{\phi(t)}{\Delta}\right),$$

hence

$$p_I(t \mid \mathcal{IP}) = -\xi\phi'(t)\exp\left(\frac{\phi(t)}{\Delta}\right)$$

where $\xi = \varsigma/\Delta$. The constant ξ is a function of the probability of intruder presence, σ_I.

To summarise, we have found a leaving density $p_R(t|\mathcal{RP})$ and to within a constant, a return time density $p_I(t|\mathcal{IP})$ that yield constant payoffs, if the supports of the two players are equal.

Are the supports of the players equal, as required for an ESS? When considering pure strategies in Section 4.3, an upper bound time $\widehat{t}$ was found such that if players left/returned after this time their best possible payoff would be less than that of leaving at the commencement of the game. A strategist adopting time $t = 0$ would be selected over a strategist adopting time $\widehat{t} + \epsilon$, where ϵ is an arbitrarily small positive constant.

Now consider the case when $\sigma_R < 1$ and $\sigma_I < 1$. The supports of the resident and intruder cannot be equal if we consider the upper bound times, as is shown in the following lemma.

Lemma 3 *If $\sigma_I < 1$, then supp$(R^*) \neq$ supp(I^*).*

Proof

The proof is based on calculating the upper bound times for leave/return strategies. Leaving at the commencement of the game will not be selected over guarding till time t, whilst

$$res_p + \phi(t) > \sigma_I res_{sp} + (1 - \sigma_I)res_p + \phi(0).$$

Here, the probability of the intruder being absent is factored into the payoff from leaving at the commencement of the game. At equality, let this time be denoted by $\widehat{t_R}$, which satisfies $\phi(0) = \phi(\widehat{t_R}) + \Delta\sigma_I$. Similarily, an upper bound return time for the intruder, $\widehat{t_I}$, will satisfy

$$int_{sp} + \phi(\widehat{t_I}) = \sigma_R int_p + (1 - \sigma_R)int_p + \phi(0).$$

Considering the above expression, the intruder's payoff from returning immediately is composed of the habitat payoff, $\phi(0)$, plus the payoff if the resident is present, $\sigma_R int_p$ and the payoff if the resident is absent $(1 - \sigma_R)int_p$. Contrast this with the payoff from leaving immediately given to the resident, if the intruder is present

$\sigma_I res_{sp}$ and absent $(1 - \sigma_I)res_p$. Once the waiting game commences, the resident does not partake in any further parasitism or superparasitism of the patch, whereas the intruder will superparasitise if it returns after the resident, hence the payoffs from returning or leaving immediately will be different for both players. The time $\widehat{t_I}$) will therefore satisfy $\phi(0) = \phi(\widehat{t_I}) + \Delta$. As $\sigma_I < 1$, this implies that $\widehat{t_R} < \widehat{t_I}$.

Now let the fitness of the resident adopting leaving time density $p_R(t|\mathcal{RP})$, against an intruder adopting return time density $p_I(t|\mathcal{IP})$, if present, be denoted by $E(R|p_R, p_I, \mathcal{BP})$. If the resident has a positive probability $\Pr(t_R > \widehat{t_R})$ of guarding within the interval $(\widehat{t_R}, \widehat{t_I}]$ then it will be selected against by a mutant assigning this probability to leaving at the commencement of the game since

$$\begin{aligned} E(R|p_R, p_I, \mathcal{RP}) &= \Pr(t_R \leq \widehat{t_R})E(R|p_R, p_I, \mathcal{RP}) + \Pr(t_R > \widehat{t_R})E(R|p_R, p_I, \mathcal{RP}) \\ &< \Pr(t_R \leq \widehat{t_R})E(R|p_R, p_I, \mathcal{RP}) + \Pr(t_R > \widehat{t_R})E(R|0, p_I, \mathcal{RP}). \end{aligned}$$

Thus $supp(R^*) \cap (\widehat{t_R}, \widehat{t_I}] = \emptyset$ if the resident strategy R^* is an evolutionary stable local strategy. This is not the case for the intruder, as in $t \in (\widehat{t_R}, \widehat{t_I})$

$$int_{sp} + \phi(t) > \sigma_R int_p + (1 - \sigma_R)int_p + \phi(0),$$

thus the fitness payoff from waiting surpasses that of leaving at the commencement of the game. These observations imply that when $\sigma_I < 1$, the intruder can choose to return after the resident and still gain fitness points, thus $supp(R^*) \neq supp(I^*)$, so the distributions listed above cannot form an ESS.

□

Originally, we studied the problem of finding pure strategy ESS's when both players were present, $\sigma_I = \sigma_R = 1$, (Section 4.3). Can mixed strategies form an ESS when $\sigma_I = \sigma_R = 1$? Consider the support structure

$$supp(R) = supp(I) = [0, \widehat{t}].$$

If we calculate the expected fitness of the intruder, given that it adopts return time distribution $p_I(\tau|\mathcal{IP})$

$$E(I|p_I, R, \mathcal{BP}) = \int_0^{\widehat{t}} \left[\int_0^{\tau} \frac{-\phi'(t)}{\Delta} \Big(int_{sp} + \phi(\tau) \Big) dt \right] p_I(\tau \mid \mathcal{IP}) dt$$

$$
\begin{aligned}
&+ \int_0^{\widehat{t}} \left[\int_\tau^{\widehat{t}} \frac{-\phi'(t)}{\Delta} \Big(int_p + \phi(\tau) \Big) dt \right] p_I(\tau \mid \mathcal{RP}) dt \\
&= \frac{1}{\Delta} \Big((int_{sp} + \phi(t))(\phi(0) - \phi(t)) + (int_p + \phi(t))(\phi(t) - \phi(\widehat{t})) \Big).
\end{aligned}
$$

The first integral corresponds to the payoff when the intruder returns *after the resident has left,* the second to *before the resident has left.* Recalling the definition of $\widehat{t}$, $\phi(0) = \Delta + \phi(\widehat{t})$, the non-constant terms in the intruder's expected fitness vanish and we are left with

$$E(I|R, p_I, \mathcal{BP}) = int_{sp} + \phi(\widehat{t}).$$

The fitness obtained by the intruder is therefore the same as that of leaving at the commencement of the game,

$$E(I|0, R, \mathcal{BP}) = E(I|p_I, R, \mathcal{BP}),$$

since

$$int_{sp} + \phi(\widehat{t}) = int_p + \phi(0),$$

thus at best, the mixed strategies derived here are only *neutrally stable* and cannot form an ESS, since we have two candidate strategies, not a unique ESS.

The next step in the search for a mixed ESS would be to consider assignment of atoms of probability and to consider the supports of the resident and intruder to be some subset of the interval $[0, \widehat{t}]$. There are two reasons why this approach is not considered as profitable. The first is that this would take us away from the main findings of this chapter, that of the instability of pure strategies. The second reason comes from invoking Selten's Theorem, stating that only pure strategies can form an ESS in an assymetric game (Selten,[72], Maynard Smith,[54]). When considering the support as the interval $[0, \widehat{t}]$, we found the reason as to *why,* neutral stability, the leave/return distributions could not form an ESS, which is not achieved by simply invoking Selten's Theorem.

4.5 Critique and Conclusions

The importance of this chapter lies in the refinement of the hypothesis of information exchange in patch leaving. Though the leave/return times observed show some stochasticity, there is a general form of patch defence behaviour found across many species of patch guarding parasitoids (Wilson,[86]). The resident guards the patch for a time dependent on the patch size and investment. Following its departure, the intruder returns to superparasitise (Field, Calbert and Keller,[21]). Barring injuries, in over eighty observations of pairwise patch contests, this was the pattern observed (Field,[19]).

In the eighty four patch contests observed there were four cases of injury of a contestant. Upon injury, these contestants immediately become intruders (Field, Calbert and Keller,[21]). Of the four injured contestants, only one was seriously injured, with the severance of the distal part of its antennae, causing the contestant to leave (Field , Calbert and Keller,[21]). Though it is possible that a guarding resident may not have an opponent, the rarity of severe injuries makes it unlikely that the patch leaving strategy of the resident would be selected to maximise fitness, with the possibly of intruder absence. Instead, patch leaving strategies *should be based on the assumption that the intruder will return.*

One other assumption of this chapter needs refinement, that of constant payoffs from superparasitism. As mentioned in the introduction (Section 4.1), the payoff from superparasitism decreases over the course of time. If the resident guards for a significant period of time, then this factor must be taken into account.

Having shown that a pure strategy ESS does not exist, does not decrease the importance of the instability results as there has been considerable attention paid to the dynamics of strategies in recent years (Hines, [33]). Within assymetric contests, a game considering the "battle of the sexes" was shown to have stable cyclical strategies (Schuster and Sigmund,[71]).

Information transfer of the resident's leaving time is the minimal requirement for the existence of a stable strategy in the waiting game. In fact there is ample evidence that both the resident and intruder adopt behaviour to maximise the chances of obtaining information about the opponent's status, whilst minimising any information transfer that would be advantageous to the opponent.

During the waiting game, a resident will mainly sit motionless on the patch, occassionally punctuated by excursions to search the patch periphery (Field, Calbert and Keller,[21]). This period of quiescence is thought to maximise the chances of detecting movement associated with the intruder's return and to "bluff" the intruder into perceiving the resident has left (Land,[42], Field, [19]). The intruder is observed to intermittantly return close to the patch, presumably to assess the presence of the resident (Field, Calbert and Keller,[21]). Indeed, the resident's strategy of remaining stationary, to maximise detection of intruder's movements may be seen to counteract the intruder's strategy of partial return (Field,[19]).

In summary, the waiting game was introduced in this chapter, with the assumption that no information is exchanged to the intruder on the resident's leaving time, if the resident leaves prior to the intruder. With no information exchange, no ESS exists, regardless of initial conditions of the resident leaving strategy or the intruder return strategy. By simulating the evolution of leave/return times, it was shown that strategies evolved cyclically when the initial return time of the intruder is greater than that of the resident's leaving time. The resident's leaving time drifted, due the absence of selection, when the return time of the intruder was less than that of the resident's leaving time. Mixed strategies were briefly considered, but were shown at best, to be neutrally stable.

The results of this chapter point to a construction of a new model with information exchange of the resident's leaving time passed to the intruder and the leaving time decision of the resident based on the knowledge that the intruder will return to superparasitise, (Chapter ??).

Chapter 5

The Waiting Game with Information Exchange

A Stackelberg Equilibrium.

5.1 Introduction and Chapter Overview

The previous chapter addressed possible leaving strategies taken by the resident and return strategies for the intruder. In this chapter, models of leave/return strategies are constructed, under a different set of assumptions.

There are two central reasons why ESS leave/return times did not exist, with two assumptions presented in the previous chapter. The first, is the assumption that the only information concerning departure or return times exchanged by players occurred if the intruder returned early to a guarded patch. No information about a resident's early departure was exchanged to the intruder. A constant superparsitism payoff to the intruder, denoted by Δ, no matter what the time of intruder return, formed the second assumption.

No ESS will exist if Δ does not change because the following intuitive reason. If there is no change in payoffs from superparasitism, the resident's best strategy is either "leave immediately" or "guard indefinitely." Consider the "guard indefinitely" strategy. An intruder's best response to this strategy was to return immediately, collecting maximal habitat payoffs after being removed by the resident. The "guard indefinitely" strategy is optimal for the resident as there is no opportunity for superparasitism. This intruder response, in turn, negates any selection pressure on the resident's strategy, thus leaving times will drift from the "guard indefinitely" strategy. Thus, "guard indefinitely" cannot be an ESS. Applying similar arguments, to the co-evolution of the leave/return times, denies the strategy "leave immediately" as an ESS candidate when Δ is constant.

What of the possibility of uncertainty in opponent presence or absence in the game? Through patch contest injury or predation, there may be a small probability that a guarding resident has no corresponding intruder, awaiting an opportunity to superparasitise. The motive for this assumption was the observation that in four of eighty experiments, players were injured, with severed antennae, during the contest for residency (Field, Calbert and Keller,[21]). A game of timing approach of finding a leaving probability density and return probability density yielding constant payoffs, when used against an opponents strategy was applied. Because of presence uncertainty, such constant payoff leave/return densities where derived, but were not shown to generate a ESS model of leave/return behaviour, because of the neutral stability of the strategies calculated (see Chapter 4).

Before proceeding with another model of the waiting game, another aspect of the biology of embryo development is discussed as a precusor to the new set of assumptions listed below. Once parasitised, the stages of development, rate of embryonic growth and time since previous parasitism will determine how vulnerable a particular host egg will be to successful superparasitism (Field,[19], Godfray,[26]). Experiments have been conducted to determine the level of success for conspecific superparasitism, under different times from the first to the second oviposition (Field,[19]). When the time difference between first and second ovipositions is small, results showed that the superparasitising conspecific had a higher probability of yielding a successful fitness return (Field,[19]). Any initial advantage to the superparasitising female decreases over the course of approximately six hours, when the first embyro is sufficiently developed (Field,[19]).

Including this observation motivates the first change in the assumptions of the previous two models, allowing the intruder's payoff, from successful superparasitism, to decrease over the course of time, that is the superparasitism payoff, Δ, now changes to a positive decreasing function of time, defined to be $\Delta(t)$.

$$\Delta(t) \longrightarrow 0 \text{ as } t \longrightarrow \infty.$$

Under this assumption, it may be possible to apply to a games of timing approach of finding leave/return probability densities that yield constant payoffs. This will not be the approach taken here, since an extra observation regarding information transference between players is modelled.

During the course of the final waiting game, an intruder is observed to move closer to the edge of the patch without making a complete return (Field, Calbert and Keller,[21]). Though the intruder, if present, may not have complete information as to the time of leaving of the resident, it is hypothesised that it can infer estimates of the resident's presence or absence by making a *partial return* to the patch (Field,[19], Wilson,[86]). To incorporate this observation into a mathematical model, a learning rule should be applied giving time dependent updates of information ascertained by a waiting intruder. For example, any consistent model of presence, absence estimates must assign a high probability of resident presence if the time interval of the intruder's last resident observation is small (Sih,[73]). Incomplete inference as to the presence or absence of the opponent can then be modelled by the use of Bayes' Theorem (McNamara and Houston,[57]) or other learning algorithms (Mangel,[48]).

Having observed that an intruder can partially infer presence or absence of the opponent, this information can be used to make a safe return to the patch to accrue superparasitism returns. Fitness returns are largest if the intruder returns as soon as possible after the resident's leaving time, the time gap depending on the quality of information the intruder has of the presence of the resident (Field,[19]). Though this seems to imply that the intruder has the intrinsic advantage in the waiting game, selection would adjust the resident's leaving strategy to maximise fitness, in light of the intruder's imminent return.

Knowledge of the intruder's return, gives the resident the information advantage, as its leaving time constrains the possible return times of the intruder. Games in which a player has an intrinsic information advantage over an opponent have been studied extensively in economics, for example, within mathematical models of company investment in a product, in which the company knows other competing firms will invest in research and development in the product some subsequent time (Fudenberg and Tirole,[24]). Economists have applied a new notion of equilibrium centered on this information assymetry. Rather than calculating game strategies around the notion of the Nash Equilibrium, in which both players simultaneously calculate their respective optimal strategies, the notion of *Stackelberg Equilbrium* applies naturally to games in which one player has the information advantage over the opponent.

Experiments of pairwise contests indicate that the intruder always returns to the patch to superparasitise when it is not injured (Field, [19]). Consequently, selection will adjust the resident's leaving strategy to take this fact into account. Rather than simultaneously optimise strategies, the intruder maximises its fitness, by returning after some time set by the resident. Knowing this, the resident then maximises its fitness return, by choice of appropriate leaving time, balancing increasing patch payoffs, due to decays in superparasitism payoffs, with decreasing habitat payoffs.

When viewed as a Stackelberg game, none of the instability problems found in the last chapter appear. Strategies adopted by both the resident and intruder are pure strategies, in accordance with a fundamental theorem on ESS's, stating that only pure stategies can exist for an assymetric game (Selten,[72]). In advantage to the resolution of the instability problems, the resident leaving times are biologically consistent.

Following this introduction, section 5.2 places the new biological assumptions within a mathematical foundation. Section 5.3 derives the Stackelberg equilibrium, for the case of decreasing patch vulnerability to superparasitism and perfect resident presence/absence information. Subsequently, the assumption of equal "perceptions" of habitat payoffs is questioned. Eliminating the assumption of perfect resident presence information is the topic of the next section 5.3.2 followed by the Discussion and Conclusion, Section 5.4.

5.2 New Assumptions

Before proceeding with the model of patch leave/return behaviour, the new assumptions derived from the preceeding biological observations are listed

- Residents choose a time to leave and serach for new patches in the environment. This leaving time, denoted by t_R, is chosen with the knowledge that the intruder will return to superparasitise at some subsequent time,

  $$t_I = t_R + \beta.$$

  The time gap between the resident's departure and the intruder's return is clearly β.

- Suppose the resident leaves at time t_R and the intruder returning at time t_I, [1] then the payoff to the resident $E(R \mid t_R, t_I, \mathcal{BP})$, given both players are present, takes the form

  $$E(R \mid t_R, t_I, \mathcal{BP}) = \begin{cases} res_p + \phi(t_I) & \text{if} \quad t_I < t_R, \\ res_p - \frac{1}{2}\Delta(t_I) + \phi(t_I) & \text{if} \quad t_I = t_R, \\ res_p - \Delta(t_I) + \phi(t_R) & \text{if} \quad t_I > t_R, \end{cases}$$

---

[1] here we allow both times to be in the interval $[0, H]$, to illustrate the payoffs if the intruder returns to a defended patch

and the payoff to the intruder $E(I \mid t_I, t_R, \mathcal{BP})$ satisfies

$$E(I \mid t_I, t_R, \mathcal{BP}) = \begin{cases} int_p + \phi(t_I) & \text{if} \quad t_I < t_R, \\ int_p + \frac{1}{2}\Delta(t_I) + \phi(t_I) & \text{if} \quad t_I = t_R, \\ int_p + \Delta(t_I) + \phi(t_I) & \text{if} \quad t_I > t_R. \end{cases}$$

Both $\phi(t)$ and $\Delta(t)$ are assumed to be monotone decreasing, differentiable functions of t.

- The intruder estimates the presence or absence of the resident. It is assumed that there is variation in the leaving time of the resident. If t_R^* is the optimal resident leaving time, the realised leaving time follows some distribution, due to such factors as variation of the estimate of patch worth, and variation of the estimate of habitat worth. If the actual leaving time be denoted by t_R, then it is assumed that this time is normally distributed with mean t_R^* and variance σ^2,

  $$t_R \sim N(t_R^*, \sigma^2),$$

  where the variance is small compared to t_R^*.

5.3 The Stackelberg equilibrium

When one player can constrain the set of optimal actions taken by another player, then the Stackelberg equilibrium is the appropriate definition for evolutionary stability (Sjerps and Haccou,[74]). If we define the player that constrains the opponents actions as the leader, and the opponent as the follower, then a Stackelberg equilibrium can be described in the following terms.

Let S_L and S_F be the respective set of pure strategies that the leader and follower can adopt, leave/return times being the pure strategies adopted here. Similarily P_L and P_F are the fitness payoffs to the leader and follower players respectively, these functions depending on the pure strategies adopted by the leader and follower. Since the leader can constrain the actions of the follower, the set of pure strategies adopted by the follower S_F, depends on on the pure strategies adopted by the leader S_L. In functional notation, for any $l \in S_L$,

$$S_F = S_F(l).$$

Suppose the leader adopts a pure strategy $l \in S_L$, then the set of strategies that forms the follower's best response to the pure strategy l, denoted by $B_f(l)$, is defined to be

$$B_f(l) = \{f^* \in S_F, \text{ such that } P_F(l, f^*) \geq P_F(l, f), \text{ for all } f \in S_F(l)\}.$$

A Stackelberg Equilibrium Strategy is the best response strategy of the leader l^*, given the follower adopts a strategy in $B_f(l^*)$. Therefore, if the payoff gain of the follower is the payoff loss of leader, as in a zero sum or constant sum game, then the equilibrium pair (l^*, f^*) satisfies

$$\begin{aligned} P_L(l^*, f^*) &= \max_{l \in S_L} P_L(l, f^*) \\ &= \max_{l \in S_L} \min_{f \in S_F(l)} P_L(l, f). \end{aligned}$$

Now suppose the intruder possessed perfect information as to the presence or absence of the resident. The resident's fitness return for leaving at time t_R, is given by

$$F_R(t_R, t_I) = res_p - \Delta(t_I) + \phi(t_R),$$

thus from the assumption listed above,

$$F_R(t_R) = res_p - \Delta(t_R + \beta) + \phi(t_R).$$

Since the resident decides the optimal time, t_R^*, to leave, this time is found by solving the equations $\frac{\partial F_R(t_R^*)}{\partial t} = 0$, $\frac{\partial^2 F_R(t_R^*)}{\partial t} \leq 0$. Thus t_R^* must satisfy

$$\frac{\phi'(t_R^*)}{\Delta'(t_R^* + \beta)} = 1.$$

Note here the similarity with Charnov's marginal value theorem (Stephens and Krebs, [77]). If $\beta = 0$, then it is optimal to leave the patch when the marginal rate of gain from the habitat equals that of the patch, the latter being caused by decreased superparasitism payoffs (Charnov and Skinner,[6]).

As the intruder is assumed here to have perfect information as to the status of the patch, defended or undefended, the optimal time for returning is ϵ time units greater than the resident's departure time, for an arbitrarily small positive ϵ. Thus

$$t_R^{*+} = t_R^* + \beta = t_R^* + \epsilon = t_I^*.$$

Given that the intruder, because of the possibility of being injured, cannot return before the resident has left, its return time to superparasitise minimises the resident's fitness. Therefore the time t_R^* satisfies

$$\begin{aligned} F_R(t_R^*) &= \max_{t_R \in [0,H]} \min_{t_I \in (t_R,H]} F_R(t_R, t_I) \\ &= \max_{t_R \in [0,H]} \min_{\beta \in (t_R, H-t_R]} F_R(t_R). \end{aligned}$$

Note that as β is a constant, ϵ, then under perfect information the function $F_R(t_R, t_I)$ is simply a function of one variable, the resident's departure time t_R.

Under the assumption of perfect information, the pair $(t_R^*, t_R^{*+}) = (t_R^*, t_I^*)$ forms a Stackelberg equilibrium *if* these times are a global optimum for the payoffs of both players (Sjerps and Haccou,[74]). The global optimality of equilibrium point (t_R^*, t_R^{*+}) will in general depend on the nature of the patch vulnerability $\Delta(t)$ and the post-patch habitat fitness $\phi(t)$. Before asserting that the pair

$$(t_R^*, t_I^*) = (t_R^*, t_R^{*+})$$

is a Stackelberg equilibrium, it must be checked that the intruder's return time is indeed a global maximum, this being achieved by comparing the intruder's fitness returns from leaving at the begining of the waiting game, where maximal expected habitat returns are found, to that of leaving at t_R^{*+}. Thus if $t_I^* = \arg\max\,(F_I(0), F_I(t_R^{*+}))$ then we have a global Stackelberg equilibrium. As an example, consider the following simple model of payoff from superparasitism,

$$\Delta(t) = \Delta_{max} \exp(-kt),$$

k being the constant that determines the decay in payoffs from superparasitism and

$$\phi(t) = \alpha\Big(1 - (\frac{t}{H})\Big).$$

A global optimum is achieved for some parameters α, k and Δ_{max}, with the resident's maxima shown in the following Figure 5.3.1.

5.3.1 $\phi(t)$ for both Players?

Is it reasonable to assume that both players have the same estimate of the post-patch habitat payoff $\phi(t)$? If reference is made back to the Introduction, an article was cited, regarding the patch leaving strategies of predators, with intra-specific competition for the resource patches (Yamamura,[88]). The ratio of patches to predators, or the *competitive intensity,* was cited as the most important parameter determining patch leaving decisions (Yamamura,[88]).

It is not unreasonable to apply the same rationale, when attempting to model patch leaving decisions of residents and intruders. If an individual is to achieve maximal lifetime fitness, learning the competitive intensity may be a major adaptive advantage. In a particular patch conflict, the resident may have higher estimates of post-patch habitat fitness than the intruder. In experiments conducted to observe fighting and patch leaving, female *T. basalis* had no previous experience in patch fighting, thus the losing intruder may have a lower estimate of post-patch habitat payoffs, due to a higher estimate of competitive intensity,

$$\phi_I(t) \leq \phi_R(t).$$

These observations have implications for the global optimality of the Stackelberg equilibrium. If an intruder chooses to return after the resident leaves at its optimal

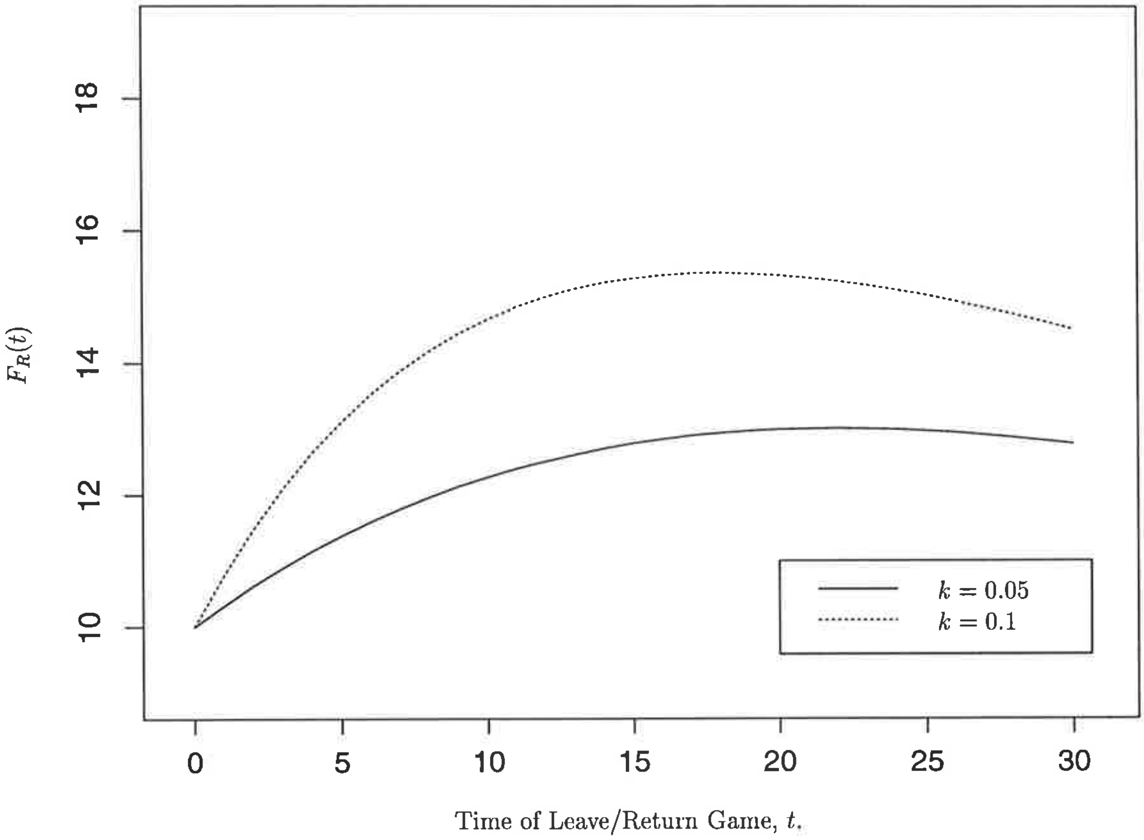

Figure 5.3.1: Fitness of the Resident $F_R(t)$, at time t for the patch vulnerability constant $k = 0.05, k = 0.1$ under the assumption that the intruder returns immediately after, that is $\beta = 0^+$. The parameters used in the figure were $\Delta_{max} = 10, \alpha = 5$ and $res_p = 15$.

time t_R^*, then its payoff must be greater than that of leaving immediately, forgoing superparasitism returns, but collecting maximal habitat returns,

$$F_I(t_I^*) = F_I(t_R^{*+}) \geq F_I(0).$$

Thus the fitness gain from superparasitism must be greater than or equal to the habitat gains,

$$\Delta(t_I^*) \geq \phi_I(0) - \phi_I(t_I^*).$$

Note that this is under the assumption of perfect information, as to the resident's presence or absence.

Two necessary conditions for the resident's strategy t_R^* to be globally optimal are

1. There is a fitness gain from leaving at t_R^* then at 0 and so, the resident's fitness difference in guarding $\Delta(0)-\Delta(t_R^*)$ must be greater than the resident's habitat fitness difference in not guarding, $\phi_R(0) - \phi_R(t_R^*)$ thus

$$\Delta(0) - \Delta(t_R^*) \geq \phi_R(0) - \phi_R(t_R^*).$$

2. there is greater habitat fitness gains for the resident than superparasitism gains at t_R^*, so

$$\phi_R(t_R^*) \geq \Delta(t_R^*).$$

Thus the habitat fitness losses, $L_I = \phi_I(0) - \phi_I(t_I^*)$ and $L_R = \phi_R(0) - \phi_R(t_R^*)$ from leaving must satisfy

$$L_I \leq \Delta(t_R^*) \leq \Delta(0) - L_R,$$

if indeed the pair $(t_R^*, t_I^*) = (t_R^*, t_R^{*+})$ is globally optimum. This inequality provides a necessary condition, in the habitat fitness losses between the two players, for stability, as illustrated in the following Figure 6.2.

For guarding to be profitable, gains to the resident from decreasing intruder superparasitism payoffs must supplement losses in habitat gains. This observation will have implications for patch competition with multiple conspecifics. With many competitors, each player will parasitise a smaller proportion of the patch, thus the fitness loses from superparasitism may decrease, lowering $\Delta_n(0)$, where $n, n > 2$ is the number of players. As a consequence, the times where

$$\Delta_n(0) - \Delta_n(t_R^*) \geq \phi_R(0) - \phi_R(t_R^*)$$

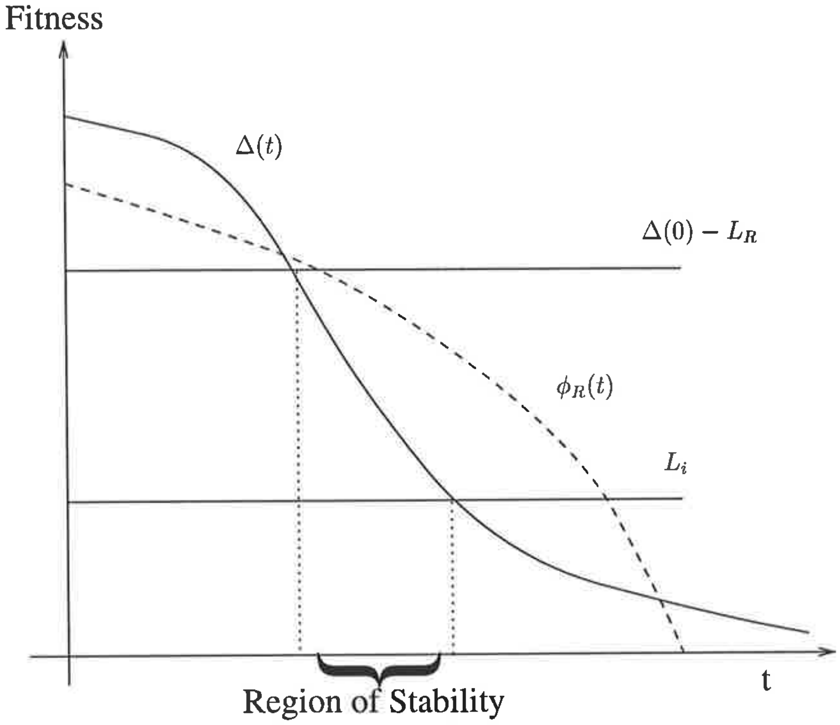

Figure 5.3.2: For stability of resident and intruder strategies, the leave/return times necessarily belong to the interval indicated in the diagram.In the region of stability, payoffs are better than those obtained by leaving or returning at the beginning or end of the game. Both $\phi_R(t), \phi_I(t)$ and $\Delta(t)$ are monotonic decreasing functions of t.

will decrease. Thus, with multiple competitors, residency times are expected to decrease, as seen in field observations (Field, personal observation).

The hypothesis of lower habitat quality estimates for an intruder may be tested, by variation of the life histories of a group of parasitoids. If one group of parasitoids experiences a higher proportion of residency in patch competition, as compared with another group that become intruders, then both the leaving times and return times of the second group should be longer than that of the first, indicative of lower habitat quality estimates. So far, patch defence experiments, over multiple patches, have not commenced, but may provide useful insight into the nature of patch leaving decisions.

5.3.2 Learning Resident Presence or Absence

Previously it was assumed that the intruder had perfect knowledge as to the occupancy of the patch. Under this assumption the intruder's return time formed a Stackelberg equilibrium. To remove the assumption of perfect information, a measure of an intruder's precision to infer patch occupancy must be defined. Furthermore, a time dependent learning rule is to be constructed, defining the estimate of the presence of the resident at any moment in time.

Bayes' Theorem

$$\Pr(A|B) = \Pr(B|A)\frac{\Pr(A)}{\Pr(B)}$$

serves as a probabilistically consistent learning model that incorporates imperfect information and time dependent estimates of resident presence. To see how this theorem is applied, let $\mathcal{O}(h)$ be the event that the intruder observes the resident, in some small time interval of length h. Let $\mathcal{P}$ be the event that the resident is present. A measure of the quality of the information an intruder can ascertain as to patch occupancy, is given by the limit

$$\theta = \lim_{h \to 0} \frac{\Pr(\mathcal{O}(h) \mid \mathcal{P})}{h}.$$

Parameter θ measures the probability per unit time for observing the resident, given it is present. As $\theta \longrightarrow \infty$, the intruder's occupancy information becomes more reliable, since in the limit, the presence of the resident is immediately detected by the intruder.

Now let ($\mathcal{P}$ at t) be the event that the resident is present at time t, with ($\mathcal{NP}$ at t) being the event that the resident is not present at time t. With similar notation, let ($\mathcal{NO}$ from τ) be the event that the intruder has made no observations of the resident from time τ. The definition of the intruder's estimate of the resident's presence at time t, given no observations from time $t, \tau \leq t$, is given by

$$\mathcal{B}(t \mid \tau) = \Pr(\mathcal{P} \text{ at } t \mid \mathcal{NO} \text{ from } \tau).$$

By Bayes' theorem, this is equal to

$$\frac{\Pr(\mathcal{NO} \text{ from } \tau \mid \mathcal{P} \text{ at } t) \Pr(\mathcal{P} \text{ at } t)}{\Pr(\mathcal{NO} \text{ from } \tau).}$$

Conditioning on the denominator, using the Theorem of total probability, this expression is just

$$\frac{\Pr(\mathcal{NO} \text{ from } \tau \mid \mathcal{P} \text{ at } t) \Pr(\mathcal{P} \text{ at } t)}{\Pr(\mathcal{NO} \text{ from } \tau \mid \mathcal{P} \text{ at } t) \Pr(\mathcal{P} \text{ at } t) + \Pr(\mathcal{NO} \text{ from } \tau \mid \mathcal{NP} \text{ at } t) \Pr(\mathcal{NP} \text{ at } t).}$$

Now as $\lim_{h \to 0} \frac{\Pr(\mathcal{O}(h) \mid \mathcal{P})}{h} = \theta$, this implies, that of small $h, \Pr(\mathcal{O}(h) \mid \mathcal{P}) \approx \theta h$, so the observations of the resident are exponentially distributed (Ross, [69]). Thus the probability of not observing the resident at time τ, given its presence at time $t, \tau \geq t$ is

$$\Pr(\mathcal{NO} \text{ from } \tau \mid \mathcal{P} \text{ at } t) = \exp(-\theta(\tau - t)).$$

As noted before, since the actual leaving time of the resident t_R is drawn from a distribution, assumed to be Gaussian with mean t_R^*, let the survivor function, $\Pr(t_R > t)$, be denoted by $S(t)$ and the distribution itself be denoted by $\Pr(t) = 1 - S(t)$.

Therefore $\Pr(\mathcal{P} > t) = S(t)$ and by integration over all the possible leaving times of the resident

$$\Pr(\mathcal{NO} \text{ from } \tau \mid \mathcal{NP} \text{ at } t) \Pr(\mathcal{NP} \text{ at } t) = \int_{\tau}^{t} \exp(-\theta(l - \tau)) d\Pr(l).$$

These observations lead to the estimation of the presence of the resident at time t, given the last time of observation was at τ, as

$$\mathcal{B}(t \mid \tau) = \begin{cases} 1 & \text{if} \quad t \leq \tau, \\ \frac{\exp(-\theta(t-\tau))S(t)}{\exp(-\theta(t-\tau))S(t) + \int_{\tau}^{t} \exp(-\theta(l-\tau)) d\Pr(l)} & \text{if} \quad t > \tau. \end{cases}$$

A graph of $\mathcal{B}(t \mid \tau)$, for different values of the quality of information exchange, θ is shown in Figure 5.3.3.

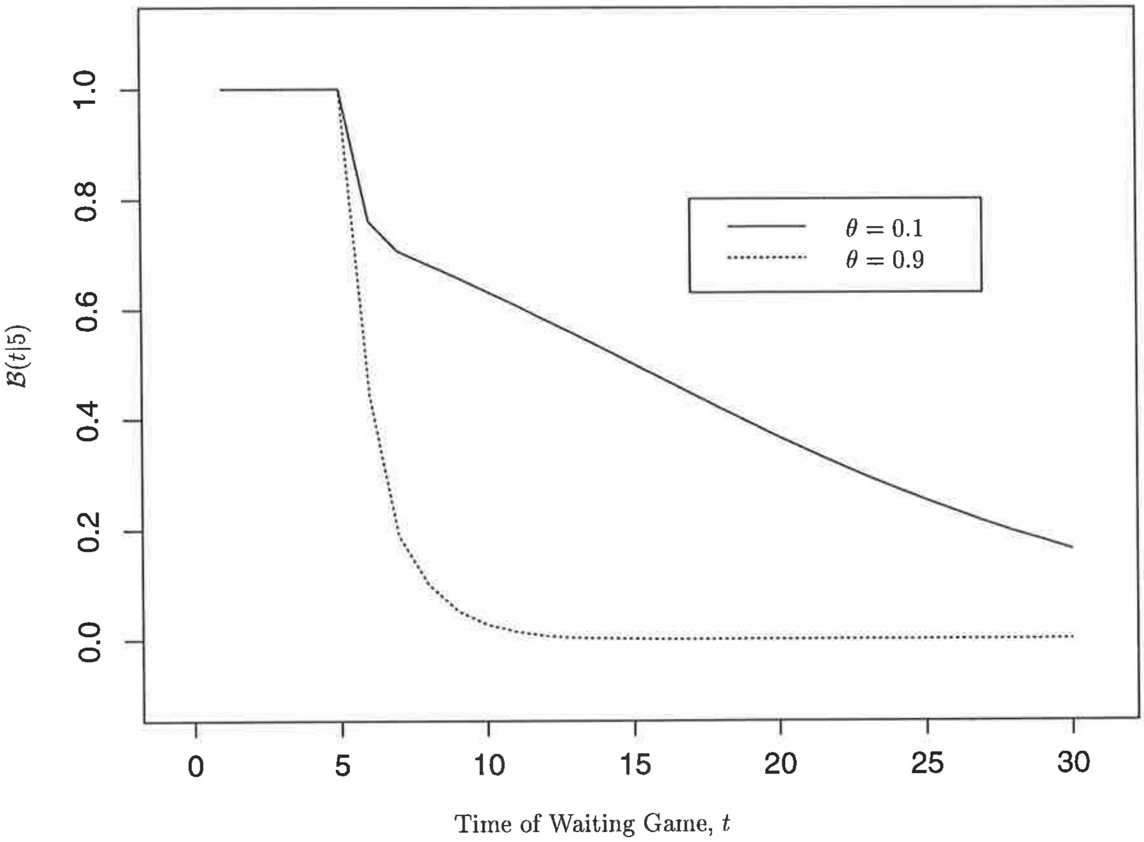

Figure 5.3.3: Intruders estimation of the presence of the resident, given that the last observation of the resident was made at $\tau = 5, \mathcal{B}(t \mid 5)$. In this figure the expected time of leaving $t_R^* = 5$ and the variance is $\sigma^2 = 2$, thus the actual leaving time $t_R \sim N(5, 2)$. This estimate of occupancy is plotted for $\theta = 0.1$ and $\theta = 0.9$.

Having constructed a model for the intruder's estimate of the presence of patch occupancy, the perceived fitness of the intruder $F_I(t, \tau)$, can be calculated where t is the since the beginning of the waiting game and τ is the time of last observation of the resident.

$$F_I(t,\tau) \quad = \quad \mathcal{B}(t \mid \tau)\Big(int_p + \phi_I(t)\Big) + (1 - \mathcal{B}(t \mid \tau))\Big(int_p + \Delta(t) + \phi_I(t)\Big)$$

$$= int_p + \phi_I(t) + (1 - \mathcal{B}(t \mid \tau))\Delta(t).$$

Comparing the resident's optimal time of leaving with the intruder's return time will give the time delay of the intruder's return β. It is noted that this time delay will depend on the time of the intruder's last observation and this time is assumed to be the actual leaving time of the resident t_R, although this assumption is questioned in the next paragraph.

What happens if the intruder mistakenly concludes the resident is not present, returning to the patch? There are several possibilities. A resident may have commenced a temporary search of the patch periphery, a behaviour occuring several times before leaving (Field, Calbert and Keller,[21]). In this case the resident, most likely, will return to intercept the intruder. Another possibility is the return of the intruder whilst the resident is on the patch, again with the result of interception and removal of the intruder (Field, personal communication).

The premature return of the intruder is very rare and the simplest explanation for this observation it that an intruder has high quality information about the resident's presence. When guarding, the resident's position is localised, usually it the patch center. As the intruder approached the patch it would gain information. In contrast, the intruder may be in any one of the peripheral areas surrounding making information exchange of the intruder's presence poor. Thus, the localisation of resources, thus resident position, has the effect of giving the intruder the presence information advantage.

If $t_I^* \in (t_R, H]$ is the return time, that maximises the intruder's perceived fitness then

$$\beta = \arg \max_{t_I \in (t_R, H]} F_I(t_I, t_R) - t_R.$$

With the assumption of imperfect information, the leaving time of the resident and the return time of the intruder

$$(t_R^*, t_I^*) = (t_R^*, t_R^* + \beta)$$

do not form a Stackelberg equilibrium pair in the strict sense, but are here defined to be a *partial information Stackelberg pair.* To calculate the partial information Stackelberg pair, the return time of the intruder t_I^*, is first calculated for each resident leaving time t_R. Differentiating the intruder's perceived fitness and checking that we have a global optimum, t_I^* will satisfy

$$\phi_I'(t_I^*) + (1 - \mathcal{B}(t_I^*|t))\Delta'(t_I^*) = \mathcal{B}'(t_I^*|t)\Delta(t_I^*).$$

Owing to the monotonicity of the functions $\phi_I(t)$ and $\Delta(t)$, then $F_I(t_I^*) > F_I(t)$, for all $t \in [t_I^*, H]$, thus the global optimality condition applies.

Having found the optimal time between the resident's departure and intruder return,

$$\beta = t_I - t_R,$$

this is substitued into the resident's fitness equation to find the optimal return time t_R^*, generating (t_R^*, t_I^*).

In general, partial information Stackelberg pairs are calculated with the following method.

- For each possible resident leaving time t_R, calculate the intruder's perceived best return time β so

$$\beta = \arg \max_{t_I \in (t_R, H]} F_I(t_I, t_R) - t_R.$$

- Calculate the optimal leaving time for the resident t_R^*,

$$t_R^* = \arg\max F_R(t_R, t_R + \beta),$$

given the intruder returns β time units thereafter.

With this algorithm, the resident's leaving time is calculated, and a sensitivity analysis is done over different rates of decay of patch vulnerability k, as seen in figure 5.3.4.

From the graph of resident leaving times, the following observations can be

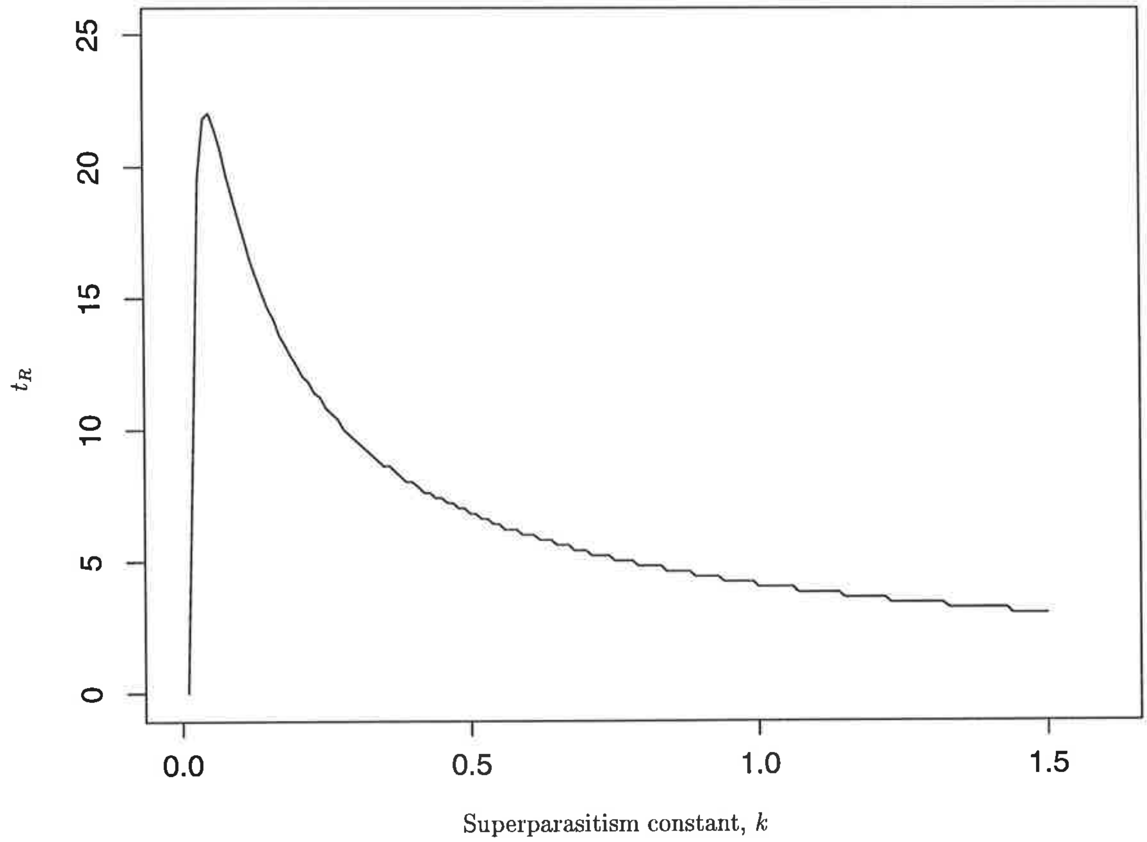

Figure 5.3.4: Stackelberg leaving times for the resident as a function of the superparasitism constant k which ranges from 0.0 to 1.6. The parameters used in this figure are $res_p = 15, int_p = 5, \Delta_{max} = 10, \alpha = 5, H = 30, \sigma^2 = 2.0$ and $p = 0.3$.

made. If there is no decay in patch vulnerability over time, then the resident's best response is to cease patch defence immediately. In light of the fact that in this situation, no matter when the intruder returned to superparasitise, full fitness returns are given to the intruder, there cannot be any fitness advantage to resident guarding, thus it pays to minimise habitat fitness losses and leave the patch immediately.

At the other extreme, if the decay in patch vulnerability is large, then the resident should not guard for long periods of time, since the patch becomes relatively safe from superparasitism after a short period of time. Again the best resident fitness returns come from adopting an early leaving strategy. Intermediate to the two extremes described, a guarding resident must balance the tradeoff in leaving early, for maximal habitat gain, and guarding the patch, enabling the egg parasitoid larvae to develop its mandibular defence physiology (see the Introduction and Overview, Chapter 1).

If it is assumed that β is small (high quality information exchange to the intruder), the habitat payoff, $\phi_R(t)$ and superparasitism payoff, $\Delta(t)$ are infinitely differentiable, then by application of Taylor's theorem $\Delta(t) = \sum_{n=0}^{\infty} \Delta^{(n)}(0)\frac{t^n}{n!}, \phi(t) = \sum_{n=0}^{\infty} \phi_R^{(n)}\frac{t^n}{n!}$. Upon substitution into the equation that yields the optimal return time of the resident,

$$\frac{\phi'(t_R^*)}{\Delta'(t_R^* + \beta)} \approx \frac{\phi_R'(0) + \phi_R''(0)t_R^*}{\Delta'(0) + \Delta''(0)t_R^*}.$$

Hence

$$t_R^* \approx -\frac{\phi_R'(0) - \Delta'(0)}{\phi_R''(0) - \Delta''(0)}.$$

Thus the balance between resource decay and rate of resource decay determines the optimal patch leaving time for the resident. Examination of the denominator shows that t_R^* will be greatest when the marginal rates of decay in habitat and superparasitism payoffs are approximately equal.

5.4 Discussion and Conclusion

This discussion focuses on the comparison of the three models constructed in the last two chapters and further work that may be germane to the understanding of the waiting game. As noted before, the first model based on the assumption of constant patch vulnerability to superparasitism and no information transfer to the intruder as to patch occupancy, exhibited no stability at all (Chapter 4). The leaving times of the resident, though correlated with those of intruder's, drifted. The second model again showed neutral stability, though is was noted that the leaving time distributions for the resident and the return time distributions for the intruder cannot be evolutionarily stable as only pure strategies can satisfy stability requirements (Hammerstein,[30]).

The Stackelberg equilibrium must be the appropriate definition for the behavioral strategies of the resident and intruder. Return times will be selected to maximise the fitness of the intruder, essentially "doing the best of a bad job" (Stephens and Krebs,[77]). This in turn puts selection pressure on the resident to adopt a strategy taking the intruder's imminent return into account. This argument is the same as that adopted by researchers studying the adjustment of clutch size in parasitoids (Sjerps and Haccou,[74]). The authors reasoned that if the first player to oviposit within a host has knowledge that a conspecific will superparasitise some time shortly thereafter, then it will adjust its clutch size to take the conspecific's superparasitism into account (Sjerps and Haccou,[74]).

It should be noted that the Stackelberg equilibrium will break down if the costs to the intruder, on return to a guarded patch are not as great as those of returning early. This may be the case when the intruding parasitoid is nearing the end of its expected life or has low egg load, making risky strategies profitable (Mangel,[46]). However if either of these situations apply, then it is expected that the player would choose to show greater persistence in fighting for patch possession and would therefore achieve residency status. Studies of the effect of varying egg load on the aggression level of competing females of the species *T. basalis* have not been conducted systematically, nevertheless females that achieve high levels of residency have been noted to have lower egg load upon subsequent dissection (Field, personal observation).

The final model of the waiting game assumed the intruder's last observation of the resident concurred with the actual time of leaving of the resident. Behavioural observations indicate that the resident adopts a complicated patch leaving strategy. Following the stationary period of patch defence in which the resident remains motionless, it commences a series of radial searches around the patch before returning to check the patch for the presence of an intruder. Following this it leaves

(Field,[19]). On evolutionary grounds, it could be argued that this search has two adaptive components. The first, is to find the intruder, to prevent superparasitism. The second is to deceive the intruder, increasing the time of last observation of the resident, hence increasing the probability of an early intruder patch return. The radial search strategy of the resident essentially decreases the quality of information exchange given to the intruder, as measured in our model, by the parameter *theta*. Leaving to search the surrounding area may come at a cost, since the intruder could return to partially superparasitise the patch before the resident has re-checked patch occupancy.

Clearly there are further modelling tasks that may provide more information as to the evolutionary forces influencing resident/intruder leave/return times. When the ratio of patches to parasitoids is low, there will be multiple intruders in any typical patch competition. This will alter the leaving time of the resident, as both the fitness loss, by multiple intruder superparasitism and the habitat fitness returns will change.

Models of resource guarding behaviour with multiple competitors have been studied in the context of male mate guarding (Yamamura,[87, 89]) both for infinite and finite time periods. These models again predicted the existence of pure guarding time strategies for males. The predicted guarding time depended crucially on the level of sperm competition with previous and subsequent male matings of the female. Here sperm competition is analoguous to the larval competition within host eggs after superparasitism. If sperm competition is intense, males remained with their mate for a time period sufficiently long to circumvent the success of sperm from subsequent male matings(Yamamura,[87, 89]).

How close to the patch should the intruder return in an attempt to ascertain the resident's presence or absence? As there is a tradeoff between increasing the quality of presence/absence information and being caught by the resident this is an important question that should be studied.

In summary, this chapter deals with the final departure of the resident, making the transition from patch defence, to foraging for further patches to superparasitise, and the return of the intruder, to superparasitise the patch. Attempts to model the waiting game without appropriate information exchange between the resident and intruder showed little signs of stability. Assuming that the intruder possessed partial information as to the presence of the resident implies that any evolutionary equilibrium will be of the form of a Stackelberg equilibrium, that is, an equilibrium in which the resident adopts a strategy of leaving, to maximise its fitness in the knowledge of an imminent intruder return. This equilibrium predicts a small leaving time, for both small and large rates of decay of patch vulnerability and a large leaving time, when the decay rate of patch superparasitism is approximately equal to the decay rate of habitat returns over the day. In applying the intruder first, resident last optimisation procedure, only pure leave/return strategies are generated these showing intrinsic stability.

Chapter 6

Further Research Directions and Conclusions

6.1 Topics for Further Study

In the mind of the author, this dissertation had raised many possible directions for further research. As the decisions made by parasitoids exhibiting patch defence are quite complicated, a large proportion of time was devoted to constructing simplified assumptions that made the modelling tasks tractable. Pairwise, single patch competition, with simple fitness functions, formed the basis of this thesis. It is therefore important to provide directions of research, in order to break down some of the simplifying assumptions behind this thesis.

What follows, is a brief outline of some topics that may bring more insight into the evolution of patch defence. In Section 6.1.1, issues associated with constucting a model of patch fitness return, as a function of player investments is discussed. Equations governing the evolution of leave/return times, as a function of competitive intensity follow in Section 6.1.2. The incorporation of learning, to model strategies used by residents guarding against multiple intruders, is the focus of the next section.

Recently, a seminal paper discussing techniques of finding $\epsilon-$ perfect, suboptimal strategies in evolutionary game theory was applied to both static and dynamic games (McNamara, Webb, Collins, Szekely and Houston,[60]). This approach to finding strategies is applied to finding an $\epsilon-$perfect resident's best response to an intruder's return in Section 6.1.4. Spatial issues, such as resident search strategies and oviposition placements are discussed in Section 6.1.5, with the general conclusion to this thesis in Section 6.2.

6.1.1 Fitness obtained from one Patch?

At the core of the modelling approach used in this thesis was the assumption that patch defence can be broken up into a series of sub-games, though these sub-games are connected. In order to make the sub-game connections as general as possible, fitness functions for each stage of competition were chosen to be as simple as possible, whilst keeping the essence of the process by which one player can gain fitness at the expense of the opponent.

When fighting (Chapter 2), fitness was broken up into role dependent contributions from present and future ovipositions, these depending on the coefficents α, β and γ, the proportions of self, opponent and future total patch investment given to the resident. Once residency was decided (Chapter 3), two coefficients specified the cost to the parasitoid itself of one opponent oviposition, these being C_I and C_R, the unit cost of an opponents oviposition to self fitness. Finally the time-dependent payoff from superparasitism (Chapter 5) was reflected in the payoff from intruder superparasitism $\Delta(t)$, where t is the time from commencement of the leave/return game. If the notation $A \longrightarrow B$ is used to state that B depends on the input of A then the following relationship between coefficients

$$\alpha, \beta, \gamma \longrightarrow C_I, C_R \longrightarrow \Delta(t)$$

will hold. Furthermore, if we let x, y denote the respective investments of the resident and intruder, immediately after residency has been decided, then

$$x, y \longrightarrow C_I, C_R.$$

The complexity of the relationships between investments and payoff coefficients will be large, and aside from separating games for tractability, this is yet another reason for the sub-games approach.

If x is the investment of the resident, y that of the intruder, then at least, the dependency of the coefficients in intruder returns would satisfy

$$\begin{array}{cc} \frac{\partial C_R}{\partial x} > 0, & \frac{\partial C_I}{\partial y} > 0, \\ \frac{\partial C_R}{\partial y} < 0, & \frac{\partial C_I}{\partial x} < 0. \end{array}$$

Dependency between investments, upon role resolution and the payoff from intruder superparasitism would have to satisfy

$$\frac{\partial \Delta(t)}{\partial x} > 0, \frac{\partial \Delta(t)}{\partial y} < 0.$$

A simple model of fitness returns from parasitism/superparasitism may be constructed if the number of superparasitising ovipositions is small enough to avoid three ovipositions in a single egg and the resident does not superparasitise.

Suppose, following the investment of x resident embryos and y intruder embryos, $x + y = E$, fitness is derived subsequent to the intruders superparasitism of $z, z \leq E$ embryos. Let the intruder's fitness be defined as $f_I(z, y, x)$. As a reasonable approximation, fitness returns of the resident will then be $f_R(z, y, x) = E - f_I(z, y, x)$.

How can the intruder's fitness be calculated? Noting that the intruder does not self-superparasitise in the current round of ovipositions (Field, [19]), host eggs will be in five states, unparasitised hosts (assumed to be zero in number, Field,[19]), those parasitised with resident or intruder embryos, denoted by R and I or those superparasitised by the intruder, denoted by RI and II. If a_R, a_I, a_{RI} and a_{II} are the respective fitness values to the intruder of host eggs in these states, then

$$0 = a_R < a_{RI} < a_I \leq a_{II}.$$

All that remains is to calculate the proportions of R, I, RI and II eggs. If the intruder does not self-superparasitise in the current round of ovipositions then the distribution of RI eggs will follow the *hypergeometric* distribution (McCullagh and Nelder,[56]). Essentially, intruder superparasitism is analogous to choosing an egg at random to superparasitise *without replacing* this egg for further superparasitism. Thus the probability that k of the z superparasitised host eggs is of the type RI will be

$$\Pr(k \text{ type } RI|z) = \frac{\binom{x}{k}\binom{y}{z-k}}{\binom{E}{z}}.$$

Thus, after superparasitism, there will be k type RI eggs, $z - k$ type II eggs and $(y - z + k)$ type I eggs with probability $\Pr(k \text{ type } RI|z)$. The fitness of the intruder will then take the form

$$f_I(z, y, x) = \sum_{k=0}^{x} \frac{\binom{x}{k}\binom{y}{z-k}}{\binom{E}{z}} \Big(a_I(y - z + k) + a_{RI}k + a_{II}(z - k)\Big).$$

Even this expression does not encapsulate all the requirements for a successful definition of fitness. In a locally mating species, as is *T. basalis,* the effects of the *sex ratio,* known to be female biased, on fitness returns cannot be ignored since emerging males fight for possession of the patch to maximise the number of female matings (Godfray,[26], Wagge,[83], Wilson,[86]). Superparasitism may cause the emergence of two related males, their competition for female matings a waste of eggs.

Large investments in superparasitism also waste time (Charnov and Skinner,[8]). Thus combining sex ratio and time costs, another expression for fitness may take the form

$$F_I(z, y, x) = \exp(-\varphi z) f_I(z, y, x).$$

where the parameter φ measures the comibined effects of male competition and time costs associated with the superparasitism of z host eggs.

Applying this expression to models of intruder return frequencies would make

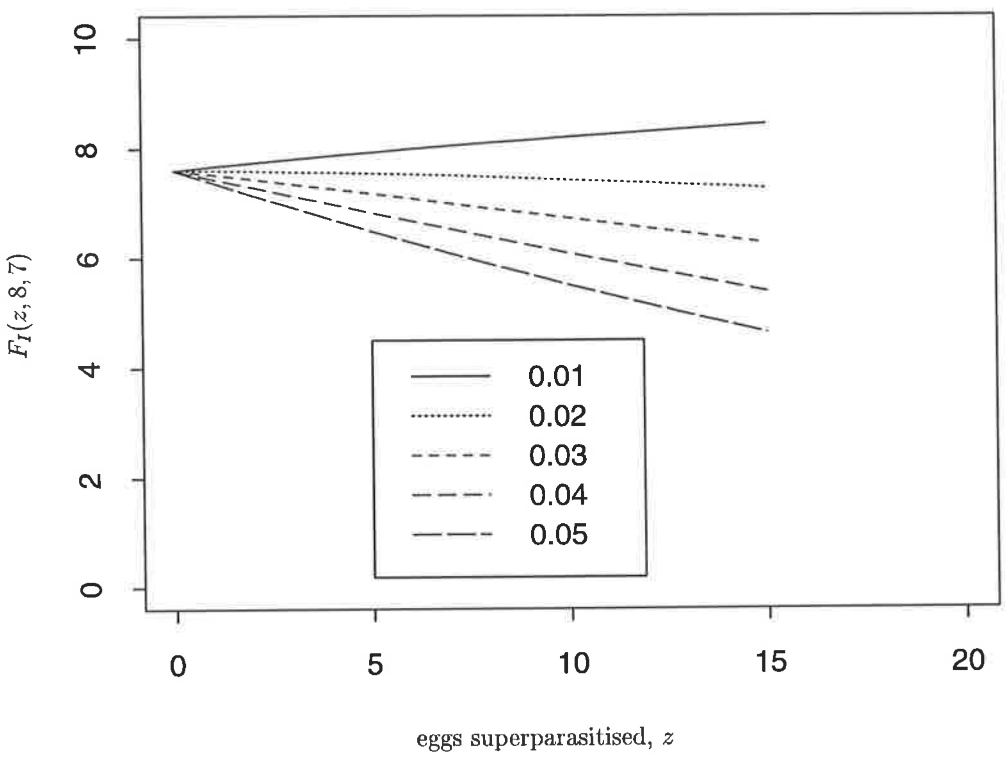

Figure 6.1.1: Sensitivity analysis of patch fitness, as calculated for the function $F_I(z, y, x)$ as z ranges from 0 to 15. Parameters used are $a_I = 0.95, a_{II} = 0.7, a_{RI} = 0.6, x = 8, y = 7$. The parameter φ ranges from 0.01 to 0.05.

any optimisation very difficult indeed. Furthermore, notice that the expectation is "parameter rich", a problem intrinsic to adopting models of increased complexity (Mangel and Clarke,[50]).

These observations point to a need for further experimental work to find empirical total fitness *from a patch,* given variation in the inter-arrival times of the two females. An empirical approach has the advantage of avoiding the forementioned parameter richness problems as well as encapsulating fitness values directly from observations. An approach to incorporating empirical fitness values with state dependent models was taken for a stochastic dynamic programming model of superparasitism of the gregarious parasitoid *Trichogramma evanescens* (Hymenoptera, Trichogrammatidae) (Mangel and Clarke,[50]).

6.1.2 Evolutionary dynamics Revisited

In deriving the leave/return strategies of a resident and intruder as a Stackelberg equilibria (chapter 5), the strategy dynamics were not considered, in the case of non-constant payoffs from superparasitism. Of potential interest, the evolutionary dynamics of patch defence, as studied through the partial differential equations that given waiting times may yield interesting results.

In order to derive a set of coupled differential equations that govern the evolution of resident departure times and intruder return times, let the leave/return times be taken from the set $[0, 1]$. [1] The evolution of resident/intruder strategies will depend on the competitive intensity of the habitat, thus we define

$$\mathcal{C} = E(\text{proportion of times residency is achieved}).$$

Further, let $f_R(t, g)$ and $f_I(\tau, g)$ be the respective expected fitness gain of a resident/intruder adopting leave/return time t, τ in generation g, and $\overline{f}_R(g), \overline{f}_I(g)$ the expected resident/intruder fitness returns over all times $t, \tau \in [0, 1]$. Generations are assumed to be continuous.

A strategy in any generation time g is defined by the vector $(t(g), \tau(g))$. Strategies will propagate if they do well against the background of competition, thus if the fitness obtained by adopting $(t(g), \tau(g))$ is greater than that of the population average, or

$$\mathcal{C}(f_R(t, g) - \overline{f}_R(g)) + (1 - \mathcal{C})(f_I(\tau, g) - \overline{f}_I(g)) > 0$$

then this strategy will propagate into the future (Hines,[33]).

Thus, let $p_R(t, g)$ be the proportion of individuals adopting departure time t, at

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[1] Any other compact interval may be re-scaled to $[0, 1]$.

generation g when resident and let $p_I(\tau, g)$ be the proportion of individuals in the population adopting return time τ, at generation g when intruder. Partial differential equations that govern the trajectories $(t(g), \tau(g))$ will satisfy

$$\begin{aligned}
\frac{\partial p_R(t,g)}{\partial g} &= k_R\Big(\mathcal{C}\big(f_R(t,g) - \overline{f}_R(g)\big) + (1-\mathcal{C})\big(f_I(\tau,g) - \overline{f}_I(g)\big)\Big)p_R(t,g), \\
\frac{\partial p_I(\tau,g)}{\partial g} &= k_I\Big(\mathcal{C}\big(f_R(t,g) - \overline{f}_R(g)\big) + (1-\mathcal{C})\big(f_I(\tau,g) - \overline{f}_I(g)\big)\Big)p_I(\tau,g),
\end{aligned}$$

with k_R and k_I constants governing the evolution rate of leave/return strategies. Together with the normalisation conditions on the interval $[0, 1]$,

$$\begin{aligned}
\int_0^1 p_R(t,g)dt &= 1, \\
\int_0^1 p_I(t,g)dt &= 1,
\end{aligned}$$

these equations may be candidates for describing the evolution of patch defence strategies.

Of importance in the structure of these evolutionary equations is the coupling of the roles of resident and intruder. When competition is intense, with residency being rare, most selection may take place on the intruders return strategy. What remains to be modelled are biologically realistic models for fitness obtained from a patch, superparasitised by many intruders. In fact, the expected fitness of a resident or intruder will depend on the competition intensity and hence C, with $\overline{f_R}$ and $\overline{f_I}$ decreasing as $\mathcal{C} \longrightarrow 0$.

6.1.3 One Resident, many Intruders

Chapter 5 addressed the leaving strategies of the resident. The optimal leaving time was found from a tradeoff of waiting till patch investments were relatively "safe" from superparasitism, whilst maximising potential fitness benefits from the habitat. A resident could choose this strategy because an intruder was constrained to return subsequent to the resident's departure.

At high levels of competition intensity, a resident may defend the patch from multiple intruders (Field,[19]), thus further work should focus on strategies that model patch defence times, given multiple intruders return to superparasitise. A model of patch leaving, with multiple intruders, should be constructed with two components. The first is a learning component, that models estimates of the number of intruders waiting to superparasitise. Estimating the number of opponents is a difficult problem because a learning procedure must map the number of encounters with multiple intruders to the number of intruders themselves. If learning the intruder number occurs during competition for the patch, how can the current resident "be sure" that an opponent is a new female to arrive on the patch, or just an opponent previously encountered? Similarily, whilst guarding, a resident may usurp an opponent, but was this a new arrival to the patch, or one of the previous contestants?

As with any other behavioral model, a hypothesis must be made about the information the resident uses to assess the number of opponents. One simple starting point would be to assume that the resident uses the encounter rate with opponents, during competition for residency, to estimate their number. This hypothesis may be tested experimentally, by replacing a resident guarding a patch from multiple intruders, with a resident guarding a patch from only a single intruder. The later's strategy, based on opponent number "estimates," if assessed during patch competition, may be to leave, on average earlier than resident who fought multiple intruders.

Return strategies of the intruders must also be considered. The assumption, for pairwise conflict, that intruders are constrained to return after the resident leaves may breakdown. Because of the high level of patch superparasitism, there may be a threshold combination of patch parasitisation, attained before or during competition for residency, in which a player removed through competition will leave.

6.1.4 $\epsilon-$ Perfect Strategies

$\epsilon-$ perfect strategies are sub-optimal strategies adopted by competing players. The analysis of $\epsilon-$ perfect strategies has a long history in models of economic competition (Fudenberg and Tirole,[24]). Recently, $\epsilon-$perfect game theory has been applied to the study of animal behaviour (McNamara, Webb, Collins, Szekely and Houston,[60]). The authors of this paper were motivated by "the cycling problem" found in finding state dependant strategies of dynamic games (Houston and McNamara,[36]). The cycling problem occurs when there is divergence of strategies from a Nash Equilibria. Instead strategies, found from applying the best response function $Br(.)$ cycle, with $Br(s_1) = s_2, Br(s_2) = s_1, Br(s_2) = s_1$, and so on. The authors of this paper identified the reason for this cycling came from the discontinuity of the best response function and by "smoothing" the best response function, convergence to an $\epsilon-$perfect equilibria was guaranteed (McNamara, Webb, Collins, Szekely and Houston,[60]).

Consider the following example, drawn from work done in Chapter 3, on the optimal guarding strategy of the resident. An optimal return frequency, dependent on the cost of superparasitism, C_I, was found for the intruder, $\lambda_I^*(C_I)$. The best response of the resident, to the intruder's return, was to either search for remaining unparasitised eggs, or to commence guarding. Which strategy to use depended on the difference of payoffs from the strategies. With the expected payoffs from guarding defined to be $E(R|\lambda_{s/o} = 0)$ and from host searching $E(R|\lambda_{s/o} = \infty)$, the proportion of time spent guarding, as a function of the intruder's return rate will satisfy

$$Br(\lambda_i^*(C_i)) = \begin{cases} 0 & \text{if } E(R|\lambda_{s/o} = 0) - E(R|\lambda_{s/o} = \infty) < 0, \\ \text{either strategy} & \text{if } E(R|\lambda_{s/o} = 0) - E(R|\lambda_{s/o} = \infty) = 0, \\ 1 & \text{if } E(R|\lambda_{s/o} = 0) - E(R|\lambda_{s/o} = \infty) > 0. \end{cases}$$

Now consider the Heaviside step function, defined to be

$$H(x) = \begin{cases} 0 & \text{if } x < 0, \\ \frac{1}{2} & \text{if } x = 0, \\ 1 & \text{if } x > 0. \end{cases}$$

then almost surely

$$Br(\lambda_i^*(C_i)) = H(E(R|\lambda_{s/o} = 0) - E(R|\lambda_{s/o} = \infty)).$$

What is an $\epsilon-$ perfect best response? Consider the following continuous approximation to the heaviside step function

$$H_\epsilon(x) = \frac{1}{1 + \exp(-\frac{x}{\epsilon})}.$$

$H_\epsilon(x)$ is an approximation to $H(x)$ since

$$H_\epsilon(x) \longrightarrow 0 \quad \text{as} \quad x \longrightarrow -\infty,$$
$$H_\epsilon(x) \longrightarrow 1 \quad \text{as} \quad x \longrightarrow \infty,$$

and

$$H(0) = \frac{1}{2}.$$

Furthermore, $H_\epsilon(x)$ converges to $H(x)$ as $\epsilon \longrightarrow 0$, in the sense that [2]

$$\lim_{\epsilon \to 0} \int_{-\infty}^{\infty} |H_\epsilon(x) - H(x)| dx = \lim_{\epsilon \to 0} \epsilon(\ln(2) - \ln(1)) = 0.$$

An $\epsilon-$ perfect best response may be defined as

$$Br_\epsilon(\lambda_i^*(C_I)) = H_\epsilon(E(R|\lambda_{s/o} = 0) - E(R|\lambda_{s/o} = \infty)).$$

When the costs of guarding versus host searching are large, that is $(E(R|\lambda_{s/o} = 0) - E(R|\lambda_{s/o} = \infty))$ is large, then the $\epsilon-$ perfect best response will approximate that of the best response, as seen in Figure 6.1.2. However, if the relative cost of

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[2] This is convergence with the L^1 metric.

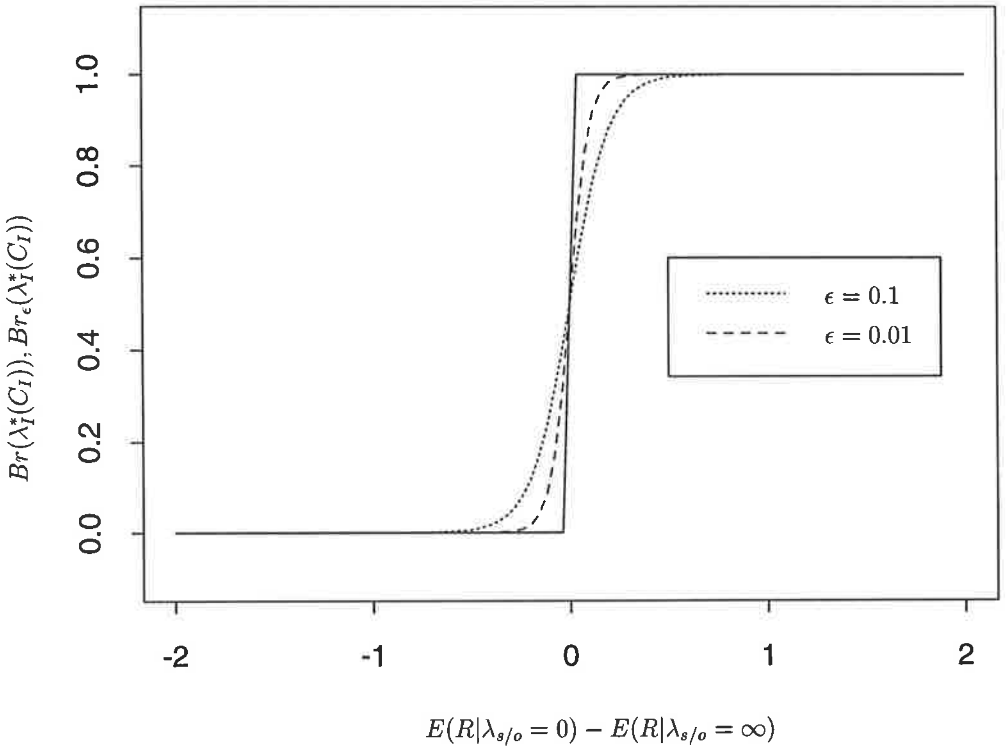

Figure 6.1.2: Comparison of the best response function $Br(\lambda_I^*(C_I))$ and the $\epsilon-$perfect best response functions for $Br_\epsilon(\lambda_I^*(C_I))$ for $\epsilon = 0.1, 0.01$. Here, $E(R|\lambda_{s/o} = 0) - E(R|\lambda_{s/o} = \infty)$ is the difference in costs of guarding versus host searching

guarding versus host searching is small, then the $\epsilon-$perfect best response predicts that a certain time will be spent guarding, before commencing host searching.

Why study these strategies? The resident's best response will depend on its estimate of the return frequency of the intruder. It is unlikely that the resident's strategy will evolve exactly to that of the ESS, because of environmental variability. Furthermore, biologically realistic models must include mistakes in strategies (McNamara, Webb, Collins, Szekely and Houston,[60]) or mistakes in the assessment of the opponents state (Enquist and Leimar,[16]), thus models where players occassionally make errors, when the cost of making those errors is small, should be explored. Observations of *T. basalis* indicate that during the intruder's return phase, a certain proportion of time is spent in patch defence and searching (Field,[19]). Apportionment of time to both strategies emerges from the $\epsilon-$ perfect best response function.

6.1.5 Spatial Issues

Most models of parasitoid host searching do not include adaptive search strategies, instead, models focus on strategies to secure resources, once the host of patch has been found. There is however, a growing body of work regarding host search strategies, taking into account spatial distributions of hosts into account. One example of this, is the spatial structure function, which determines the probability of find a host, some particular distance from the current host (Mangel,[48]).

Three classes of behaviour in *T. basalis* have spatial structure as the core issue. The first is the oviposition pattern of contestants. Upon patch arrival, players are seen to oviposit in the boundary eggs first, moving to the interior, as remaining unparasitised eggs diminish (Field,[19], Wilson,[86]). What are the costs and benefits of this strategy? It may seem like an obvious strategy to adopt, however, when resident and intruder roles are determined, an intruder superparasitises the exterior eggs (Field,[19]). If the exterior eggs are intruder superparasitised, this makes them a riskier investment, thus shouldn't they be parasitised last? The costs and benefits of exterior first/interior last, interior first/exterior last or random oviposition strategies are yet to be examined.

Observation of *T. basalis* show that the searching strategy involves travelling up and down the stems of the plant that support host patches (Personal observation). As host patches are found on the undersides of leaves, this seems to be a sensible search strategy. This strategy, as opposed to a random sample of positions on the host plant, may have consequences for the the arrival of conspecifics to a patch.

In models where predators estimate the numbers of prey at a site, as is the case of a sit and wait forager such as a trap door spider, interarrival times of prey are assumed to exponentially distributed (Mangel and Clarke, [50]). However, conspecific *T.basalis* may arrive in "bursts" due to the search strategy adopted. There is some evidence for this in the wild, from estimates of the coefficient of variation of numbers of competitors on sampled patches (Field, personal communication). If competitors do arrive in bursts, what are the implications for patch defence strategies? The optimal leaving time of a resident was calculated, assuming the intruder superparasitises some time afterwards. Models that include multiple arrivals, with different inter-arrival time structures, should be constructed.

The final behavioral pattern that has clear spatial issues is that of the resident's patch departure. As mentioned in the previous chapter, a resident, when leaving, commences a series of radial searches of the surrounding area, these searches punctuated with a return to check the patch (Field, Calbert and Keller,[21]). Each time a new search commences, the radius is increased. In this authors mind, there is clear adaptive value in this behaviour.

Consider the following abstraction. Suppose an object is located some distance from some central point. The probability of the object being a specified distance from the center follows a two dimensional Gaussian distribution, with the origin at this central point. What is the optimal search trajectory, given imperfect detection of the object? The discipline of *search theory* (Koopman,[41]) covers such topics as these. Authors have shown that the optimal search strategy, in this situation, is to search within a series of circles of ever increasing radius (Koopman,[41]). There is a clear need to apply some of the topics of search theory to the behaviour of *T. basalis* and other guarding parasitoids. Search theory has indeed been applied to the subject of ant navigation (Wehner and Srinivasan,[85]).

6.2 General Conclusion

The work in this thesis could be broadly classed as theoretical behavioral modelling of parasitoids that defend patches from conspecifics. Two issues were studied.

- The resolution of roles from patch competition.
- Role dependent strategies used to maximise potential fitness gains from a patch.

The first part of the thesis focussed on the mechanisms by which residency is decided. By qualititive comparison with observed data (Field,[19]), the rule of persistence in fighting, in proportion to your current investment was proposed. With this assumption, a persistence time, in the case of continuous risks in fighting, could be found by finding the ESS scaling factor u^*, that scaled current investment to time of fighting. A persistence time was replaced with a persistence level, or risk of injury, with the graduated risks model. Below some threshold current patch investment, players did not risk being injured, thereafter fighting occurred at a level that maximised the probability that one player would be injured.

The host searching strategy of *T. basalis,* by local anntenation of the patch required that the assumptions of perfect information about the oppenents investment, assumed in many war of attrition models was not correct (Mesterson-Gibbons,[63]). The competitors in these games for residency were assumed to have knowledge of self-investment and only knowledge of the distribution of possible opponent investments.

Having lost residency, the strategies by which an intruder could maximise fitness returns were studied. Under the assumption that the patch is most vulnerable to intruder superparasitism when the resident is itself ovipositing, an optimal intruder return frequency was calculated, assuming an exponential return time distribution. As the intruder has only partial information of the behaviour of the resident, the optimal return frequency was calculated under the further assumption that the intruder could estimate the residents oviposition rate, but not the times of oviposition. Assuming that the resident, in response, adopted the strategies of search/oviposit or guard, a threshold return rate of the intruder was found, below which, the best response was to continue searching. The intuitive explanation for this is clear. If the return tendency of the intruder is low, there will be more time to search for remaining unparasitised host eggs, making this strategy profitable.

Through multiple returns, the intruder may learn which strategy is more profitable, returning to search for hosts, possibly with a resident interception cost, or playing the waiting game.

Once the costs of attempts to steal ovipositions become to great, the only strategy open to the intruder is to return after the resident leaves to superparasitise. If the intruder has partial information as to the presence or absence of the resident, then its best strategy is to return when the probability of resident being present is sufficiently low that the rewards from superparasitism outweigh the risks in returning while the resident is still present.

Given that the resident's costs of intruder superparasitism decrease with time, the best response of the resident is to leave the patch at a time which maximises fitness gains in light of the intruders return. The situation of resident departure and intruder return, with the resident having the information advantage, forms a Stackelberg equilibria of leave/return times.

At the commencement of this thesis, it was hoped that models would be constructed that were at the very least partially descriptive of the behavioural phenomena studied in Dr. Scott Fields thesis (Field,[19]). This aim has been achieved though in constructing these models, it has became clear that some assumptions about patch vulnerability and information assymetry need to be tested experimentally.

Is the patch more vulnerable to intruder oviposition while the resident is itself ovipositing? An initially high return rate may in fact be due to incomplete "perception" of the role of this player as the intruder as it may still "perceive" it is a resident. Can parasitoids "count" the number of ovipositions, or are decisions made with a rate based currency? Currently, the assumption that the parasitoids use counts of the previous number of ovipositions, rather than the rate of ovipositions as a cue for fighting is more favourable because there seems to be huge variation in the mean rate of encounter with unparasitised hosts as patch parasitisation progresses (Field,[19]). The only reliable information possessed by the parasitoid seems to be current number of self ovipositions.

Do there exist simple rules of thumb that govern the behaviour of the resident and intruder? All of the models in this thesis assumed pairwise competition. However, large variation in host patch sizes and competitor numbers is the most likely background under which patch defence behaviour has evolved, this being the direction for future research in parasitoid patch defence.

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