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A GAME THEORY ANALYSIS OF RESOURCE DEFENCE AND OBSERVATIONS ON THE BEHAVIOUR OF JUVENILE LIMNOPORUS NOTABILIS STÅL (HETEROPTERA: GERRIDAE)

by

Andrew John Tyre

B.Sc. University of Alberta 1991

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A GAME THEORY ANALYSIS OF RESOURCE DEFENCE
AND OBSERVATIONS ON THE BEHAVIOUR OF JUVENILE
LIMNOPORUS NOTABILIS STÅL (HETEROPTERA: GERRIDAE)

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Abstract

Resource defence has been studied for decades in many different contexts, from mate acquisition to foraging. The occurrence of resource defence has been best explained by the concept of economic defensibility. In relation to foraging, economic defensibility has been tested most often in the form of the food threshold hypothesis, with resource defence being the optimal foraging strategy at intermediate levels of food availability between an upper and a lower threshold. The food threshold hypothesis provides a reasonable qualitative fit to observations in many systems. However, considerable unexplained variation still exists. In particular, it is still unclear why alternate foraging strategies coexist with resource defence at food levels at which defence is the optimal strategy according to the food threshold hypothesis.

Multiple strategies and other considerations suggest that resource defence should be modelled as a game played "against the field". A game theory model of resource defence demonstrates that mixed equilibria of territory owners and floaters should be common under a wide variety of circumstances. In addition, the model predicts that lower food thresholds will exist only when evicting floaters is costly. Upper food thresholds exist only when there is a maximum rate of energy intake.

I examined the behaviour of juvenile water striders *Limnoporus notabilis* to determine if they use aggressive behaviour in the acquisition of food. I assume that juvenile water striders use vibration signals on the water surface to communicate aggressive intent to competitors. In a growth experiment, increased food supply increased some components of fitness, particularly survival and growth rate in the first two instars. Based on these observations, the food threshold model predicts that aggressive behaviours should occur most frequently at intermediate levels of food availability. Contrary to these predictions, changing food availability had no effect on the frequency of aggressive behaviours in individual water striders.

Overall, the results of this thesis suggest that more attention needs to be paid to alternative strategies for acquiring resources when considering resource defence. Explaining the existence of alternative strategies as being employed by competitively inferior individuals is not always an adequate explanation.

For my parents.

Without your encouragement I would never have started,
and without your support I would never have finished.

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Chapter 1:

General Introduction

> "...the struggle almost invariably will be most severe between the individuals of the same species, for they frequent the same districts, require the same food, and are exposed to the same dangers." Charles Darwin, *The Origin of Species*

As noted by Darwin, all organisms must consume resources in order to survive and reproduce, and those resources are limited. In scramble competition, resources such as space, mates, or food are divided up among competitors in a population on a "first come, first served" basis. In interference competition, competitors frequently use aggression to increase their share of resources over what they would have received in pure scramble competition (Milinski and Parker 1988). Aggressive behaviour generates a variety of social structures, most notably territory defence and dominance. In both cases aggression, a behaviour with a variety of potential costs, is used in order to increase a competitor's share of a limited resource. This thesis is composed of two studies, both of which consider how changes in food availability can affect aggression during foraging. First, I construct a game theory model of resource-based aggression. Second, I examine the behaviour of juvenile water striders (Heteroptera: Gerridae: *Limnoporus notabilis* Stål) for evidence of food-related aggression, and perform manipulative experiments to look for effects of food availability on aggressive behaviour.

Although territorial behaviour has been defined in many ways (reviewed in Kaufmann 1983), the definition of a territory that applies to the widest taxonomic range is "an area occupied more or less exclusively by an animal or group of animals by means of repulsion through overt defence or advertisement" (Wilson 1975). The key component of this definition is: the defence of an area against conspecifics or other users of the resource. This definition applies across a range of temporal scales. At the shortest temporal scale, an individual may be observed responding only to competitors within some distance immediately adjacent to itself. As the temporal scale of the observations increases, a larger region within which the aggressor exerts its influence may or may not become apparent. Wilson (1975) refers to a defended area immediately adjacent to an individual as a "floating territory". While such areas are not fixed in space, similar economic considerations apply to the defence of both floating and fixed territories.

Dominance behaviour is defined as, "...the assertion of one member of a group over another in acquiring access to a piece of food, a mate, a place to display, a sleeping site or any other requisite that adds to the genetic fitness of the dominant individual" (Wilson 1975). However, if dominant animals only exert their dominance over subordinates within some specified maximum distance (as must be the case), and if dominance behaviour can be considered costly in a manner similar to territory defence, then economic models of territory defence can also be applied to dominance behaviours. The primary difference between dominance and territoriality is that territory owners direct aggression at all other individuals, while individuals in a dominance hierarchy direct aggression only at subordinates.

Early attempts at understanding territorial behaviour sought to elucidate a function for territoriality in the tradition of ethology. The conclusion was that territoriality served different functions in different species, making generalization impossible (Brown and Orians 1970). Attention then shifted to understanding the factors that may lead to the evolution of territorial behaviour. A number of hypotheses have been proposed to explain the adaptive significance of territorial behaviour (e.g. Brown 1964; Verner 1977). Of these, Brown's (1964) concept of economic defensibility has enjoyed the greatest longterm success.

The concept of economic defensibility may be summarized as follows. If the benefit derived from a resource exceeds the cost of defending it, then a resource can be defended economically. However, whether we expect a resource to be defended depends on how the net benefit of defence compares with the net benefit of alternative strategies for acquiring the same resource. This distinction is often overlooked. The benefit of defence is generally the acquisition of (or continued access to) the resource. The costs of defence are varied, and can include energetic expenditures on evicting intruders (e.g. Frost and Frost 1980; Puckett and Dill 1985), the time cost of evicting intruders (Davies and Houston 1981, Tye 1986; Ydenberg and Krebs 1987), risk of injury while evicting intruders (Jaeger 1981; Mathis 1991), and increased risk of mortality from predators (Martel 1992). Benefits will be determined by the abundance, availability, and distribution (uniform, random, or clumped) of resources in the environment, whereas costs will be a function of the number of competitors present, the persistence of those competitors, and the proportion of those competitors also engaging in aggressive defence of resources.

Most demonstrations of resource defence as an alternative food acquisition strategy have been with birds. For example, Carpenter and Macmillen (1976) showed with a simple energetic model that defence by Hawaiian honeycreepers (*Vestiaria coccinea*) should be favoured only at intermediate levels of food availability. At low levels of food availability the energetic costs of defence exceed the benefits that can be extracted from the limited area defended. At high levels of food availability the overabundance of food makes the cost of defence wasteful. In contrast, at intermediate levels of food availability defence is the best way to maximize energetic intake.

Another way to consider these predictions is to think of upper and lower thresholds of food availabilities. Defence is advantageous between these threshold levels, whereas outside of the thresholds an alternative strategy will be better (Figure 1.1). Carpenter and Macmillen (1976) compared the results of their model with data on Hawaiian honeycreepers, and found a reasonable qualitative fit to their prediction.

Davies and Houston (1981) described resource defence in the pied wagtail (*Motacilla alba*). Pied wagtails defend stretches of river bank, consuming insects that wash up on shore. The feeding rate of a defender depends on the time between visits to a particular area, as the food supply is replenished at a fixed rate. The alternative strategies are to exclude all competitors from the foraging area, or to permit a satellite resident to coexist on the foraging area. In all cases in their study, defence increased the owner's feeding rate by preventing intruders from depleting the food supply. Satellites were tolerated only on days of high food availability. Equally important, when food became scarce defenders abandoned their foraging area, and when food was super-abundant defenders ignored intruders and satellites altogether. These observations fit the food-threshold model.

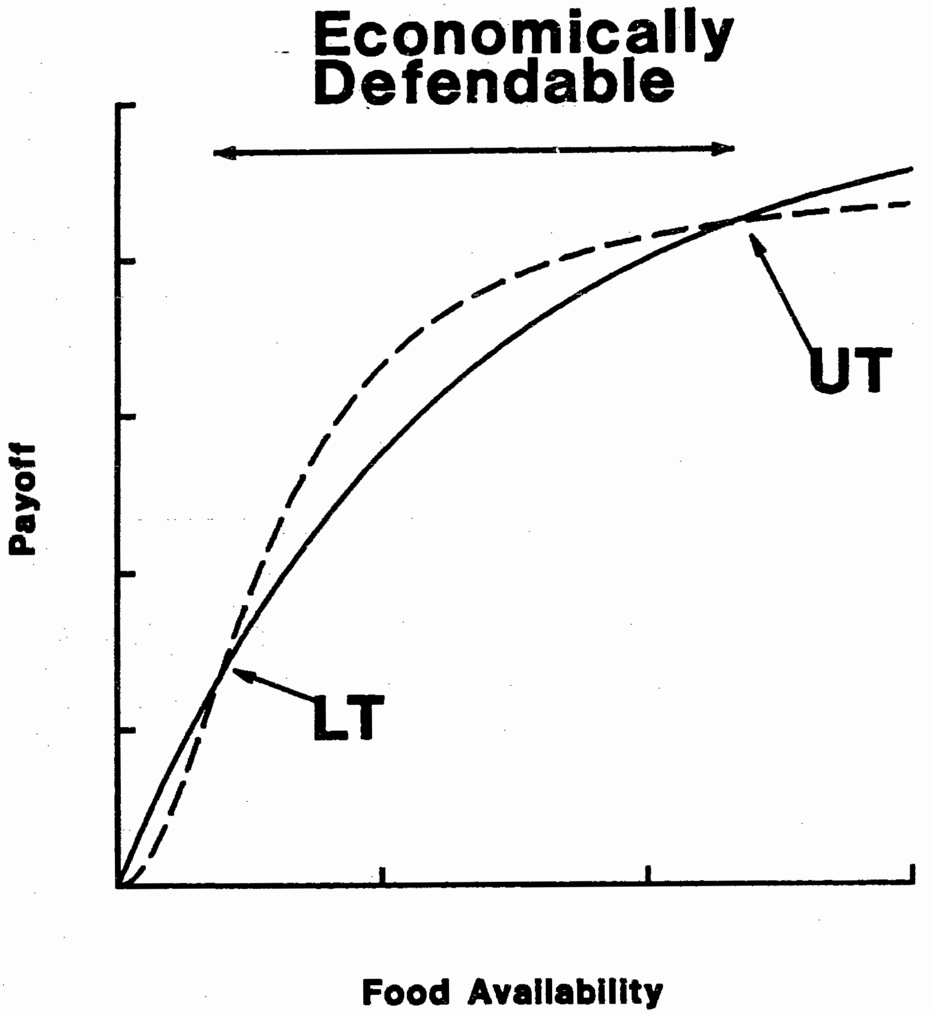

Figure 1.1 Relationship between food availability and the occurrence of resource defence. Food availability increases from left to right on the ordinate. The dashed line is the payoff to aggressive animals, and the solid line is the payoff to non-aggressive animals. Below the lower threshold (LT), the cost of resource defence is greater than the benefit obtained, so non-aggression is a superior strategy. There is a maximum amount of food that can be consumed, and once this level is reached non-aggressive animals do better because they do not pay defence costs. This creates the upper threshold (UT).

Wilcox and Ruckdeschel (1982) demonstrated food threshold resource defence in the water strider, *Aquarius* (=*Gerris*) *remigis* (Heteroptera: Gerridae). In a laboratory experiment they deprived water striders of food and observed that within one day most individuals entered a phase of aggression. After one week without food the animals ceased all activity. Wilcox and Ruckdeschel (1982) interpreted the initiation of aggression as evidence for an upper food threshold, and the cessation after a week as evidence for a lower food threshold. In a field experiment they provisioned animals that were defending a foraging area with flies and showed that animals ceased aggressive defence within a few days, demonstrating the existence of an upper threshold. The alternative strategy in the field study was home range maintenance, in that animals maintained site-fidelity but did not actively defend that site from conspecifics.

From the previous examples it is clear that the food-threshold model does a reasonable job of describing resource defence behaviour in a variety of species, at least qualitatively. However, in many of these studies there is a substantial amount of unexplained variation in behaviour. At least three sources could contribute to this variation. First, in many cases it is difficult to quantify the costs and benefits of alternate strategies; there may be conditions under which a decision to defend resources seems like a poor one, but perhaps the alternatives under those same conditions are even worse. Second, the costs of defence depend on the number of intruders, which may vary independently of food availability (Myers et al. 1981). Third, the number of intruders may depend on the frequency with which defence behaviour is occurring within the population (Davies 1980). Individuals who are defending territories should have less time to explore the environment beyond the boundaries of their territory. Therefore, the frequency of intrusions should decrease as the frequency of resource defence behaviour in the population increases. This dependence of the costs and benefits of a behaviour on the frequency of the behaviour in the population, and the dependence of the frequency of the behaviour on the costs and benefits of alternative strategies, suggests that modelling resource defence as a game would be appropriate (e.g. Poethke and Kaiser 1985).

Game theory is a branch of probability theory that deals with the outcome of games. A game is any situation involving an interaction between more than one individual in which each individual has a different desired outcome of the interaction, and only partial control over what the eventual outcome will be (Maynard Smith 1982). Resource defence can be considered in a game context. Each individual would "like" (in a non-cognitive sense) the largest possible share of the available resources, and each individual controls only its own behaviour: to aggressively defend resources or not. The outcome, the share of the available resources that an individual receives, depends both on the individual's behaviour and on the behaviour of other members of the population.

In the next chapter I construct a game theory model of resource defence, and demonstrate that it is possible to have stable mixed strategy equilibria between defenders and non-defenders competing for a resource, in the absence of any initial asymmetries between individuals. This model takes into account the dependency of costs and benefits of resource defence on the frequency of the behaviour in the population. The model makes the same predictions as simpler food threshold models (Carpenter and Macmillen 1976; Myers et al. 1981). More importantly, the model is unique in that it predicts <u>variation</u> in the occurrence of resource defence within a single population. Traditional food threshold models predict a single optimal strategy at each level of food availability.

For the experimental portion of this study, I elected to work on juvenile water striders, *Limnoporus notabilis* Stål. *L. notabilis* are convenient for experimental work on aggression because: (1) they are common in B.C., (2) they are large, (3) previous work has shown that juvenile *A. remigis* defend foraging areas (Blanckenhorn 1991; Wilcox and Ruckdeschel 1982), and (4) adult male *L. notabilis* defend areas to increase their encounter rates with females (Spence and Wilcox 1986). Therefore, I was interested in determining whether or not *L. notabilis* also engaged in food-based aggression. I chose to study juveniles in order to remove mate-acquisition as a reason for aggressive behaviour (e.g. Wyman and Hotaling 1988).

In Chapter 3 I examine the behaviour of juvenile *L. notabilis* in the laboratory. I assume that the vibration signals generated by juvenile water striders signal aggressive intent, and in a growth experiment I show that food availability influences the development rate and survival of waterstriders in the laboratory. Finally, in an attempt to relate food availability to aggression, I subjected juvenile bugs to different food levels and observed their tendency to signal aggressive intent to competitors. Contrary to expectation, food levels did not alter signalling behaviour in any predictable manner.

List of References

Brown JL (1964) The evolution of diversity in avian territorial systems. The Wilson Bulletin 76:160-169

Brown JL, Orians G (1970) Spacing patterns in mobile animals. Annual Review of Ecology and Systematics 1:239-262

Blanckenhorn WU (1991) Fitness consequences of food-based territoriality in water striders, *Gerris remigis*. Animal Behaviour 42:147-149

Carpenter FL, Macmillen RE (1976) Threshold model of feeding territoriality and test with a Hawaiian honeycreeper. Science 194:639-642

Davies NB (1980) The economics of territorial behaviour in birds. Ardea 68:63-74

Davies NB, Houston AI (1981) Owners and satellites: the economics of territory defence in the pied wagtail, *Motacilla alba*. Journal of Animal Ecology 50:157-180

Frost SK, Frost PGH (1980) Territoriality and changes in resource use by sunbirds *Leonotis leonurus* (Labiatae). Oecologia 45:109-116

Jaeger RG (1981) Dear enemy recognition and the costs of aggression between salamanders. American Naturalist 117:962-974

Kaufmann JH (1983) On the definitions and functions of dominance and territoriality. Biological Reviews 58:1-20

Martel G (1992) Influence of predation risk on the territorial behaviour of juvenile coho salmon, *Oncorhynchus kisutch*. PhD. Dissertation. Simon Fraser University, Burnaby, B.C., Canada. 150pp.

Mathis A (1991) Territories of male and female terrestrial salamanders: costs, benefits, and intersexual spatial associations. Oecologia 86:433-440.

Maynard Smith J (1982) Evolution and the theory of games. Cambridge University Press, Cambridge. 224 pages

Milinski M, Parker GA (1988) Competition for resources. pp. 137-168. In: Krebs JR, Davies NB (Eds.) Behavioural Ecology: An Evolutionary Approach. Blackwell Scientific Publications, Oxford

Myers JP, Connors PG, Pitelka FA (1981) Optimal territory size and the sanderling: compromises in a variable environment. pp 135-159. In: Kamil AC, Sargent TD (eds) Foraging Behaviour: Ecological, Ethological, and Psychological Approaches. Garland STPM Press, New York.

Poethke HJ, Kaiser H (1985) A simulation approach to evolutionary game theory: the evolution of time-sharing behaviour in a dragonfly mating system. Behavioral Ecology and Sociobiology 18:155-163

Puckett KJ, Dill LM (1985) The energetics of feeding territoriality in juvenile coho salmon (*Oncorhynchus kisutch*). Behaviour 92:97-111

Spence JR, Wilcox RS (1986) The mating system of two hybridizing species of water striders (Gerridae). II. Alternative tactics of males and females. Behavioral Ecology and Sociobiology 19:87-95

Tye A (1986) Economics of experimentally-induced territorial defence in a gregarious bird, the fieldfare *Turdus pilaris*. Ornis Scandinavica 17:151-164

Verner J (1977) On the adaptive significance of territoriality. The American Naturalist 111:769-77

Wilcox RS, Ruckdeschel T (1982) Food threshold territoriality in a water strider (*Gerris remigis*). Behavioral Ecology and Sociobiology 11:85-90

Wilson EO (1975) Sociobiology. Belknap Press, Cambridge Massachusetts. 367pp.

Wyman RL, Hotaling L (1988) A test of the model of the economic defendability of a resource and territoriality using young *Etroplus maculatus* and *Pelmatochromis subocellatus kribensis*. Environmental Biology of Fishes 21:69-76

Ydenberg RC, Krebs JR (1987) The tradeoff between territorial defence and foraging in the great tit (*Parus major*) American Zoologist 27:337-346

Chapter 2:

A game-theoretic approach to resource defence: when does being a bully pay?

Introduction

In most territorial systems only some members of the population defend territories. The remaining members are non-territory holders, or floaters. Floaters have traditionally been considered to be individuals who are unable to acquire territories because of low resource holding potential (RHP; Robertson et al. 1976), or because of late arrival (Smith 1978). In this chapter I present a game theory model of territoriality that challenges these assumptions and demonstrates that populations can be at mixed strategy equilibria, with some members of the population defending territories and others floating.

Game theory is a branch of probability theory that deals with the outcome of games. A game is any situation involving an interaction between more than one individual in which each individual has a different desired outcome of the interaction, and only partial control over what the eventual outcome is (Maynard Smith 1982). A game theory analysis will describe a game in terms of the best strategies to use at an equilibrium, where all participants in the game have the same <u>expected</u> payoffs. Such equilibrium points can be either pure, where all participants use the same strategy, or mixed, where some proportion of the participants use one strategy and the remaining participants use a different strategy. It is important to keep in mind that at a mixed equilibrium point, all inidivuals receive the same payoff, regardless of the strategy used. In addition, strategies (both pure and mixed) may be conditional: what each individual does depends on conditions in the environment (Parker 1984).

There are two points about territoriality that suggest that a game theory approach is appropriate. First, intruders are often of the same species as territory owners, and presumably part of the same population. This begs the questions: where do intruders come from, and what do they do when they are not intruding? Clearly, they are either territory owners themselves, or they are using an alternative strategy to territory defence to acquire the same resource. A model of the decision of when to defend a territory must include an analysis of the payoffs to using alternative strategies, in addition to considering the payoffs to territory holders. Second, the costs and benefits of territory ownership may change with the proportion of the population that is using the strategy of "territory owner", as interactions with other territory owners may carry a different cost (either higher or lower) than interactions with non-territory owners. More importantly, the number of individuals available to intrude decreases as the number of territory owners increases. Both of these considerations suggest that a game theory approach to the problem will be fruitful.

Previous game theory models of territory defence have examined the decision of how to defend a territory given that the animal already owns it (e.g. Getty 1987; Grafen 1987; Hurd 1992; Maynard Smith 1982). Such models explain how territory owners maintain their territories, and why escalated fights with rivals are uncommon. Again, these models are limited in that they make the implicit assumption that all animals would be territory owners if they could because there is no other way to acquire the resource. This is not always the case: Robertson et al. (1976) demonstrated that striped parrotfish can use either a territorial or a non-territorial schooling strategy to acquire food. The decision about whether or not to defend a territory at all, as opposed to how to defend a territory, is a game against all other members of the population (e.g. "a game against the field"; Poethke and Kaiser 1985), rather than a game between two individuals.

The two main kinds of resources that territory owners defend are food and reproductive opportunities (or resources needed for reproduction). These two resources need not be mutually exclusive. Male red-winged blackbirds (*Agelaius phoenicius*) defend feeding territories to acquire food for raising offspring (Shutler and Weatherhead 1991). However, in order to simplify the task of modeling the decision of whether to defend a territory, I restrict my analysis to non-breeding populations of animals. Territorial defence under such a condition is not uncommon. For example, hummingbirds (*Selasphorus rufus*) defend feeding territories during migrations (Gass et al. 1976). Similarly, pied wagtails (*Motacilla alba*; Davies and Houston 1981), robins (*Turdus migratorius*; Sallabanks 1983), and harriers (*Circus cyaneus*; Temeles 1990) defend feeding territories during the non-reproductive season. Juvenile coho salmon (*Oncorhynchus kisutch*) defend feeding territories in streams prior to migrating out to sea (Puckett and Dill 1985; Martel 1992). Juvenile water striders (*Aquarius remigis*) also defend feeding territories (Wilcox and Ruckdeschel 1982). Although my analysis will be restricted to non-breeding situations, many of the insights from this model can be extended to include reproductive situations.

In the game there are two strategies: floating and territory ownership. Each of these strategies specifies the actions used by a player of that strategy to acquire the resource. Floaters locate and consume food as they move randomly through the environment. A population of all floaters is engaging in scramble competition. Floaters never defend food and always retreat when faced with an aggressor. Territory owners, on the other hand, restrict their foraging to a particular area of the environment which they defend aggressively from competitors. Territoriality is a mechanism of interference competition. While I assume here that territories remain fixed in place, the subsequent development of the model is no different if territory owners defend territories that move with them as they move through the environment. In fact, the use of a specific area can be abandoned altogether without changing the mathematics, resulting in a form of dominance hierarchy. As long as dominant individuals have an individual distance within which they respond to competitors, and these responses are costly, the predictions will be similar. For the remainder of this chapter I will use "territory owner" to refer to competitors who use aggression to increase their share of limited resources.

It is possible to describe intuitively the mechanisms that will lead to stable mixed equilibria of territory owners and non-territory owners (floaters). First, consider why a single floater, in a population consisting completely of floaters, would find it beneficial to switch to a territorial strategy. Floaters are engaging in scramble competition for food, and in a high density population competition will be intense. A territory owner gets more or less exclusive access to the food on its territory. Provided that the cost of territory defence is low enough, a lone territory owner could obtain more food than a floater. Now consider the advantage of a single floater in a population of territory owners. If the cost of interacting with other territory owners is high, then a territory owner that abandons territory defence in favour of floating will no longer pay that high cost. Assuming that floaters can acquire some food in a habitat completely covered with territory owners, then the net payoff to a floater in a population of territory owners could be higher than the net payoff to a territory owner.

The above conditions define what happens when everyone is either a territory owner or a floater. When there is a mixture of territory owners and floaters, there is an important distinction (see Brown 1969). As the proportion of territory owners increases from zero, there is enough space that each new territory owner does not have to fight other territory owners to acquire a territory. However, once the entire habitat is covered with territories, a new territory owner can acquire a territory only by usurping all of another territory, or parts of several territories. Therefore, the payoff to territory owners of defending will increase until the habitat is covered with territories, because the number of floaters that must be evicted is decreasing. Once territories saturate the habitat the payoff to territory owners will start to decrease with further increases in the number of owners. Territories must shrink in size to accommodate each new territory owner, and territory owners will need to interact with each other in order to maintain the boundaries of their territories. At the same time, the payoff to floaters will initially be decreasing because less and less area is available for them to forage in outside of territories. Once the entire habitat is covered with territories the payoffs to floaters will depend on how efficiently territory owners can detect and evict them, because the only food available to floaters is that which can be obtained from territories, assuming that territories pack completely with no leftover space (i.e. that territories are hexagonal; e.g. Barlow 1974; Buckley and Buckley 1977).

This modeling exercise has two goals: first, to determine whether food thresholds in resource defence can be obtained in a game-theory context; second, to explain intrapopulation variation in the occurrence of resource defence as a mixed strategy equilibria.

Assumptions

Territories have been defined in various ways. The two most widely used definitions are: "an area occupied more or less exclusively by an animal or group of animals by means of repulsion through overt aggression or advertisement" (Wilson 1975), and that animals are spaced out more than expected from a random occupation of the habitat (Davies 1978). In this chapter, I use the first definition because the second can result through mutual avoidance as well as aggression. The two key components to territoriality in this definition are: (1) the more or less exclusive use of an area, and (2) defence of that area against conspecifics or other users of the resource. It is important to keep in mind that defence does not necessarily imply physical attack; advertisment that results in an intruder leaving the territory is also "defence".

I make several assumptions to simplify the analysis:

(1) All food that arrives is consumed by either territory owners or floaters.

(2) Food arrives in the environment randomly at a constant rate, and consumption does not alter the rate (i.e. patches do not deplete). Random arrival means that the position of an arriving food item has no bearing on where the next food item will arrive, and that no point in the environment has a higher probability of receiving food than any other point.

(3) All competitors are equal in their ability to capture and consume food, and all territory owners are equal in their ability to defend territories.

(4) All activities, such as feeding and territory defence, are instantaneous, or at least not mutually exclusive. This prevents conflicts between the time required for various activities from occurring in the model.

(5) Territories are either flexible in geometry or hexagonal. In other words, when the habitat is completely covered with territories there are no refuges.

(6) Animals have a preferred territory size, and this preference does not vary with competitor or food density. However, territories may be smaller than preferred under pressure from surrounding territory owners. Examples of such territories have been found in desert spiders (*Agelenopsis aperta*) in which territory size does not vary with either food or competitor density (Riechert 1981), and sanderlings in which territory size varies only with intruder density (Myers et al. 1981).

The Model

To begin, assume that all competitors are floaters. Since all competitors are equal the probability of any one individual being the first to reach a food item is inversely proportional to the density of competitors. Therefore, the payoff to a single floater is

$$E(F,I) = \frac{f}{n} \tag{2.1}$$

where $E(F,I)$ is the payoff to an individual playing F (floater) in a population playing strategy I (which is the average strategy played by all other individuals), f is the density of food, and n is the density of competitors (all symbols used in the model are listed in Table 2.1). Now consider what happens if one competitor switches to the strategy of territory owner. First, there is a decrease in the number of floaters amongst which the food is shared. Second, the total amount of space available to floaters for foraging decreases by some amount, because the territory owner does not permit trespassing.

The effect of some proportion p of individuals in the population switching to territory ownership on the denominator of (2.1) is to reduce the proportion of the population amongst which the remaining food is shared to $(1 - p)$.. Therefore, the amount of food is divided up among $(1 - p)n$ competitors.

The amount of space to which floaters will lose access is related to the proportion of competitors that switch to territory ownership, the density of competitors, and the size of territories defended. An expression for this

Table 2.1 List of symbols used in the game theory model.

Symbol	Description
$E(F,I)$	Expected payoff to a floater in a population playing the average strategy I.
$E(T,I)$	Expected payoff to a territory owner in a population playing the average strategy I.
f	Density of food.
n	Density of competitors.
p	Proportion of the population playing territory ownership.
T	Preferred territory size.
ϕ	Dimensionless measure of territory density (Equation 2.2).
t	Realized territory size (Equation 2.3).
P	Proportion of area covered with territories (Equation 2.4).
a	Efficiency of exclusion when $p = 0$.
$e(p)$	Proportion of food monopolized by a territory owner (Equation 2.7).
b	Parameter controlling the steepness of the exclusion function $e(p)'$ (Equation 2.11 and Figure 2.3).
c_t	Cost to a territory owner of interacting with other territory owners (Equation 2.12).
c_f	Cost to a territory owner of interacting with floaters (Equation 2.13).
c_1	Parameter controlling the cost of interacting with other territory owners when the habitat is covered with territories.
c_2	Parameter controlling the cost of interacting with floaters.
c_3	Cost to floaters of evading territory owners.
$C(f)$	Function describing rate of energy intake (Equation 2.25)
m	Maximum rate of energy intake

dimensionless number is

$$\phi = nTp \tag{2.2}$$

where T is the preferred territory size (in units of area per competitor).

It is possible for ϕ to exceed 1, which corresponds to the entire environment being covered with territories. I refer to the point where $p = 1/nT$ as the "critical point". When p is below the critical point there is room for more territories without having to decrease the size of a territory. When p exceeds the critical point, territory owners must reduce territory size because they are equivalent in their ability to defend territories, and the entire environment is filled. The realized territory size t is

$$t = \begin{cases} T \text{ } if \text{ } \phi \leq 1 \\ \frac{1}{np} \text{ } if \text{ } \phi \geq 1 \end{cases} , \tag{2.3}$$

and therefore, the proportion of the available area that is covered with territories is

$$P = n\,t\,p\,. \tag{2.4}$$

P equals zero when there are no territory owners, and one when the entire area is covered with territory owners. P

never exceeds one, no matter how many territory owners are present. The total amount of area available to floaters is then $(1 - P)$, and the amount of food available to be divided up among floaters is $(1 - P)f$. Therefore, the payoff to a floater is

$$E(F,I) = \frac{(1 - P)f}{(1 - p)n} \ . \qquad (2.5)$$

The payoff to a territory owner is simply the density of food multiplied by the size of a territory

$$E(T,I) = tf \ . \qquad (2.6)$$

The payoff curves for equations (2.5) and (2.6) are shown in Figure 2.1 for two sets of parameter values. When $T > 1/n$ (Figure 2.1A), $p = 1$ is the only stable equilibrium point. If the area per territory owner is greater than the area per floater (the inverse of density when $p = 0$) then the payoff to territory owners is always greater than the payoff to floaters, and everyone should defend a territory. In addition, once ϕ exceeds 1 the entire habitat is covered with territories and floaters receive a payoff of 0. When $T < 1/n$ (Figure 2.1B), $p = 0$ is the only stable equilibrium point. If the area per territory owner is less than the area per floater then no one should defend a territory. Unlike the first case, ϕ never exceeds 1, and the payoff to floaters is always greater than that of territory owners. When $T = 1/n$ the payoffs of defending and floating are equal regardless of which strategy is being played, because

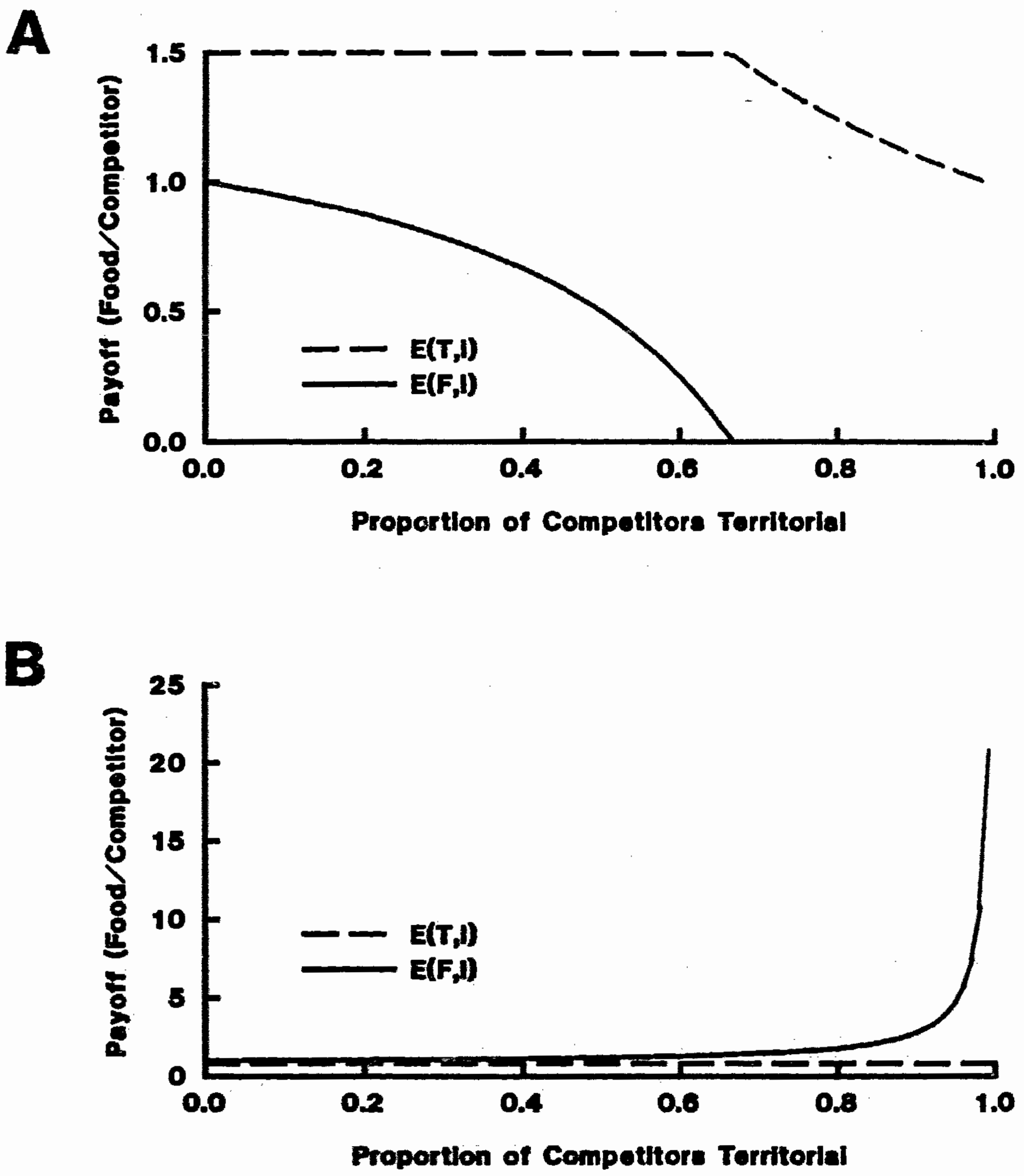

Figure 2.1 Plot of payoff equations (2.5) and (2.6). The solid line is the payoff to floaters, and the dashed line is the payoff to territory owners. The vertical dashed line marks the critical point where $\phi = 1$. Parameters are (A) $T = 1.5$, $n = 1$, $f = 1$, and (B) $T = 0.8$, $n = 1$, $f = 1$.

territory owners and floaters each have the same amount of area in which to acquire food.

The feature of the above equations which makes a mixed equilibrium impossible (except trivially, when $T = 1/n$) is that when the entire area is covered with territory owners, floaters cannot obtain food. This implies that exclusion is perfect, which is unrealistic. A solution to this problem is to allow floaters to consume some proportion of the food that lands on a territory. It is reasonable to assume that when there are fewer floaters exclusion will be more efficient. When $p = 1$, there are no floaters, therefore no intruders to be repelled, and exclusion should be perfect. In the simplest case, each floater that switches to being a territory owner reduces the intruder pressure on territory owners by the same amount, regardless of how many floaters remain in the population, or the proportion of the area that is covered with territories. The proportion of food on a territory monopolized by the owner is described by the linear function

$$e(p) = a + (1-a)p \qquad (2.7)$$

where a is the efficiency with which the first territory owner (when $p = 0$) excludes intruders. This exclusion efficiency is the ratio between the rate of intrusion and the rate of eviction when there is only one territory owner in the population. With this complication, the payoff to territory owners is

$$E(T,I) = tfe(p) \ . \tag{2.8}$$

The amount of food available to floaters from the space occupied by territories is the proportion of the total area covered with territories (P) times the portion of food not monopolized by territory owners ($1 - e(p)$) times the density of food, so the new payoff to floaters is

$$E(F,I) = \frac{(1 - P)\,f + (1 - e(p))\,Pf}{(1 - p)\,n} \ . \tag{2.9}$$

These payoffs are shown in Figure 2.2.

I have calculated the stability conditions for these payoff equations. Equilibrium points occur at $p = 0$, $p = 1$, and wherever the payoff curves cross (i.e. wherever the payoffs to both strategies are equal). The equilibrium at $p = 1$ is always stable, because the payoff to territory owners is always greater than the payoff to floaters at that point. The equilibrium at $p = 0$ is stable only when the share of food a territory owner could get (Ta) is less than the share of food a floater gets ($1/n$). The mixed equilibrium at

$$p = \frac{\frac{1}{nT} - a}{1 - a} \tag{2.10}$$

is never stable (Figure 2.2B, where the payoff curves cross), because a small increase in p yields a higher payoff for territory owners, causing p to increase to the next equilibrium point at $p = 1$. A slight decrease in p creates

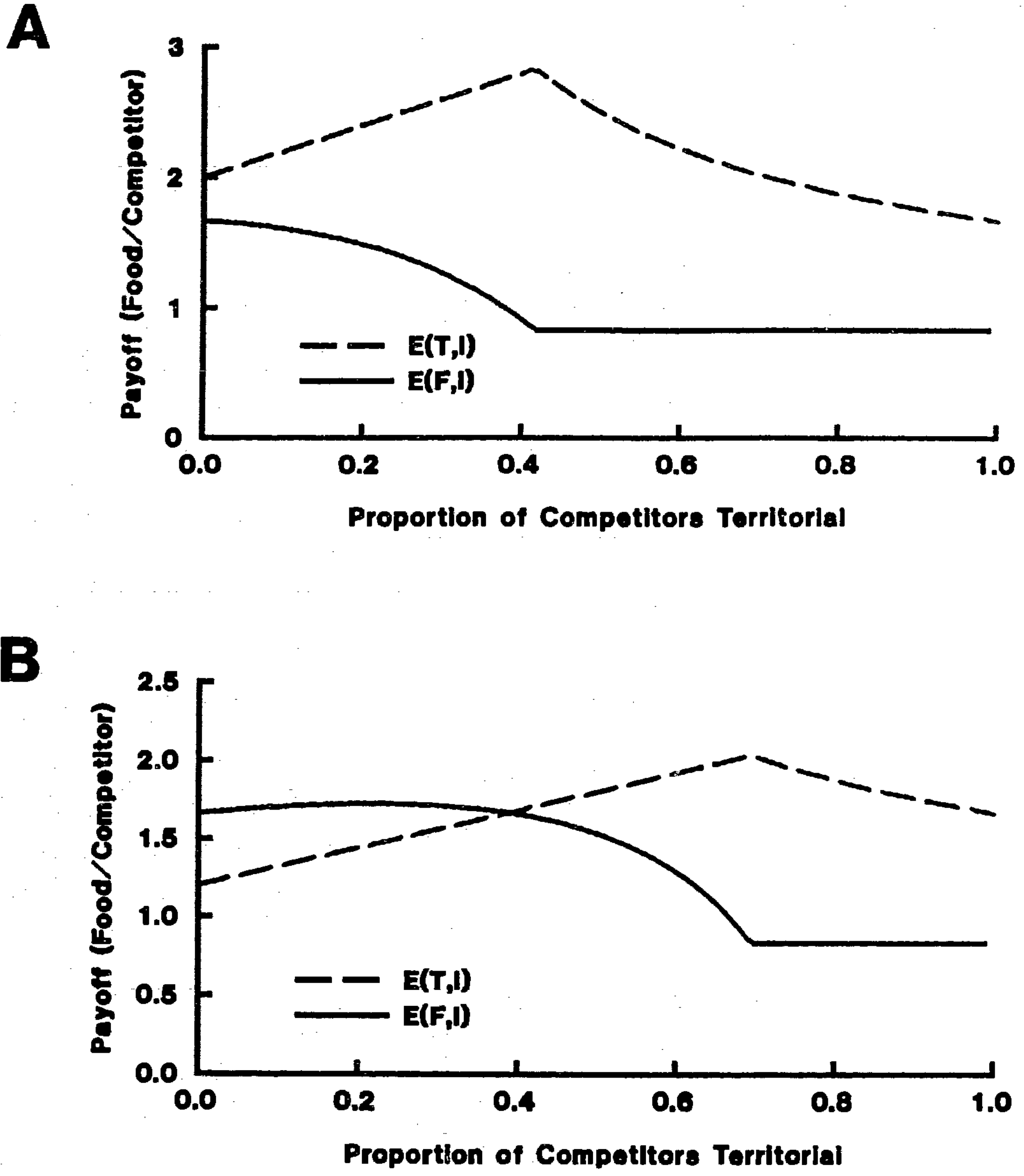

Figure 2.2 Plot of payoff equations (2.8) and (2.9). All symbols and lines as in Figure 2.1. Parameters are (A) T = 2, n = 1.2, f = 2, a = 0.5, and (B) T = 1.2, n = 1.2, f = 2, a = 0.5.

a higher payoff for floaters, causing p to decrease to 0. Under these assumptions, it is always possible for everyone to defend territories, whereas the absence of territory defence is possible only under certain conditions (e.g. Figure 2.2B). Increasing density decreases the range of conditions under which no territory defence ($p = 0$) is a stable strategy, as does increasing territory size. The density of food has no effect on the dynamics of the model. Increasing or decreasing f does not change the stability of the equilibrium points ($p = 0$, $p = 1$, and equation [2.10]). This is not a satisfying conclusion since empirical work has demonstrated the dependence of territorial behaviour on the availability of food (Carpenter and Macmillen 1976; Wilcox and Ruckdeschel 1982; Wyman and Hotaling 1988).

The basic payoff equations can be further modified in a variety of ways corresponding to relaxing different assumptions about the model, thereby increasing its biological realism. The first relaxes the assumption that there are no conflicts between time spent interacting with other territory owners and evicting floaters (assumption [4]). This makes the exclusion function $e(p)$ non-linear. I analyse the dynamics of this modification graphically. The second modification relaxes the assumption that territory defence carries no energetic cost, and this model is analyzed in detail.

As the number of territories increases the amount of space available for floaters to exist outside of territories decreases. If a floater has somewhere to wait until a territory owner is occupied (i.e., a refuge), then intrusion is more likely to succeed. Therefore, excluding floaters becomes easier as the space available for floaters to exist outside of territories decreases (as P approaches 1). Once the entire environment is covered with territories floaters must keep moving from territory to territory, only remaining in an area until the owner evicts them. At the same time, territory owners are spending time interacting with other territory owners. This decreases the ability of territory owners to exclude floaters. This is described by a sigmoid function with the inflection point at $\phi = 1$. Replace equation (2.7) with

$$e(p)' = \frac{(1-a)p^b}{\left(\left(\frac{1}{nT}\right)^b + p^b\right)} + a \qquad (2.11)$$

(Figure 2.3). As before, a is the exclusion efficiency of the first territory owner in the population, and b is a constant which is directly related to how steeply the function rises around the inflection point.

One possible set of payoffs from these equations is shown in Figure 2.4. The equilibrium at $p = 0$ is stable under the same conditions as the earlier model: a floater does better than a territory owner in a population consisting entirely of floaters. The equilibrium point at

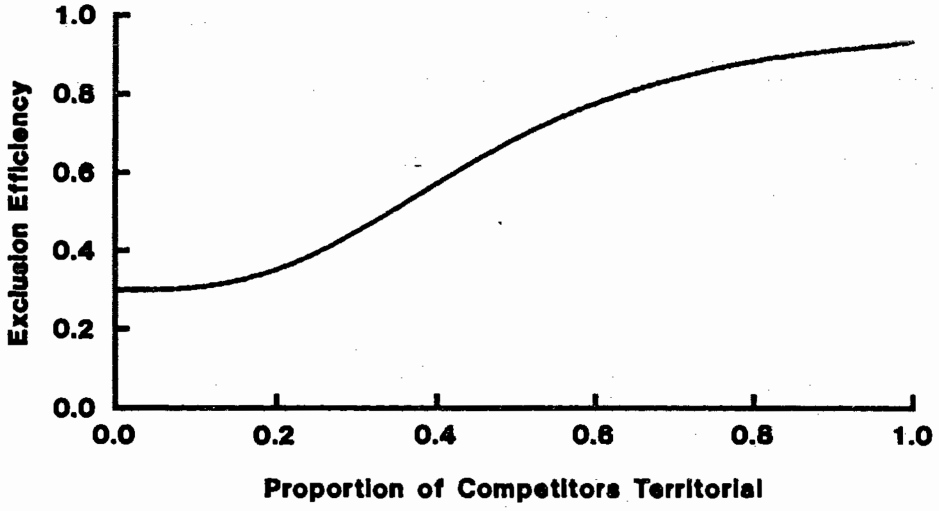

Figure 2.3 Efficiency of exclusion as a function of the proportion of competitors that are territorial. Parameters are $a = 0.3$, $T = 1.8$, $n = 1.2$, $b = 3$.

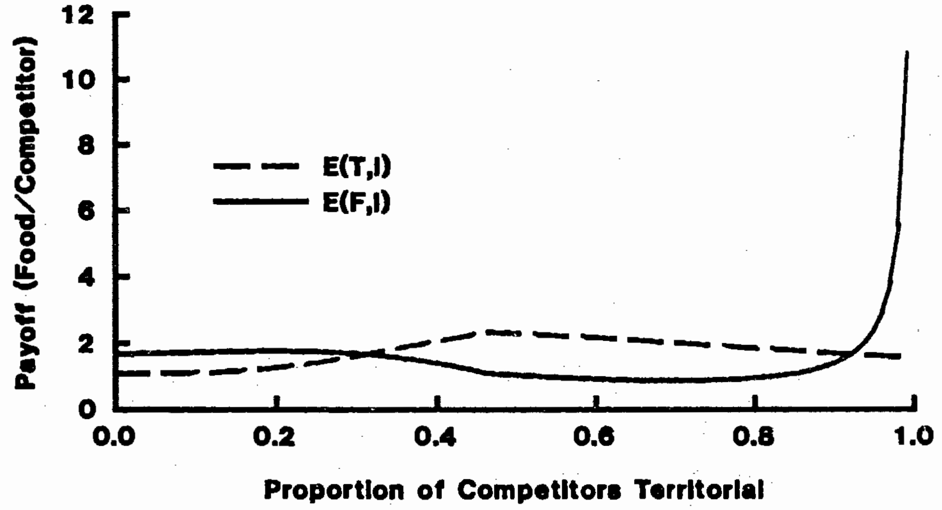

Figure 2.4 Payoff equations (2.8) and (2.9) with $e(p)$ replaced with $e(p)'$ (equation [2.11]). All symbols and lines as in Figure 2.1. Parameters are $a = 0.3$, $T = 1.8$, $n = 1.2$, $b = 3$, $f = 2$.

p = 1 is not stable because as the number of floaters decreases, each individual floater's share of the non-monopolized food increases; simultaneously, the ability of territory owners to exclude those floaters is decreasing because of increased interactions with other territory owners. Therefore, there is more food (less efficient exclusion by territory owners) for fewer floaters (p is increasing), and so the payoff to being a floater is high when p is close to or equal to 1. The left hand mixed equilibrium point is unstable. A small perturbation of p in either direction will result in p moving to the next stable point in that direction. The mixed equilibrium point on the right is stable against small perturbations of p. If the number of territory owners increases, the payoff to territory owners decreases, and it will pay some territory owners to switch back to floating. The reverse is true if p decreases. At this stable mixed equilibrium point the entire habitat is covered with territories ($P = 1$), and both floaters and territory owners receive the same payoff.

Modifying $E(T,I)$ to include costs of territoriality is straightforward. There are two sources of costs: floaters and other territory owners. Cost of territory defence should increase with the density of competitors involved, and with the size of the territory. Interactions with other territory owners should not be costly until all available space has been covered with territories ($\phi \geq 1$). When space is available, territorial animals whose territories overlap by chance will move until their territories do not overlap. Then the cost of interacting with other territory owners is

$$c_t = \begin{cases} 0 \ if\ \phi < 1 \\ c_1 \ if\ \phi \geq 1 \end{cases} . \tag{2.12}$$

The cost of interacting with other territory owners is a constant because it is a cost per neighbour, and the number of neighbours is constant regardless of territory size. This is true unless a territory exists on a boundary of the habitat, but that possibility is not considered here.

The cost of defending a territory from floaters is a function of the number of floaters, the territory size, and a cost constant representing the energy required to evict one floater:

$$c_f = c_2\ n\ t\ (1 - p) . \tag{2.13}$$

The resultant payoff equation is

$$E(T,I) = t\ f\ e(p) - c_f - c_t . \tag{2.14}$$

To be consistent, I include a cost to floaters in this model. This cost could be the risk of injury involved in escaping territory owners, increased predation risk, etc.. The resultant payoff equation is

$$E(F,I) = \frac{(1 - P)\ f + (1 - e(p))\ P\ f}{(1 - p)\ n} - c_3 . \tag{2.15}$$

These payoff equations are plotted in Figure 2.5.

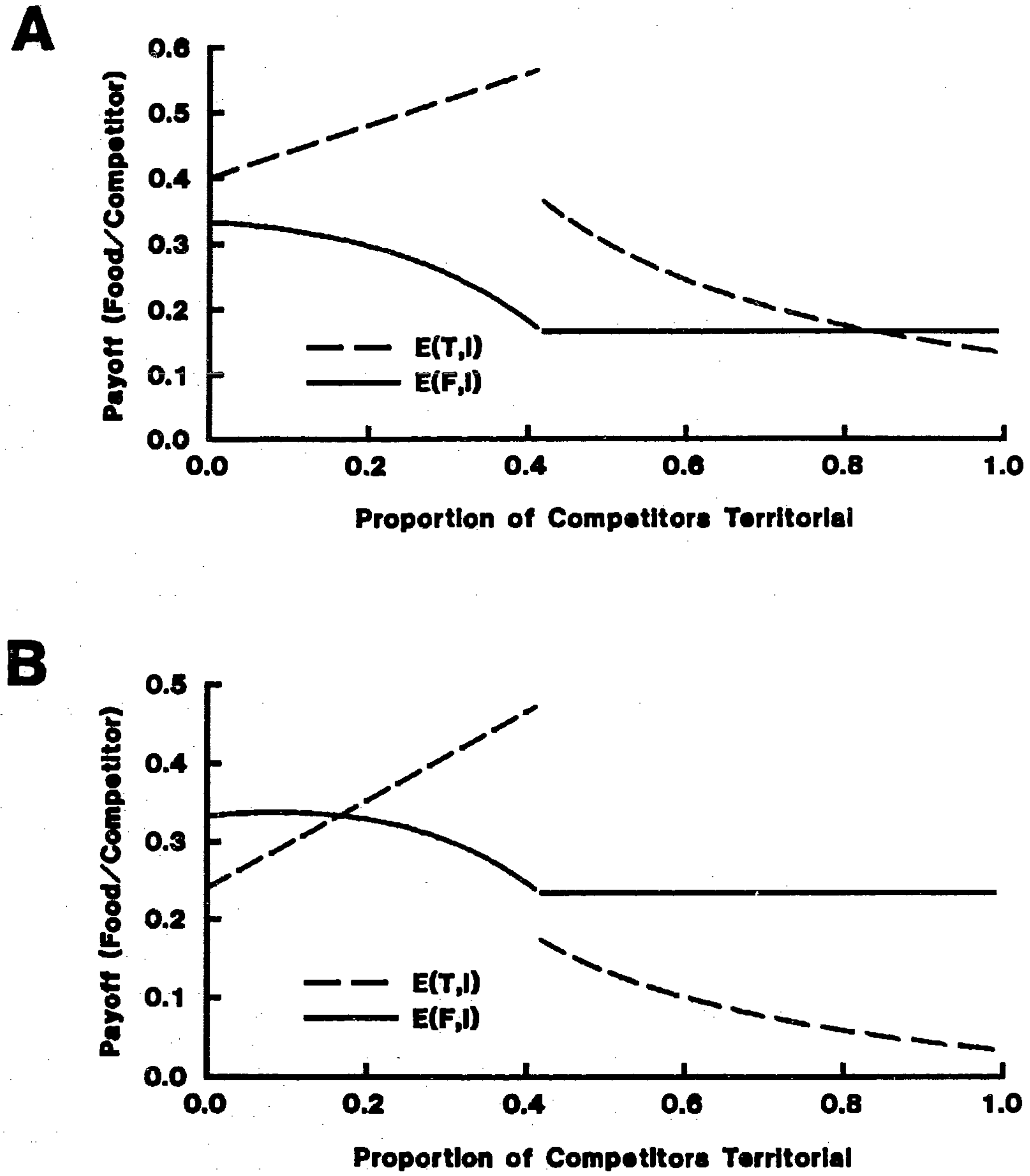

Figure 2.5 Payoff equations (2.14) and (2.15). All symbols and lines are as in Figure 2.1. Parameters are (A) $a = 0.5$, $T = 2$, $n = 1.2$, $f = 0.4$, $c_1 = 0.2$, $c_2 = 0$, $c_3 = 0$ and (B) $a = 0.3$, $T = 2$, $n = 1.2$, $f = 0.4$, $c_1 = 0.3$, $c_2 = 0$, $c_3 = 0$.

In order to simplify the stability analysis of this model I assume that c_2 and c_3 are both 0, i.e., there is no cost to territory owners to interacting with floaters, and no cost to floaters to evading territory owners. Therefore the loss to territory owners from floaters ($1 - e(p)$) is a function of the length of time floaters can remain undetected on a territory. As soon as a territory owner detects a floater, it signals ownership, and the floater abandons the territory. No struggle is involved, so the cost is negligible to both floaters and territory owners. The detailed calculations of the stability conditions are contained in Appendix A. Here I present the stability conditions in terms of f, the density of food.

The equilibrium point at $p = 1$ is stable when

$$f \geq \frac{nc_1}{a} \ . \tag{2.16}$$

If territory owners become more efficient at excluding intruders (a is increased), then a population consisting of all territory owners is more likely to be stable (increasing a decreases the level of f required to make $p = 1$ stable). Similarly, decreasing the density or the cost of interacting with other territory owners also makes a population of all territory owners stable under a wider range of parameter values. The mixed equilibrium point that occurs above $\phi = 1$ can be calculated using

$$p = \frac{fa}{nc_1}\ , \tag{2.17}$$

and this point is stable when

$$f \le \frac{n\ c_1}{a} \tag{2.18}$$

which is the converse of the stability property for the equilibrium at $p = 1$. Where the two conditions overlap is where $p = 1$ in (2.17). It appears from inspecting (2.18) that increasing the efficiency of territory defence, or decreasing density and cost are going to make the equilibrium at (2.17) less likely to be stable. However, when (2.18) is not met, the equilibrium described by (2.17) is greater than 1, and therefore does not exist. In that case, the stable solution is for all individuals to defend territories. Increasing the exclusion efficiency or the availability of food has the expected effect of increasing the proportion of the population that will defend territories (increasing a or f in (2.17) increases p), while increasing density or the cost of territoriality decreases the proportion of the population defending territories.

Because of the discontinuous nature of the payoff equations, the above solution is valid only for the mixed equilibrium when $p \ge 1/nT$ (the critical point; Figure 2.5).

Therefore, we can use equation (2.17) for the mixed equilibrium only when

$$f \geq \frac{C_1}{Ta} \ . \tag{2.19}$$

When condition (2.19) is false, equation (2.17) is no longer valid. However, as long as the unstable equilibrium below the critical point persists, the critical point itself is a stable "equilibrium" point. This can be seen in Figure 2.5B. Below the critical point the payoff to territory owners is greater than the payoff to floaters, and so p should increase. Above the critical point, territory owners do worse than floaters and p will decrease.

This equilibrium point at $p = 1/nT$ has interesting properties. Unlike other mixed equilibria, the payoffs of floaters and territory owners are not equal at the critical point. In fact, at the critical point territory owners have two payoffs: one from the form of the payoff equation that is used at and below the critical point, and one from the payoff equation used at and above the critical point. The question arises, which payoff does a territory owner get when the system is at this equilibrium point? It may help to think of a real territorial system, where the dynamics are discrete rather than continuous (i.e. a fraction of a territory owner cannot exist). With enough territory owners to make p slightly less than the critical point territory owners will be receiving a higher payoff than floaters.

Should a floater switch to being a territory owner? If adding one more territory owner makes p exceed the critical point, then that new territory owner will receive a lower payoff than it did as a floater. Therefore, it does not pay that floater to switch to territory ownership. The system will rest at or slightly below the critical point, territory owners will have a higher payoff than floaters, and this is a stable equilibrium point. This point corresponds to the minimum number of territory owners to completely cover the habitat with territories without having to reduce territory size. Another way to think of this equilibrium point is as a pure conditional strategy: defend a territory if the habitat can support another territory, otherwise float.

The stability of this equilibrium point must be described by two conditions, one for each side. The point is stable when dp/dt' (the rate of change in p with time when p is at or above the critical point) is less than 0 at the critical point, and when dp/dt (the rate of change in p with time when p is at or below the critical point) is greater than 0 at the critical point. The first condition is satisfied when

$$f \leq \frac{C_1}{Ta} \ . \tag{2.20}$$

This condition is the converse of the condition that the upper mixed equilibrium (2.17) must satisfy in order to be less than 1. The second condition is satisfied when

$$nT \geq 1 \ . \tag{2.21}$$

Therefore, whenever the critical point is less than 1, the lower stability condition for the critical point is satisfied. Intuitively this makes sense, because if the critical point is greater than or equal to 1 then it no longer exists as an equilibrium point.

Finally, the stability conditions for the equilibrium at $p = 0$ and the lower mixed equilibrium can be described. A population of all floaters is stable when

$$Ta \leq \frac{1}{n} \tag{2.22}$$

which is the same condition as in the game without costs. If each floater gets a larger share of food than a territory owner gets in a population of all floaters, then a population of all floaters is stable. The mixed equilibrium below the critical point (Figure 2.5B) is calculated with

$$p = \frac{1 - nTa}{nT - nTa} \tag{2.23}$$

and this equilibrium cannot be both stable and greater than 0. This equilibrium is less than the critical point when

$$nT \leq 1 \tag{2.24}$$

which is the converse of one of the stability conditions for the equilibrium at the critical point (equation (2.21)).

As food availability is one of the parameters in this game, the stability conditions can be used to determine if the model predicts the occurrence of food thresholds. In the model analyzed above (payoff equations (2.14) and (2.15)), there are no food thresholds. Food availability has no effect on the stability of a population consisting entirely of floaters (f does not appear in (2.22)). Food also does not affect the occurrence of the unstable mixed equilibrium (2.23), and consequently has no effect on the bottom side stability of the stable equilibrium at the critical point. Increasing food availability cannot eliminate the equilibrium of all floaters. Likewise, increasing food availability does not eliminate the equilibrium of all territory owners. Therefore, this model does not predict the occurrence of either upper or lower thresholds.

Are there any biologically meaningful modifications that could generate food thresholds in this model? If it becomes costly to evict floaters ($c_2 > 0$), then a lower threshold appears in the model. In general, as long as the costs of territoriality are never 0, a lower threshold will exist. This is shown in Figure 2.6. In Figure 2.6A, the only stable equilibrium is a population consisting of all floaters. By changing only food availability, a new equilibrium appears with some individuals defending territories (Figure 2.6B). The lower stable equilibrium with all floaters still exists at this point. Increasing food availability further causes this equilibrium of all

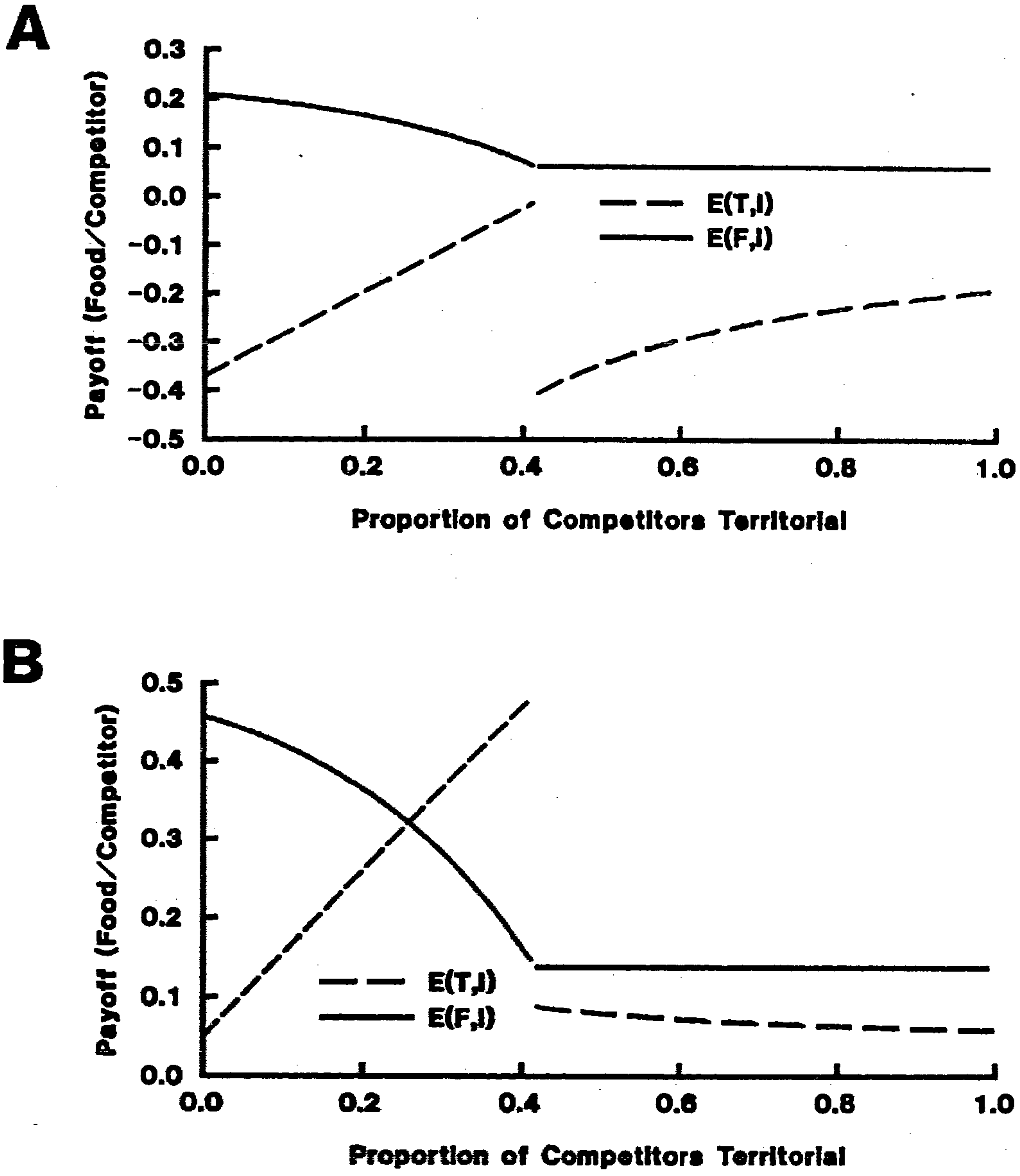

Figure 2.6 Payoff equations (2.14) and (2.15) with the cost of evicting floaters greater than 0. These 3 plots show the effect of increasing food supply, demonstrating the existence of a lower food threshold. All symbols and lines as in Figure 2.1. Parameters are (A) $a = 0.7$, $T = 2$, $n = 1.2$, $f = 0.25$, $c_1 = 0.4$, $c_2 = 0.3$; (B) the same as (A) except $f = 0.55$; (C) the same as (A) but $f = 1.4$

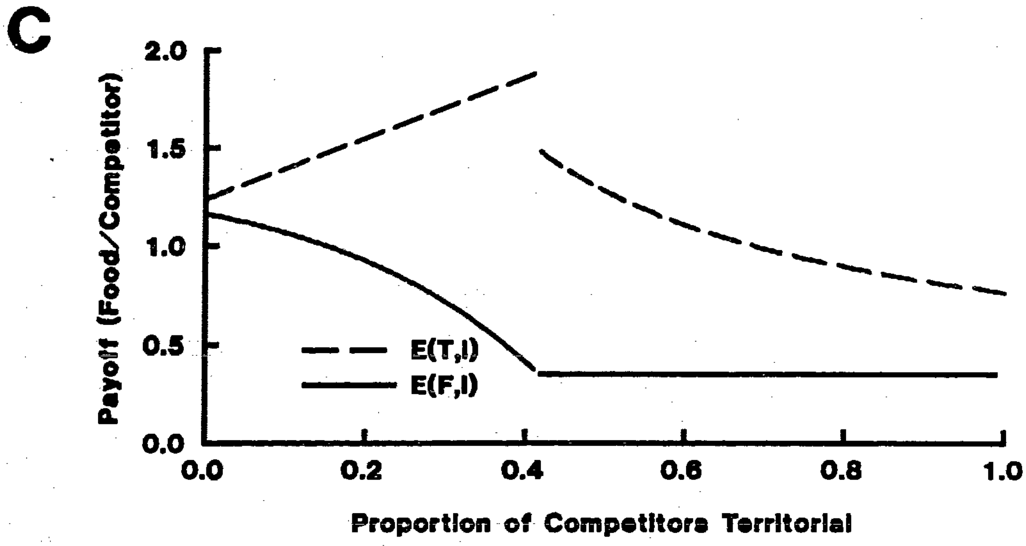

Figure 2.6 Continued from previous page.

floaters to disappear (Figure 2.6C). Increasing the food availability still more causes the population to move to an equilibrium of all territory owners. However, no upper thresholds exist in this case.

There are at least two mechanisms that could generate upper thresholds. First, if c_f were an increasing function of f as well as n and t, then the payoff to territory owners would decrease as f increased. This could occur if floaters are more persistent in their intrusions when food is more available. A second mechanism would be the incorporation of a maximum consumption rate. At some point the amount of food available to a territory owner on its territory will exceed the amount that it can consume. Once this occurs, the extra food on the territory will become available to floaters, thereby increasing their benefit. Eventually the amount of food available to floaters will also exceed an individual's ability to consume it. At this point, the benefit to both floaters and territory owners will be equal. As floaters do not pay the cost of territory defence, floating will have a higher payoff than territory defence, thereby creating an upper threshold. I will now develop and graphically analyze a set of payoff equations that take this last mechanism into account.

I begin by choosing a suitable constraint function *C(energy)*: it should reach an asymptote at some maximum energy intake rate m, and the function must be less than its operand throughout its range (it is not possible to eat more food than is available). A modification of the Holling disc equation (Holling 1966) meets these criteria:

$$C(energy) = \frac{m\ energy}{m + energy}\ , \tag{2.25}$$

where m is the maximum intake, and *energy* is the value that is to be limited to m. Including this maximum feeding rate in the payoff to territory owners yields

$$E(T,I)' = C(tfe(p)) - c_f - c_t\ . \tag{2.26}$$

The payoff for floaters can be computed similarly, but first the amount of food that is not eaten on territories by territory owners must be included in the food available to floaters. Recall that the amount of food available to a territory owner is given by equation (2.8). The proportion of food on a territory that is not eaten by the territory owner is the ratio of food eaten to food available:

$$\frac{C(tfe(p))}{tfe(p)}\ . \tag{2.27}$$

Simplifying yields

$$\frac{m}{m + tfe(p)}\ . \tag{2.28}$$

The amount of food available to floaters from territories will be the proportion of area covered with territories times one minus the amount eaten by territory owners, which will be the proportion of food defended ($e(p)$) times the proportion actually consumed (equation 2.28):

$$E(F,I) = \frac{(1 - P)\, f + \left(1 - \frac{e(p)\, m}{m + tfe(p)}\right) P\, f}{(1 - p)\, n} \; . \qquad (2.29)$$

This is similar to equation (2.15), but the proportion of food eaten by territory owners is reduced by including equation (2.28) into the second term of the numerator. Equation (2.29) can then be used in the constrained payoff equation for floaters:

$$E(F,I)' = C(E(F,I)) - c_3 \; . \qquad (2.30)$$

As before, by varying the availability of food (f) systematically, I can examine payoff equations (2.26) and (2.30) for food thresholds in the occurrence of equilibria. At very low levels of food availability the stable equilibrium is all floaters, provided that evicting floaters is costly for territory owners ($c_2 > 0$; Figure 2.7A). As the availability of food increases, the mixed strategy equilibrium at $\phi = 1$ becomes stable (Figure 2.7B). This equilibrium persists as the only stable equilibrium in the system, until the availability of food exceeds an upper threshold (Figure 2.7C). After this point, the only stable equilibrium is all floaters again. In contrast to earlier payoff equations, the system never moves to an equilibrium with all territory owners; there are some floaters at every possible stable equilibrium. However, it should be

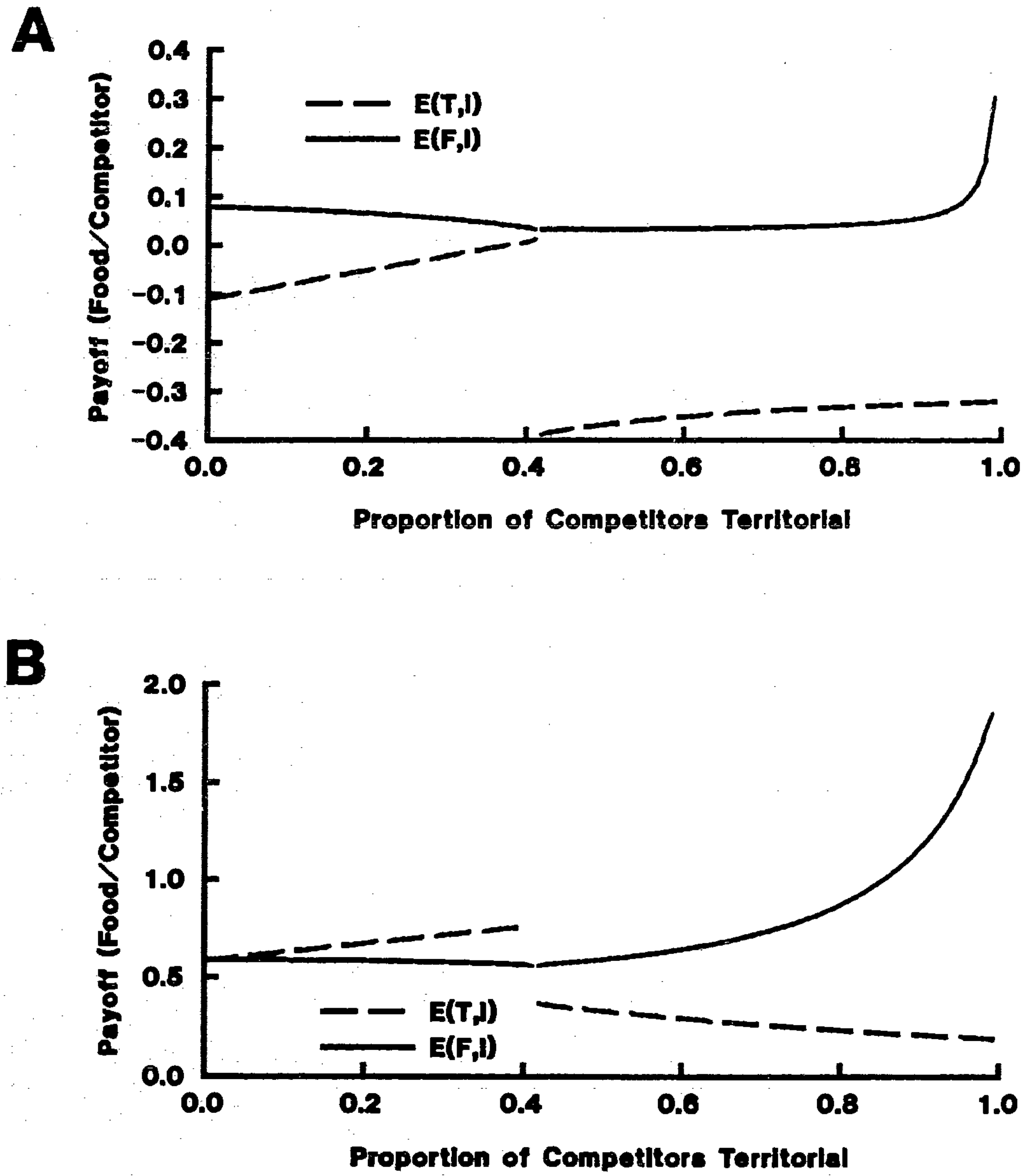

Figure 2.7 Payoff equations (2.26) and (2.30) with an upper limit on the amount of food that can be consumed. These 3 plots show the effect of increasing food supply, demonstrating the existence of both an upper and lower food threshold. All symbols and lines are as in Figure 2.1. Parameters are (A) a = 0.7, T = 2, n = 1.2, f = 0.1, c_1 = 0.4, c_2 = 0.1; (B) the same as (A) except f = 1; (C) the same as (A) except f = 6.

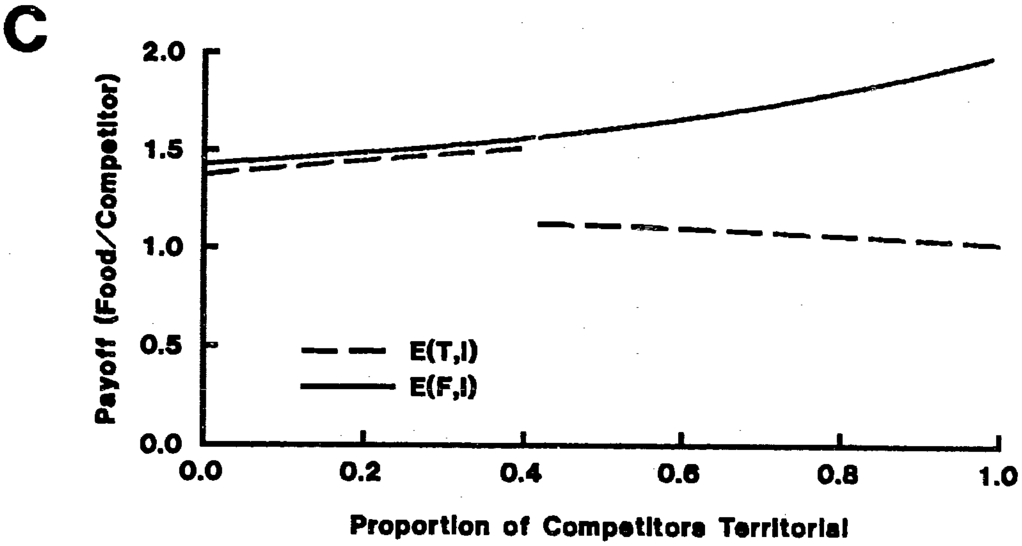

Figure 2.7 Continued from previous page.

emphasized that this graphical analysis examines the stability of equilibria for only one combination of parameters. A global understanding of the stability properties of this system requires an analytical solution of (2.26) and (2.30).

Discussion

The primary motivation for developing this model was to explain intrapopulation variation in territory defence as mixed strategy equilibria between territorial and non-territorial individuals. The insight gained is that when considering the decision of whether or not to defend a territory, the payoffs to non-territorial animals must be considered, as mixed strategy equilibria are possible. Moreover, not all mixed equilibria in the game lead to identical payoffs for the two strategies; it is possible to have pure conditional strategies that depend on the frequency of territory defence. Simply comparing the payoffs of territory owners to those of floaters is not sufficient to determine the existence (or non-existence) of an ESS. What happens to the payoffs when the proportion of territory owners is changed must also be determined. As an example, Dhondt and Schillemans (1983) measured the reproductive success of both territorial and non-territorial pairs of Great Tits in Holland. On average, territorial pairs fledged twice as many chicks as non-territorial pairs.

They concluded that territory defence was not a mixed ESS with non-territory defence. However, if non-territorial pairs could do better by "intruding" than by trying to force another territory into the system, then the system is at an evolutionary stable equilibrium, even though the payoffs to one strategy are lower. Such an equilibrium is a pure conditional strategy (Parker 1984), where animals defend territories if the habitat is not filled with territories.

The stability analysis of (2.14) and (2.15) was carried out under the assumption that both c_2 and c_3 were equal to 0. It can be argued that this leaves the game open to cheating by territory owners. If all a territory owner has to do to evict a floater is signal ownership, and if signalling ownership is not costly, then territory owners should signal ownership constantly whether or not a floater has been detected on the territory. There are two responses to this problem. First, if territory owners signal constantly there should be selection on floaters to distinguish between signals given when they have been detected and when they have not, and respond to signals only when they have been detected. Second, if signalling territory ownership is costly ($c_2 > 0$), then signalling is more likely to be honest. Given that the evolution of honest signalling is an entire game theory problem on its own, it is beyond the scope of this paper. However, graphical explorations of the effects on the model of making

$c_2 > 0$ (Figure 2.6) have been conducted. In general, the stability conditions given above become more complex, but the relations between them do not change. This is true so long as the cost of evicting floaters (c_2) is less than the cost of interacting with other territory owners (c_1). When this condition is not met the qualitative nature of the game changes. Making it costly for floaters to interact with territory owners ($c_3 > 0$) similarly has little qualitative effect on the nature of the equilibria as long as the cost to floaters is small compared to the cost to territory owners of interacting with other territory owners.

The requirement that the cost of interacting with other territory owners be greater than the cost of evicting floaters seems to contradict a large amount of literature on the "dear enemy" or neighbour-stranger hypothesis (reviewed by Ydenberg et al. 1988). This literature seeks to explain the observation that territory owners often respond less aggressively to neighbouring territory owners than to strangers. Studies where this phenomenon has been documented are all cases of breeding territories (Ydenberg et al. 1988). In contrast, Temeles (1990) observed harriers on winter feeding territories and observed increased aggression towards neighbouring territory owners compared with aggression directed at floaters. The explanation provided was that intruding territory owners sought to expand their territories at the expense of the owner, while floaters were simply looking for food. Therefore, the longterm cost of allowing another territory owner to intrude is greater than the cost of allowing floaters to intrude. The kind of simulated intrusion that is used in "dear enemy" studies is that of a strange territory owner. Therefore, what these studies have generally shown is that territory owners react more strongly to strange territory owners than to neighbouring territory owners. The current model does not address this issue. Instead, it distinguishes between floaters that are intruding and territory owners that are intruding. As in the harriers observed by Temeles (1990), it seems reasonable to suppose that floaters are less costly to evict than other territory owners, because a floater does not permanently remove a piece of the owner's territory, whereas another territory owner will. It is this difference in aggressivness between intruders that are territory owners and intruders that are floaters that leads to the eviction of floaters being less costly than border interactions with other territory owners.

Another assumption that was made to simplify the analysis was that all competitors were equal in foraging and territory defence ability. If this assumption were relaxed, then individuals with superior competitive ability would be the ones defending territories when territoriality is the better option. When the stable equilibrium in the game is a population consisting entirely of floaters, individuals of all competitive abilities will float. This will be true unless superior competitors pay no costs to defend territories.

A final simplifying assumption is that of complete packing. This results in the habitat being completely covered with territories without refuges when a large proportion of the population is territorial. Relaxing this assumption would lead to food being available off territories. The effect of this would be to further increase the benefit available to floaters. This would tend to reduce the differences in net payoff between floaters and territory owners that occur at the special equilibrium point when $\phi = 1$.

This model could be extended in a number of ways. The assumption of uniform distribution of food could be relaxed, as could the assumption of identical competitive ability. It would also be valuable to build time into the model in a more explicit manner, allowing the time conflict between different behaviours to be directly incorporated.

In summary, this model demonstrates that it is not necessary to invoke differences among individuals in order to explain the observation that not all individuals defend territories. Mixed strategy equilibria of floaters and territory owners occur when interactions between territory owners are costly. Lower thresholds appear when it is costly for territory owners to evict floaters, and upper thresholds occur only when there is a maximum rate of energy intake. Future studies of territoriality should consider whether it is possible to obtain the same resources without being territorial. In addition, it is particularly important to consider how the costs of defence may vary with the type of intruder.

List of References

Barlow GW (1974) Hexagonal territories. Animal Behaviour 22:876-878

Brown JL (1969) Territorial behaviour and population regulation in birds. The Wilson Bulletin 81:293-329

Buckley PA, Buckley FG (1977) Hexagonal packing of royal tern nests. The Auk 94:36-43

Carpenter FL, MacMillen RE (1976) Threshold model of feeding territoriality and test with a Hawaiian honeycreeper. Science 194:639-641

Davies NB (1978) Ecological questions about territorial behaviour. pp 317-351. In: Krebs, JR, Davies, NB (eds) Behavioural Ecology. Blackwell, Oxford

Davies NB, Houston, AI (1981) Owners and satellites: the economics of territory defence in the pied wagtail, *Motacilla alba*. Journal of Animal Ecology 50:157-180

Dhondt AA, Schillemans J (1983) Reproductive success of the great tit in relation to its territorial status. Animal Behaviour 31:902-912

Gass CL, Angehr G, Centa J (1976) Regulation of food supply by feeding territoriality in the rufous hummingbird. Canadian Journal of Zoology 54:2046-2054

Getty T (1987) Dear enemies and the prisoner's dilemma: why should territorial neighbors form defensive coalitions? American Zoologist 27:327-336

Grafen A (1987) The logic of divisively asymmetric contests: respect for ownership and the desperado effect. Animal Behaviour 35:462-467

Holling CS (1966) The functional response of invertebrate predators to prey density. Memoirs of the Entomological Society of Canada 48:1-86

Hurd P (1992) Evolutionary analysis of threat and fighting in the american coot (*Fulica americana*). MSc. Thesis, Simon Fraser University, Burnaby, B.C., Canada. 121pp.

Martel G (1992) Influence of predation risk on the territorial behaviour of juvenile coho salmon, *Oncorhynchus kisutch*. PhD. Dissertation. Simon Fraser University, Burnaby, B.C., Canada. 150pp.

Maynard Smith J (1982) Evolution and the Theory of Games. Cambridge University Press, Cambridge. 224 pages

Myers JP, Connors PG, Pitelka FA (1981) Optimal territory size and the sanderling: compromises in a variable environment. pp 135-159. In: Kamil, AC and TD Sargent (eds) Foraging Behaviour: Ecological, Ethological, and Psychological Approaches. Garland STPM Press, New York

Parker GA (1984) Evolutionarily stable strategies. pp 30-61. In: Krebs JR and Davies NB (eds) Behavioural Ecology: An Evolutionary Approach. Second Edition. Sinauer Associates, Sunderland, Massachusetts

Poethke HJ, Kaiser H (1985) A simulation approach to evolutionary game theory: the evolution of time-sharing behaviour in a dragonfly mating system. Behavioral Ecology and Sociobiology 18:155-163

Puckett KJ, Dill LM (1985) The energetics of feeding territoriality in juvenile coho salmon. (*Oncorhynchus kisutch*). Behaviour 92:97-111

Riechert SE (1981) The consequences of being territorial: spiders, a case study. The American Naturalist 117:871-892

Robertson DR, Sweatman HPA, Fletcher EA, Cleland MG (1976) Schooling as a mechanism for circumventing the territoriality of competitors. Ecology 57:1208-1220

Sallabanks R (1993) Fruit defenders vs. fruit thieves: winter foraging behavior in American robins. Journal of Field Ornithology 64:42-48

Shutler D, Weatherhead PJ (1991) Owner and floater red-winged blackbirds: determinants of status. Behavioral Ecology and Sociobiology 28:235-241

Smith SM (1978) The "underworld" in a territorial sparrow: adaptive strategy for floaters. The American Naturalist 112:571-582

Temeles EJ (1990) Northern harriers on feeding territories respond more aggressively to neighbors than to floaters. Behavioral Ecology and Sociobiology 26:57-63

Wilcox RS, Ruckdeschel T (1982) Food threshold territoriality in a water strider (*Gerris remigis*). Behavioral Ecology and Sociobiology 11:85-90

Wilson EO (1975) Sociobiology. The Belknap Press, Cambridge, Massachusetts. 366 pages

Wyman RL, Hotaling L (1988) A test of the model of the economic defendability of a resource and territoriality using young *Etroplus maculatus* and *Pelmatochromis subocellatus kribensis*. Environmental Biology of Fishes 21:69-76

Ydenberg RC, Giraldeau LA, Falls JB (1988) Neighbors, strangers, and the asymmetric war of attrition. Animal Behaviour 36:343-347

Chapter 3:

Field Observations and Laboratory Experiments on Juvenile *Limnoporus notabilis* Stål

Introduction

A complete understanding of animal aggression in relation to resource acquisition must account for aggressive behaviours in all kinds of species, regardless of taxonomic affinities. To date, however, most studies of resource defence have focused on vertebrates, particularly birds and fish (reviewed in Lott 1984). Demonstrations of resource defence in invertebrate species are rarer (reviewed in Hart 1987; see also Stimson 1970, 1973), and should be investigated in order to further our understanding of the phenomenon. Here I attempt to show that juvenile water striders, *Limnoporus notabilis*, use aggression in resource acquisition.

Water striders that live on ponds could benefit from defending priority of access to food if food is limiting. In a pond, food (e.g. dead terrestrial insects) falls onto the water surface from the surrounding vegetation. In this case, it is the water strider that is closest to a given food item that is most likely to encounter and consume it. By chasing nearby competitors a water strider could clear a larger space around itself of competitors than would be the case in the absence of aggression, increasing the probability that it will be the closest bug to a particular food item.

I chose to examine the behaviour of juvenile *L. notabilis* for two reasons. First, food threshold defence

(defence at intermediate levels of resource availability) has been demonstrated in juvenile *Aquarius remigis*, another water strider species (Wilcox and Ruckdeschel 1982; Blanckenhorn 1991). Second, adult male *L. notabilis* aggressively defend areas to increase their encounter rates with females. They use a surface vibration signal to communicate territory ownership (Spence and Wilcox 1986; Wilcox and Spence 1986).

The food threshold model (Carpenter and Macmillen 1976) predicts that at intermediate levels of food availability, juvenile *L. notabilis* will utilize aggression to acquire food. Such a prediction has not previously been made for this species, since previous workers did not believe that juveniles used aggressive resource defence under any conditions (L. Rowe, personal communication). This prediction requires two assumptions: first, that juvenile water striders do perform aggressive behaviours, and second, that increased food results in correspondingly higher fitness.

The first assumption, that juveniles use aggression, has not been tested. However, adult male *L. notabilis* defend territories with a surface vibration signal (Spence and Wilcox 1986; Wilcox and Spence 1986), and this signal resembles the surface vibrations generated by juveniles (personal observation). The surface vibrations generated by juveniles do not resemble the "courtship" signal also generated by adult male *L. notabilis*. Based on these observations I assume for the purposes of this study that the function of surface vibrations in juveniles is to aggressively repel competitors, rather than to practice sexual behaviour.

Assuming that juvenile *L. notabilis* use aggressive behaviour to increase foraging success, I attempted to reproduce these behaviours in the laboratory under controlled conditions. The goal was to manipulate food availability and observe the response of aggression. I did these experiments in two parts. First, I controlled the availability of food in order to determine the effect different food levels would have on growth rate and size. If food availability does not affect development rate or final larval size, then I would not expect foragers to behave in a manner that maximizes foraging rate. This tests the assumption made above that increasing food increases fitness. Second, I performed an experiment to test the response of aggressive behaviour of individuals to their recent foraging experience.

Does food availability influence growth rate, size, and survival?

In order to demonstrate that a resource is limiting, it must first be shown that increasing the amount of the resource increases some component of an individual's fitness. Increasing food supplies to water striders should increase their size and development rates. Small bugs are more susceptible to predation both from larger conspecifics and other predators. Therefore, the quicker a small bug reaches a large size the higher its fitness (Spence and Cárcamo 1991; personal observations), if fitness is only considered as the probability of surviving to molt. Understanding how changes in food availability affect fitness is a first step to being able to predict the levels of food availability that might lead to resource defence.

Methods

I raised *L. notabilis* in individual 500 ml cups (7 cm in diameter) from the day of hatching until adulthood, or until death, under four different regimes of food availability: low - 1 fruit fly/3 days, medium - 1 fruit fly/2 days, high - 1 fruit fly/day, and ultra-high - 2 fruit flies/day. Sample sizes for each treatment group and instar are given in Table 3.1. The plastic cups used to raise water striders had vents cut in the sides and bottom. Those vents were covered with plastic window screen. Fifteen cups were placed in a 20 x 55 cm tray of water, and food treatments were randomly assigned to each cup. The photoperiod was held at 19L:5D. I recorded the number of days required for each individual to complete an instar and

Table 3.1 The number of bugs in each treatment group and instar of the growth experiment. Numbers decrease within treatment groups due to mortality both within instars, and during molting.

Instar	Low Food	Medium Food	High Food	Ultra-High Food
1st	20	20	20	21
2nd	16	15	20	19
3rd	13	15	20	19
4th	8	11	18	18
5th	1	3	6	5

the age at death. After each molt, I measured the mid- and hind-tibia lengths of the exuvia.

The effects of food treatment on the mid-tibia length and the number of days required to complete an instar were analyzed using a repeated measures ANOVA in SAS (Sas Institute 1990). I did not include hind-tibia lengths in any analyses because hind-tibia lengths were significantly correlated with mid-tibia lengths ($r^2 = 0.93$; $F(1,264) = 3470$; $p < 0.001$). Within-instar effects of treatment were analyzed using procedure ONEWAY in SPSS-X (SPSS Inc. 1988). Survival time was analyzed with procedure SURVIVAL in SPSS-X.

Results and Discussion

Better fed bugs should increase in size more during a molt. In first instar animals the effect will be absent because leg size is set by egg food reserves prior to hatching. This expectation was borne out in the repeated measures analysis (Table 3.2), and by the data themselves (Figure 3.1). I could not generate within-instar comparisons of treatment effect with the repeated measures ANOVA because of the number of individuals that died during the experiment. However, because both the effect of instar, and the interaction between instar and treatment were significant, oneway ANOVAs were used to estimate treatment effects within each instar (Figure 3.1). There was no

Table 3.2 Summary of Repeated Measures ANOVAs on Growth Experiment data. The effect of instar is significant for both mid tibia length and days spent in an instar. The treatment effect is stronger for days per instar than for mid tibia length, and the interactions between instar and treatment are significant. Each column has the F-value(df) and p-value for the effect.

Response Variable	Treatment Effect	Instar Effect	Treatment by Instar Interaction
Mid Tibia Length	2.75(3,77) p=0.049	153.40(4,191) p=0.0001	2.64(12,191) p=0.0027
Days per Instar	29.54(3,66) p=0.0001	155.86(4,125) p=0.0001	12.03(9,125) p=0.001

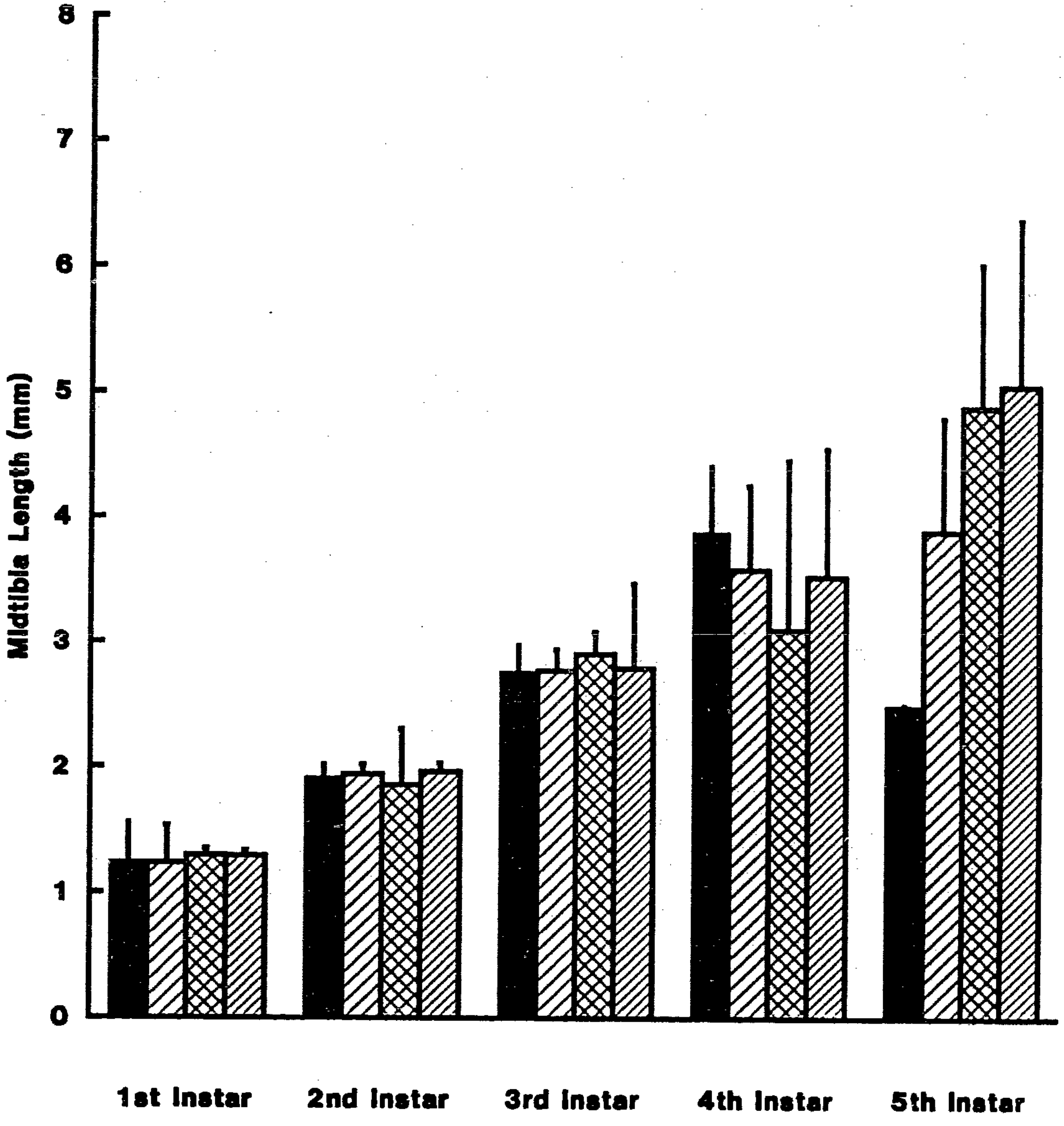

Figure 3.1 Bar plot of the average midleg tibia length (+SE) in mm for each instar in each treatment group. Better fed bugs are larger in the 5th instar, but no within instar effects are significant according to oneway ANOVAs. Treatment groups are: Solid = 1 fruit fly / 3 days, Coarse Hatched = 1 fruit fly / 2 days, Cross Hatched = 1 fruit fly / day, Fine Hatched = 2 fruit flies / day.

significant effect of treatment on mid-tibia length within any instar, despite the estimate of an overall treatment effect by the repeated measures ANOVA. The trend is in the correct direction for the 5th instar animals, with better fed animals being larger on average than poorly fed animals.

There was a negative relationship between food level and duration of each instar (Figure 3.2); better fed bugs molted more rapidly. The results of a repeated measures ANOVA indicate that treatment effects and instar effects were both significant, and that the treatment effect increases in older instars (Table 3.2 and Figure 3.2). Within-instar effects are significant in all instars (Figure 3.2). The apparent weakening of the trend in the 4th instar in statistical terms is caused by a loss of power due to the small number of bugs surviving to the 4th instar.

Analysis of survival time is complicated because many of the bugs in the ultra-high food group (2 Fruit Flies/Day) succumbed to an unknown cause over a one week period. As this occurred at the same time as a widespread die-off among late instar bugs kept in the laboratory, I do not believe that this is an effect of the treatment. A higher proportion of ultra-high bugs were in the later instars at the time this problem occurred. Therefore, I have excluded the ultra-high food animals from the analysis. Cumulative proportion surviving did not differ between the low and medium food groups, nor between the medium and high food

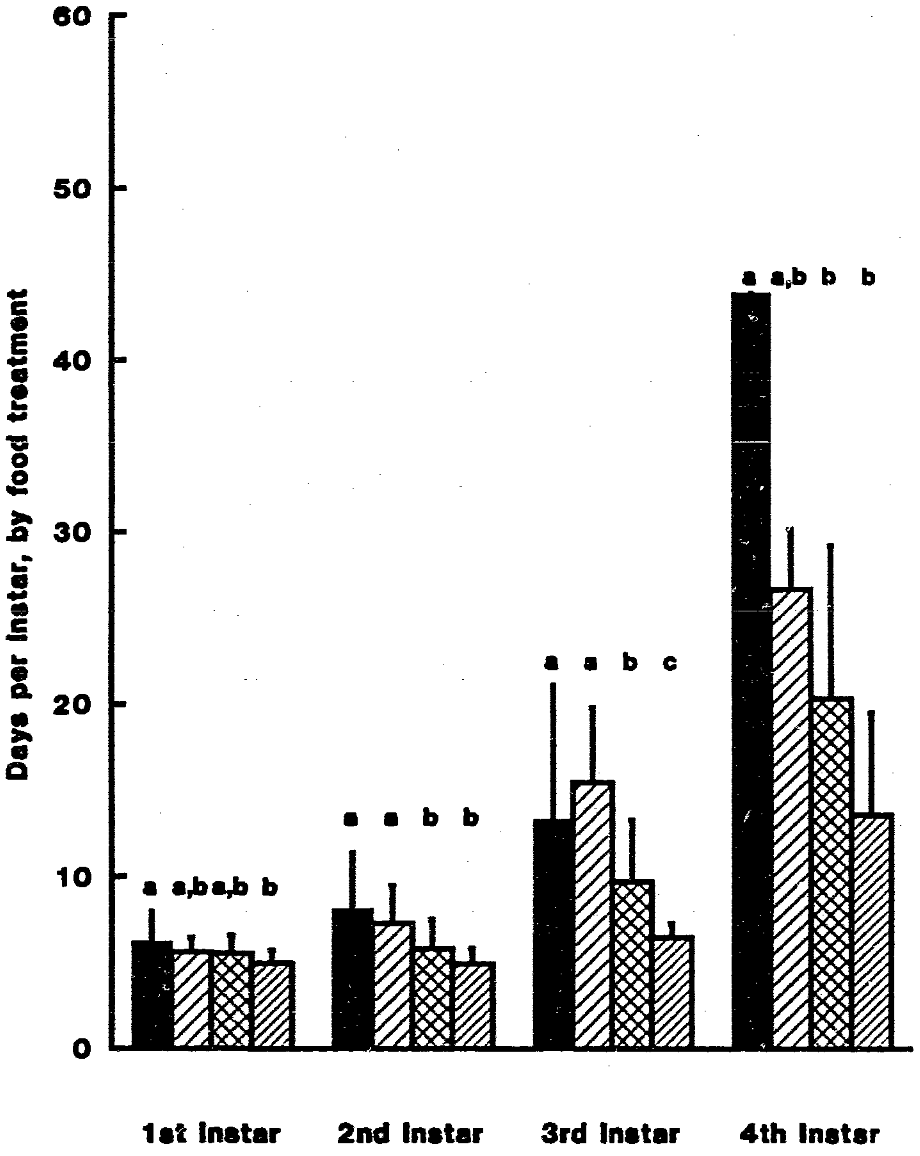

Figure 3.2 Bar plot of the average number of days (+SE) spent in each instar for each treatment group. Plot only includes individuals who did not die during that particular instar. Treatment groups are: Solid = 1 fruit fly / 3 days, Coarse Hatched = 1 fruit fly / 2 days, Cross Hatched = 1 fruit fly / day, Fine Hatched = 2 fruit flies / day. Bars with different letters within each instar are significantly different from each other. Better fed bugs spend less time per instar.

Table 3.3 Summary of Survival tests by treatment. Comparison refers to the treatment groups being compared, and the statistic being calculated is distributed as a chi-square. Treatment groups are Lo = 1 Fruit Fly / 3 Days, Med = 1 Fruit Fly / 2 Days, High = 1 Fruit Fly / Day. The ultrahigh treatment (2 Fruit Flies / Day) was eliminated from this analysis. Survival in treatment High is different from survival in treatment Lo.

Comparison	D statistic	D.F.	
Lo with Med	1.06	1	0.3038
Lo with High	12.09	1	0.0005
Med with High	0.90	1	0.3435

groups; however, the low and high food groups were significantly different from each other (Table 3.3). Examination of the data directly reveals a more complex picture (Figure 3.3). Early in the experiment bugs in the high food group survived better than both lower food level groups, but after day 55 the situation was reversed between the medium and high food groups. During the last 20 days of the experiment very little difference in survival is evident among the treatment groups.

Despite the fact that none of the bugs in this experiment survived to adulthood, increased food tends to affect development in a positive manner. Considering survival in the early instars (1 and 2) it is clear that a larger amount of food improves one component of fitness. However, larger bugs require more food than smaller bugs, and the fact that the diet did not change as bugs increased in size meant that the mortality due to starvation increased in all treatment groups as bugs increased in size. In nature, a larger animal could attempt to increase its consumption rate; experimental animals did not have this option. If I had allowed the treatment diets to increase as the bugs grew, I may have avoided this increase in mortality. Prior to the experiment however, I did not have any information about the number of fruit flies per day required for development, and so I elected to maintain the treatments at a constant level throughout.

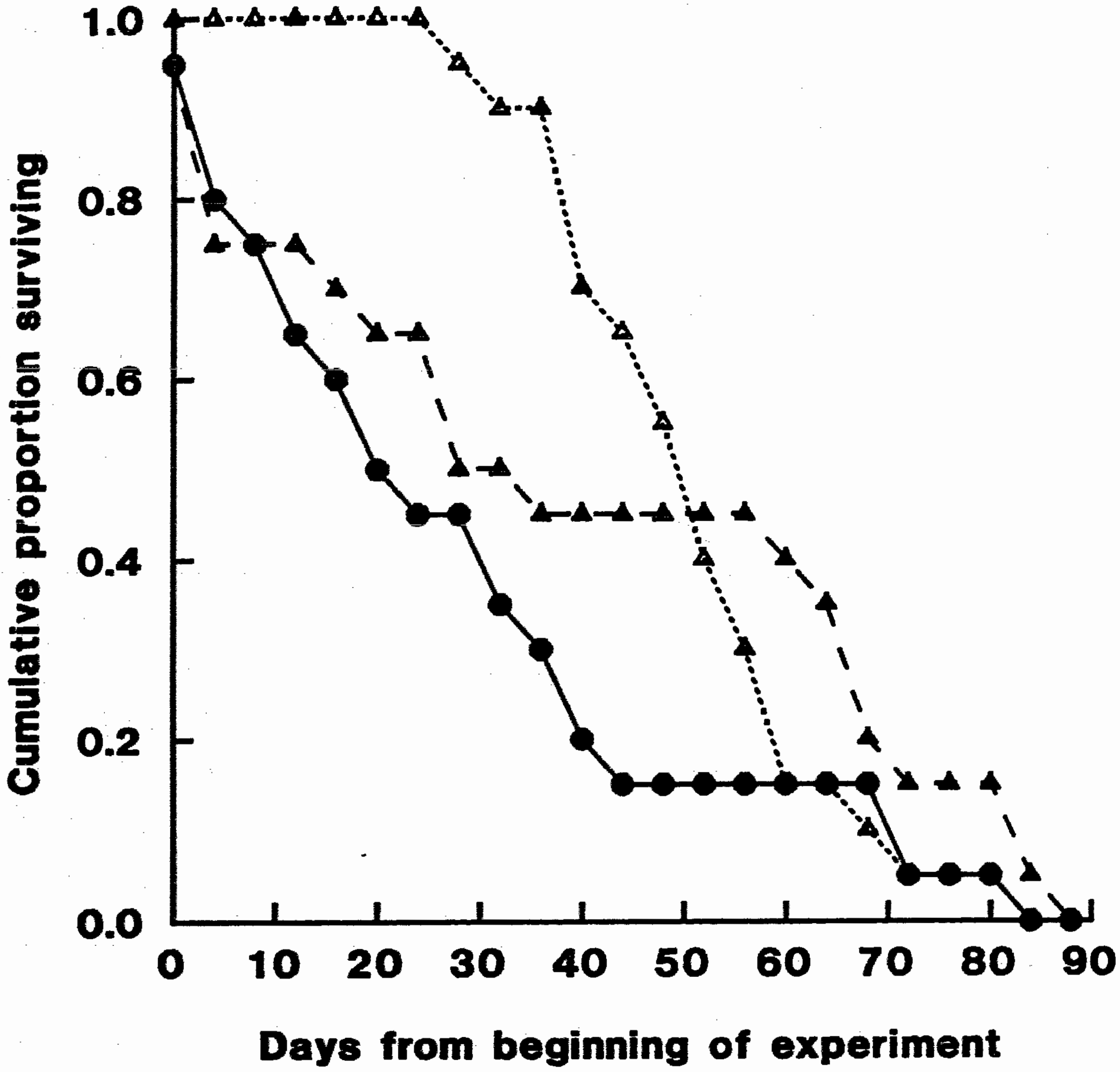

Figure 3.3 Plots of cumulative proportion of juvenile striders alive against time for three different diet treatments. Solid circles = 1 Fruit fly / 3 days, Solid triangles = 1 Fruit fly / 2 days, Open triangles = 1 Fruit fly / day. Better fed bugs survive better early in the experiment, but once they reach a large size they require more food than was provided in the treatment.

Because mortality tends to increase with decreasing food, it is likely that providing different numbers of fruit flies per day affects the survival of bugs. In addition, better-fed bugs grow faster, rather than larger, and therefore tend to reach adulthood quicker than bugs with less food. Thus, food availability probably has an impact on fitness (considered only as survival to the next molt), as a bug's risk of predation is greater when it is smaller (Spence and Cárcamo 1991; personal observations).

Aggression Experiment

Given that the amount of food eaten has effects on fitness, it is likely that juvenile water striders will behave in such a way as to maximize their food intake, subject to other considerations such as minimizing predation risk. One way by which water striders could maximize food intake is to aggressivly defend their foraging space. Juvenile *L. notabilis* use several behaviours in the field that could be interpreted as resource defence: vibration signals, lunges, and fighting (personal observations). Assuming that these behaviours represent aggressive defence of resources, I set up an experiment placing pairs of water striders in a contest situation in order to measure the frequency with which they signaled, attacked, and fought after two days experience with a particular food level.

Aggressive resource defence can be used to acquire a wide variety of resources such as mates (Davies 1978; Poethke and Kaiser 1987; Spence and Wilcox 1986) and food (Blanckenhorn 1991; Carpenter and MacMillen 1976; Davies 1980; Davies and Houston 1981; Dill 1978; Dill et al. 1981; Gass et al. 1976; Kodric-Brown and Brown 1978; Martel 1992; Puckett and Dill 1985; Temeles 1990; Tye 1986; Wilcox and Ruckdeschel 1982; Ydenberg 1984; Ydenberg and Krebs 1987). To date, the most successful explanation of resource defence is Brown's (1964) concept of economic defensibility. For resource defence in relation to food, the food threshold model (Carpenter and Macmillen 1976) is the best developed and best tested version of the economic defensibility concept.

The food threshold hypothesis predicts that at low levels of food availability, resource defence is not a viable option because the costs of defence exceed the benefit available from the foraging area. As food availability increases, eventually the benefit of defence exceeds the cost; this is the lower threshold of defence (see Figure 1.1). As food availability continues to increase, one of several mechanisms can bring about an upper food threshold for defence (Myers et al. 1981). The costs of defence can rise as the number of intruders increases; however, this assumes that increasing food availability on the local foraging area is not matched by an increase in the habitat outside the defended area. Alternatively, an upper limit to the amount of food that can be consumed could be reached. After reaching this limit, further increases in food availability do not increase the benefits of defence, and a higher payoff can be obtained only by ceasing to pay the costs of defence.

In Chapter 2 of this thesis I developed a game theory version of the food threshold model. There are two predictions of the game theory model that should be kept in mind for this experiment. First, it is possible for more than one strategy to be optimal at the same time; mixed strategy equilibria of aggressive and non-aggressive foragers (territory owners and floaters in Chapter 2) are common. In the non-game food threshold model only one strategy is predicted to be optimal for a given food level. Second, the availability of food affects the occurrence of aggressive behaviour only when the cost to aggressors of interacting with non-aggressive individuals is positive.

Methods

On the first day of each run of the experiment, approximately 20 4th or 5th instar *L. notabilis* were weighed, measured, and placed individually into 500 ml cups (diameter 7 cm). On day 2, each water strider received between 2 and 2.5 h of foraging time in a tray identical to the one in which the contest trial would take place. During this time, from one to four frozen fruit flies were placed into the tray at half-hour intervals. All animals in a particular run of the experiment received the same number of flies. This procedure was repeated on day 3. On day 4, all surviving animals that had not molted were re-weighed and matched into pairs based on weight (mean percentage difference(range)=4.0%(0-14)). Each pair of bugs was placed into a pair of upside down cups in the centre of a tray and allowed to acclimate for 1 min. After the acclimation period, the cups were lifted and the frequency of strides, signals, attacks, and fights were recorded for 10 minutes. An observation was terminated if one of the animals jumped out of the experimental arena. Individuals were only used once in the study. An exception to the protocol was made in the last run: 5th instars from the previous run were re-weighed and provided with 10 fruit flies/day in an effort to generate a wider range of weight changes.

Analysis of the data was performed on a standardized aggression score, calculated by summing the number of signals and the number of physical attacks for each individual, and then dividing by the number of seconds in an observation period. Change in condition was calculated as the final experimental weight minus the initial experimental weight, divided by the cube of mid-tibia length. All analyses were run in SPSS-X (SPSS Inc. 1988).

Results and Discussion

Based on the food threshold model of resource defence, I expected to see aggression first increase in frequency with increasing food availability, and then decrease. This prediction was not supported by the data (Figure 3.4). A oneway ANOVA of total aggression by treatment revealed that there was no significant effect of treatment (F=0.87; df=4,32; p=0.4908). Moreover, the pattern does not qualitatively conform to that predicted by the food threshold hypothesis.

A problem with the experimental setup was that there was no guarantee that a water strider would consume all of the fruit flies it was provided. While food threshold models are generally formulated in terms of food availability, there is an implicit assumption that the animals eat, or are able to eat, all of the food provided. Animals must estimate food availability based on their encounter rate with food items, or their foraging success. One indicator of an individual's foraging success is its change in condition over the four day period of the experiment. Figure 3.5 shows the average change in condition for an individual in each of the treatment groups. Water striders with greater access to food tended to improve more in condition, at least among treatment groups 1 to 4. The variation among individuals within a treatment group is still high.

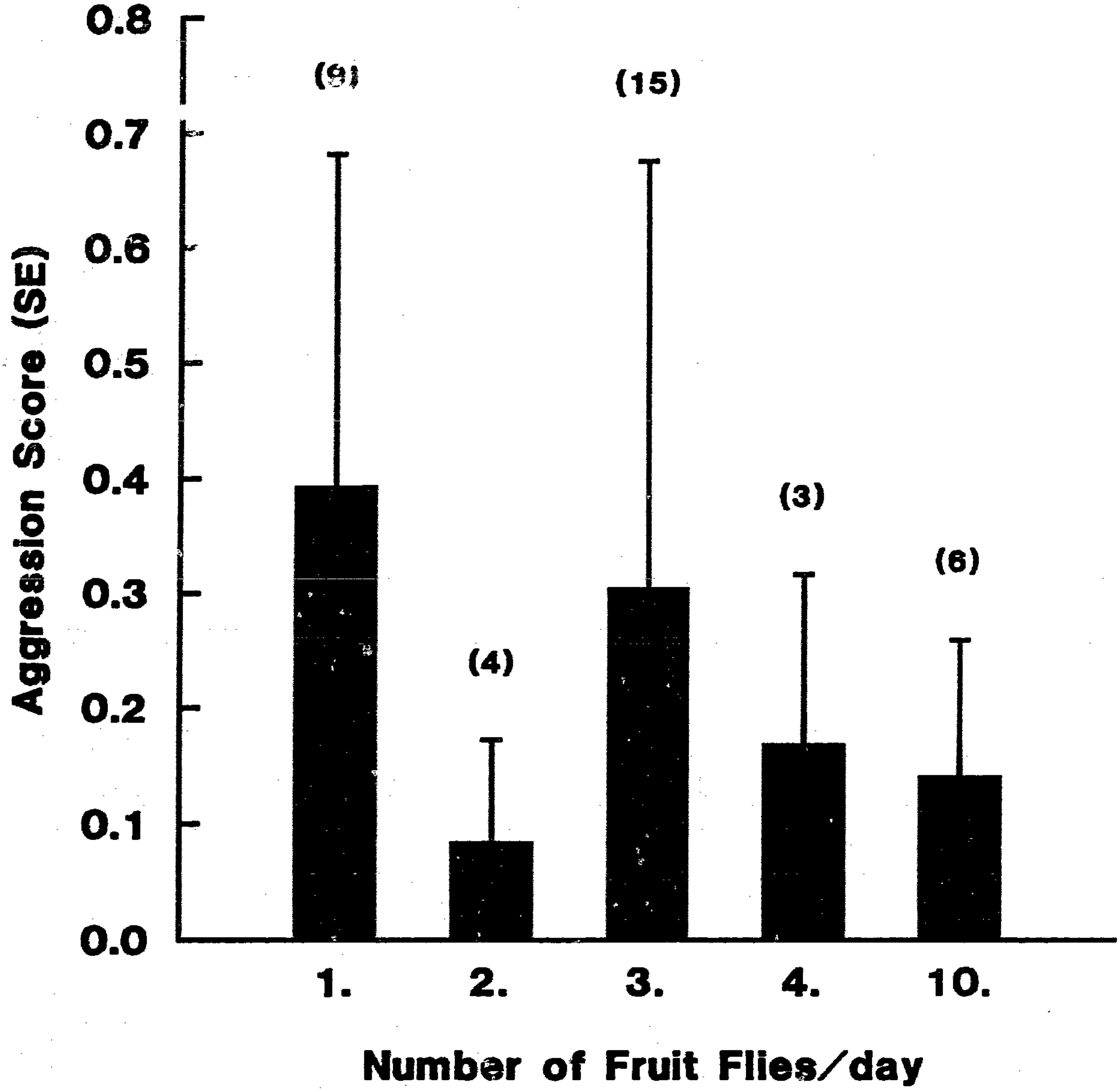

Figure 3.4 Bar plot of the average aggression scores (+SE) in each treatment group. Aggression scores are summed over both bugs in an observation. Numbers in parentheses are the number of pairs of bugs observed in that treatment group. The pattern of aggression frequency does not match the pattern predicted by the food threshold model.

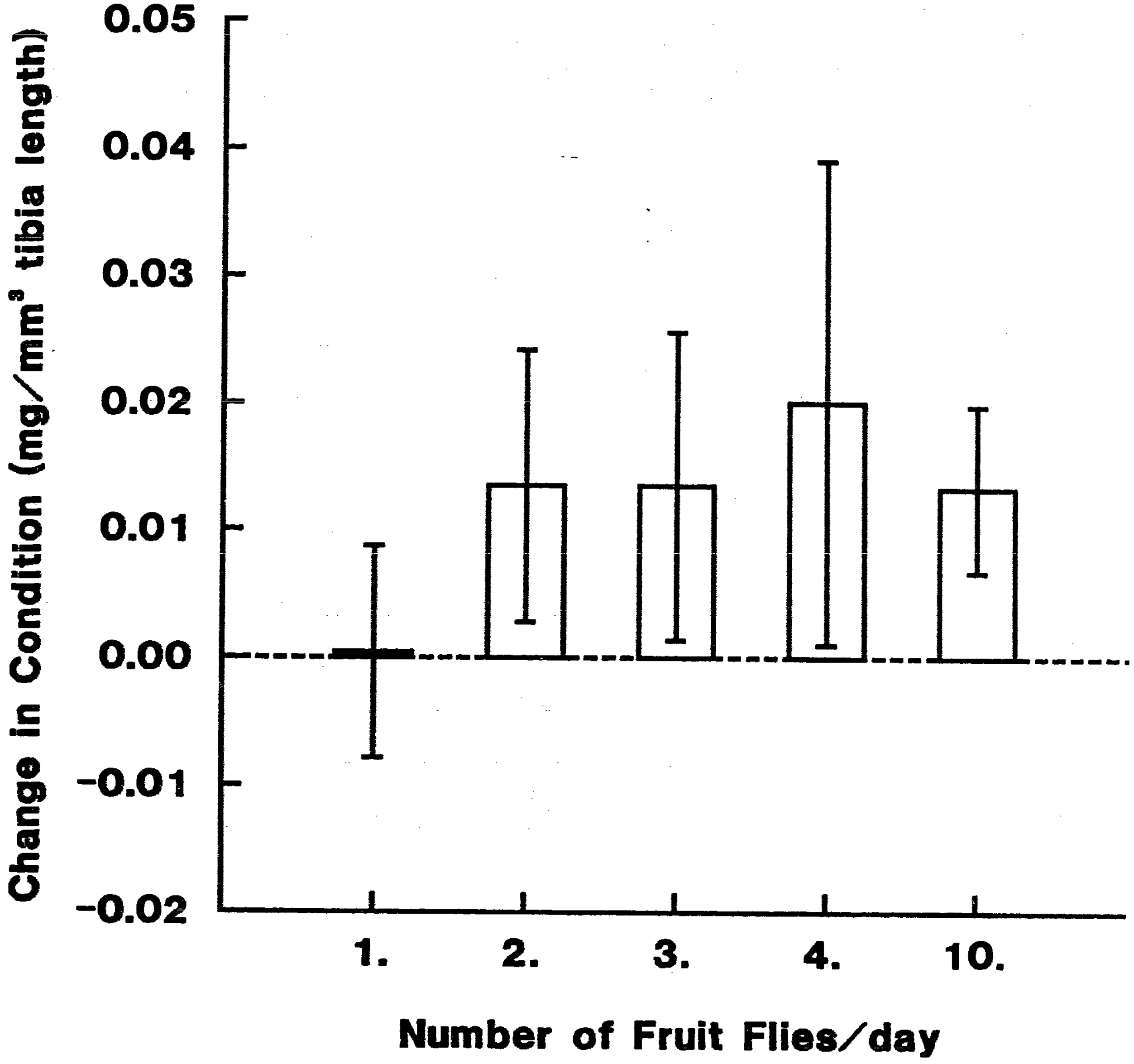

Figure 3.5 Bar plot of average change in condition for all individuals in each treatment of the aggression experiment. Error bars represent standard errors. Sample sizes are double the sample sizes in Figure 3.4. There is a significant effect of treatment on change in condition (F=5.67, df=4,69, p=0.001), although only treatment 1 is significantly less than the others by a Tukey multiple comparisons test.

Figure 3.6 shows the relationship between an individual's aggression score and its change in condition. I have attempted to analyze this distribution in several ways. All methods involved splitting change in condition (a continuous variable) into categories, and analyzing the resulting group means, or frequencies of aggressive versus non-aggressive bugs within each group. A loss in condition is biologically different from a gain, so the first category chosen was all bugs that lost condition during the experiment. Bugs that gained condition were split into two categories, low and high gain, at the point halfway between zero change in condition and the maximum change in condition observed. The frequency table was calculated by counting the number of individuals in a group that behaved aggressively, and those that showed no aggression at all. Table 3.4 summarizes the contingency test, and Table 3.5 summarizes the ANOVAs. None of tests shows a response in the expected direction. The trend in Table 3.4 is in the right direction, but this could easily be due to chance; there are many fewer observations in the loss and high gain categories than in the low gain category. Analyzing this table with a monte carlo simulation method, freeing the analysis from assumptions about the underlying distribution, yields p-values greater than 0.1

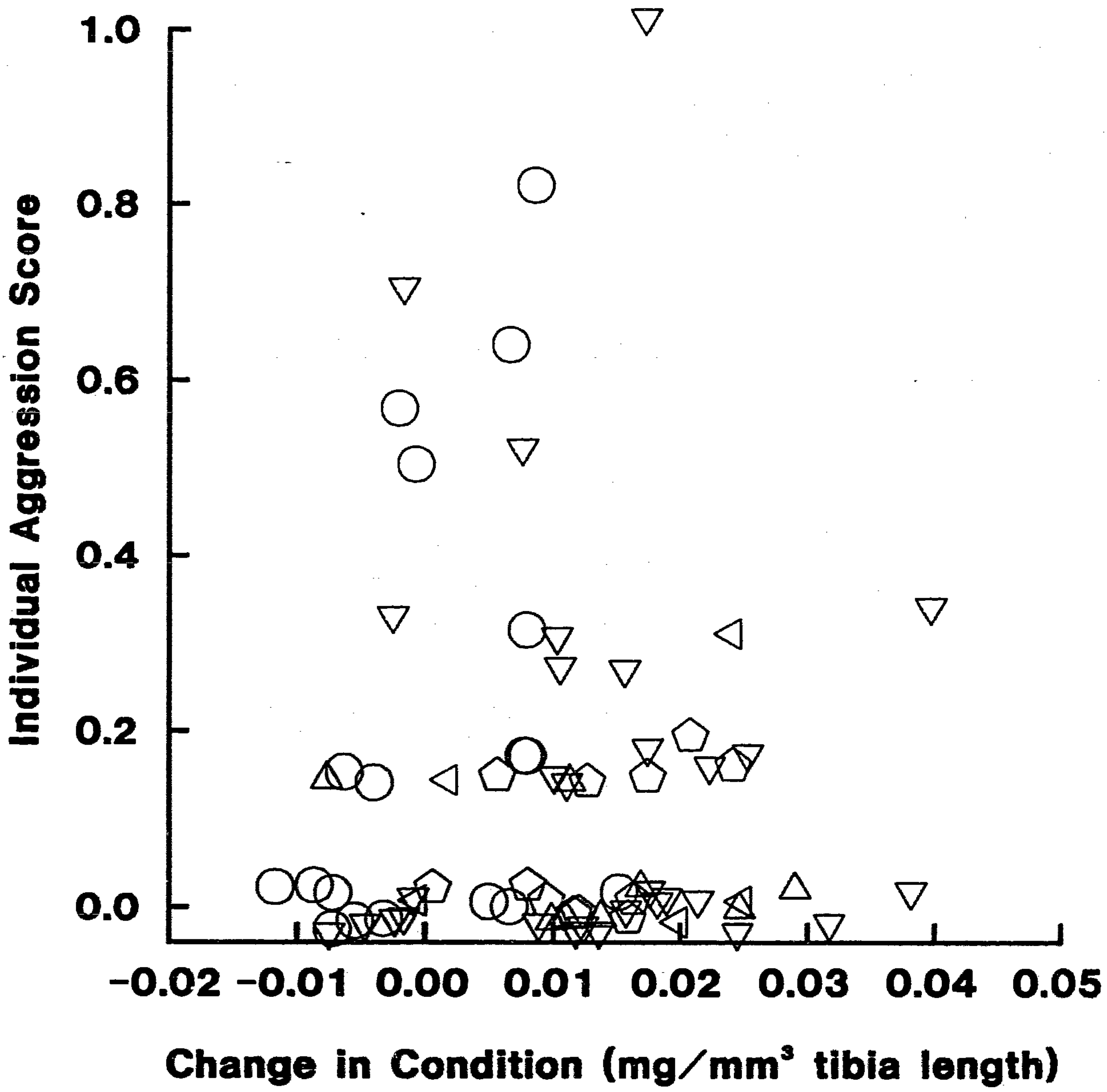

Figure 3.6 Scatter plot of the aggression score for each individual against that individual's change in condition during the aggression experiment. Different symbols represent different treatments: circles = 1 fruit fly/day, triangles = 2 fruit flies/day, upside down triangles = 3 fruit flies/day, sidewise triangles = 4 fruit flies/day, and pentagons = 10 fruit flies/day. There is no trend.

Table 3.4 Contingency test of aggression by change in condition. Values within the table are the numbers of individuals who match those criteria. Aggression and change in condition are independent of each other ($\chi^2 = 3.74$, DF = 2, p = 0.154).

	No Aggression	Aggression
Loss of condition (<0.000 mg/mm^3)	12	6
Gain in condition (<0.025 mg/mm^3)	25	24
Gain in condition (>= 0.025 mg/mm^3)	6	1

Table 3.5 ANOVAs of aggression score by change in condition. The first row includes all individuals, and the second includes only those individuals who behaved aggressively. Change in condition was broken into the same three groups as in Table 3.3. None of the groups is significantly different from any of the others. The degrees of freedom are the between groups and within groups values, respectively.

	DF	F	p
Including all Individuals	2,71	0.76	0.4723
Including only Aggressive Individuals	2,28	0.09	0.9059

General Discussion

In this study I have demonstrated that food availability affects the growth rate and survival of juveniles. Assuming that surface vibrations and lunges represent aggressive behaviour, and that natural selection favours rapid growth by juvenile water striders, there is good reason to suspect that juveniles should exhibit food defence at intermediate levels of food availability. Therefore, I manipulated food availability to look for effects on the occurrence of aggression. I failed to find an effect of food availability.

As an increased amount of food appears to increase an individual's fitness, I expected that water striders should attempt to maximize their net energy intake. One way to do this is to utilize aggression to increase an individual's share of a limited food supply. Juvenile water striders generate surface vibrations that I assume communicate aggressive intent to competitors; however, these behaviours do not vary with food supply as predicted by the food threshold hypothesis. There are three reasons why this may have occurred: first, vibration signals may not represent aggression; second, vibration signals may be aggressive, but may not increase foraging success; third, individuals may not have transferred their estimates of foraging success to the experimental arenas. I will deal with each of these considerations in turn.

As stated in the introduction, I assumed that surface vibrations represent aggression by the vibrator. I have not tested this assumption, and therefore it is possible that my failure to detect an effect of food availability on aggression is due to the fact that I was not recording aggression at all, but some other behaviour. A conclusive test of the function of surface vibrations would require record-and-playback experiments.

Vibration signals, whether they represent aggression or not, could potentially increase foraging success by inhibiting competitors. In a preliminary trial in which I provided fruit flies at 10 minute intervals to a group of four similarly-sized water striders in a 20 x 55 cm tray, one individual began signalling and lunging at the other three after it had consumed the first fruit fly. After 10 minutes of this, the other three water striders were restricted to a 2 cm strip along one end of the tray, and the signaller received the remaining fruit flies in the trial without interference from the others. In this one case, signals and lunges were used to keep competitors from foraging, increasing the energy intake rate of the signaller.

In the aggression experiment itself, at least 24 hours elapsed from the time each bug was last provided with food to the experimental encounter. In that time the bug was moved twice, from the foraging arena to its cup, and from the cup to the experimental arena. It is conceivable that the bugs were unable to transfer estimates of food availability obtained in the foraging arena to the experimental arena. This could account for the lack of a response to manipulations of food availability. How might a bug estimate food availability? Two possible mechanisms are monitoring change in condition over some time period, or by keeping track of the average interval between capture attempts.

I measured change in condition as change in body weight over a 2 day period divided by the cube of mid tibia length. There are two ways in which this measure could differ from the measure used by the bugs themselves. First, fat content, or the amount of some nutrient, may be more important than weight. Second, bugs could be averaging their body condition over a longer or shorter period of time. If food availability in the field fluctuates rapidly, then they might not alter their behaviour on the basis of a short-term deviation from the average taken over a longer time period. Alternatively, they might average on a much shorter time scale. In this case it is likely that all bugs would have had similar estimates of food availability, as they had all been denied food for 24 hours. Similarly, if bugs measure the interval between encounters with food items, all of the bugs in the experiment would have had similar expectations of food availability because of the lag between the last time food was provisioned and the actual experimental confrontation. If any of these measures of foraging success is used instead of food per day, the effect would be to reduce differences in expected food availability among treatments.

I cannot conclude anything about the effect of food availability on the occurrence of aggression from these experiments. However, bugs still varied in both the intensity and occurrence of aggression, as predicted by the game theory model developed in Chapter 2. A second consideration is that the game theory model only predicts the occurrence of food thresholds when interactions with non-aggressive individuals are costly for aggressive individuals. If this is not the case, then the game theory model predicts that food availability will have no effect on the occurrence of aggression, in direct contrast to the predictions of the simpler cost-benefit model of food thresholds (Carpenter and Macmillen 1976). I have no data to evaluate this possibility, but it is at least possible that vibration signals carry a negligible cost when directed at non-aggressive individuals. Signals could still be costly when directed at other aggressive individuals, as those individuals may respond with signals of their own, leading to a more involved interaction.

Future research on the aggressive behaviour of juvenile *L. notabilis* needs to consider three things. First, the function of vibration signals should be evaluated using playback experiments. Second, the costs (particularly predation risk, energy, and time) and benefits (energy) of aggressive behaviour need to be evaluated directly in longer term laboratory experiments. Finally, longer term field observations need to be conducted to evaluate the use of these behaviours by individuals over longer time scales.

List of References

Brown JL (1964) The evolution of diversity in avian territorial systems. The Wilson Bulletin 76:160-169

Blanckenhorn WU (1991) Fitness consequences of food-based territoriality in water striders, *Gerris remigis*. Animal Behaviour 42:147-149

Carpenter FL, Macmillen RE (1976) Threshold model of feeding territoriality and test with a Hawaiian honeycreeper. Science 194:639-642

Davies NB (1978) Territorial defence in the speckled wood butterfly (*Pararge aegeria*): the resident always wins. Animal Behaviour 26:138-147

Davies NB (1980) The economics of territorial behaviour in birds. Ardea 68:63-74

Davies NB, Houston AI (1981) Owners and satellites: the economics of territory defence in the pied wagtail, *Motacilla alba*. Journal of Animal Ecology 50:157-180

Dill LM (1978) An energy-based model of optimal feeding-territory size. Theoretical Population Biology 14:396-429

Dill LM, Ydenberg RC, Fraser AHG (1981) Food abundance and territory size in juvenile coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Zoology 59:1801-1809

Gass CL, Angehr G, Centa J (1976) Regulation of food supply by feeding territoriality in the rufous hummingbird. Canadian Journal of Zoology 54:2046-205

Hart DD (1987) Feeding territoriality in aquatic insects: cost-benefit models and experimental tests. American Zoologist 27:371-386

Kodric-Brown A, Brown JH (1978) Influence of economics, interspecific competition, and sexual dimorphism on territoriality of migrant rufous hummingbirds. Ecology 59:285-296

Lott DF (1984) Intraspecific variation in the social systems of wild vertebrates. Behaviour 88:266-325

Martel G (1992) Influence of predation risk on the territorial behaviour of juvenile coho salmon, *Oncorhynchus kisutch*. PhD. Dissertation. Simon Fraser University, Burnaby, B.C., Canada. 150pp.

Martin P, Bateson P (1986) Measuring Behaviour: An Introductory Guide. Cambridge University Press. 200pp

Myers JP, Connors PG, Pitelka FA (1981) Optimal territory size and the sanderling: compromises in a variable environment. pp 135-159. In: Kamil AC, Sargent TD (eds) Foraging Behaviour: Ecological, Ethological, and Psychological Approaches. Garland STPM Press, New York.

Poethke HJ, Kaiser H (1987) The territoriality threshold: a model for mutual avoidance in dragonfly mating systems. Behavioral Ecology and Sociobiology 20:11-19

Puckett KJ, Dill LM (1985) The energetics of feeding territoriality in juvenile coho salmon (*Oncorhynchus kisutch*). Behaviour 92:97-111

SAS Institute (1990) SAS Procedures Guide: Version 6 (3rd Edition). Cary, NC. 705 pp

Spence JR (1986) Relative impacts of mortality factors in field populations of the waterstrider *Gerris buenoi* Kirkaldy (Heteroptera: Gerridae). Oecologia 70:68-76

Spence JR, Wilcox RS (1986) The mating system of two hybridizing species of water striders (Gerridae). II. Alternative tactics of males and females. Behavioral Ecology and Sociobiology 19:87-95

Spence JR, Cárcamo HA (1991) Effects of cannibalism and intraguild predation on pondskaters (Gerridae). Oikos 62:333-341

SPSS Inc. (1988) SPSS-X Users Guide (3rd Edition). Chicago, Ill. 1072 pp

Stimson J (1970) Territorial behaviour of the owl limpet, *Lottia gigantea*. Ecology 51:113-118

Stimson J (1973) The role of the territory in the ecology of the intertidal limpet *Lottia gigantea* (Gray). Ecology 54:1020-1030

Temeles EJ (1990) Northern harriers on feeding territories respond more aggressively to neighbors than to floaters. Behavioral Ecology and Sociobiology 26:57-63

Tye A (1986) Economics of experimentally-induced territorial defence in a gregarious bird, the fieldfare *Turdus pilaris*. Ornis Scandinavica 17:151-164

Wilcox RS (1979) Sex discrimination in *Gerris remigis*: role of a surface wave signal. Science 206:1325-1327

Wilcox RS, Ruckdeschel T (1982) Food threshold territoriality in a water strider (*Gerris remigis*). Behavioral Ecology and Sociobiology 11:85-90

Wilcox RS, Spence JR (1986) The mating system of two hybridizing species of water striders (Gerridae). I. Ripple signal functions. Behavioral Ecology and Sociobiology 19:79-85

Wilson EO (1975) Sociobiology. Belknap Press, Cambridge Massachusetts. 367pp

Ydenberg RC (1984) The conflict between feeding and territorial defence in the great tit. Behavioural Ecology and Sociobiology 15:103-108

Ydenberg RC, Krebs JR (1987) The tradeoff between territorial defence and foraging in the great tit (*Parus major*). American Zoologist 27:337-346

Chapter 4:

Concluding Remarks

The goal of this thesis was to conduct two independent explorations into the nature of aggressive defence of resources. The first, a game theory model of resource defence, shows that mixed strategy equilibria not only occur in systems where resource defence is an alternative food acquisition strategy, but that they are common. The second, a set of empirical observations on the behaviour of the water strider *Limnoporus notabilis*, provides indirect evidence that juveniles use aggression to enhance foraging success, and describes an attempt to manipulate the occurrence of resource defence. What do these two studies together say about resource defence and the effect of food availability?

First, both the model and the empirical observations reinforce the need to account for within population variation in the occurrence of aggressive defence of resources. Not all water striders generate surface vibrations in the presence of competitors. Yet, presumably, these silent individuals are also engaged in foraging for the same resources. Discarding half of a population as deficient in competitive ability is an inadequate explanation; the model clearly shows that it is possible for populations where all competitors are equal in ability to have individuals that do not employ aggressive defence as a foraging strategy. Particular attention needs to be paid to comparing the payoffs of alternative strategies for acquiring a resource.

Second, the literature on resource defence is divided on semantic issues: there are nearly as many definitions of territoriality as there are papers discussing it (see Kaufmann 1984). Individuals defend territories to acquire a larger share of limited resources. Classical definitions of territoriality with their emphasis on a defended area of space appear to overlook this essential point. Territories are about acquisition of resources, not about space (except when space itself is a limiting resource). Replacing a conceptually loaded term, territoriality, with a more neutral one, resource defence, pushes the emphasis back where it belongs: on the use of aggression to increase a competitor's share of limited resources. It moves a large number of disparate studies under the same conceptual umbrella, and removes much of the taxonomic biases that have resulted from studies of territoriality in birds.

List of References

Kaufmann JH (1983) On the definitions and functions of dominance and territoriality. Biological Reviews 58:1-20

Appendix A

Here I present the detailed stability analysis of the complete territory model with costs. Following Maynard-Smith (1982), if W_i is the fitness of an individual who adopts strategy i, and W is the mean fitness of the population, then

$$W_i = C + \sum_j p_j E(i, j)$$

$$\overline{W} = \sum_i p_i W_i \tag{A.1}$$

where C is a positive constant, p_i is the proportion of individuals in the population that are playing strategy i, and $E(i, j)$ is the expected payoff to strategy i when playing against j. Assume that the population is reproducing in a haploid asexual fashion, then the proportion of individuals in the next generation that play i is

$$p_i' = p_i \frac{W_i}{\overline{W}}. \tag{A.2}$$

Equations (A.1) and (A.2) describe the dynamics of the population in finite difference form. They can be rewritten (Maynard-Smith 1982)

$$p_i' - p_i = \frac{p_i(W_i - \overline{W})}{\overline{W}}$$

which, if the difference between generations is not too great, can be replaced with the differential equation

$$\frac{dp_i}{dt} = \frac{p_i(W_i - \overline{W})}{\overline{W}}. \qquad \text{(A.3)}$$

Note that the t in the left hand side of (A.3) is time, not territory size. Because the right hand side of the set of equations represented by (A.3) is divisible by the same function $\overline{W}$, the flows and stationary points are identical for the equations

$$\frac{dp_i}{dt} = p_i(W_i - \overline{W}). \qquad \text{(A.4)}$$

For the territory model

$$W_T = C + E(T, I),$$

$$W_F = C + E(F, I),$$

$$\overline{W} = pW_T + (1 - p)W_F.$$

Substituting into (A.4) and simplifying

$$\frac{dp}{dt} = p(W_T - (pW_T + (1 - p)W_F))$$

$$= p((1 - p)W_T - (1 - p)W_F)$$

$$= p(1 - p)(W_T - W_F)$$

$$= p(1 - p)((C + E(T,I)) - (C + E(F,I)))$$

$$= p(1 - p)(E(T,I) - E(F,I)) \qquad \text{(A.5)}$$

Equilibrium points occur wherever dp/dt = 0. By inspection, equilibrium points will occur at $p = 0$, $p = 1$, and when

$$E(T,I) - E(F,I) = 0 \;. \qquad \text{(A.6)}$$

In order to calculate where the mixed equilibria occur, (A.6) must be solved. Because of the discontinuous nature of the payoff equations in this model, this equation must be solved twice, once assuming that p is less than the critical point, and again assuming that p is greater than the critical point. The resulting solutions for the mixed equilibria must then be bounded by the conditions under which they apply. Solutions obtained assuming that p is less than the critical point are only valid when p is greater than 0 and less than $1/nT$ (recall that $p = 1/nT$ is the critical point), while solutions assuming that p is greater than the critical point are valid when p is less than 1 and greater than $1/nT$.

To begin, I solve (A.6) assuming that p is greater than the critical point. I substitute equations (2.14) and (2.15) into (A.6), assuming that c_2 and c_3 are equal to zero.

$$\frac{f(a+(1-a)p)}{np}-c_1-\frac{1-a-(1-a)p)f}{(1-p)n}=0$$

$$\frac{f(a+(1-a)p)}{p}-\frac{1-a-(1-a)p)f}{(1-p)}=nc_1$$

$$\frac{(fa+fp-fap-fap-fp^2+fap^2)-(fp-fap-fp^2+fap^2)}{p(1-p)}=nc_1$$

$$\frac{fa-fap}{p(1-p)}=nc_1$$

$$\frac{fa(1-p)}{p(1-p)}=nc_1$$

$$p=\frac{fa}{nc_1} \qquad (A.7)$$

This point is less than 1 when

$$f \leq \frac{nc_1}{a} \qquad \text{(A.7.1)}$$

and it is greater than $1/n$T when

$$p = \frac{fa}{nc_1} \geq \frac{1}{nT}$$

$$f \geq \frac{c_1}{Ta}. \qquad \text{(A.7.2)}$$

Next, I solve (A.6) assuming that p is less than $1/nT$, and again assuming that c_2 and c_3 are equal to zero. Substituting (2.14) and (2.15) in (A.6)

$$Tf(a+(1-a)p) - \frac{f(1-nTp)+f(1-a-(1-a)p)nTp}{(1-p)n} = 0$$

$$Tfa+Tfp-Tfap- \frac{(f-nTfp+nTfp-nTfap-fTfp^2+nTfap^2)}{(1-p)n} = 0$$

$$nTfa+nTfp-nTtfap-nTfap-nTfp^2+nTfap^2-$$
$$(f-nTfp+nTfp-nTfap-nTfp^2+ntTfap^2) = 0$$

$$nTfa+nTfp-nTfap-f = 0$$

$$nTa+nTp-nTap-1 = 0$$

$$(nT-nTa)p = 1-nTa$$

$$p = \frac{1-nTa}{nT-nTa} \tag{A.8}$$

This equilibrium is greater than 0 when

$$(1-nTa) \geq 0$$

$$-nTa \geq -1$$

$$Ta \leq \frac{1}{n} \tag{A.8.1}$$

This equilibrium is less than $1/nT$ when

$$\frac{1-nTa}{1-a} \leq 1$$

$$nTa \geq a$$

$$nT \geq 1. \tag{A.8.2}$$

An equilibrium point will be stable if d(dp/dt)/dp is negative at the equilibrium point. d(dp/dt)/dp must be calculated separately for the cases above and below the critical point. Beginning with the case above the critical point, substitute (2.14) and (2.15) into (A.5), simplify, and take the derivative with respect to p

$$\frac{dp}{dt} = p(1-p)\left(\frac{f(a+(1-a)p)}{np} - c_1 - \frac{(1-a-(1-a)p)f}{(1-p)n}\right)$$

$$= p(1-p)\left(\frac{fa+fp-fap}{np} - c_1 - \frac{f-fa-fp+fap}{(1-p)n}\right)$$

$$= \frac{(1-p)(fa+fp-fap) - np(1-p)c_1 - p(f-fa-fp+fap)}{n}$$

$$= \frac{(fa+fp-fap-fap-fp^2+fap^2) - (fp-fap-fp^2+fap^2) - nc_1p+nc_1p^2}{n}$$

$$= \frac{fa-fap-nc_1p+nc_1p^2}{n}$$

$$\frac{d\left[\frac{dp}{dt}\right]}{dp} = -\frac{fa+nc_1-2nc_1p}{n}\,. \qquad \text{(A.9)}$$

And for the case where p is less than the critical point

$$\frac{dp}{dt} = p(1-p)\left(Tf(a+(1-a)p) - \frac{f(1-nTp)+f(1-a-(1-a)p)nTp}{(1-p)n}\right)$$

$$= p(1-p)\left(Tfa+tfp-Tfap- \frac{(f-nTfp+nTfp-nTfap-nTfp^2+nTfap^2)}{(1-p)n}\right)$$

$$=p\left(\frac{nTfa+nTfp-nTfap-nTfap-nTfp^2+nTfap^2}{n} - \frac{(f-nTfap-nTfp^2+nTfap^2)}{n}\right)$$

$$= p\left(\frac{nTfa+nTfp-nTfap-f}{n}\right)$$

$$= \frac{(nTf-nTfa)p^2 + (nTfa-f)p}{n}$$

$$\frac{d\left[\frac{dp}{dt}\right]}{dp} = \frac{2(nTf-nTfa)p+(nTfa-f)}{n} \ . \qquad \text{(A.10)}$$

Expressions (A.9) and (A.10) can be used to test the stability of the equilibrium points to which they apply.

Starting with the equilibrium at $p = 1$, substitute $p = 1$ into (A.9)

$$\frac{d\left[\frac{dp}{dt}\right]}{dp} = -\frac{fa-nc_1}{n} \leq 0$$

$$fa-nc_1 \geq 0$$

$$f \geq \frac{nc_1}{a} \; . \qquad (A.11)$$

Therefore, $p = 1$ is a stable equilibrium when (A.11) is true. Substituting (A.7) into (A.9)

$$\frac{d\left[\frac{dp}{dt}\right]}{dp} = -\frac{nc_1-fa}{n} \leq 0$$

$$nc_1-fa \geq 0$$

$$-fa \geq -nc_1$$

$$f \leq \frac{nc_1}{a} \; . \qquad (A.12)$$

Therefore (A.7) represents a stable equilibrium when (A.12) is true. (A.12) and (A.7.1) are identical, so if (A.7) exists, it is stable. Continuing with the equilibrium at $p = 0$ and (A.10)

$$\frac{d\left[\frac{dp}{dt}\right]}{dp} = \frac{nTfa-f}{n} \leq 0$$

$$nTa-1 \leq 0$$

$$Ta \leq \frac{1}{n} . \tag{A.13}$$

And finally, the equilibrium at (A.8) is stable when

$$\frac{d\left[\frac{dp}{dt}\right]}{dp} = 2(1-nTa)+nTa-1 \leq 0$$

$$1-nTa \leq 0$$

$$Ta \geq \frac{1}{n} . \tag{A.14}$$

However, (A.14) contradicts (A.8.1), so it is not possible for (A.8) to both exist and be stable.

When (A.7.2) is violated, (A.7) is no longer a valid equilibrium. From a graphical analysis (Figure 2.5B) it appears as though the critical point itself becomes an equilibrium of a special sort under these conditions. At this point, there are two equations for dp/dt. The first set is valid for the stability of the point when *p* is decreased below the critical point, while the other set is valid for the stability of the point when *p* is increased. For the lower side of the point, dp/dt must be greater than 0 for the point to be stable. For the upper side, dp/dt must be negative for the point to be stable. From the calculation of d(dp/dt)/dp above the critical point the simplified version of dp/dt is

$$\frac{dp}{dt} = \frac{fa-fap-nc_1p+nc_1p^2}{n} \leq 0 \ .$$

Substitute $p = 1/nT$

$$\frac{c_1}{T}-nc_1-fa \leq -nTfa$$

$$nTfa-fa \leq nc_1-\frac{c_1}{T}$$

$$Tfa(nT-1) \leq c_1(nT-1)$$

$$f \leq \frac{c_1}{Ta}\ , \quad \textit{if and only if}\ nT \geq 1. \qquad (A.14)$$

The equilibrium point at $1/nT$ does not exist when nT is less than 1. The simplified dp/dt for below the critical point comes from the calculations for (A.10)

$$\frac{dp}{dt} = \frac{(nTf-Tfa)p^2+(nTfa-f)p}{n} > 0\ .$$

Substituting $p = 1/nT$

$$\frac{\dfrac{(1-a)+(nTa-1)}{nT}}{n} > 0$$

$$nTa-a > 0$$

$$nT > 1\ . \qquad (A.15)$$

Therefore, when $nT > 1$ and $f \leq c_1/Ta$, $p = 1/nT$ will be stable.