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Misinformation and Assessment Uncertainty in the Ecology of Information Use

By:

Marten A. Koops

A Thesis
Submitted to the Faculty of Graduate Studies
in Partial Fulfillment of the Requirements
for the Degree of

DOCTOR OF PHILOSOPHY

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Winnipeg, Manitoba

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**MISINFORMATION AND ASSESSMENT UNCERTAINTY IN THE
ECOLOGY OF INFORMATION USE**

BY

MARTEN A. KOOPS

**A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University
of Manitoba in partial fulfillment of the requirements of the degree**

of

DOCTOR OF PHILOSOPHY

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For Michelle and Eiryn.

“In the beginning there was information. The word came later.”

- Fred I. Dretske (1981)
Knowledge and the Flow of Information

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General Abstract

The purpose to acquiring and using information is to improve the decision process. But not all information improves decisions. Some information is incorrect, i.e. misinformation, or variable, leading to assessment uncertainty. Both misinformation and uncertainty can result in erroneous decisions. In this thesis, I investigate the role of misinformation and assessment uncertainty in the decision process, specifically considering situations where animals cannot distinguish when information is incorrect. I start by theoretically investigating the influence of reliability on the value of information. Here, I demonstrate that the higher the marginal costs of information, the lower the minimum reliability of information. I further demonstrate that tolerance to misinformation will be affected by a feature of the animal's life history - how current payoffs map to fitness. The greater the fitness consequences of current payoffs, the greater the tolerance to misinformation. Animals may also make erroneous decisions from assessment uncertainty associated with sampling. I develop the Z model of perceptual constraints to model the decision process when perceptual ability is constrained by assessment uncertainty. The Z model predicts that perception will be constrained when differences are small, variability is high, or information is limited. A group of foragers constrained by uncertainty are predicted to conform best to the distribution of resources, i.e. exhibit an ideal free distribution, when food is abundant, competitors are few, or memory is good. With individual differences in competitive ability comes the potential to exploit information niches, with good competitors predicted to exhibit shorter memory than poor competitors. A potential source of information about the quality of food patches is the aggression of foragers. In

an experiment with female guppies, *Poecilia reticulata*, I find that even though I affect a change in the distribution of aggression, the distribution of foragers is unaffected. This suggests that guppies do not use aggression as public information about patch quality. High variability makes aggression unlikely to be a reliable source of information about patch quality.

Chapter 1: General Introduction

Information, as a resource, has great importance to the life of any organism. Information is not important because of any direct influence on fitness. Having more information does not necessarily lead to greater fitness. However, having information can increase fitness through activities such as finding food, avoiding or surviving encounters with predators, or acquiring mates. Without information, decisions about foraging, fighting, fleeing, and mating can be more costly and less beneficial to the decision maker. Initial investigations into behavioral decisions made the simplifying, often implied, assumption that decision makers had perfect information (see Stephens & Krebs 1986 for foraging examples). Predictions based on an assumption of perfect information were often qualitatively supported, though animals continued to perform behaviours inconsistent with the theory. The importance of information to decision making is quite apparent, and though much research has been conducted on information problems, most of this work is restricted to questions about specific aspects of an organism's life.

Consider an animal moving through its environment. For simplicity, assume that this animal is currently interested in finding food while not becoming food. Under such circumstances, decisions will be based on the available information about the distribution and abundance of both food and predators. What are the possible sources of information available to this animal? First, information about food can be obtained directly through senses such as sight, smell, hearing, vibrations, etc. Sensing food directly can provide accurate information, but will be limited to a fine scale of search (Poysa 1992).

Information can also be acquired from the behaviour of other individuals. Observing

feeding behaviour (Krause 1992, Templeton & Giraldeau 1995, 1996), or fights over food (Kennedy & Gray 1994), or a group searching in a limited area (Reebs & Gallant 1997, Laland & Williams 1997, Lachlan et al. 1998) can all be sources of information about the presence or abundance of food. Other features of the environment can also provide information. For example, evidence of the recent passage of prey or the presence of a prey's preferred habitat or food. In addition, this animal may also have information acquired through previous experience with its environment which, even if the environment has changed, may provide a better starting point than no information. Thus, a quick consideration of the foraging information available to an organism reveals three types of information sources: (i) direct experience; (ii) observation of correlated traits; and (iii) past experience. Of course, our animal is also concerned with the possible risk of predation. The same three types of information sources used for foraging can provide information about predators. Directly, predators can be sensed (seen, smelt, heard, felt). Indirectly, the behaviour of conspecifics, or of species with a shared predator, can provide information about the presence of predators. And finally, past experience can provide an expectation of danger, e.g. foraging beside a bush that a predator may hide behind.

I will focus on the ecology of information use from the general perspective that both the acquisition and use of information have been subject to evolution by natural selection. This perspective is traditional for behavioural ecologists, but is not a common approach within cognitive science (Dukas 1998). Given the importance of the ecology of an organism to experienced selection pressures, an ecological perspective may provide the most comprehensive approach with the most explanatory power.

1.1 Information Flow

Animals are faced with the problems of acquiring information from a noisy environment, deciphering the information content, and making a decision (Fig. 1.1a). The flow of information starts with an information source generating a pattern that can provide information. For the moment I refer to this as a pattern to avoid any implication that the transfer of information is intentional or not, or that the source is biotic or abiotic. To this pattern is added some unspecified amount of environmental noise, so that when the pattern reaches the receiver, it is a combination of the original pattern and some amount of non-informative noise. The pattern is received at the level of the senses, and is passed to the central nervous system where it must be translated before the information content is perceived by the receiver. After the information has been perceived, the use of the information will depend on the value of information to the receiver. At this point, the behaviour of the current receiver can be a source of information for another receiver. Thus, information transfer can be divided into four stages: transmission, reception, perception, and application (Fig. 1.1b).

The four stages of information transfer provide researchers with different approaches to the study of information. The first stage, the generation and transmission of an information pattern, can lead to questions about the evolution of communication displays (Johnstone 1997). When transmitting information, the signaller must balance reception by both the intended receiver and potential eavesdroppers. For example, when predators are present, signallers may change the structure of their calls to reduce the possibility of localization by predators (e.g. Ryan 1983, Klump et al. 1986).

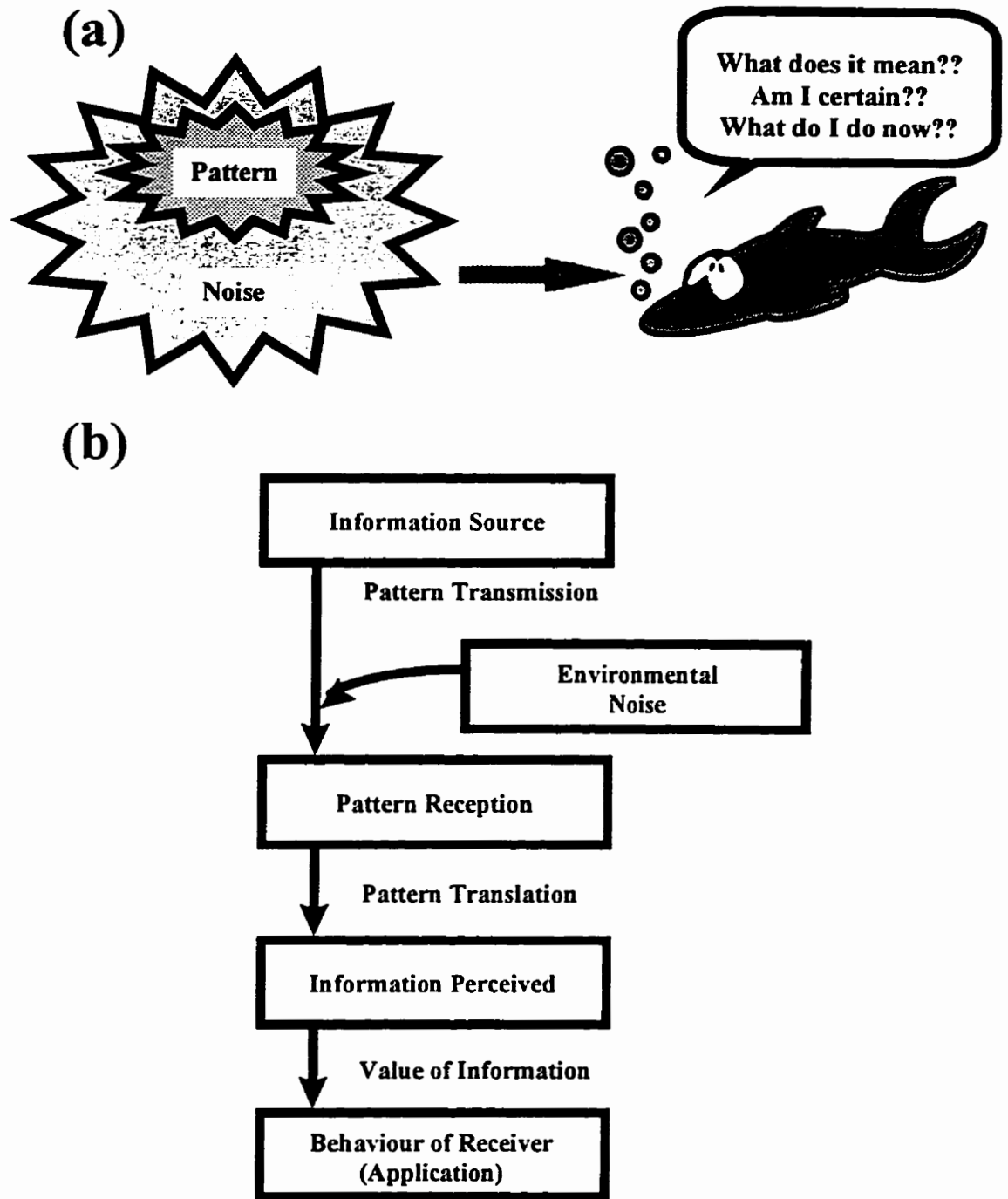


Figure 1.1. (a) When an organism acquires information from its environment, that information will be mixed with meaningless noise, and the organism is faced with the problem of deciphering the information and deciding what to do with it. (b) The four stages of information flow: transmission, reception, perception and application. Adapted from Shannon and Weaver (1949).

The second stage of information transfer is covered by the field of sensory ecology (Dusenbery 1992) and represents an area of overlap between ecology and sensory physiology. This field asks questions about the reception of information through sensory organs. This can lead to research into the conspicuousness of signals in the environment under which they evolved (e.g. Dawkins & Guilford 1994), or biases in the responsiveness of receivers to exaggerated signals (e.g. Enquist & Arak 1998).

The third stage of information transfer is the domain of cognitive ecology and represents an area of overlap between ecology and psychology (Yoerg 1991, Real 1992). The central question is how precisely the transmitted pattern can be translated into the desired meaning so that the information will be accessible and manipulatable by the receiver. If a pattern contains information of importance to an animal's fitness, then there should be selection for the appropriate interpretation of the pattern. There is always the possibility, however, that errors occur in this interpretation (Wiley 1994), and the effectiveness of a pattern may be diminished by environmental noise. Questions about how an organism represents information in its cognitive domain would also be covered by cognitive ecology.

The fourth stage of information transfer is the ecology of information use. At this level, questions concern the influence of ecological surroundings on behaviour, how information modifies behaviour, and what information animals use to make decisions (e.g. Giraldeau 1997). The use of information depends on the value of information to the decision maker (*sensu* Gould 1974, Stephens 1989). Any ecological conditions that change the value of information will influence the formation of assessments and the decision process.

I limit the research presented in this thesis to the final step: from the perception to the application of information. First I will cover the necessary terminology, then I will present a framework for the study of information use, and finish with a brief prospectus of my thesis. My aim is to provide a cohesive view of information use by animals, equally applicable regardless of the behaviour of interest.

1.2 Terminology

Before I continue, some terms should be defined. To start, I will look at what has been termed animal intelligence. Kamil (1994) defined animal intelligence as “those processes by which animals obtain and retain information about their environments and use their information to make behavioral decisions” (p.21). This definition is consistent with the generally accepted view that intelligence includes the ability to adapt behaviour to specific conditions. Without the ability to acquire information, animals would be hard pressed to make adaptive decisions under changing environmental conditions. Animal intelligence, as defined by Kamil (1994), is a broad topic encompassing pattern translation, information perception and the application of information (Fig. 1.1b), so I will further limit myself to the study of how animals use information about their environment.

But what is information? There are few attempts to define information in the biological literature (see Table 1.1), and beyond biology, there is no generally accepted definition of information (Hauser 1996). While I may not be able to find a generally acceptable definition of information, I can list some of the characteristics of what is considered to be information. First, information per se can not be transferred on its own,

but can be transferred when encoded in a pattern. Second, a pattern encoding information can be produced by anything, i.e. life or consciousness is not a requirement. Finally, information is only acquired when the pattern is decoded or interpreted. The information may provide data about the world, but this data need not be true, accurate or precise. This allows for the existence of misinformation as a type of information.

1.2.1 *Information Transfer*

So far I have referred to information as transmitted in a pattern. In the literature, most references to the transfer of information refer to signals or cues. A distinction can be made based on the function of information transfer, so I follow Seeley (1989, Dusenbery 1992) and define a signal as a pattern that conveys information and has been shaped for this purpose by natural selection. This means that both the pattern generated by the transmitter and the interpretation of the pattern by the receiver are shaped by evolution. On the other hand, patterns that contain information but have not been shaped by natural selection specifically to convey information shall be referred to as cues (Seeley 1989, Dusenbery 1992). This suggests that the source of a cue, animate or inanimate, does not experience selection for the improved transmission of information, but the receiver's interpretation should be subject to natural selection. For an alternative view of signals and cues see Hauser (1996).

Table 1.1. A sampler of some published definitions of information, from both biology and other fields. Square brackets are my additions to the quote.

| Definition | Reference |
|--|-----------------------------------|
| “...information in communication theory relates not so much to what you do say, as to what you could say” (p.100) | Shannon & Weaver (1949) |
| information “...describes an abstract quantity which is almost impossible to measure, so we [in communication theory] do not attempt to assess the actual content of messages but stick to possible information content” (p.5) | Rosie (1973) |
| “...information is as fundamental an abstraction as the concept of energy. Whereas energy is the capacity to do work, information is the capacity to organise a system” (p.39) | Stonier (cited in Dusenbery 1992) |
| meaningful information is “...that which has form, can help create or maintain form, and does so by representing states of the environment and inducing behaviors appropriate to them” (p.108) | Wright (1989) |
| information is “...the general assembly of...pattern[s] of objects or events that relate to an adaptive way to behave... animals perceive [these patterns], but what they interpret is information” (p.147) | Templeton & Franklin (1992) |
| information is “...a message which alters probabilistic perceptions of random events” (p.707) | Chavas & Pope (1984) |
| information is “...an object for the communication of knowledge, made up of a support AND a significance” (p.140) | Vincent (1993) |

Communication and passive information transfer can be distinguished based on their use of signals and cues. The use of signals selected to transmit information constitutes a communication system (see Hauser [1996] for a sampler of the diversity of available definitions of communication). Passive information transfer is the transfer of information through a pattern not selected for this purpose, i.e. a cue. This distinction suggests that communication should be selected for the unambiguous transfer of information, at least between communicants. In contrast, passive information transfer, as a by-product of another process, will usually be subtle (Seeley 1989). This will be especially true under conditions where evolution selects against the production of cues, such as a predator selected to move quietly through the forest to avoid alerting its prey. Using these definitions of signals, cues, communication and passive information transfer, information interactions can be classified by the benefits and costs to participants (Table 1.2). Starting with signals, if both the signaler and receiver benefit from information transfer, this is honest communication. If, however, the signaler benefits from the transfer of information at the cost of the receiver, this is deceptive communication. This is the scenario described by Dawkins and Krebs (1978, Krebs and Dawkins 1984) where an arms race develops between the signaler (manipulator) and the receiver.

Altruistic communication occurs when the signaler transfers information beneficial to the receiver at a cost to itself. When both participants experience a cost from the transfer of information, an error has occurred and information transfer can be classified as mis-communication (Wiley 1994). Undoubtedly, this classification will not appropriately categorize all examples of communication (consider white lies or spite), but it is a starting point.

Table 1.2. Classification of information interactions. + indicates a benefit to sending or responding to information, - indicates a cost to sending or responding to information, and NA indicates that there is no benefit or cost, either due to the source being inanimate or because the benefit/cost comes from the function of the behaviour and not the transfer of information.

| <u>Signals</u> | | |
|----------------|----------|---------------------------|
| Signaller | Receiver | Classification |
| + | + | Honest Communication |
| + | - | Deceptive Communication |
| - | + | Altruistic Communication |
| - | - | Mis-Communication (error) |

| <u>Cues</u> | | |
|-------------|----------|------------------------------|
| Source | Receiver | Classification |
| NA | + | Passive Information Transfer |
| NA | - | Misinterpretation |

When information is transferred through the use of cues, referring to the benefit or cost to the source may be inappropriate since (i) the source may be inanimate, or (ii) if animate, the cue is produced as a by-product of another behaviour, and thus it is the benefits accrued from the other behaviour that are selected. This is not to imply that there are no costs to the production of cues, or that any costs are not important, simply that these costs are not necessary to classify information transfer by cues. So, if the receiver benefits from the information acquired from a cue, passive information transfer has occurred. When the receiver experiences a cost from attending to a cue, the cue has been misinterpreted.

While defining and classifying information transfer as signals or cues and communication or passive information transfer is important for understanding the evolution of information transfer, this is not the focus of my thesis. Instead, the important feature of these definitions for the ecology of information use is the common theme of the transfer of information. I include them here only in an attempt to clarify their usage. Hereafter, I will focus on the use of information, and only consider the source when it is important in determining information use.

1.2.2 Types of Information

Information, whether it is obtained from a signal or cue, can be broadly categorized as either: (i) prior information or (ii) current information. Current information is information that an individual is in the process of acquiring. After information is acquired, it becomes prior information, and over time, loses its accuracy due to the stochastic nature of the

world. The distinction between current and prior information may be difficult to determine. The easiest distinction would be that information is current in the instant it is acquired, but becomes prior information immediately thereafter. While this may be the easiest way to define current and prior information, it is overly simplistic for the real world. The acquisition of information takes time, and not all information is old by the time it is acquired. Thus, the length of time that information remains current will be situation specific, however, little research has been conducted on ecological conditions that influence the discounting of prior information (e.g. Valone 1992a).

Prior information is any information previously acquired as current information. Valone (1991) used the term pre-harvest information to refer to information available prior to patch exploitation, however, pre-harvest information is not all prior information. Pre-harvest information is composed of both prior information, and information about patch quality available before the forager enters the patch, such as the smell of food. This last part is not prior information, but rather a source of current information. Prior information is any information an organism has from the past, regardless of its source.

Current information can be divided into information from two types of sources: (i) direct and (ii) indirect. Direct information is acquired from the source of interest, e.g. foraging rate, or the smell of food items. Indirect information is acquired from a source correlated with the source of interest, e.g. observing other forager's success and activity.

Previously, current information was classified as either personal or public information. Personal information is current information acquired through experience with the environment. Some have used the term personal sample information (e.g. Templeton & Giraldeau 1995a) to refer to information acquired by direct experience with

the object of interest. Current information about the environment acquired through the behaviour of other individuals is public information (Valone 1989), though it has also been called social information (Kennedy & Gray 1994).

Public information, as first coined by Valone (1989), was used solely as “information about the quality of a patch that can be obtained by observing the foraging success of other individuals in that patch” (p.357). Valone (1989, 1993) went on to demonstrate that the use of public information can, theoretically, keep social foragers from underusing patches, and allowed social foragers to realize harvest rates almost as high as solitary foragers, though Ruxton (1995) rebuts Valone's contention that group foraging must lead to reduced harvest rates. To date, the term public information has mostly been used to refer specifically to information about patch quality, though it should not be limited to patch assessment (see Forbes & Kaiser 1994, Boulinier & Danchin 1997, Danchin & Wagner 1997, Giraldeau 1997, Danchin et al. 1998, Nordell & Valone 1998).

1.3 Value of Information

The decision to use information will be based on the value of information. Information should improve the decision processes, thereby increasing expected fitness. The value of information (VI) can be defined as the increased payoff obtained with information (Gould 1974, Stephens & Krebs 1986, Stephens 1989):

$$VI = H(t_i^*|s_i) - H(t'|s_i) \quad (1.1)$$

where H is the payoff function associated with choosing tactic t conditional on s as the state of the environment. So, $H(t_i^*|s_i)$ is the informed payoff obtained from using the

optimal tactic t_i^* when the environment is in state s_i , and $H(t'|s_i)$ is the uninformed payoff obtained from using the best average tactic t' when the environment is in state s_i .

The value of information as defined above is the value of free information, i.e. no acquisition costs have been included, and therefore, the value of information is always positive. This is because the uninformed payoff is the best average payoff, whereas the informed payoff is the best possible payoff. Thus, t_i^* always provides a payoff at least as good, if not better, than t' . This leads to the conclusion that because the value of costless information is positive, any information free of acquisition costs cannot be detrimental to the decision maker (Gould 1974, Chavas & Pope 1984, Templeton & Franklin 1992). Chavas and Pope (1984) developed a model of information that agreed with these conclusions about the value of costless information, and went on to show that being able to revise future plans as new information becomes available, such as being Bayesian (McNamara and Houston 1980), tends to make the decision maker better off, and better information tends to improve the decision process.

1.3.1 *Variance and the Value of Information*

Intuitively, it would seem that the more possible states of the environment, the more valuable the information that narrows the options. This is the conclusion drawn from Shannon's measure of information (Shannon & Weaver 1949). However, this is not necessarily true if the value of information is defined by equation (1.1) (Gould 1974, Chavas & Pope 1984). The reason for this divergence of opinions is that Shannon's measure of information only considers the states of the environment, whereas Gould's

value of information deals with the payoffs associated with decisions based on information. Using Gould's definition of the value of information, it can be shown that variance in the state of the environment does not influence the value of information, but rather, it is variance in the availability of tactics or responses that influences the value of information (Gould 1974, Stephens & Krebs 1986, Stephens 1989). Using Gould's definition of the value of information, Stephens (1989) showed that increased variance in the state of the environment will increase the value of information only when the variance of available tactics increases. This means that there is value to information that distinguishes between state i and state j only when there is a different best tactic for each state, t_i^* and t_j^* respectively and $t_i^* \neq t_j^*$. Thus, information has value only when it can change decisions.

1.3.2 Accuracy

The accuracy of information refers to the amount of inherent error (Templeton & Franklin 1992). This error may be caused by environmental noise, interpretation errors (Wiley 1992), or by the variability of the information source. For example, if a forager is assessing patch quality, a source of accurate information would be to personally sample the patch. Another, less accurate, source of information would be to watch the behaviour of other foragers sampling the patch. Their level of activity should be correlated with the value of the patch, but the amount of uncertainty from such an assessment would be much greater than personally sampling the patch. So, while personal information may allow a forager to assess the patch as a good patch, the less accurate public information may

assess the patch as mediocre to excellent. Templeton and Franklin (1992) show how two sources of information can be combined to increase the accuracy of an assessment. As yet, no one has shown how accuracy will influence the value of information. Decreased accuracy should lead to a decrease in the value of the information, but the form of this relationship is unknown. The use of less accurate sources of information may also be a trade-off between accuracy and acquisition costs.

1.3.3 *Acquisition Costs*

Most investigations of the value of information make the simplifying assumption that information is free of acquisition costs. In some situations this is a valid assumption. For example, the information acquired from the warning coloration of a poisonous snake is free for all to see. In fact, this is the purpose of warning coloration. Free information is also present in some communication settings such as food calls. While there may be a cost to the signaller, there is no cost to receiving the information, though there may be a cost to using the information. It is important to distinguish acquisition costs from usage costs. With usage costs, the cost of using information is experienced as a lower payoff, possibly negative, compared to the payoff obtained without information, i.e. from the uninformed response. Acquisition costs, however, must be paid up front before the information is used. These costs are incurred even if the decision maker acquires the information and then decides to discard the information. Acquisition costs will decrease the value of information by reducing the magnitude of the payoff obtained from an informed response. So, the value of information will decrease as the cost of acquiring information increases.

The purpose of acquiring information is to decrease uncertainty about the possible states of the environment, and improve the decision process. The uninformed response is the best tactic to use when the exact state of the environment is unknown, and is based on prior expectations of the probability of each possible state of the environment. As information is acquired, this set of probabilities is modified. In the case where perfect information is acquired, as in the definition of the value of information shown in equation (1.1), the probabilities of all possible states are reduced to zero, except the true state of the environment. As the decision maker acquires more information, reducing uncertainty about the possible state of the environment, the cost of information acquisition will increase. The form of this increase will depend on the situation, but is probably subject to diminishing returns. The payoff with information can be expected to increase as more information is acquired. By assuming that the benefit to acquiring more information levels off as a state of perfect information is approached, it is possible to produce cost and benefit curves as illustrated in figure 1.2. The value of information with acquisition costs will be:

$$VI = [H(t_i^*|s_i) - C(s_i)] - H(t'|s_i) \quad (1.2)$$

where $C(s_i)$ is the cost of acquiring the information. The optimal amount of information to acquire maximizes the value of information, which occurs when $H(t_i^*|s_i) - C(s_i)$ is maximized (Fig. 1.2).

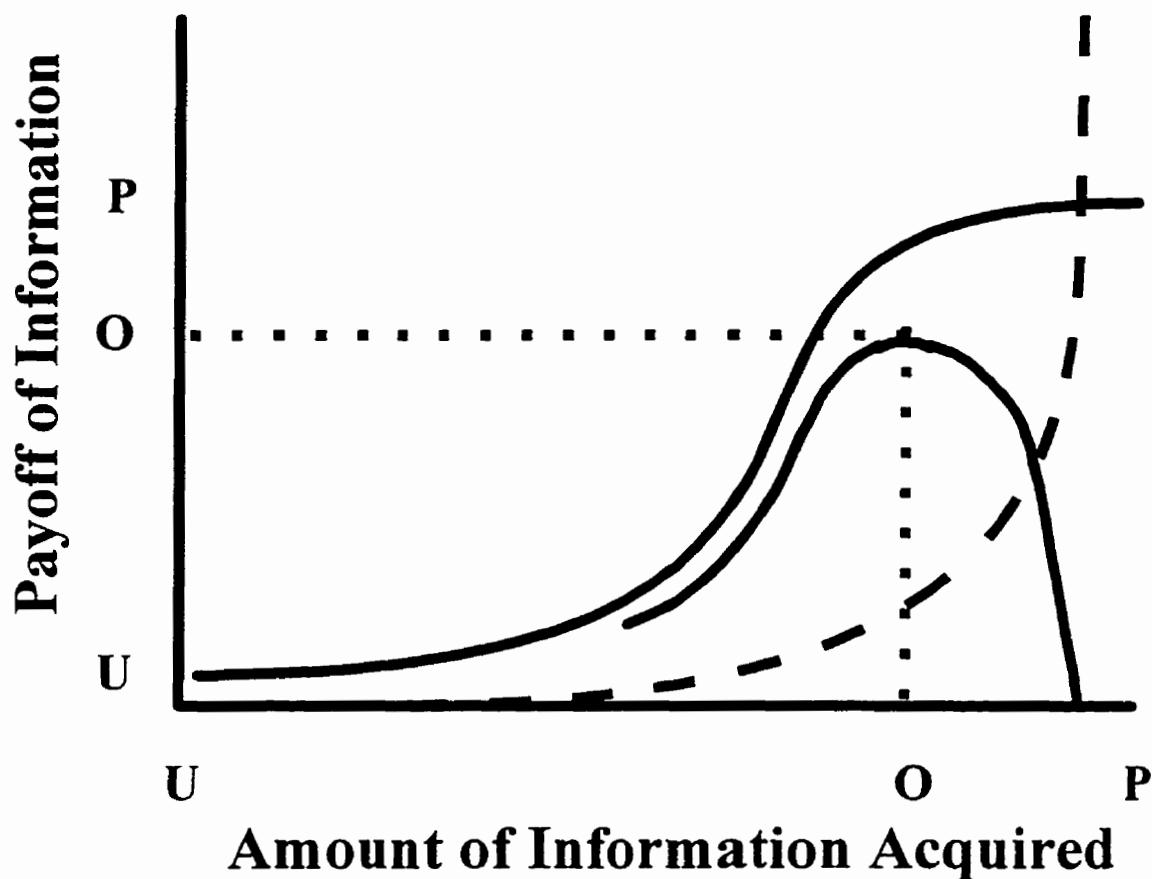


Figure 1.2. Some arbitrary cost (dashed line) and benefit (solid line) curves for increasing amounts of information. As the amount of information acquired increases, the cost increases exponentially, but the benefits plateau. The payoff for costly information is based on the cost and benefit curves. The optimal amount of information to acquire is represented by O, the uninformed amount of information by U, and perfect information by P.

1.4 Memory

Memory is the mechanism by which prior information is weighted in a current assessment. The use of prior information is expected to depend on its reliability. As information ages, it becomes less reliable due to the probability that the environment has changed since the information was acquired. There are three mechanisms for the inclusion or weighting of prior information in current decisions: (i) a memory window where all information less than a certain age is used; (ii) a decay function that weights older information less than newer information; or (iii) a probabilistic memory that is more likely to exclude older information.

1.4.1 *Memory Window*

With a memory window, all information is used equally to make current decisions, and prior information is used continually until it reaches a certain age, then the information is dropped (Fig. 1.3; Krebs & Cowie 1976, Cowie 1977). Originally, memory windows were proposed as an explanation for the observation that recent experience was used while older experience was ignored. The only theoretical investigation of memory windows was published by Valone (1992a) where he showed that the optimal size of a memory window would increase as travel time increased, but is relatively insensitive to the distribution of resources among patches (uniform vs. clumped). Generally, memory windows are considered to be unrealistic (Devenport & Devenport 1994), especially in light of

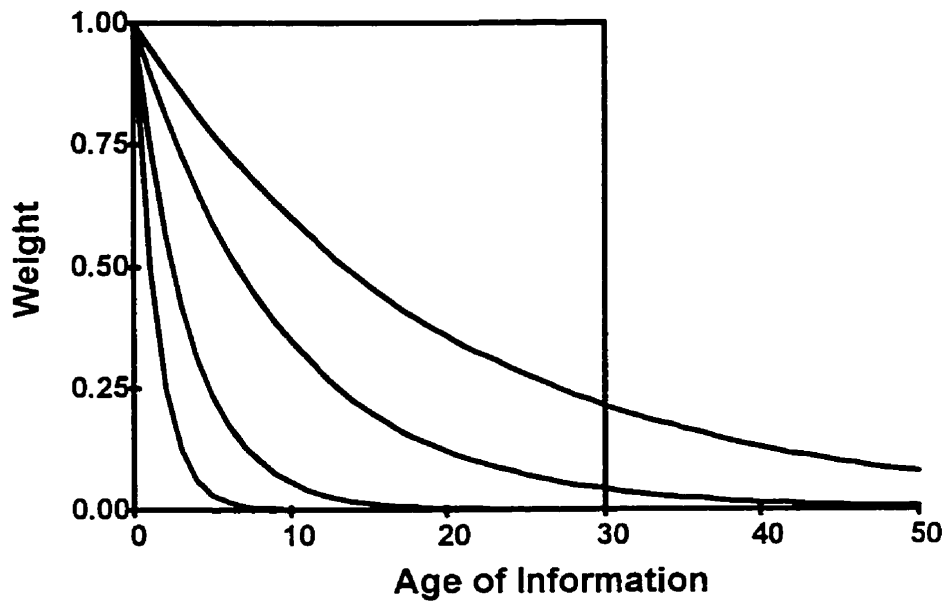


Figure 1.3. Weighting of prior information as it ages. Curves from left to right represent decay functions of the form αt with α values of 0.50, 0.75, 0.90, 0.95 respectively. The step function represents the weighting of prior information for a memory window of 30 time steps.

were proposed as an explanation for the observation that recent experience was used while older experience was ignored. The only theoretical investigation of memory windows was observations that recent experience has a greater impact on current decisions than older experience (Cuthill et al. 1990).

1.4.2 Decay Functions

With a decay function, recent information is highly valued, and the value decays exponentially as a function of age (Fig. 1.3). Most of the original memory decay models were linear operators of the general form:

$$P_i(t+1) = \alpha Q_i(t) + (1-\alpha)P_i(t) \quad (1.3)$$

where $P_i(t)$ is the probability of option i paying off at time t , $Q_i(t)$ is the amount of reinforcement, e.g. number of food items, from option i at time t , and α ($0 < \alpha < 1$) determines the relative weight of recent and past information (Kacelnik et al. 1987).

McNamara and Houston (1987) propose that the optimal weighting could be exponential with $\alpha(t) = \alpha^t$, where t represents age of the information and the rate of decay is determined by the value of α (c.f. Mangel 1990).

A decay function that does not require any free parameters is the temporal weighting rule (TWR) proposed by Devenport and Devenport (1994). Weight is defined as:

$$W_x = \frac{1/t_x}{\sum_{k=1}^n 1/t_k} \quad (1.4)$$

t_x is the time since the acquisition of information x (i.e. age), and $\sum_{x=1}^n W_x = 1$. The result of this weighting is that as information ages, the value of the weighted mean approaches the unweighted mean.

The main difference between the TWR and most decay functions is the influence of age. In most decay functions, information is weighted by its absolute age. So, even if an animal only has access to old information, this prior information is given very little weight. With the TWR, it is relative age that is important. Thus, if all the information an animal has is old, the TWR will weight it as if it were all recent.

1.4.3 *Probabilistic Memory*

Probabilistic memory is a combination of the memory window and decay function mechanisms. Like a memory window, any information that is included is included equally. Like a decay function, older information is less likely to be used in current decisions. α^t does not define weighting, but defines the probability that an experience of age t is used. Thus, α is the probability of using a piece of information that is one time step old. With probabilistic memory, the expectation of the mean should be the same as for the decay function with recent information having a greater influence than older information.

1.4.4 *Memory and Assessment Uncertainty*

The effect of memory is to reduce the amount of information a decision maker has, which will increase uncertainty in an assessment. The problem is choosing the appropriate

measure for uncertainty. An obvious way to measure uncertainty is variance, since it describes the spread of the distribution of experiences that form an assessment. Table 1.3 shows the effect of each memory mechanism on assessment and uncertainty when recent experience is (a) good and (b) bad. When recent experience is good and old experience is bad (RGOB) or recent experience is bad and old experience is good (RBOG), the mean behaves as expected for all three memory mechanisms. The mean under RGOB is higher than the mean under RBOG, as expected when recent experience is weighted more heavily than old experience (e.g. Cuthill et al. 1990).

Should experience order have an effect on uncertainty? Since uncertainty describes a decision maker's confidence in its assessment, experience order should not affect uncertainty. It does not matter if an option switches from good to bad or bad to good. The equivalent change in state should be followed by an equivalent level of uncertainty. If uncertainty is measured by variance, experience order does not affect uncertainty when the memory mechanism is a memory window or decay function (either α^t or TWR). Under probabilistic memory, measuring uncertainty by variance increases uncertainty when the value of recent experience increases.

Mangel (1990) uses coefficient of variation (CV) to measure uncertainty, and this may be more appropriate since CV scales for the effect of the mean. Hilborn and Mangel (1997) argue that CV is a better measure of variability since absolute variability is less important than relative variability when making decisions (Hogarth cited in Hilborn & Mangel 1997). If CV describes uncertainty, the order of experience has no effect on uncertainty under probabilistic memory, but changes with the other mechanisms, increasing uncertainty as the value of recent experience decreases.

Table 1.3. Means^{*} (\bar{x}), variances[†] (s^2), and coefficients of variation (CV) of ten experiences with an option based on weightings with the temporal weighting rule (TWR), α^{\dagger} decay function with $\alpha = 0.85$, a memory window (6.666667[‡]), and a probabilistic memory with $\alpha = 0.85$ based on 1000 iterations. Ageing of information are one datum per time unit for ten time units. Recent good, old bad (R.G.O.B.) calculations based on $x_1 = 10, x_2 = 10, x_3 = 10, x_4 = 10, x_5 = 10, x_6 = 1, x_7 = 1, x_8 = 1, x_9 = 1, x_{10} = 1$. Recent bad, old good (R.B.O.G.) calculations based on $x_1 = 1, x_2 = 1, x_3 = 1, x_4 = 1, x_5 = 1, x_6 = 10, x_7 = 10, x_8 = 10, x_9 = 10, x_{10} = 10$. For unweighted data: $\bar{x} = 5.5, s^2 = 22.5, CV = 0.86$.

| | TWR | α^{\dagger} | Memory Window | Probabilistic Memory |
|-----------|-------|--------------------|---------------|----------------------|
| R.G.O.B. | | | | |
| \bar{x} | 8.02 | 7.23 | 7.79 | 5.92 |
| s^2 | 15.47 | 17.63 | 17.36 | 8.89 |
| CV | 0.49 | 0.58 | 0.54 | 0.49 |
| R.B.O.G. | | | | |
| \bar{x} | 2.98 | 3.77 | 3.21 | 2.91 |
| s^2 | 15.47 | 17.63 | 17.36 | 2.32 |
| CV | 1.32 | 1.11 | 1.30 | 0.49 |

$$* \bar{x} = \frac{\sum w_i n x_i}{\sum w_i n} = \frac{\sum w_i x_i}{\sum w_i}$$

$$† s^2 = \frac{\sum w_i n (x_i - \bar{x})^2}{\sum w_i n - 1}$$

‡ Size of the memory window is calculated as $1/(1-\alpha)$ with $\alpha = 0.85$, which should make the memory window equivalent to a decay function with $\alpha = 0.85$ (Dow & Lea 1987).

In each of these mechanisms for memory, the use of prior information is expected to be limited due to a reduction in the reliability of prior information as it ages. Very little work, however, has been done on the ecological factors that influence memory or the reliability of prior information (Giraldeau 1997). Experimental work by Valone and Brown (1989) and Valone (1991, 1992b) suggests that environmental variability will influence the use of prior information (see section 1.5.1). Valone (1992a) provides the only theoretical investigation, to date, into the influence of ecological factors on optimal memory. Similar work should be carried out on all the memory mechanisms to provide a theoretical foundation for predicting optimal rates of forgetfulness (Healy 1992). Experimental work also needs to look into the potential for individuals to modify their use of prior information. Is memory simply a matter of using prior information when it pays, otherwise ignore it (Giraldeau 1997)? Or is memory constrained by cognitive architecture to a constant rate of decay?

1.5 Assessment and Information Use

To start, I return to the introductory example of an animal moving through its environment. Suppose this animal is interested in foraging, but has been off performing other activities. Therefore, this animal does not have any current information about the quality of foraging sites, but it does have past experience that forms a prior expectation of patch quality. For simplicity, I assume that this animal has the choice of foraging in two different, but fairly proximal locations. Since the animal only has a prior expectation of patch quality, it may start by foraging in the patch that was previously of highest quality.

As the animal searches for food, it also acquires current information about patch quality, which is used to update its assessment. Thus, a forager's current assessment of patch quality will use both prior and current information:

$$\text{current assessment} = \rho_p(\text{prior information}) + \rho_c(\text{current information})$$

where prior information and current information are weighted by their respective reliability, ρ_p and ρ_c . The reliability of prior information is expected to decrease as information ages, but is the age of information the only factor that influences the reliability of prior information?

1.5.1 *Environmental Variability*

Environmental predictability, or variability, should influence the use of prior information. Stephens (1991) developed a model of the evolution of learning, which I will consider to be the use of prior information. Stephens' model predicts that the variability an individual experiences within its lifetime is most important in determining whether prior information should be used. When the environment is persistent within a generation, prior information can allow an individual to learn and adapt to its environment. Since environments fall along a continuum of predictability (Fig. 1.4), the relative weighting of prior information should be influenced by this predictability, so that when the environment is highly predictable, a decision maker could rely completely on prior information and appear prescient. At the other extreme, the environment is so unpredictable that prior information has no value, and a decision maker must rely on current information alone.

This perspective (Fig. 1.4) is consistent with experimental work carried out by

Valone (Valone & Brown 1989, Valone 1991, 1992b). Valone and Brown (1989) worked on desert granivores to determine how patch quality is assessed. They produced a shift from a low to high variance environment by increasing variance in the amount of food placed in feeding trays. In the high variance environment, Merriam's kangaroo rat, *Dipodomys merriami*, the Arizona pocket mouse, *Perognathus amplus*, and the round-tail ground squirrel, *Spermophilus tereticaudus*, all used a Bayesian assessment strategy. In the low variance environment, kangaroo rats appeared to be prescient (appearing to have perfect information) while the pocket mouse and ground squirrel switched to a fixed time strategy (abandon patch after x time units). These results are consistent with the proposed influence of environmental variability on the reliability of prior information. As environmental variability declines, the environment becomes more predictable, the reliability of prior information decays at a slower rate, and foragers need less current information to make decisions that are optimal.

Valone (1991) studied patch assessment by Inca doves, *Columbina inca*, while manipulating the temporal predictability of patches. Again, he found that when a patch was predictable, foragers appeared to use a prescient foraging strategy. When predictability was reduced, foragers appeared to switch to a Bayesian assessment strategy. As with Valone and Brown's (1989) study, there is no need to assume a shift in assessment strategy, instead, by increasing the temporal predictability of a patch, Valone (1991) increased the reliability of prior information, and removed the need for current information to make optimal decisions. Valone (1992b) again manipulated environmental variability and found that black-chinned hummingbirds, *Archilochus alexandri*, combined prior information with current information in the low variance environment, but started to

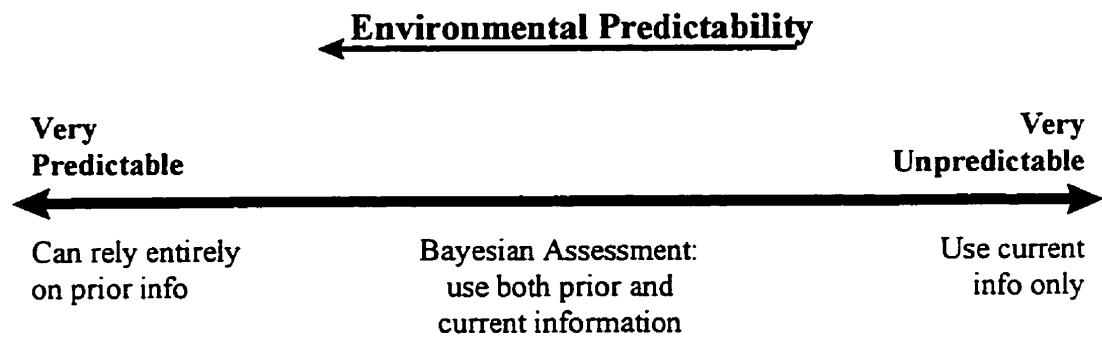


Figure 1.4. The proposed influence of environmental predictability on the relative use of prior and current information.

drop the use of prior information in the high variance environment. Again, this supports the proposed influence of environmental predictability on the reliability and use of prior information (Fig. 1.4). However, not all the hummingbirds dropped their use of prior information in the high variance environment (Valone 1992b). It would be interesting to know if this is caused by individual differences in their assessment of environmental predictability, or innate differences in the use of information (c.f. Roitberg 1990).

1.5.2 Public Information

The use of public information in assessment has only been tested in a few studies. Valone and Giraldeau (1993) found that foraging budgerigars, *Melopsittacus undulatus*, used prior and patch sample information and ignored the available public information. This is contrary to Templeton and Giraldeau's (1995a) finding that European starlings, *Sturnus vulgaris*, used public information when making patch departure decisions. However, the use of public information was dependent on the compatibility of public information with personal information. If starlings could easily acquire public information, it was included in their assessment. However, when the acquisition of public information was incompatible with the acquisition of personal information, public information was ignored, and assessments were based on personal information alone. When Templeton and Giraldeau (1996) decreased the ability of foragers to acquire accurate personal information, starlings made use of the available public information, however, when accurate personal information could be easily acquired, public information was ignored.

There is also some evidence that fish will use public information when choosing

patches (e.g. Krause 1992). However, this use of public information depends on the ability to acquire personal information. Three-spined sticklebacks, *Gasterosteus aculeatus*, prevented from personally sampling a patch, fail to choose the more profitable patch (Gotceitas & Colgan 1991), instead, preferring the patch with more conspecifics. Goldfish, *Carassius auratus*, seem to use public information when they can acquire food in low quantity, but ignore public information when no food is available (Pitcher & House 1987). Together with Templeton and Giraldeau's (1995a) study, these results suggest that for public information to have value, an animal needs to be able to acquire personal information. If an animal cannot acquire personal information, either to evaluate the reliability of public information or to provide a context for the interpretation of public information, the default may be to ignore public information.

Foraging is not the only context where animals use public information. There is mounting evidence that females use public information about male quality by copying the mate choices of other females (e.g. Dugatkin 1992, Gibson & Hoglund 1992, Pruett-Jones 1992). The use of mate copying also depends on its reliability. For example, young female guppies, *Poecilia reticulata*, are more likely to copy older females than vice versa (Dugatkin & Godin 1993). By virtue of their age, older females are more likely to provide reliable public information about the quality of a male than young females.

Animals also use public information about predators. This was first documented by Verheijen (1956, also by Magurran & Higham 1988) who showed that a fright reaction could be transmitted from a school of European minnows, *Phoxinus phoxinus*, in one tank to a school in an adjoining tank. Public information can also travel through a flotilla of a marine insect, the ocean skater *Halobates robustus*, in what has been called the Trafalgar

effect where “the rate of transmission of avoidance behaviour throughout a group can exceed the speed of an approaching predator” (Treherne & Foster 1981:912). The common vole, *Microtus arvalis*, uses public information about predators, exhibiting a response when they can see and hear conspecifics (Gerkema & Verhulst 1990). When voles could see but not hear conspecifics, the reaction to public information about predators declined very rapidly as the distance between voles increased. Again, this suggests that animals are quick to ignore public information when its reliability is suspect.

1.5.3 *Sequential Assessment*

Sequential assessment refers to the act of sampling repeatedly through time to acquire information to form an assessment. I borrowed this term from contest theory, where the sequential assessment model (SAM) was proposed to explain the repeated use of behavioural sequences to settle contests (Enquist & Leimar 1983). The SAM assumes that fighting behaviour provides contestants with information about the fighting ability of their opponent. Each repetition of a behaviour provides another piece of information. An individual forms an assessment of its opponent’s fighting ability by sequentially sampling its opponent against itself. Enquist et al. (1990) found that the SAM did well predicting the structure of contests between males of the South American cichlid *Nannacara anomala*. The structure of contests between convict cichlids, *Cichlasoma nigrofasciatum*, are also consistent with the idea of sequential assessment of an opponent’s fighting ability (Koops & Grant 1993). Other predictions of the SAM have been supported in contests among net-spinning caddis larvae, *Arctopsyche ladogensis* (Englund & Olsson 1990),

male bowl and doily spiders, *Frontinella pyramitela* (Leimar et al. 1991), and fiddler crabs, *Uca annulipes* (Jennions & Backwell 1996).

Sequential assessment can also be seen in mate choice. For example, Dale and Slagsvold (1994) found that when female pied flycatchers, *Ficedula hypoleuca*, were assessing males by repeatedly returning to a male's territory to sample for his presence on the territory. This is an effective sampling strategy in this system since males can establish a second territory, and females sampling for their presence assesses the probability that they are single territory males. Polyterritorial males tend to be poor mates since they invest most of their parental care in their first territory (Dale & Slagsvold 1994). Thus, sequential assessment is not a strategy specific to contest resolution, but is equally applicable to other information problems.

1.5.4 *Assessment Uncertainty*

Not all information is the same. Going back to the introductory example, an animal may progress for a time without finding any food, then find several food clumps in quick succession. Or, the animal may find one large food item followed by several small food items. The result of this type of food discovery is variability in the forager's experience and information, resulting in uncertainty about the assessment of patch quality. Now, the forager is faced, not just with the problem of choosing among foraging patches, but choosing among patches assessed with uncertainty. Uncertainty reduces the ability to discriminate among options, and when animals are unable to discriminate, they need to use another method of making a decision. Abrahams (1986), in proposing the perceptual

limits model, assumed that when an animal could not distinguish among options, it would choose randomly. Valone and Brown (1989) assumed that foragers unable to assess a difference would use a fixed time strategy. Both of these approaches assume that animals only make decisions on the basis of one currency. It is also possible that animals may make decisions on the basis of uncorrelated traits, such as go where there are more conspecifics (Gotceitas & Colgan 1991). While there is theoretical work showing how updating rules influence uncertainty (e.g. Mangel 1990), in behavioural ecology no one has provided a model of decision making explicitly including uncertainty.

1.6 Prospectus

The ecology of information use is a newly emerging area of research within behavioural ecology (Giraldeau 1997, Dukas 1998) which overlaps a number of other fields. I have tried to bring together studies and ideas from various areas of behavioural ecology into a synthesis, however, this is difficult since many researchers are interested in specific information problems. Thus, work on the general problems of information use have sometimes been ignored. For example, there have been no further investigation into the value of information since Stephens' (1989) demonstration of the influence of variance. Yet, to understand information use, it is important to understand the value of information. There are many factors that can influence the value of information to an animal, such as reliability, context, and content, but there is no structure to these ideas.

There are also many ecological factors that could potentially influence memory. As seen in section 1.4, environmental variability is one of these ecological factors,

however, this only scratches the surface. Valone and Brown (1989) and Valone (1991, 1992b) have shown that manipulating environmental variability will influence the use of prior information, however, this has not been followed up with investigations into the influence of the magnitude, rate or probability of change. Valone (1992a) has provided one of the only theoretical investigations into the influence of an environmental factor on optimal memory for memory windows. There is the possibility for an ecological theory of optimal forgetfulness (Healy 1992), but more knowledge is needed about the fitness value of memory and the influence of ecological conditions.

Both of these areas relate to questions about why animals use some but not all information. For example, why do some animals ignore public information (e.g. Valone & Giraldeau 1993)? For this reason, I start by looking at how reliability influences the value of information (chapter 2). This work follows directly from Gould's (1974) definition and the work by Stephens (1989) on variance and the value of information (section 1.3). From section 1.5, it is apparent that reliability plays a role in the information used in the formation of assessments. Reliability also plays a role in the transfer of information in communication systems (section 1.2.1). Many authors have approached honest communication from the perspective of the signaller, yet it is the receiver that decides whether or not to use information. Even though many authors refer to reliability, no one has defined what reliability is or how it influences the value of information. The use of information will be affected by its value, and a reduction in reliability leads to a reduction in value. But how reliable must information be to have value and be used?

If animals do use information that is not completely reliable, they have imperfect information which could result in large estimation errors. In chapter 3, I look at the

influence of life history on an animal's tolerance to imperfect information. This is a slightly different approach to looking at the value of information by considering how poorly an individual does with imperfect information. Previous research suggests that tolerance to imperfect information can be large (e.g. Bouskila & Blumstein 1992), however, these conclusions need to be qualified by considering the biology of the decision maker (Koops & Abrahams 1998, chapter 3).

A more realistic look at assessment and imperfect information takes into account the sequential nature of assessment. As pointed out in section 1.5, an animal uses information to form assessments, but these assessments will have a measure of uncertainty about them. This assessment uncertainty constrains the ability of an animal to accurately choose optimal tactics. In chapter 4, I extend the perceptual limits model (Abrahams 1986) into a stochastic decision rule where the perceptual ability of an animal is constrained by assessment uncertainty. Even though assessment uncertainty is included in various publications on Bayesian assessment (e.g. Mangel 1990), none has provided a decision rule.

The Z model of perceptual constraints developed in chapter 4 is a general decision rule applicable to any situation where an animal must choose among options assessed with uncertainty. In chapter 5, I present an individual-based model of a group of foragers choosing between two food patches that must be assessed. Each forager assesses the quality of each patch with uncertainty, then chooses a patch using the Z model as a decision rule. This is an ideal free distribution (IFD) foraging situation (Fretwell & Lucas 1970), and was chosen since it corresponds to Abrahams (1986) application of the perceptual limits model.

In this individual-based model, foragers form assessments on the basis of personal information alone. To keep the model as simple as possible, I excluded the use of public information in patch assessment. In chapter 6, I present the results of an experiment with guppies, *Poecilia reticulata*, testing Kennedy and Gray's (1994) hypothesis that aggressive interactions are used as public information about patch quality.

If none of these chapters interest you, yet the general topic of the ecology of information use does, I suggest you skip directly to chapter 7 for the general discussion. There I present some of the general conclusions from chapters 2 through 6, and I discuss my view of the future of behavioural ecology in general with specific regard to the ecology of information use.

1.7 References

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Chapter 2: Reliability and the Value of Information

2.1 Abstract

The reliability of acquired information will influence the value of information. The value of information is defined as the difference in payoff obtained based on decisions with versus without information. Reliability is defined as the probability that the information is correct. By introducing reliability into the definition of the value of information, we find that reducing the reliability of information reduces the value of information. Furthermore, there is a minimum reliability, below which information should be ignored. This minimum reliability is dictated by the ratio between the cost of being misinformed and the benefit of being informed. The greater the benefits of being informed relative to the costs of being misinformed, the greater the potential for information to be unreliable and still have positive value. We also find that free information will never be required to have perfect reliability. The costs associated with being misinformed can be greater than the benefit of being informed, and with highly reliable information, the costs of misinformation can be orders of magnitude above the benefits of correct information. Finally, if misinformation leaves a decision maker better off than with no information, but worse off than with correct information, e.g. white lies, then the frequency of these white lies can never be high enough to cause information to completely lose its value.

2.2 Introduction

Organisms are constantly bombarded by information, some useful and some not.

Obviously, not all information is processed, and much available information is left unacquired, possibly due to time or processing constraints (Dukas & Ellner 1993). When information is available without acquisition costs, organisms should make use of all available free information to make decisions (Gould 1974; Chavas & Pope 1984; Templeton & Franklin 1992). If there is a cost to acquiring information, we expect organisms to only acquire information worth the cost. Thus, we can think of the value of information as the maximum cost offset by the benefit of acquiring information.

In its simplest form, the value of information (VI), as defined by Gould (1974; though here I follow Stephens' [1989] notation), is the difference in payoff obtained when informed versus uninformed, or:

$$VI = H(t_i^* | s_i) - H(t' | s_i) \quad (2.1)$$

where H is the conditional-payoff function, t is the tactic chosen and s is the state of the environment. t' is the best tactic to use when s is unknown and is chosen to maximize the average payoff so that:

$$\sum_i p_i H(t' | s_i) = \max_t \sum_i p_i H(t | s_i) \quad (2.2)$$

where p_i is the probability that the environment is in state i and the set of all p_i represents the decision maker's perception of the environment based on prior information. Thus, t' is the tactic that, on average, provides the highest payoff across all possible states of the environment and should be used whenever the specific state of the environment is unknown. t_i^* , however, is the best tactic to use, and provides the highest payoff when the

environment is in state i , and is defined as:

$$H(t_i^* | s_i) = \max_t H(t | s_i) \quad (2.3)$$

Thus, $H(t' | s_i)$ is the payoff obtained without additional information, $H(t_i^* | s_i)$ is the payoff obtained with additional information, and equation (2.1) defines the value of acquiring perfect information free of acquisition costs.

Stephens (1989) showed that increased variance in the state of the environment will increase the value of information only when the number of available tactics also increases. Therefore, it is only of value to distinguish between state i and state j when there is a different best tactic for each state, t_i^* and t_j^* respectively. This demonstration leads to the conclusion that information has value only when it can change decisions, i.e. when $t_i^* \neq t_j^*$.

Stephens' demonstration can be used to explain the occurrence of general classes of communication calls, such as alarm calls. Belding's ground squirrels, *Spermophilus beldingi*, give a single-note whistle as an alarm call when aerial predators appear, which is quite distinct from the multiple-note trills used for terrestrial predators (Turner 1973; Sherman 1985). When the alarm call for aerial predators is heard, Belding's ground squirrels take cover in the nearest burrow since any burrow will provide protection from an aerial predator. When the alarm call for terrestrial predators is heard, Belding's ground squirrels selectively choose burrows with a second exit over closer burrows since some terrestrial predators will follow squirrels into a burrow (Turner 1973). Since the anti-predator behaviour used for aerial predators is independent of the species of predator, Stephens' demonstration predicts no value to a collection of predator specific alarm calls. With no value and no selective pressure, there is no evolution beyond a general alarm call

for aerial predators.

From this definition of the value of information, information is valued only in terms of how it is used, as defined by the unspecified conditional-payoff function H (Gould 1974; Stephens 1989). Furthermore, the value of costless information is non-negative and any information free of acquisition costs cannot be detrimental to the decision maker (Gould 1974; Chavas & Pope 1984). This conclusion follows from the fact that, according to equation (3), the informed payoff, $H(t_i^* | s_i)$, is the largest payoff a decision maker could possibly acquire, therefore the uninformed payoff, $H(t' | s_i)$, cannot be larger than the informed payoff. Since $H(t_i^* | s_i) \geq H(t' | s_i)$, the value of information, as defined by equation (2.1), cannot be less than zero. When information has acquisition costs, these conclusions may change, and new conclusions will depend on how the cost function is defined (Gould 1974).

By considering biological situations where animals have access to information that is free, or nearly free, of acquisition costs, we can easily think of situations where we might expect the value of information to be less than zero. Examples of information that may fall into this categorization (see Dawkins & Krebs [1978] for some other examples) include Batesian mimicry, false alarm calls (e.g., Munn 1986), and bluffed threats (e.g., Steger & Caldwell 1983). The common feature here is that the reliability of the information has been decreased through deception.

Many models of honest signaling have focused on the signaler and the cost of deception (e.g., Zahavi 1977; Grafen 1990; Maynard Smith 1991; Adams & Masterton-Gibbons 1995), however, less attention has been focused on the receiver and the decision to use information (Guilford & Dawkins 1991; Harper 1991). Some authors refer to

factors, such as the reliability of information, when discussing how animals use information (e.g. Zahavi 1977; Devenport & Devenport 1994; Fenton 1994; Shannon et al. 1994; Adams & Masterton-Gibbons 1995), however, standardized definitions have not been provided, leaving some usages ambiguous. In this paper I define reliability based upon current usage, and theoretically examine the influence of reliability on the value of information.

2.3 Reliability of Information

Reliability has been referred to as the quality of information (Sih 1992), and sometimes is used synonymously with the accuracy of information, though accuracy and reliability describe different aspects of information (Templeton & Franklin 1992). For simplicity, I define the reliability of information (ρ) as the probability that the information is correct. Thus, if $\rho = 1$, the information is always correct, and if $\rho = 0$, the information is never correct.

Consider a world where the environment has only two states. Information that the environment is in state i is correct with probability ρ , the reliability of the information. We can calculate the value of this information, following equation (1), as the weighted average of the value of correct and incorrect information. So the value of partially reliable information can be written as:

$$\rho \left[H(t_i^* | s_i) - H(r' | s_i) \right] - (1 - \rho) \left[H(t_i^* | s_j) - H(r' | s_j) \right] \quad (2.4)$$

This equation describes a situation where a decision maker is misinformed about the state of the environment. The information says the environment is in state i , and the value of

information is diminished when the environment is actually in state j and the decision maker is left with the misinformed payoff, $H(t_i^*|s_j)$.

We can now ask: what is the minimum reliability (ρ_{\min}) before partially reliable information loses its positive value? We can determine this by setting equation (2.4) equal to 0 and solving for ρ_{\min} , which leads to:

$$\rho_{\min} = \frac{-[H(t_i^*|s_j) - H(t'|s_j)]}{[H(t_i^*|s_i) - H(t'|s_i)] - [H(t_i^*|s_j) - H(t'|s_j)]} \quad (2.5)$$

From equation (2.5) we can see that ρ_{\min} is close to zero when the value of incorrect information, $[H(t_i^*|s_j) - H(t'|s_j)]$, is close to zero. The closer the payoff obtained responding to false information, $H(t_i^*|s_j)$, is to ignoring false information, $H(t'|s_j)$, the more unreliable information can be and still have positive value. This is equivalent to saying that the smaller the marginal costs of misinformation, the more unreliable information can be and still have positive value (see Appendix 2A).

Now there are two situations to consider: (i) when it is better to be uninformed than misinformed and the value of incorrect information is negative, and (ii) when it is better to be misinformed than uninformed and the value of incorrect information is positive. First, when the value of incorrect information is negative, i.e. $H(t_i^*|s_j) \leq H(t'|s_j)$, it is better to be uninformed than misinformed. Since we already know that $H(t_i^*|s_i) \geq H(t'|s_i)$ we can rewrite equation (2.5) in terms of the benefit of being informed, B , and the cost of being misinformed, C , where:

$$\begin{aligned} B &= [H(t_i^*|s_i) - H(t'|s_i)] \\ C &= -[H(t_i^*|s_j) - H(t'|s_j)] \end{aligned} \quad (2.6)$$

Substituting (2.6) into equation (2.5), we get:

$$\rho_{\min} = \frac{C}{B + C} = \frac{C/B}{1 + C/B}. \quad (2.7)$$

If the benefit of being informed is zero, $H(t_i^*|s_i) = H(t^*|s_i)$, and equations (2.5) and (2.7) are of no interest because additional information has no value.

If we consider ρ_{\min} as a function of C/B (Fig. 2.1), we find that: (i) the minimum reliability of information is 0 when $C = 0$; (ii) as long as $\rho > 0.5$ the cost of being misinformed can be greater than the benefit of being informed, i.e. $C > B$; and (iii) no matter how great the cost of misinformation, ρ_{\min} will never reach 1 as long as $B \neq 0$. So, there is always room for some unreliability, or deception, in valuable information. Finally, from equation (2.7), we see that as the value of correct information increases, and C/B decreases, the minimum reliability decreases. This means there is greater potential for unreliability when correct information is more valuable. This is equivalent to saying that the greater the marginal costs of acting without correct information, the more unreliable information can be and still have positive value (see Appendix 2A). So, the more costly it is to be misinformed, the more likely a decision maker is to respond to partially reliable information and be misinformed.

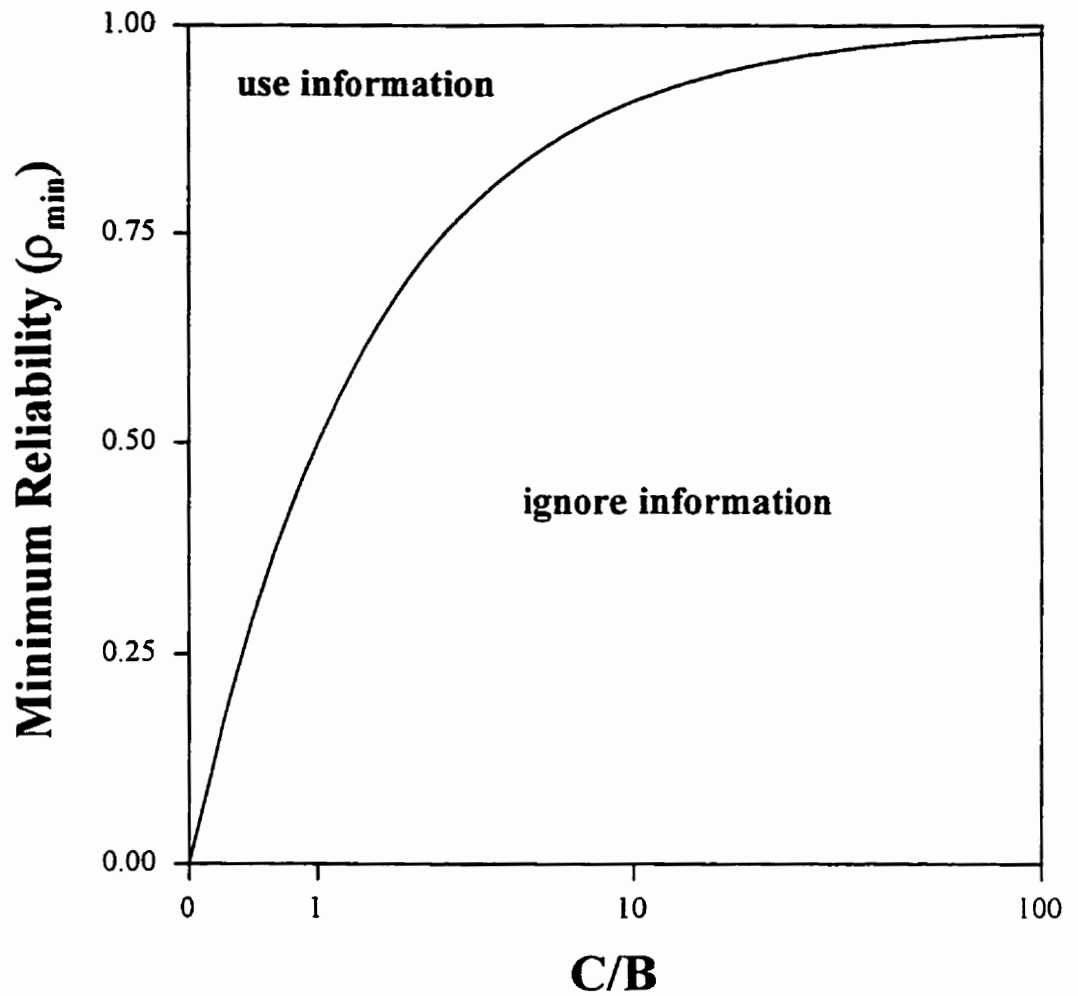


Figure 2.1. The minimum reliability of information (ρ_{\min}) as a function of the ratio of the cost of being misinformed to the benefit of being informed plotted on a logarithmic scale, $\log_{10}(C/B + 1)$. Above the curved line is the region where information has positive value and should be used, below the curved line is the region where the value of information is negative and should be ignored. For a given reliability, the value of information increases as C/B decreases, and for a given C/B ratio, the value of information increases as the reliability increases.

The second situation to consider in relation to equation (2.5) is when it is better to be misinformed than uninformed, i.e. $H(t_i^*|s_j) \geq H(t'|s_j)$. In this situation, the "cost" of misinformation is only a cost relative to the benefit of being informed. Now the value of incorrect information is positive, $[H(t_i^*|s_j) - H(t'|s_j)] \geq 0$, and $\rho_{\min} \leq 0$. Since, by definition, reliability ranges between 0 and 1, $\rho_{\min} = 0$ when the misinformed payoff is better than the uninformed payoff. Lloyd (1983) defined white lies as a situation where a signal is used inappropriately to the mutual benefit of both sender and receiver. In the situation considered here, white lies, regardless of their frequency, will not cause information to lose its positive value.

So far, we have only considered the dichotomous situation where the environment is either in state i or state j . Equation (2.4) can be expanded to consider situations where the possibilities are more numerous. When the possible states of the environment are greater than two, the value of partially reliable information becomes:

$$\rho \left[H(t_i^*|s_i) - H(t'|s_i) \right] + (1 - \rho) \sum_{j \neq i} \pi_j \left[H(t_i^*|s_j) - H(t'|s_j) \right] \quad (2.8)$$

where $\sum \pi_j = 1$ and π_j is the probability that $s = s_j$ when misinformation says $s = s_i$ but $s \neq s_i$. The conclusions associated with equation (2.7) still hold true, except that now:

$$C = - \sum_{j \neq i} \pi_j \left[H(t_i^*|s_j) - H(t'|s_j) \right] \quad (2.9)$$

One major difference that arises from increasing the number of subtypes of the environment from the dichotomous situation occurs when $\rho \leq 0.5$. In a dichotomous situation, decreasing reliability below 0.5 could be considered to increase the reliability of information about the opposite situation. This is analogous to the situation where an individual always says "yes" when the answer is actually "no", and vice versa. To hear this

individual say "yes" could be reliable information that "no" is actually true, however, this would occur only in the dichotomous situation considered by equation (2.4), and is probably not of interest to most situations where numerous subtypes are possible.

2.3.1 Deception

Deception occurs when signalers benefit at the expense of receivers. In communication systems, deception involves misinformation about the state of the environment, such as the use of false alarm calls. Munn (1986) reported observations of two species of Amazonian flycatchers, *Lanio versicolor* and *Thamnomanes shistogynous*, which act as sentinels, and also appear to use alarm calls to distract other birds and increase their own chances of catching arthropods. Matsuoka (1980) and Møller (1988) describe situations where great tits, *Parus major*, use false alarm calls to gain priority access to food sources. The use of false alarm calls represent situations where we might expect that when reliability is low, receivers will still respond to alarm calls as if a predator were present. The benefit of being informed is high, leading to increased probability of escape from predation, whereas the cost of being misinformed can be fairly low, resulting in the loss of some food.

To evaluate the occurrence of false alarm calls in the context of reliability and the value of information obtained from an alarm call, let us assume that when great tits hear an alarm call they have two options: respond with an anti-predator response (t_i^*) or ignore the signal (t'). If a bird chooses to ignore the alarm call, we shall assume its payoff would be the same as if it received no information about predation risk in the environment, $H(t'|s_i)$. If the alarm call always provides information about the presence of a predator (s_i),

and the bird responds, the optimal payoff for this state of the environment, $H(t_i^*|s_i)$, is obtained and the value of information provided by the alarm call would be defined by equation (2.1), the value of correct information. If the alarm call is only partially reliable, however, the value of information would be diminished due to the receiver being deceived when it responds to a false alarm call. The payoff received using the optimal tactic for the wrong state of the environment, i.e. responding to a false alarm call, is $H(t_i^*|s_j)$. We know that $H(t_i^*|s_i) > H(t^*|s_i)$ by equation (2.3) and, in this situation, we expect that $H(t_i^*|s_j) < H(t^*|s_j)$. So, it is better to respond to a true alarm call than ignore it, and it is better to ignore a false alarm call than to respond. The value of information contained in the partially reliable alarm call then becomes a weighted average of the value of a true alarm call and the value of a false alarm call, as defined by equation (2.4).

Møller (1988) observed that 63% of alarm calls were false. This gives a reliability of 0.37 for alarm calls by great tits, which suggests that either ignoring alarm calls is very costly or responding to false alarm calls is cheap. If we use $\rho = 0.37$ in equation (2.7), we find that the cost to great tits of responding to a false alarm call must be less than 58.7% of the benefit of responding to a true alarm call, i.e. $C/B \leq 0.587$. As the cost drops from there, the value of indiscriminately responding to alarm calls increases. This contrasts with the reliability of threat displays used by *Gonodactylus bredini*, a stomatopod crustacean. When molting, *G. bredini* is vulnerable and cannot escalate a fight, however, it will bluff by using the threat display (Steger & Caldwell 1983; Adams & Caldwell 1990). *G. bredini* only appears to bluff when it is molting, so, given that one in five residents using the threat display had molted in the previous five days, the threat display has a reliability of at least 0.80 (Steger & Caldwell 1983). This means that, if there

are no acquisition costs, the cost of responding to a bluff as if it were a real threat display can be up to four times the benefit of responding to a true threat display ($C/B = 4$ when $\rho_{\min} = 0.80$).

2.3.2 Unreliable Cues

The examples I used in the above explanation centered around communication systems. I do not wish to leave the impression that misinformation can only occur with dishonest, or partially reliable communication. Viitala et al. (1995) found that kestrels, *Falco tinnunculus*, could detect the runaways of voles, *Microtus agrestis*, which are marked with urine and feces and are visible and detectable by kestrels in ultraviolet light. Viitala et al. proposed that kestrels could use this information to assess vole numbers, allowing the detection of high quality foraging patches without prior knowledge of local food resources. The reliability of this cue, however, may well be less than perfect. Johnson (1975), working on the bank vole, *Clethionomys glareolus*, found that the quantity of urination differed between two races. The race from the island of Skomer, *C.g. skomerensis*, is relatively free of predation, and produces a higher quantity of urine per urination than the race from mainland Britain, *C.g. britannicus*. While not the only explanation, this would be consistent with the hypothesis that *C.g. britannicus* has experienced selective pressure to reduce the reliability of cues available to at least one of its predators, the kestrel.

2.4 Discussion

Stephens (1989) showed that the value of information can be influenced by variability in the environment if acquiring information allows the recipient to distinguish between alternative choices. As we have seen in this paper, the value of information is also influenced by the reliability of information. As reliability decreases, the value of information decreases, as would be expected. When reliability is introduced into our definition of the value of information we get the following results. First, due to the possibility of being misinformed, the value of information can be less than zero. This means that the conclusion of earlier authors that information free of acquisition costs can only benefit the recipient (Gould 1974; Chavas & Pope 1984; Templeton & Franklin 1992) is not strictly valid. If the reliability of information is low, information can be costly to use. Second, when the misinformed payoff is close to the uninformed payoff, there is greater latitude in the reliability of information. Thus, if information is acquired through communication, the option is available for signalers to deceive receivers without degrading reliability beyond the point where no response will be elicited. And finally, the more valuable information is when it is correct, i.e. the greater the marginal costs of correct information, the greater the potential for information to be unreliable yet still have value.

2.4.1 Sources of Unreliability

When information is acquired from communication, there is the potential for lowered reliability due to deceptive signaling. This was demonstrated earlier with the false alarm calls and bluffed threats. Zahavi's (1975) handicap principle provides one hypothesized

mechanism for keeping the reliability of communication high through costly signaling. Signals will be kept reliable either through a cost of performing the signal so only honest signalers can afford the signal, or a cost on dishonest signaling so the benefit to dishonest signalers will be reduced or removed. This hypothesis, however, only works when receivers are in a position to abandon unreliable signals. In the case of false alarm calls, the cost of ignoring an honest alarm call may be too great to select for a more reliable, or less corruptible, signal. In this case, if honest and false alarm calls are indistinguishable, it may pay individuals to respond to all alarm calls indiscriminately as long as the reliability remains above ρ_{\min} . This is not to imply that there will be no selective pressure to distinguish between reliable and unreliable sources of information. Even though the reliability of information will not be required to be perfect, there will still be selection to distinguish between reliable and unreliable information to avoid the payoff associated with a misinformed response, $H(t_j^* | s_i)$, possibly leading to an arms race between the receiver and the deceptive signaler (Dawkins & Krebs 1978; Krebs & Dawkins 1984). However, as the costs associated with misinformation decline, we should see tolerance to unreliable or imperfect information (Roitberg 1990; Bouskila & Blumstein 1992; Abrams 1994; Koops & Abrahams 1998, chapter 3).

An alternative source of reduced reliability of information would be through misinterpretation (Dusenbery 1992) or errors (Wiley 1994). These mistakes would be subject to similar selection pressures away from misinformed responses. We would expect individuals to be selected to reduce costs associated with misinformed responses, either through a more appropriate interpretation of acquired information, or the combination of multiple sources of partially reliable information to form more reliable assessments

(Franklin & Templeton 1992). If, however, the cost of misinterpretation is small or, as in the case of white lies, the misinterpretation is better than no information, there may be tolerance to these errors even though they reduce the reliability of the information.

2.4.2 *Bayesian Assessment*

In Bayesian assessment, an animal combines prior information with current information to obtain an updated assessment of ecological conditions (McNamara & Houston 1980). p_i in equation (2.2) represents this prior information. The best tactic to use when the state of the environment is unknown, t' , is determined based upon a prior expectation of the environment. Prior information, as it ages, becomes a less reliable indicator of the current status of the environment, and some experimental evidence indicates that animals discount aging information according to a decay function (e.g., Devenport & Devenport 1994). The value of partially reliable information can provide a measure of the value of prior information, and ρ_{\min} predicts when prior information should no longer be used in a current assessment. Thus, in most cases, prior information should be discarded before its reliability reaches zero. From figure 2.1 we can see that if the reliability of information starts high, information with a low C/B ratio should continue to be used longer than information with a high C/B ratio. The higher the cost incurred from an erroneous decision, the quicker prior information should be discarded.

2.4.3 *Content and Context*

Reliability is not the only factor that may influence the value of information. The value of information can be increased through decreased acquisition costs (Gould 1974), increased variance in the possible states of the environment (Gould 1974; Stephens 1989) or a decrease in the rate of fitness gains (Koops & Abrahams 1998, chapter 3). We would also expect the content of information to affect its value. Content refers to how informative the cue or signal is, and will influence the value of information through the unspecified conditional-payoff function, H . The higher the content of information, the more the information will narrow the options an organism must choose among. Magurran and Higham (1988) investigated the transfer of information across shoals of European minnows, *Phoxinus phoxinus*, under threat of predation from a pike, *Esox lucius*, model. Information about predation risk was transferred as evident from the change in behaviour of the receiver minnows. The receiver minnows, however, exhibited a delayed and less extreme reaction compared to the transmitter minnows. Magurran and Higham (1988) hypothesized that this difference may be due to insufficient information about the threat. The transmitter minnows had access to information about the size, appearance and motivation of the predator. The content of the information available to the receiver minnows was substantially less, resulting in a larger array of available tactics.

The context of information may also influence the value of information. Context refers to additional sources of information available to a recipient (Smith 1977). The idea of context has been used in the study of animal communication since the 1950s, however, it is applicable to any source of information (Templeton & Franklin 1992). Magurran et al. (1996; Irving & Magurran 1997) proposed that the response of European minnows,

Phoxinus phoxinus, to Schreckstoff, a chemical alarm substance, is context dependent. Irving and Magurran (1997) found that, in a laboratory setting, European minnows responded strongly to Schreckstoff, however, in a semi-natural setting, the minnows exhibited a decreased and transitory response. In the wild, Magurran et al. (1996) were unable to find any response to Schreckstoff. These findings suggest that in confined settings (Irving and Magurran 1997), where additional sources of information are limited and the possibility of escape from a predator is low, the marginal cost of acting without or ignoring correct information is high and the value of information from Schreckstoff is enough to elicit a response. In a wild setting (Magurran et al. 1996), the additional sources of information and lower marginal costs of acting without information, provide a context where the value of information from Schreckstoff is too low to elicit a response. This provides an example of how context can influence the value of information, but still leaves open the question of what is the reliability of Schreckstoff? How often do minnows experience Schreckstoff in the presence of predation?

2.4.4 *Conclusions*

By introducing reliability into the definition of the value of information, I have shown that the use of information by a receiver will depend on the relative benefits and costs of information and misinformation, and free information can be detrimental to the decision maker. This theory assumes that information is free of acquisition costs, makes no assumptions about the source of information, and therefore, there is no specific requirement for information to be costly or highly reliable to be of value to a receiver.

This theory provides a framework for investigations about the use of information, and why animals may use information from one source but not another. What remains to be discerned are other ecological factors that can influence the value of information.

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2.5 Appendix 2A - The Marginal Costs of Information

We start with the payoff obtained with information, $H(t_i^*|s_i)$. This is a concave function on t (Fig. 2.A1) with the maximum payoff occurring at the optimal tactic t_i^* . Therefore, by definition, the first and second derivatives are :

$$\begin{aligned} \frac{dH(t_i^*|s_i)}{dt} &= 0 \\ \frac{d^2H(t_i^*|s_i)}{dt^2} &< 0 \end{aligned} \tag{2.A1}$$

respectively. Now, following Stephens (1989), we can approximate the value of $H(t|s_i)$ for any t using a second-order Taylor series:

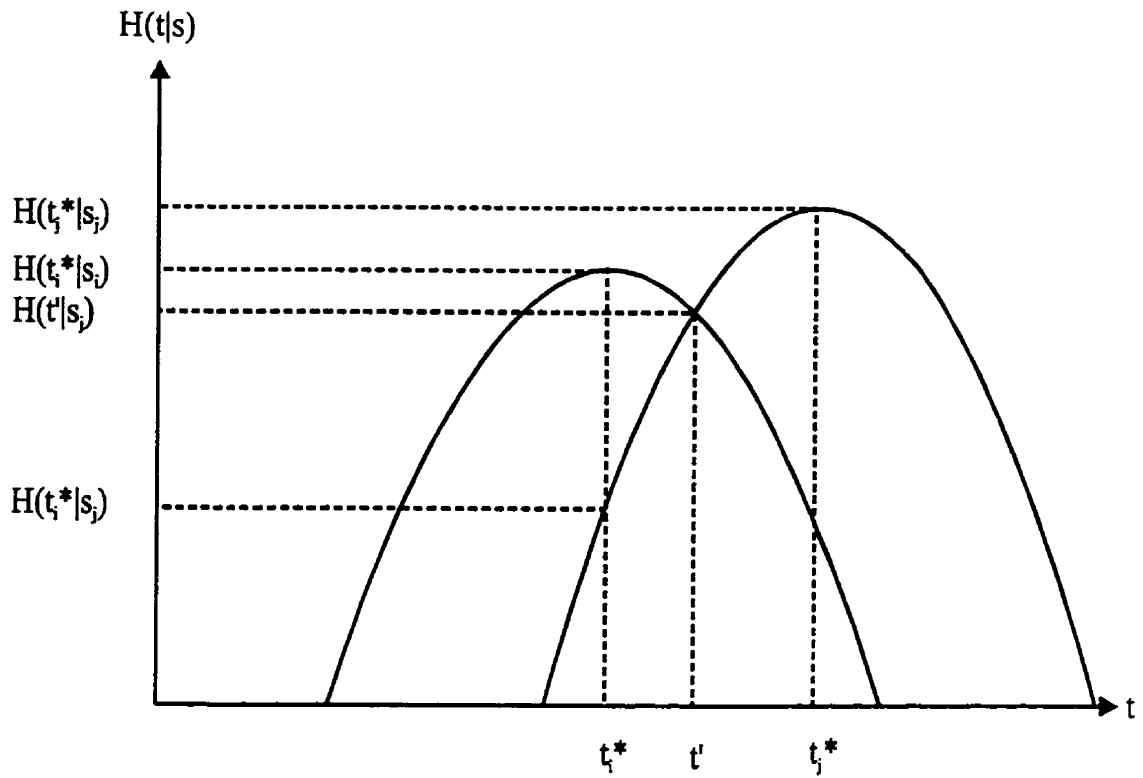


Figure 2A.1. The concave conditional payoff function $H(t|s)$ as a function of t . The first curve is $s = s_i$, the second curve is $s = s_j$.

$$\begin{aligned}
H(t|s) &\approx H(t_i^*|s_i) - \frac{(t_i^* - t)^2}{2} \frac{d^2 H(t_i^*|s_i)}{dt^2} \\
&\approx H_i^* - c_i (t_i^* - t)^2
\end{aligned} \tag{2.A2}$$

where $H_i^* = H(t_i^*|s_i)$, the optimal payoff, and $c_i = -\frac{1}{2}d^2H(t_i^*|s_i)/dt^2$, which is the marginal cost of deviations from the local optimum. The value of correct information (VCI) can be written as:

$$\begin{aligned}
VCI &= H(t_i^*|s_i) - H(t'|s_i) \\
&\approx H_i^* - \left[H_i^* - c_i (t_i^* - t')^2 \right] \\
&\approx c_i (t_i^* - t')^2
\end{aligned} \tag{2.A3}$$

and the value of correct information is the marginal cost of acting without information using t' . Incidentally, this also demonstrates that the value of information increases with increasing variance in the available tactics, $(t_i^* - t')^2$, not increasing variance in the states of the environment (Gould 1974; Stephens 1989). We can also re-write the value of incorrect information (VII) as:

$$\begin{aligned}
VII &= H(t_i^*|s_j) - H(t'|s_j) \\
&\approx \left[H_j^* - c_j (t_j^* - t_i^*)^2 \right] - \left[H_j^* - c_j (t_j^* - t')^2 \right] \\
&\approx c_j \left[(t_j^* - t')^2 - (t_j^* - t_i^*)^2 \right]
\end{aligned} \tag{2.A4}$$

And, putting (2.A3) and (2.A4) together, the value of partially reliable information (VPRI) is:

$$\begin{aligned}
VPRI &= \rho \left[H(t_i^*|s_i) - H(t'|s_i) \right] + (1 - \rho) \left[H(t_i^*|s_j) - H(t'|s_j) \right] \\
&\approx \rho \left[c_i (t_i^* - t')^2 \right] + (1 - \rho) \left[c_j \left((t_j^* - t')^2 - (t_j^* - t_i^*)^2 \right) \right]
\end{aligned} \tag{2.A5}$$

This shows that the value of partially reliable information is dependent on three features:

(i) the reliability of information, ρ ; (ii) the marginal costs of deviating from the optimal

tactic, c ; and (iii) the variance of the distribution of available tactics, $(t_i^* - t')^2$. This also shows that introducing reliability into the value of information does not change previous conclusions (Gould 1974; Stephens 1989) about the influence of variance on the value of information.

By setting (2.A5) equal to zero and solve for ρ_{\min} , we get:

$$\rho_{\min} = \frac{-\left(c_j \left[(t_j^* - t')^2 - (t_j^* - t_i^*)^2 \right]\right)}{c_i (t_i^* - t')^2 - c_j \left[(t_j^* - t')^2 - (t_j^* - t_i^*)^2 \right]} \quad (2.A6)$$

and we can see that the minimum reliability of information (ρ_{\min}) declines as the marginal costs of information (c_i) increase and the marginal costs of misinformation (c_j) decrease.

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Chapter 3: Life History and the Fitness Consequences of Imperfect Information[†]

3.1 Abstract

The acquisition of information incurs costs in time, energy, exposure to predation, and/or lost opportunity. Without information, however, animals will be unable to assess the costs and benefits of decisions. Obtaining perfect information may be impossible, but how close to perfect do animals need assessments of ecological factors, such as predation risk, before estimation errors affect fitness? A recent article suggests that animals should be tolerant to imperfect information about predation risk, possibly relying on simple rules of thumb. Using a dynamic state variable approach, we examine some of the assumptions underlying this work, and show that tolerance toward imperfect information is dependent on life history strategy. By changing the relationship between energy and fitness, assumptions about life history strategies can be modified. Calculations show that tolerance to imperfect information is sensitive to these assumptions with some life histories leading to overestimation, while other life histories result in underestimation. One consistent effect across life histories is that animals with a higher rate of increase in fitness with respect to energy should show greater tolerance to imperfect information.

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3.2 Introduction

In most environments, animals need information to make decisions that maximize fitness. Early models in behavioural ecology assumed that animals had perfect information about their environment (Stephens and Krebs, 1986). This is obviously not true, and many researchers have started to investigate how animals acquire and use information (e.g. Stephens, 1987; Valone and Brown, 1989; Mangel, 1990; Roitberg, 1990; Valone, 1991, 1992; Templeton and Giraldeau, 1995). If information is free, we expect animals to acquire enough information for perfect assessments (Chavas and Pope, 1984; Templeton and Franklin, 1992), however, we expect some cost to be associated with the acquisition of information. Even if information is free, an environment may be too variable for animals to acquire perfect assessments. Given that perfect information is desirable, but its acquisition is costly, we are left with the question: how tolerant should animals be to imperfect information?

Roitberg (1990) used a dynamic state variable approach to determine whether fruit flies should be optimistic (errors biased toward overestimation) or pessimistic (errors biased toward underestimation) about the value of foraging patches. Roitberg's model predicted, and his field data supported the prediction, that fruit flies should be optimistic in their assessment of patch quality. More recently, Bouskila and Blumstein (1992) asked if animals should be tolerant to imperfect information about predation risk. Using a similar dynamic state variable approach, they modelled the effect of error in the estimation of predation risk on the fitness of a forager. Their analysis showed that, in general, tolerance to imperfect information was predicted to be skewed toward overestimation of predation

risk, and that tolerance to imperfect information would be relatively large. This led Bouskila and Blumstein (1992) to conclude that, when there is a cost to reducing error, animals should be using simple rules of thumb leading to overestimation of predation risk.

Abrams (1994), using a deterministic model, showed that either under- or overestimation of predation risk could be expected. Abrams' model predicted that the advantage to any given bias in the estimation of predation risk would depend on the costs and benefits of foraging, i.e. on the relationship between fitness and foraging gains. This would suggest that tolerance to imperfect information should be influenced by the life history of the forager. Life history refers to those traits of an organism's life cycle that contribute to its reproductive success (Stearns, 1992). Hence, the life history of an organism would determine how foraging gains contribute to fitness (Abrams, 1983, 1991). Obviously, this is only one aspect of an organism's life history.

Newman (1991) demonstrated that by changing the relationship between energy gains and the probability of survival, the patch-residence times of modelled foragers could be significantly lengthened. Using Bouskila and Blumstein's (1992) model, we investigate how assumptions about life history influence predicted tolerance to imperfect information through modifications to the model's terminal fitness function (the fitness-foraging relationship).

Table 3.1. Parameters, parameter values and descriptions of parameters used in the basic model. When two parameter values are reported, they correspond to patch 1 and patch 2 respectively. Patch 1 is the safe but food poor patch, while patch 2 is the risky but food rich patch. Parameter values correspond to those used by Bouskila and Blumstein (1992).

| Parameter | Value(s) | Description |
|-------------|--------------|---|
| T | 25 | The final time step (time horizon) |
| t | ... | The current time step for all $t < T$ |
| α_i | 1, 1 | Energetic cost of a decision per t |
| r_i | 0.16, 1.61 | Rate of encounter with food per t |
| λ_i | 0.15, 0.8 | Probability of finding food per t |
| Y_i | 1, 2 | Units of energy obtained per successful discovery |
| β_i | 0.0001, 0.04 | Probability of death by predation per t |
| $X(t)$ | ... | State variable (energy reserves) at time t |
| x | ... | Current level of energy reserves |
| x_c | 3 | Critical level of energy reserves |
| x_{cap} | 15 | Maximum capacity of energy reserves |
| x_{sat} | 10 | Saturation point, or x required for maximum fitness |

3.3 The Model

The model used by Bouskila and Blumstein (1992) is a modified version of the patch choice model described by Mangel and Clark (1988). A forager chooses between two patches based upon parameter values of the probability of finding food (λ) which is determined by the rate of encounter with food (r), the energy obtained with each successful discovery (Y), the energetic cost of a decision (α), and the probability of death by predation (β) (see Table 3.1 for a summary). This decision is repeated for each time step, t , during a foraging period of T time steps. A forager avoids starvation by keeping its energy reserves at each time period, $X(t)$, above a critical level, x_c .

During each time period, the forager's energy reserves change depending on the patch chosen and foraging success in that patch. If a forager chooses patch i and finds food, its new energy reserves will be:

$$x'_i = x - \alpha_i + Y_i \quad (3.1)$$

where x represents current energy reserves. If the forager is unsuccessful, its new energy reserves will be:

$$x''_i = x - \alpha_i. \quad (3.2)$$

The range of possible energy reserve levels are bound by an upper maximum capacity, x_{cap} , and a minimum critical level, x_c .

The probability of finding food at each time step in patch i will be determined by the rate of encounter with food in patch i :

$$\lambda_i = 1 - e^{-r_i}. \quad (3.3)$$

The forager's expected fitness from time t to the time horizon, T , given energy reserves x is defined by the equation:

$$F(x, t, T) = (1 - \beta_i) [\lambda_i F(x'_i, t+1, T) + (1 - \lambda_i) F(x''_i, t+1, T)] \quad (3.4)$$

where x'_i , x''_i and λ_i are defined by equations (3.1), (3.2) and (3.3). The forager chooses the patch, i , at each time step to maximize $F(x, t, T)$. For a complete description of the dynamic state variable approach and stochastic dynamic programming (SDP), see Mangel and Clark (1988).

In the model described by Bouskila and Blumstein (1992), the forager makes decisions with error in one of the parameter values (e.g. estimation of the probability of death by predation in patch 2, β_2). Fitness is calculated based upon the true parameter value, allowing calculation of the effect that estimation error has on the fitness of the modelled forager. The true parameter values used in the basic model are reported in Table 3.1. Estimation errors were calculated as:

$$\% \text{ Error} = \frac{100(R - E)}{R} \quad (3.5)$$

where R is the real parameter value and E is the forager's erroneous estimate of the parameter value. Negative errors represent overestimation and positive errors represent underestimation. Calculations in our version of the model were run at 5% error intervals.

At the end of the time period, fitness is calculated based upon the forager's energy reserves, and the terminal fitness function (TFF). The TFF relates the terminal value of the state variable $X(t = T)$ (i.e. energy reserves) to fitness (Mangel and Clark, 1988). As stated earlier, one aspect of the life history of an animal determines how foraging gains contribute to fitness. The TFF determines the relationship between fitness and foraging

gains (energy reserves), and hence, is an assumption about the life history of the modelled forager.

Bouskila and Blumstein (1992) used a step function (Fig. 3.1a) as their TFF. The step function defines terminal fitness as:

$$F(x, T, T) = \begin{cases} 1 & \text{if } x > x_c \\ 0 & \text{if } x \leq x_c \end{cases} \quad (3.6)$$

An animal with this type of life history receives zero fitness if its energy reserves fall below the critical level, x_c . However, if the forager keeps its energy reserves above x_c , it can expect to receive maximum fitness. The step function, as a TFF, most likely represents a situation where the forager is avoiding starvation over a non-breeding interval, so the terminal condition is either survival (fitness = 1) or starvation (fitness = 0) (Mangel and Clark, 1988).

We define four alternative TFFs related to possible life histories. All are defined so fitness ranges between zero and one (see Table 3.2 for the values of constants) for comparability of our results to those reported by Bouskila and Blumstein (1992).

The first alternative TFF is a straight line function (Fig. 3.1b). Fitness increases linearly with increasing energy reserves up to some maximum:

$$F(x, T, T) = \begin{cases} 1 & \text{if } x \geq x_{sat} \\ a + bx & \text{if } x_c < x < x_{sat} \\ 0 & \text{if } x \leq x_c \end{cases} \quad (3.7)$$

where x_{sat} , the saturation point, is the level of energy reserves where maximum fitness is attained. A straight line TFF could describe the life history of an animal whose fitness is

Table 3.2. Constants[†] used to define the alternative TFFs in the basic model.

| TFF | a | b | c |
|------------------|--------|-------------------------------------|--------|
| Straight line | -0.429 | 0.143 | NA |
| Saturation curve | 1.000 | 0.906 | -0.604 |
| Sigmoid curve | 1.000 | 0.120 | NA |
| Abrams' equation | 1.500 | $\frac{(x - x_c)}{(x_{sat} - x_c)}$ | NA |

[†]All calculations performed with double precision, however, for clarity of presentation, the constants have been rounded to the third decimal place.

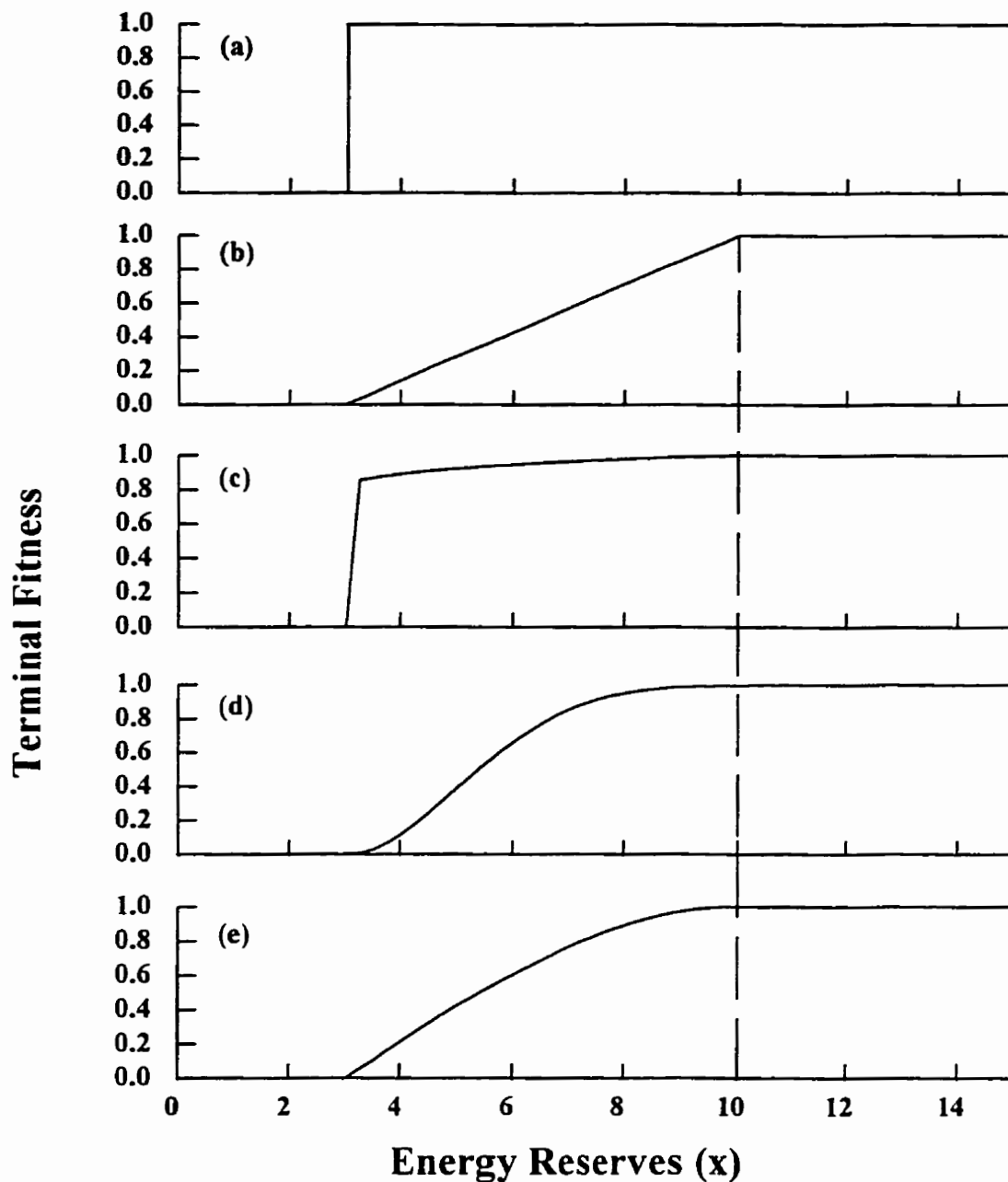


Figure 3.1. The five terminal fitness functions (TFFs) used in our dynamic state variable model representing possible life histories: (a) the step function used by Bouskila and Blumstein (1992); (b) a straight line function; (c) a saturation curve; (d) a sigmoid curve; (e) Abrams' equation. The dashed reference line represents the saturation point, x_{sat} , where maximum fitness is obtained in the basic model.

limited by the time available to gain access to resources other than food. For example, the reproductive success of a male guppy, *Poecilia reticulata*, may be limited by the time available to court females (Baerends et al., 1955; Farr, 1980). In such cases, higher energy reserves would provide more time for non-foraging activities.

If fitness increases in a curvilinear fashion with increasing energy reserves, the TFF may be described by a saturation curve (Fig. 3.1c):

$$F(x, T, T) = \begin{cases} 1 & \text{if } x \geq x_{sat} \\ \frac{a(x-c)}{1+ab(x-c)} & \text{if } x > x_c \\ 0 & \text{if } x \leq x_c \end{cases} \quad (3.8)$$

A saturation TFF represents a life history where initial increases in fitness with increasing energy reserves are quick, followed by a decreasing rate of fitness gains, requiring more energy per unit of fitness (e.g., animals investing in the quality of offspring). For example, Lemon and Barth (1992) measured reproductive success in four populations of zebra finches, *Taeniopygia guttata*, where feeding rate was manipulated. Reproductive success, as measured by offspring fledged per female, increased with increased feeding rate in a curvilinear manner similar to a saturation curve.

Alternatively, fitness could increase exponentially with increasing energy reserves, then plateau at some maximum, as described by a sigmoid curve (Fig. 3.1d):

$$F(x, T, T) = \begin{cases} a(1 - e^{-b(x-x_c)^2}) & \text{if } x > x_c \\ 0 & \text{if } x \leq x_c \end{cases} \quad (3.9)$$

A sigmoid TFF may represent the life history of female fish. Growth efficiency increases with increased food, but decreases again at high levels of food rations (Ricker 1979).

Fecundity, however, increases exponentially with the size of female fish (Bagenal, 1978).

If we consider these two relationships together, the result would be initial fitness increasing exponentially with increased energy reserves, then, due to reduced growth efficiency, fitness would plateau at high levels of energy reserves, producing a sigmoid TFF. This simplified view ignores the effects of food availability and population density (see Bagenal (1978) for review), and temperature and oxygen availability (Ricker, 1979) on fecundity and growth.

In an attempt to compare our results and the predictions of Abrams' (1994) model, we also include a TFF using an equation given by Abrams that, according to his model, shows underestimation of predation risk. We have slightly modified Abrams' equation to fit the dynamic state variable model:

$$F(x, T, T) = \begin{cases} 1 & \text{if } x \geq x_{sat} \\ 1 - a[\frac{2}{3} - b + \frac{b^1}{3}] & \text{if } x_c < x < x_{sat} \\ 0 & \text{if } x \leq x_c \end{cases} \quad (3.10)$$

Abrams' equation looks like a saturation curve when plotted in the range used in our calculations (Fig. 3.1e) and would represent a similar life history.

These calculations allow us to investigate the influence that a range of life history characters have on tolerance to imperfect information. We do this by numerically solving the dynamic programming equation (equation 4), employing backward iterations, while changing the TFF. While these alternative TFFs may not accurately represent a particular organism, they do represent a reasonable range of naturally occurring life history characters.

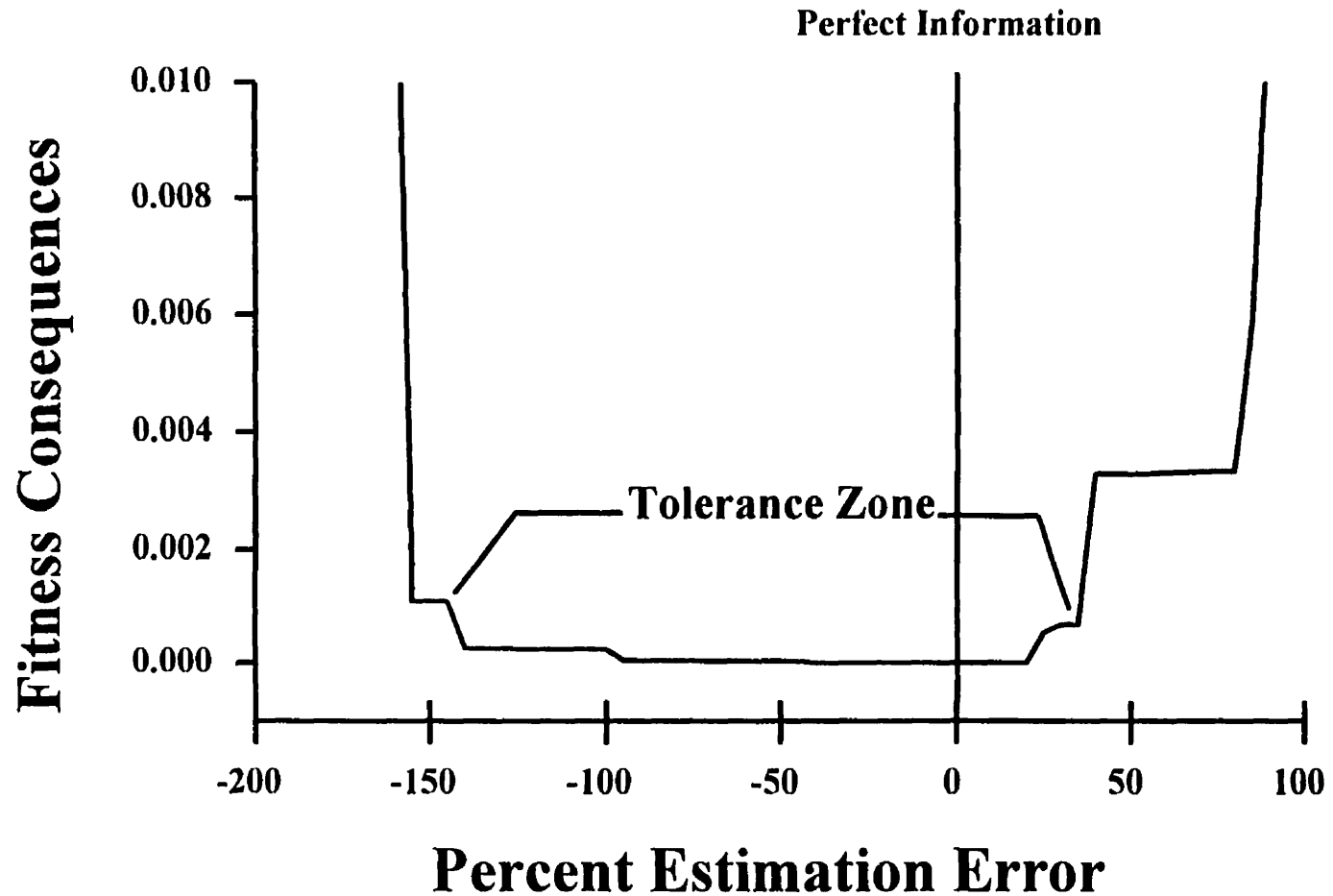


Figure 3.2. Fitness consequences of imperfect information plotted against estimation error in the probability of death by predation in the risky patch (β_2). Note that these fitness consequences refer to how much fitness is reduced by the use of imperfect information. The terminal fitness function in this case is the step function (Fig. 3.1a) used by Bouskila and Blumstein (1992). All parameter values as reported in Table 3.1, and expected fitness taken at $X(t = 0) = 13$.

3.4 Results

The results of our calculations can be presented by plotting the fitness consequences of estimation error against the percent error (Fig. 3.2) to demonstrate tolerance to imperfect information. We define fitness consequences as the effect of estimation error on fitness compared to a state of perfect information:

$$\text{fitness consequences} = \frac{(\text{fitness with perfect info}) - (\text{fitness with erroneous info})}{(\text{fitness with perfect info})}. \quad (3.11)$$

Thus, the fitness consequences range between zero and one, and zero percent estimation error (perfect information) has a fitness consequence of 0.000. As the fitness consequences increase, the experienced fitness decreases. The flat region around perfect information in Fig. 3.2 is defined as the tolerance zone. This is the region with little influence of imperfect information on the expected fitness of the modelled forager. Choosing a fitness consequence of 0.001 as our criterion for tolerance, while consistent with Bouskila and Blumstein (1992), is arbitrary. Within the tolerance zone, imperfect information has a fitness consequence less than 0.1% of the fitness with perfect information. For example, in Fig. 3.2, the tolerance zone ranges from -145% to +40% error, and the size of the tolerance zone is 185% error. Our results, however, are fairly robust to changes in this criterion. While selection will act on any fitness consequence greater than zero, we believe that this level of fitness consequence is low enough for selection to be weak.

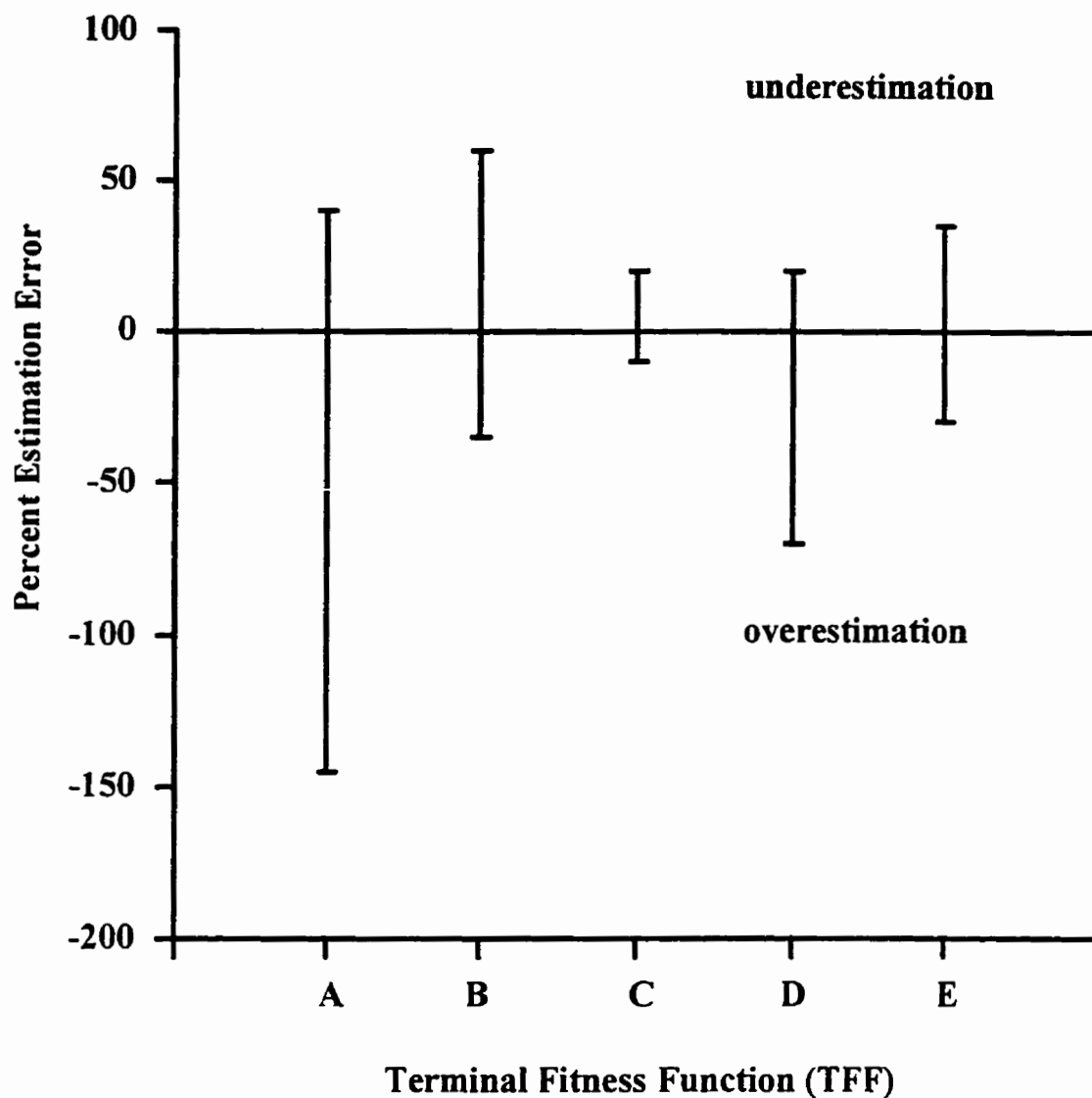


Figure 3.3. Percent estimation error in predation risk in the risky patch (β_2) showing the range of the tolerance zone for each terminal fitness function (TFF). The solid reference line shows perfect information. Below the line is overestimation, above the line is underestimation. All calculations were performed with the parameter values reported in Table 3.1; data calculated based on expected fitness at $X(t = 0) = 13$.

3.4.1 *TFFs, Tolerance and Predation Risk*

Modifications to the model's TFF had a marked influence on predicted tolerance to imperfect information. When comparing tolerance to imperfect information about predation risk (β_2), the size of the tolerance zone decreases from 185% error (range: -145% to +40%) when the TFF is a step function to 30% error (range: -10% to +20%) when the TFF is a saturation curve (Fig. 3.3). Bouskila and Blumstein (1992) concluded that tolerance to imperfect information should be relatively large and biased toward overestimation of predation risk, based on results from the step TFF (Fig. 3.3). All four alternative TFFs result in reduced tolerance to imperfect information compared to tolerance predicted with the step TFF. Furthermore, the straight line function, the saturation curve and Abrams' equation all show zones of tolerance biased toward underestimation of predation risk.

3.4.2 *TFFs, Tolerance and Patch Profitability*

To investigate the effect of error in a forager's estimate of patch profitability, we ran the model with error in the rate of encounter in the food rich patch (r_2). The size of the tolerance zone was calculated 20 times with each TFF, allowing r_2 to range from 0.25 to 5.00 at intervals of 0.25. We found that for all the TFFs, except the step function, the size of the tolerance zone follows a U-shaped curve as encounter rate increases (Fig. 3.4). This is not a surprising result if we consider the effect erroneous information about patch profitability has on fitness. At low encounter rates, erroneous estimates of r_2 have little

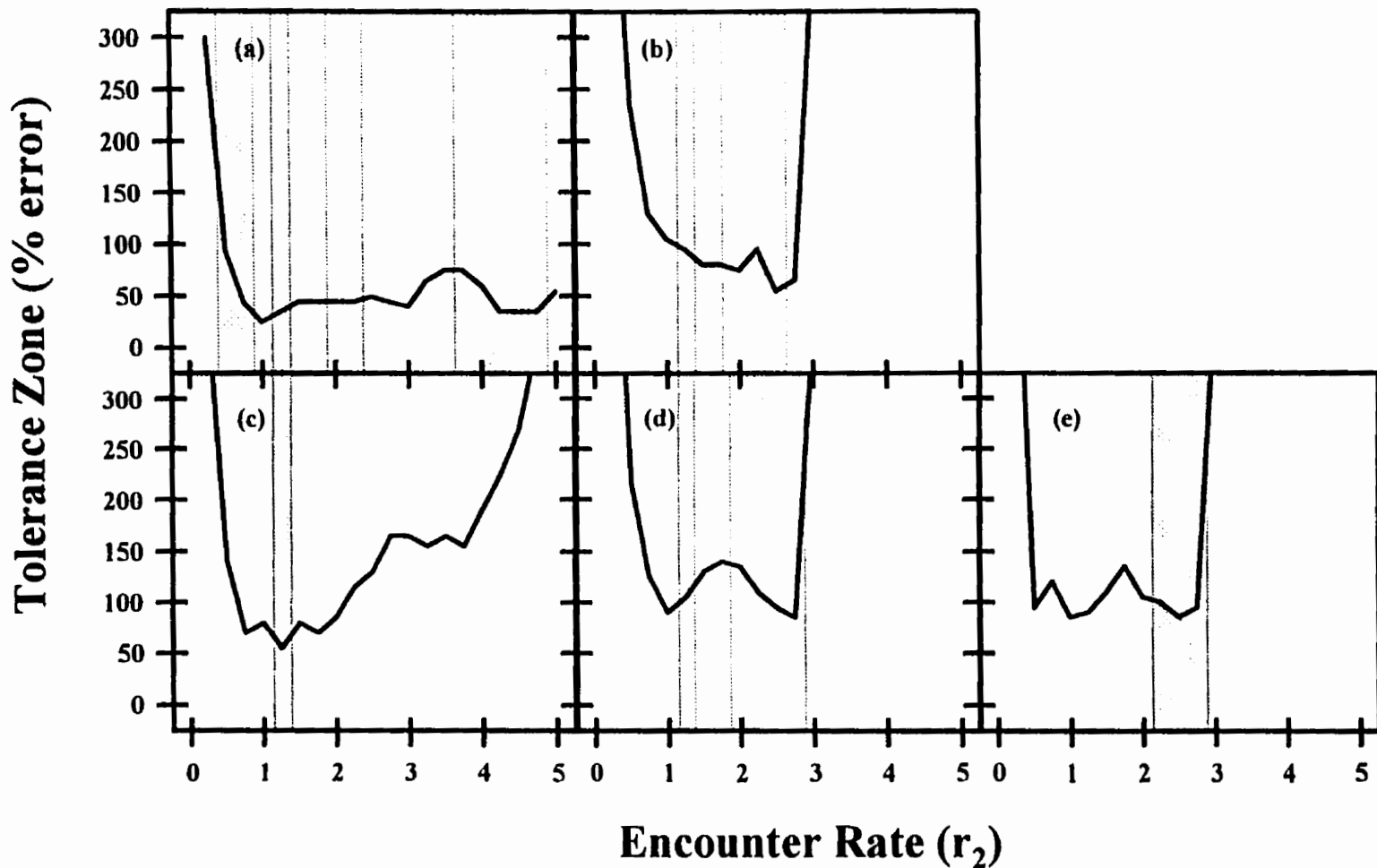


Figure 3.4. Size of the tolerance zone (measured in % error in encounter rate, r_2) over a large range of encounter rates in the food rich patch (r_2). Hatched areas represent conditions where the tolerance zone is biased toward underestimation of encounter rate, and the clear area represents conditions where the tolerance zone is biased toward overestimation of encounter rate. These results are from the dynamic state variable model when the terminal fitness function is: (a) a step function; (b) a straight line function; (c) a saturation curve; (d) a sigmoid curve; and (e) Abrams' equation. All other parameters values as reported in Table 3.1; data calculated based on expected fitness at $X(t = 0) = 13$.

influence on fitness since the probability of starvation is high. At high encounter rates, fitness consequences for alternative TFFs, i.e. all TFFs except the step function, would be small due to plateaus (see Fig. 3.1) and the small effect of variation in energy reserves on expected fitness. As for the step function, Bouskila et al. (1995) showed that foragers minimize their visits to the risky patch (their Fig. 1). Since there is no benefit to high energy reserves, erroneous estimates of patch profitability can have drastic effects on fitness if energy reserves fall below the critical level leading to relatively narrow tolerance zones.

From Fig. 3.4 we can see there are intermediate encounter rates at which foragers are predicted to have low tolerance to imperfect information about patch profitability. Over most of the range of encounter rates investigated, tolerance zones are biased toward overestimation of patch profitability, the exception mostly occurring when tolerance is relatively low. However, both the range of low tolerance and the ranges of underestimation of encounter rate are influenced by assumptions about the terminal fitness function (Fig. 3.4).

3.4.3 TFF Details

Assumptions about the TFF can be modified by changing the details without changing the TFF's overall shape. In the basic model, all alternative TFFs have a saturation point set at $x_{\text{sat}} = 10$. Thus, fitness increases with increasing energy reserves between 3 (x_c) and 10 (x_{sat}). Any forager at the end of the time period with $X(T) \geq 10$ received maximum fitness, $F(x, T, T) = 1$. However, this characteristic of the TFF can also be modified, so

Table 3.3. The effect of saturation point (x_{sat}) in defining the TFF on the size (and range) of the tolerance zone (in % error) when the straight line function, saturation curve, sigmoid curve and Abrams' equation were used in the model's TFF. Error occurs in estimation of the probability of death by predation in the risky patch (β_2). For comparison, the size of the tolerance zone for the step function is 185% error (range: -145% to +40%). $X(t=0)=13$, all other parameter values as reported in Table 3.1.

| x_{sat} | Straight Line | Saturation Curve | Sigmoid Curve | Abrams' Equation |
|-----------|----------------------|-----------------------|-----------------------|-----------------------|
| 5 | 110% (-40%, +70%) | 215% (-170%, +45%) | 145% (-110%, +35%) | 165% (-150%, +15%) |
| 10 | 95% (-35%, +60%) | 30% (-10%, +20%) | 90% (-10%, +20%) | 65% (-30%, +35%) |
| 15 | 115% (-40%, +75%) | 30% (-5%, +25%) | 50% (-25%, +25%) | 75% (-40%, +35%) |
| 20 | 115% (-40%, +75%) | 80% (-55%, +25%) | 60% (-25%, +30%) | 130% (-115%, +15%) |
| 25 | 115% (-40%, +75%) | 75% (-50%, +25%) | 55% (-30%, +25%) | 95% (-15%, +80%) |

the saturation point can occur as soon as $x = 4$ (as for the step TFF), or as late as $x = 15$ or later, in which case no forager in this model could obtain maximum fitness. The more a TFF resembles a step function (i.e. the lower the saturation point and the higher the rate of increase in fitness with respect to energy reserves), the larger the zone of tolerance (see Table 3.3).

3.5 Discussion

The model considered here predicts that the aspect of life history described by the relationship between energy and fitness is important in determining tolerance to imperfect information, and this is true whether we are discussing information about predation risk or patch profitability. Therefore, it is not possible to make general predictions about whether estimation of predation risk will be biased toward overestimation (e.g. Bouskila and Blumstein, 1992; Bouskila et al., 1995) or underestimation. This is similar to the conclusion Abrams (1994) drew from his deterministic model.

The influence of life history on tolerance to imperfect information is not too surprising in light of the aspect of life history considered, i.e. the mapping of energy on to fitness. Imperfect information about both predation risk and patch profitability will affect the state variable -- energy reserves. Underestimating predation risk or overestimating patch profitability leads to a forager spending more time in the dangerous patch than would be optimal, thus reducing fitness through increased predation risk. Overestimating predation risk or underestimating patch profitability leads to underexploitation of the most profitable patch, and reduced fitness through diminished energy reserves. Thus, we can

see why using the step function as the TFF leads to the prediction that animals should be overestimating predation risk. With the step function, fitness does not decrease as energy reserves decrease until energy reserves fall below the critical level, x_c .

Not only did we show that the shape of the food-fitness relationship (TFF) changes tolerance to imperfect information, but the details of the relationship are also important (Table 3.3). Regardless of the general shape of the relationship, as the TFF looks more like a step function (smaller x_{sat}) the tolerance to imperfect information increases. This suggests that when it is easier to attain maximum fitness (i.e. a higher rate of increase in fitness gain per unit of energy gain), tolerance to imperfect information should be greater. Specifically, the relatively large tolerance to imperfect information Bouskila and Blumstein (1992) observed was due to the extreme discontinuity of their terminal fitness function. Furthermore, additional calculations by Bouskila (1993) employed TFFs that lead to conclusions similar to Bouskila and Blumstein's (1992) conclusions about tolerance to imperfect information being biased toward overestimation of predation risk, though the zone of tolerance was smaller.

3.5.1 *Value of Information*

Stephens (1989) defines the value of information as the difference in payoff between being informed and being uninformed. The tolerance zones observed in our results can be considered the zone over which the value of information is low. There is very little difference in fitness payoff between acting with perfect information versus acting with an erroneous estimate, as long as that estimate falls within the tolerance zone. The fitness

consequences plotted in Fig. 3.2 can be viewed as the value of information (Stephens, 1989), or the maximum fitness cost a forager should willingly incur to obtain perfect information. In the present model, there is no cost to acquiring information. In fact, the modelled foragers did not acquire information at all, an erroneous estimate was assigned from the start. However, if we wish to consider the circumstances where information should be valued, this model may lend some insight. We know that information is valued only when having information leads to different decisions (Gould, 1974; Chavas and Pope, 1984; Stephens, 1989). If increasing the accuracy of the estimate from 25% to 10% error does not lead to a decision with any appreciable increase in fitness, the value of information would be low. Thus, this model shows that assumptions about the food-fitness relationship of the animal considered can have an influence on the value of information. This means that two animals in exactly the same situation, but with different life histories, may value information differently. Other life history traits, such as age of maturity, size at maturity, size of offspring, clutch size etc., should be investigated for an impact on the value of information.

3.5.2 Predation Risk

Bouskila and Blumstein (1992) used this dynamic state variable approach to conclude that foragers should overestimate predation risk. This conclusion is based upon the assumption that the relationship between foraging gains and fitness (the TFF) is a step function. Abrams (1994) objected and used a deterministic model to show that both over- and underestimation of predation risk can be expected. Bouskila et al. (1995) claimed that

Abrams' deterministic model was not comparable to their model, and that Bouskila (1993) had used alternative TFFs to show that overestimation of predation risk was still predicted. Abrams (1995) claimed that underestimation was still possible, and that none of the alternative TFFs used by Bouskila (1993) conformed to the conditions that his model claimed lead to underestimation of predation risk. The alternative TFFs used by Bouskila (1993) were similar to the sigmoid curve TFF we used, and his results are similar to ours for this TFF.

We included Abrams' (1994) equation in our calculations because Abrams' model predicts that, with this equation, tolerance should be biased towards underestimation of predation risk. In the basic run of the model with Abrams' equation as a TFF, results show tolerance biased to underestimation of predation risk (Fig. 3.3). However, when the saturation point is changed from $x_{sat} = 10$, we observe a bias toward overestimation of predation risk (Table 3.3). This does not mean that underestimation will be uncommon, but rather that Abrams' (1994) model does not necessarily make the same predictions as Bouskila and Blumstein's (1992) model concerning the underestimation of predation risk. Both models, however, do predict that some foragers will underestimate predation risk.

3.5.3 *Patch Profitability*

The only comparable work on erroneous estimates of patch profitability is Roitberg's (1990) model of fruit flies. Our results show that life history should influence tolerance to imperfect information about patch profitability. Comparing Roitberg's model results to our results may not be valid since his model does not use an explicitly stated TFF.

Instead, as fruit flies search for food items in patches, they increase fitness by laying an egg as they find an appropriate item. There is no carry over from day to day, and no benefit in failing to lay all 10 eggs available in a given day. This type of life history would be most similar to our condition of a straight line TFF. Under these conditions, we find that our results lead to the prediction that foragers should be optimistic about, or overestimate, patch profitability (Fig. 3.4b). Roitberg's (1990) data on giving up times are significantly shifted toward an over representation of optimistic fruit flies, as expected from Roitberg's (1990) model and our results. Valone (1993) shows that without the use of public information, social foragers pay a cost of foraging in groups by leaving patches too soon, i.e. social foragers underestimate patch quality compared to solitary foragers. If, however, social foragers use rules biased toward overestimation of patch profitability, then underestimation by social foragers without public information would be minimized or countered.

3.5.4 Conclusions

Our model results demonstrate that tolerance to imperfect information is sensitive enough to assumptions about life history that no general conclusions can be drawn concerning an expected observation of over- versus underestimation of predation risk. Furthermore, the size of the tolerance zone can be manipulated through the details of life history. From this model we conclude that animals will show tolerance to imperfect information, but the extent of this tolerance may change from one situation to the next. Therefore, animals may use rules of thumb, but, to avoid decreases in fitness from a lack of information, the

rules of thumb should either be flexible to local ecological conditions or lead to erroneous estimates that fall within the boundaries of the narrowest tolerance zones. We may still expect organisms to use rules of thumb, but they may not be as simple as expected from Bouskila and Blumstein's (1992) analysis. The one general prediction we can draw from our results is that the greater the rate of increase in fitness with respect to increasing energy reserves (i.e. the lower x_{sat} and the steeper the TFF), the more tolerant an animal should be to imperfect information.

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3.6 Appendix 3A - Computer Code

The following computer code for the basic model has been coded in Visual Basic, and if typed in to a module in Microsoft Excel, will output data to a spreadsheet. Remark statements are in italics, all Visual BASIC keywords are in bold.

Option Explicit

Rem Patch selection model with imperfect information

Sub ImpInfoSDP()

Rem Initialize parameters

Dim ro, i, j, TFF, Time, capacity, xcrit, alpha, horizon, npatch **As Integer**

Dim xsat, er, t, x, xprime, x2, imaxg, xqprime, erroneous **As Integer**
Dim a, b, c, vmaxg, egterm1, egterm2 **As Double**
Dim testg, qterm1, qterm2 **As Double**
Dim Y(), pgstar() **As Integer**
Dim rbeta(), rlambda() **As Single**
Dim ebeta(), elambda(), egrhs() **As Double**
Dim g0(), g1(), q0(), q1() **As Double**

capacity = 15 *'maximum capacity for energy reserves, x*
xcrit = 3 *'lower critical level for x*
xsat = 10 *'saturation point for x*
alpha = 1 *'energetic cost per t*
horizon = 25 *'maximum number of time steps*
npatch = 2 *'number of patches*
TFF = 1 *'1=step, 2=straight, 3=saturation, 4=sigmoid, 5=Abrams'*
erroneous = 1 *'1=error in lambda, 2=error in beta*
Time = 0 *'Time for output*

ReDim rbeta(npatch), rlambda(npatch), Y(npatch), ebeta(npatch), elambda(npatch)
ReDim efrhs(npatch), egrhs(npatch)
 'rhs is the right hand side of the dpe for patch i

ReDim g0(horizon, capacity), g1(horizon, capacity)
ReDim q0(horizon, capacity), q1(horizon, capacity)
ReDim pgstar(horizon, capacity)
 'g0 tracks $F(x,t,T)$ & g1 tracks $F(x,t+1,T)$ with expected values
 'pstar is the optimal patch
 'q0 & q1 tracks $F(x,t,T)$ & $F(x,t+1,T)$ with real values

rbeta(1) = 0.0001 *'rbeta = real probability of death*
rbeta(2) = 0.04

ebeta(1) = rbeta(1) *'ebeta = expected probability of death from imperfect info*

rlambda(1) = 0.15 *'rlambda = real probability of finding food*
rlambda(2) = 0.8

elambda(1) = rlambda(1) *'elambda = expected probability of finding food*

Y(1) = 1 *'energetic gain from foraging successfully in patch i*
Y(2) = 2

Rem Define terminal fitness function (TFF)

Select Case TFF

Case 1 *'TFF is a step function'*
For x = xcrit + 1 To capacity
 g1(horizon, x) = 1
 q1(horizon, x) = 1
Next x

Case 2 *'TFF is a straight line function'*
a = -0.429
b = 0.143
For x = xcrit + 1 To capacity
 If x < xsat Then
 g1(horizon, x) = a + b * x
 q1(horizon, x) = a + b * x
 Else
 g1(horizon, x) = 1
 q1(horizon, x) = 1
 End If
Next x

Case 3 *'TFF is a saturation curve'*
a = 1#
b = 0.9056970483934
c = -0.6041219597369
For x = xcrit + 1 To capacity
 If x < xsat Then
 g1(horizon, x) = (a * (x - c)) / (1 + a * b * (x - c))
 q1(horizon, x) = (a * (x - c)) / (1 + a * b * (x - c))
 Else
 g1(horizon, x) = 1
 q1(horizon, x) = 1
 End If
Next x

Case 4 *'TFF is a sigmoid curve'*
a = 1#
b = 0.12
For x = xcrit + 1 To capacity
 If x < xsat Then
 g1(horizon, x) = a * (1 - Exp(-1 * b * (x - xcrit) ^ 2))
 q1(horizon, x) = a * (1 - Exp(-1 * b * (x - xcrit) ^ 2))
 Else
 g1(horizon, x) = 1
 q1(horizon, x) = 1
 End If
Next x

Case 5 *'TFF is Abrams' equation'*
a = 3 / 2
For x = xcrit + 1 To capacity

```

If x < xsat Then
  b = (x - xcrit) / (xsat - xcrit)
  gl(horizon, x) = 1 - (a * ((2 / 3) - b + ((b ^ 3) / 3)))
  ql(horizon, x) = 1 - (a * ((2 / 3) - b + ((b ^ 3) / 3)))
Else
  gl(horizon, x) = 1
  ql(horizon, x) = 1
End If
Next x
Case Else
  MsgBox ("Undefined Terminal Fitness Function, please reset parameter TFF and try
    again")
  Exit Sub
End Select

Rem Start iterations

Rem Solve dynamic programming equation (dpe)

For er = 100 To -200 Step -5

  'set error in either lambda(2) or beta(2)
  Select Case erroneous
    Case 1
      ebeta(2) = rbeta(2) - (0 / 100) * rbeta(2)
      elambda(2) = rlambda(2) - (er / 100) * rlambda(2)
    Case 2
      ebeta(2) = rbeta(2) - (er / 100) * rbeta(2)
      elambda(2) = rlambda(2) - (0 / 100) * rlambda(2)
    Case Else
      MsgBox ("Cannot create error in that estimate, please reset parameter erroneous and
        try again")
      Exit Sub
  End Select

For t = horizon To 1 Step -1          'move backwards in time

  For x = xcrit + 1 To capacity        'cycle through energy reserve levels

    For i = 1 To npatch                'calculate fitness for all patches

      xprime = x - alpha + Y(i)          'new x if food is discovered
      If xprime > capacity Then xprime = capacity
      If xprime < xcrit Then xprime = xcrit
    
```

```

x2 = x - alpha                                'new x if no food discovered
If x2 < xcrit Then x2 = xcrit

egterm1 = elambda(i) * g1(t, xprime)
egterm2 = (1 - elambda(i)) * g1(t, x2)
egrhs(i) = (1 - ebeta(i)) * (egterm1 + egterm2)

Next i

Rem Find the optimal patch

vmaxg = 0
imaxg = 0
For i = 1 To npatch
  testg = egrhs(i)
  If testg > vmaxg Then
    vmaxg = testg
    imaxg = i
  End If
Next i

g0(t, x) = vmaxg
pgstar(t, x) = imaxg

Next x

Rem Update g1

For j = xcrit + 1 To capacity
  g1(t - 1, j) = g0(t, j)
Next j

Next t

Rem Calculate probability of survival with real beta values

For t = horizon To 1 Step -1
  For x = xcrit + 1 To capacity

    xqprime = x - alpha + Y(pgstar(t, x))
    If xqprime > capacity Then xqprime = capacity
    If xqprime < xcrit Then xqprime = xcrit

    x2 = x - alpha
    If x2 < xcrit Then x2 = xcrit

```

```

qterm1 = rlambda(pgstar(t, x)) * q1(t, xprime)
qterm2 = (1 - rlambda(pgstar(t, x))) * q1(t, x2)
q0(t, x) = (1 - rbeta(pgstar(t, x))) * (qterm1 + qterm2)

```

```
Next x
```

```

For j = xcrit + 1 To capacity           'update p1
  q1(t - 1, j) = q0(t, j)
Next j

```

```
Next t
```

```
Rem   Print parameter values
```

```
If er = 100 Then
```

```
Worksheets(1).Select
```

```
Cells(1, 1) = "xcrit = " + CStr(xcrit)
```

```
Cells(2, 1) = "capacity = " + CStr(capacity)
```

```
For i = 1 To npatch - 1
```

```
  Cells(3, 1) = "ebeta(" + CStr(i) + ") = " + CStr(ebeta(i))
```

```
Next i
```

```
For i = 1 To npatch
```

```
  Cells(3 + i, 1) = "rbeta(" + CStr(i) + ") = " + CStr(rbeta(i))
```

```
Next i
```

```
For i = 1 To npatch
```

```
  Cells(5 + i, 1) = "rlambda(" + CStr(i) + ") = " + CStr(rlambda(i))
```

```
Next i
```

```
For i = 1 To npatch
```

```
  Cells(7 + i, 1) = "Y(" + CStr(i) + ") = " + CStr(Y(i))
```

```
Next i
```

```
Cells(9, 3) = "Time = " + CStr(Time)
```

```
Cells(10, 1) = "% Error"
```

```
Select Case erroneous
```

```
  Case 1
```

```
    Cells(10, 2) = "elambda"
```

```
  Case 2
```

```
    Cells(10, 2) = "ebeta"
```

```
End Select
```

```
Cells(10, 3) = "fitness@x=4"
```

```
Cells(10, 4) = "fitness@x=13"
```

```
End If
```

```
Rem   Print fitness results
```

If er = 100 **Then** ro = 11 **Else** ro = ro + 1

Cells(ro, 1) = er

Select Case erroneous

Case 1

Cells(ro, 2) = elambda(2)

Case 2

Cells(ro, 2) = ebeta(2)

End Select

Cells(ro, 3) = ql(Time, 4)

Cells(ro, 4) = ql(Time, 13)

Next er

Beep

End Sub

3.7 References

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Chapter 4: Perceptual Constraints: A Lack of Information?

4.1 Abstract

Without perfect recognition of the available options, animals must sample the options to acquire information and assess their choices. These assessments will be formed with uncertainty, increasing the problem faced by animals trying to distinguish among the available choices. Previous work has shown how decision makers can use new information to update assessments with uncertainty, however, little work has been done on how these assessments are used or how uncertainty can constrain the decision making process. Here I propose a model based upon perceptual constraints, the Z model, to explain how animals can distinguish between options when there is uncertainty in their assessments. The Z model predicts that smaller differences and greater inherent variance will lead to increased information demands and a longer decision process.

4.2 Introduction

The need for information is a ubiquitous problem faced by animals. Without information, the ability to distinguish between options may be severely limited. Early models in behavioural ecology assumed that animals had complete information (see examples in Stephens & Krebs 1986), however, this assumption has been relaxed, and many researchers have started to investigate the effects of incomplete information on the decisions made by animals (e.g. Stephens 1987; Valone & Brown 1989; Mangel 1990; Roitberg 1990; Valone 1991, 1992; Templeton & Giraldeau 1995; Koops & Abrahams 1998, chapter 3).

Ideal free distribution (IFD) theory is one area where animals were assumed to have ideal knowledge of the distribution of resources, and predicts that in a continuous input IFD animals would distribute themselves among patches in proportion to the available resources (Fretwell & Lucas 1970). Deviations from an IFD are common, with most deviations consistently occurring toward under use of good patches and overuse of poor patches (Abrahams 1986; Kennedy & Gray 1993). Abrahams (1986), considering that these deviations could be caused by a violation of the IFD's assumption of ideal knowledge of the distribution of resources, proposed the perceptual limits model (PLM). Abrahams proposed that animals have a perceptual limit, and when the difference in quality between patches is less than the perceptual limit, the patches will be indistinguishable. Through computer simulations, Abrahams showed that when animals were limited in their ability to distinguish patch quality, they produced biased distributions consistent with many of the observed biases (c.f. Kennedy & Gray 1993; Spencer et al.

1995, 1996).

The PLM does not specify the reason for an animal's perceptual limit. If a perceptual constraint is dictated by limitations on the animal's cognitive ability to process information, then the animal has a cognitive constraint. With a cognitive constraint, any mean difference less than the perceptual limit would be indistinguishable, and there would be nothing an animal could do to discern between these options. Alternatively, a perceptual constraint could be caused by a lack of information (Mitchell 1989; Watterson 1992). In this situation, perception is constrained by limitations on the acquisition of information, and the perceptual limit is determined by the difference discernible with a given amount of information. Under an informational constraint, an animal may have the opportunity to gather more information, potentially allowing it to distinguish between previously indistinguishable options, thereby appearing to lower its perceptual limit. For example, Gray and Kennedy (1994) found that decreasing the overall input rate of food reduced the apparent perceptual limit of mallard ducks, *Anas platyrhynchos*, from 0.5 to about 0.14 food items per minute.

Abrahams' (1986) PLM assumes that, with the exception of mean differences below the perceptual limit, animals have complete information about the quality of options, i.e. options are immediately and accurately recognized. If, instead, animals must assess the options, they will have a sample distribution of the quality of each option. This sample distribution will have a mean and variance from n samples of a given option, each sample providing an observation or experience, x_i . Now, if an animal must choose between two options, it is faced with trying to distinguish between two sample distributions, each with a mean, \bar{x}_a and \bar{x}_b , and variance, s_a^2 and s_b^2 respectively (Fig.

4.1). Obviously, the more variable the sample distributions or the less difference between the means, the more difficult it will be to distinguish between the options and the greater the chance of an erroneous decision. Thus, Abrahams' (1986) approach to perceptual constraints of only considering the means, while useful, may have underestimated the effect of informational constraints, since sampling was not required.

The process described above, where an animal updates a previous assessment of an option with new information is known as Bayesian assessment. With Bayesian assessment, an animal starts with an initial expectation of the value of an option, known as the prior. This prior expectation is distributed with a mean, \bar{x}' , and uncertainty about the mean, s'^2 . The prior expectation can be based on previous experience with the option of interest, a general expectation of the average value of the option, or an evolutionarily selected expectation. When the animal samples the option, more information is acquired, having a mean, \bar{x} , and a variance, s^2 , forming the current sample distribution. Using Bayes' Theorem, the prior distribution can be combined with the current sample distribution to form an updated distribution, known as the posterior. Lee (1989) shows that, when the prior is normally distributed, the posterior distribution will have a mean:

$$\bar{x}'' = \frac{n'\bar{x}' + n\bar{x}}{n''} \quad (4.1)$$

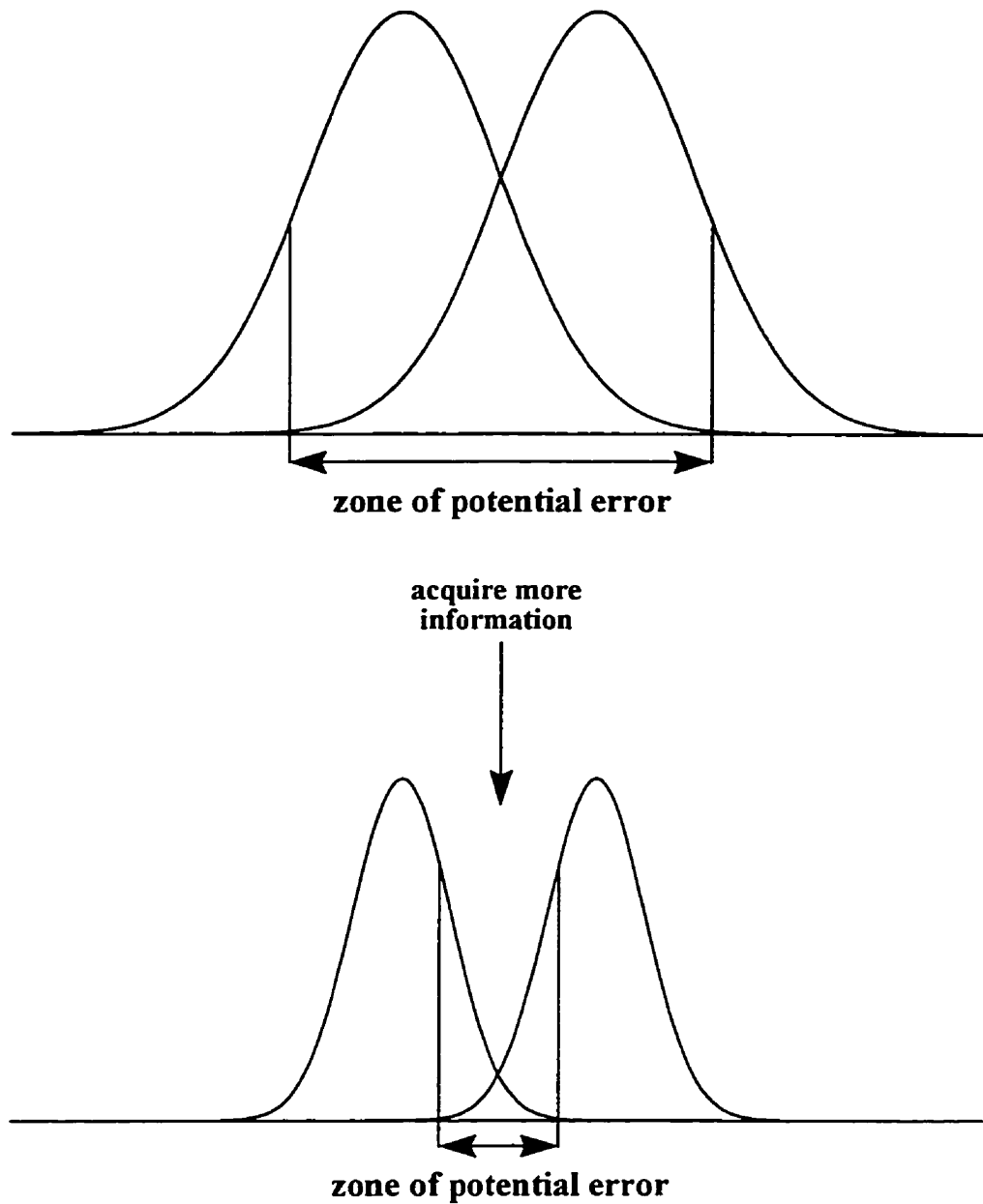


Figure 4.1. With limited information, an animal's assessment of the options may have high uncertainty, so distinguishing between the options is fraught with the dangers of an erroneous decision. By acquiring more information, uncertainty about the assessments are reduced, the chance of an erroneous decision is reduced, and true differences can be separated from differences caused by sampling error.

where n' is the prior number of experiences, n is the number of samples (pieces of information) composing the current sample, and $n'' (= n' + n)$ is the posterior sample size.

The posterior distribution will also have a variance about the mean (Lee 1989):

$$s_{\bar{x}}^{2''} = \frac{(n' - 1)s^{2'} + (n - 1)s^2 + \left[\frac{1}{n'} + \frac{1}{n} \right] [\bar{x}' - \bar{x}]^2}{n'' - 1}. \quad (4.2)$$

Notice that all prior values are denoted with a prime ('), all posterior values with a double prime (''), and all current values with no prime.

There are three points to note from equations (4.1) and (4.2). First, as with the classic equation for variance, uncertainty decreases as sample size increases. Thus, animals can reduce uncertainty about their assessment by acquiring more information. Second, the more information an animal acquires (increasing n), the less weight its prior expectation will carry. So, if an animal starts with erroneous prior information, this state can be remedied through the acquisition of information. Obviously, the more divergent the prior is from the actual state of the option to be assessed, the more information will be required to reduce uncertainty. Finally, these equations assume stationarity, i.e. the parameter being assessed does not change over the time period of the assessment or as a result of information acquisition.

A Bayesian assessment framework has been used in a number of experimental studies to explain behaviours such as mate choice (e.g. Hunte et al. 1985; Dale & Slagsvold 1994), patch departure (e.g. Valone & Brown 1989; Valone 1991), and memory decay (e.g. Kacelnik et al. 1987). Theoretical work has demonstrated how animals can use new information to update old assessments (e.g. McNamara & Houston

1980, Mangel 1990). To date, no one has provided a general model of decisions under uncertainty, where an animal must choose between two options, each assessed with uncertainty. Here I propose a general model of choice under uncertainty.

4.3 Z Model of Perceptual Constraints

Once an animal has acquired information, and has formed estimates with uncertainty as assessments of each available option, one option must be chosen. Due to the stochastic nature of the world, it may be impossible for an animal to acquire enough information to know which option is the best choice, with certainty. However, it would be useful to know the probability that one option is better than another, i.e. $p(a > b)$. If a and b are normal random variables, then $p(a > b) = \Phi(Z)$, where:

$$Z = \frac{\bar{x}_a'' - \bar{x}_b''}{\bar{s}_x} \quad (4.3)$$

\bar{x}_a'' and \bar{x}_b'' can be defined by equation (4.1), and the mean uncertainty of the two assessments:

$$\bar{s}_x = \sqrt{\frac{s_a^2''}{n_a''} + \frac{s_b^2''}{n_b''}} \quad (4.4)$$

n_a'' and n_b'' are the number of observations taken from, or experiences with, options a and b respectively. s_a^2'' and s_b^2'' can be defined by equation (4.2). $\Phi(Z)$ ranges between 0 and 1, and is a strictly monotonically increasing function over the range of Z . When Z is positive, anything that leads to an increase in Z will increase an animal's ability to distinguish between options. When Z is negative, anything that leads to a decrease in Z

will increase an animal's ability to distinguish between options.

This simple Z model of perceptual constraints predicts that an animal's ability to distinguish between options will increase, or the perceptual limit will decrease, when: (1) the mean difference increases, *as per* Abrahams (1986); (2) the mean variance decreases; or (3) the amount of acquired information (n) increases. Now, we can see that Abrahams' PLM is a special case of the Z model of perceptual constraints, where only the mean difference is considered (see Appendix 4A). This is what we would expect when animals have perfect recognition of the available options, as Abrahams' (1986) model assumes. If animals must assess the options, then we expect sample variance to have an effect on the ability of animals to perceive a difference. When options are less variable, animals will be able to assess the options more quickly, with less information, and the perceptual limit will appear to be lower. Finally, animals are able to improve their perceptual ability by increasing the amount of information they acquire from the options. Increasing acquired information, increases n in equations (2) and (4), leading to decreased uncertainty about the mean. If information is acquired continuously, rather than discretely, it can be shown that the Z model makes the same predictions (see Appendix 4B).

4.3.1 *The Confidence Function*

The $\Phi(Z)$ function defines a decision maker's confidence in a decision. When Z is close to 0, the probability that option a is better than option b is close to 0.5, and confidence is low. As Z moves away from 0, the probability that one option is better than another increases, and confidence in a decision increases. By extension of the statistics analogy,

$\Phi(Z)$ can be expressed as a cumulative probability function, and by adapting the cumulative normal probability density function found in most introductory statistic texts, we can define the confidence function (Fig. 4.2) as:

$$\Phi(Z) = \int_{-\infty}^Z \frac{1}{\sqrt{2\pi\kappa}} e^{-z^2/2\kappa} \quad (4.5)$$

where κ is the level of skepticism and occurs in the interval $0 < \kappa < \infty$. When $\kappa = 1$, equation (4.5) defines the cumulative normal probability density function for $N(0, 1)$. When $\kappa < 1$, observed differences are weighted more heavily than uncertainty, the $\Phi(Z)$ function is steeper, and less information is needed to increase confidence. Conversely, when $\kappa > 1$, uncertainty is weighted more heavily than observed differences, the $\Phi(Z)$ function is shallower, skepticism increases, and more information is needed to attain the same level of confidence in a decision.

4.4 Discussion

When animals must assess the quality of options, they are faced with the problem of distinguishing between options assessed with uncertainty. From the Z model of perceptual constraints, we find that in both the discrete and continuous cases considered here, similar factors are predicted to influence the perceptual abilities of animals. First, *as per*

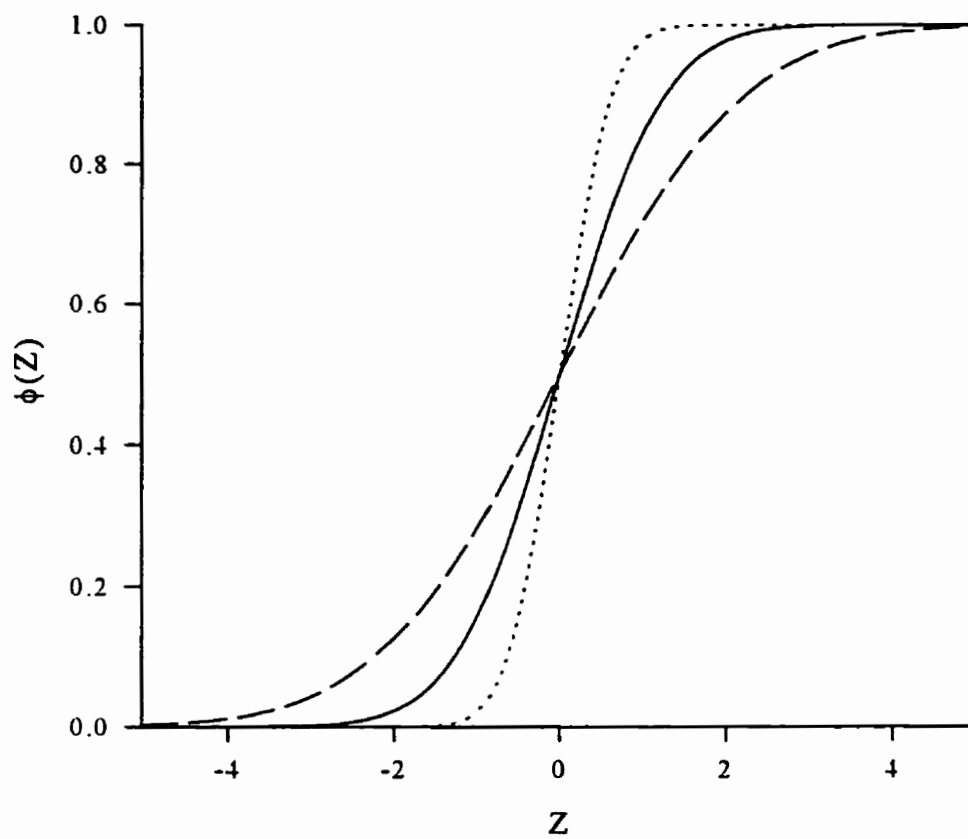


Figure 4.2. The form of the $\Phi(Z)$ function for (—) an assessment of normally distributed options with $\kappa = 1$, (.....) an optimistic decision maker with $\kappa = 0.5$, and (- - -) a pessimistic decision maker with $\kappa = 1.75$.

Abrahams (1986), it should be easier for animals to distinguish between options with greater mean differences. Second, the less variable an option, the less uncertainty around the estimated mean, which will lead to greater confidence in an observed difference. Finally, an animal can reduce its uncertainty, and increase its confidence in an observed difference by acquiring more information, i.e. boosting its sample size. A side effect of acquiring more information is that an erroneous prior expectation will have less influence on assessments as more current information is included in those assessments.

4.4.1 *Optimism vs. Pessimism*

When forming assessments, organisms can overestimate or underestimate the value of an option, what Roitberg (1990) referred to as optimism and pessimism, respectively. Using a state dependent model, Roitberg evaluated the fitness consequences of estimation errors. Roitberg's model predicted that, given the difficulty in forming a perfect assessment, fruit flies should be optimistic, overestimate patch quality, and persist in a patch longer than expected on the basis of perfect information. Field data on giving up times supported this prediction (Roitberg 1990). The reason for the predicted optimism is the smaller fitness consequences of overestimating patch quality relative to underestimation. Others have concluded that animals should show under or overestimation in assessments of both patch quality and predation risk (Bouskila & Blumstein 1992) depending on starvation curves (Abrams 1995) or life history characteristics (Koops & Abrahams 1998, chapter 3).

Biases in perception can be expressed in the Z model through the $\Phi(Z)$ function (Fig. 4.2). A bias toward optimism ($\kappa < 1$) means that an organism is willing to make a

choice at a higher level of uncertainty, creating a steeper $\Phi(Z)$ curve, and a bias toward pessimism ($\kappa > 1$) creates a shallower $\Phi(Z)$ curve representing a need for greater certainty before a choice is made. The exact form of the $\Phi(Z)$ function may depend, in part, on the cost of acquiring additional information or the cost of a misinformed decision.

4.4.2 *Sequential Assessment*

Tests of the sequential assessment model (Enquist & Leimar 1983) can provide some support for the Z model of perceptual constraints. The sequential assessment model (SAM) assumes that animal contests involve individuals assessing the fighting ability of their opponents, and the behaviour observed during contests is the most efficient way to acquire information about an opponent. The SAM predicts that individuals differing greatly in fighting ability should settle contests quickly, whereas contests between individuals with small differences should take longer to settle. The Z model makes a similar prediction. The closer two individuals are in fighting ability, the more information would be required to reduce the sample variance to the point where the difference is detectable with confidence. When one individual has enough information to determine that its opponent's fighting ability is greater than its own, this individual should quit the contest. Enquist et al. (1990) and Koops and Grant (1993) both found empirical support for this prediction in fighting cichlids, *Nannacara anomala* and *Cichlasoma nigrofasciatum* respectively, suggesting that sample variance is an important factor in detecting differences. Alternatively, if perceptual limits could be explained on the basis of mean differences alone, then as soon as information about the fighting ability of an

opponent is acquired a decision can be made, and the magnitude of the difference would not influence the time to obtain a complete assessment.

4.4.3 *Ideal Free Distributions*

Abrahams (1986) originally proposed the perceptual limits model for the ideal free distribution (IFD). When applied to the IFD, does the more general Z model of perceptual constraints make any new predictions? The continuous model (Appendix 4B) can describe a continuous input IFD with no patch depletion. Under these conditions, the Z model would predict that a foraging group should approach the IFD as individual foragers acquire more information (e.g. Milinski 1979, his Fig. 2). Information is acquired through sampling time, so the more time foragers spend experiencing the patches, the more certain they should be about their assessments, and the more stable the group distribution should become, leading to reduced variance in forager distributions. With enough time to acquire the information necessary to reduce their uncertainty, the stable distribution of foragers among patches should approximate the IFD, if deviations are caused solely by a violation of the assumption of ideal knowledge.

The pivotal difference between Abrahams' (1986) PLM and the Z model is the mechanism of perceptual constraint. In the PLM, perception is constrained by a perceptual limit (see Appendix 4A), whereas perception is constrained by uncertainty in the Z model. Thus, the PLM makes no predictions about the influence of variance in food intake on perceptual constraints, whereas the Z model predicts that increased variance in intake will increase uncertainty, leading to longer assessment times and greater variance in

forager distributions.

4.4.4 *Perfect Information*

From the Z model, one might conclude that, given the time to acquire enough information, animals should be able to distinguish between any options, regardless of how minor the difference. This, however, would be a very simplistic view of the world. It takes time for animals to acquire information. As time passes, the initially acquired information ages. We know that animals discount aging information (e.g. Kacelnik et al. 1987), and when information is old enough, it is no longer used in assessments. Discounting old information is important to maintaining a current assessment that can track a changing environment. If old information is not eliminated, current assessments will be trapped by the weight of outdated and irrelevant information. Two general mechanisms have been proposed to explain how old information can be discounted. One proposal is that animals use memory windows to keep their assessments current (Krebs & Cowie 1976; Cowie 1977; Valone 1992). Only information less than a certain age is used, anything older is ignored. Alternatively, information may be discounted according to a decay function (e.g., Harley 1981; Regelman 1986; Kacelnik et al. 1987; Devenport & Devenport 1994). As information ages, it is weighted less and less until it is eventually dropped from the assessment. Regardless of the mechanism by which aging information is discounted, the fact that information ages and acquiring information takes time, leads to a limit on the amount of information an animal can acquire, and thus a limit on its ability to distinguish between options. Aging information results in a trade-off between the ability to

discriminate current differences among options and the ability to adapt to changes in those options.

The equations used in the development of the Z model (equations 4.1, 4.2, 4.B1 and 4.B2) do not discount aging information, however, this can be rectified. Mangel (1990) provides equations for the assessment of the rate of encounter (λ) of a Poisson process, which includes a memory parameter so that prior information is discounted as it ages. Mangel's equations for the mean and variance of the rate of encounter can replace equations (4.B1) and (4.B2), providing a form of the Z model with aging information. This modification would not change the predictions of the Z model discussed so far, however, higher rates of memory decay could lead to longer assessment times and occasional sampling to reduce uncertainty about the state of alternative options.

4.4.5 Conclusions

Any support for the Z model of perceptual constraints does not mean that perceptual limits are not affected by cognitive constraints. Animals can be cognitively constrained in the amount of information they can process, or the number of information sources they can attend to at any one time, which would extend the amount of time needed to acquire the information to distinguish between options. Describing perceptual constraints as informational or cognitive constraints do not have to be mutually exclusive explanations. The ability of an animal to distinguish between sampled options is likely to depend on its cognitive ability to process information (Yoerg 1991), the amount of information acquired which determines uncertainty in assessments, and an evolutionary balance between the

costs of acquiring and processing additional information and the benefits of additional information to decision making (Stephens 1989).

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4.5 Appendix 4A - No Uncertainty

Contrary to Abrahams' (1986) perceptual limits model, the Z model of perceptual constraints does not have a specified perceptual limit. Instead, in the Z model, perception is constrained by uncertainty in assessments. However, Abrahams' perceptual limits model can be expressed as a special case of the Z model where:

$$Z = \frac{\bar{x}_A - \bar{x}_B}{PL} \quad (4.A1)$$

where \bar{x}_A and \bar{x}_B are the perceived values of options A and B, respectively, and PL is the decision maker's perceptual limit. If we define the $\Phi(Z)$ function as:

$$\Phi(Z) = \begin{cases} 0 & \text{if } Z < -1 \\ 0.5 & \text{if } -1 \leq Z \leq 1 \\ 1 & \text{if } Z > 1 \end{cases} \quad (4.A2)$$

the decision maker will choose the better option, with certainty, except when the perceived difference is less than or equal to its perceptual limit, at which point an option is chosen randomly, *as per* Abrahams (1986).

4.6 Appendix 4B - A Continuous Z Model

Information may be acquired continuously over the time an animal experiences an option. For example, the continuous acquisition of information occurs when an animal is assessing predation risk, availability of mates, or quality of foraging in alternative habitats. If we assume that events are encountered according to a Poisson process, where the occurrence of any event is random and independent of the occurrence of any other event, then the important parameter to assess is the rate of encounter, λ . Events may be encounters with predators, mates, or food items. The information an animal has access to is the amount of time spent sampling an option, t , and the number of encounters during that time period, r . These pieces of information are sufficient to estimate the rate of encounter of a Poisson process (Pratt et al. 1995). The posterior number of events observed is $r'' = r' + r$, and the posterior time spent sampling an option is $t'' = t' + t$.

Pratt et al. (1995) show that the posterior estimate of the mean rate of encounter (λ) is estimated as:

$$\bar{\lambda}'' = \frac{r' + r}{t' + t} = \frac{r''}{t''}. \quad (4.B1)$$

The number of encounters observed and the time spent sampling the option are also sufficient to calculate uncertainty about the estimated mean encounter rate (Pratt et al. 1995):

$$s_{\bar{\lambda}''}^2 = \frac{t}{t' + t} \frac{r'}{t'^2}. \quad (4.B2)$$

We can now take the estimated mean encounter rate and the variance for each

option, and ask what the probability is that option a has a greater encounter rate than option b, or $p(\lambda_a > \lambda_b) = \Phi(Z)$. This is now the same question asked in the discrete version of the Z model, so:

$$Z = \frac{\bar{\lambda}_a'' - \bar{\lambda}_b''}{\bar{s}_\lambda} \quad (4.B3)$$

which is the same form as equation (4.3). In this continuous form, the sample size is the sampling time, so the mean variance is:

$$\bar{s}_\lambda = \sqrt{\frac{s_a''}{t_a''} + \frac{s_b''}{t_b''}}. \quad (4.B4)$$

Now we can see that both the continuous and discrete versions of the Z model of perceptual constraints make the same predictions. In the continuous version, however, an increase in acquired information is accomplished by increasing the amount of time spent experiencing the options.

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Chapter 5: Assessment Uncertainty and the Ideal Free Distribution

5.1 Abstract

Previous models of the ideal free distribution (IFD) either assumed that animals had perfect information about the distribution of resources, or assumed perfect recognition with some limitation on the perception of differences. Without perfect recognition, animals must sample the options to acquire information and assess their choices. These assessments will be formed with uncertainty, increasing the problem faced by animals trying to distinguish between available options. Using a Z model of perceptual constraints as the decision rule, an individual based computer model was constructed to look at group level dynamics of foragers assessing food distributions with uncertainty. Simulation results predict that deviations from an IFD are influenced by memory, group size, and rate of encounter with food, with both the distribution of foragers and competitive abilities tending to undermatch the resource distribution. The time for a group to reach an equilibrium distribution is influenced by memory, group size, and the group's initial deviation from the distribution of resources. The greatest constraint on conformity to an IFD appears to be memory, which also influences the time to reach equilibrium. This suggests that the ability of a foraging group to conform to an IFD is limited by the ability of individuals to adapt to changing foraging conditions.

5.2 Introduction

When animals distribute themselves among patchily distributed resources, the continuous-input ideal free distribution (IFD) predicts that the distribution of animals should match the distribution of resources. The reason for this prediction is that social foraging is a game where patch selection by one forager influences the payoff to other foragers. When foragers are distributed according to the distribution of resources, no forager can improve its intake rate by unilaterally switching patches, and the IFD is the Nash equilibrium. IFD theory rests on a number of assumptions (Fretwell & Lucas 1970), not the least of which are: (i) organisms have ideal knowledge of the distribution of resources; (ii) all organisms are free to move about their environment; (iii) all competitors are equal; (iv) organisms behave to maximize their rate of resource acquisition; and (v) travel costs are negligible. While these assumptions are rarely, if ever met, some tests have shown that the IFD performs well at predicting the distribution of many animals (Milinski 1988, Milinski & Parker 1991), though not all (Kennedy & Gray 1993).

Even when animals approximate the distribution of resources, there tend to be consistent biases where animals undermatch the resource distribution, i.e. underuse the good patch, overuse the poor patch (Abrahams 1986, Kennedy & Gray 1993). To explain this consistent bias in the distribution of animals, researchers have either relaxed the assumption of equal competitors or ideal knowledge, providing a rich literature on IFDs with unequal competitors (e.g. Parker 1982, Sutherland 1983, Parker & Sutherland 1986, Houston & McNamara 1988, Hughie & Grand 1998) or perceptual constraints (e.g. Abrahams 1986, Gray & Kennedy 1994, Spencer et al. 1995, 1996). When the

assumption of ideal knowledge is relaxed, it is typically done by assuming that animals have a limit on the mean difference that can be perceived, i.e. animals have a perceptual limit (Abrahams 1986, c.f. Kennedy & Gray 1993, Spencer et al. 1995, 1996, Cartar & Abrahams 1997). However, this approach assumes that, even though animals have a perceptual limit, resource patches are immediately and accurately recognized. As Gray and Kennedy (1994) discovered, the problem with assuming a perceptual limit is that a different perceptual limit is needed to explain increased deviations from the IFD as the rate of food input is increased. Koops (unpubl. ms, chapter 4) provides an alternative approach to perceptual constraints where animals acquire information about the quality of resource patches, and use that information to form assessments with uncertainty. In this model, the perception of an animal is constrained by its assessment uncertainty, not a predefined limit. The choice of a resource patch for exploitation is then made on the probability of choosing the best patch, i.e. the patch that maximizes personal acquisition rate.

The Z model of perceptual constraints proposed by Koops (unpubl. ms, chapter 4) is a general decision rule applicable to any situation where animals make decisions under uncertainty. In this paper, we set out to build an IFD model using the Z model of perceptual constraints as the decision rule. Previous IFD perceptual constraint models (Abrahams 1986, Gray & Kennedy 1994, Spencer et al. 1995, 1996) assumed that information was free and left the mechanism of perceptual constraint unspecified. In the present model, animals must pay for information by sampling and we investigate

assessment uncertainty as the mechanism of perceptual constraint. We then use the IFD literature to independently test model predictions in a meta-analysis.

5.3 The Model

To model the patch selection decisions of imperfectly informed foragers, we used an individual-based modelling (IBM) approach. For an IBM, the behaviour of each individual within the computer simulation is coded and controlled individually. The resulting spatial distribution of the group becomes an emergent property of how individuals make patch choice decisions. Since we are modelling the patch selection behaviour of foragers with assessment uncertainty, we will compare the results of this model to the Nash equilibrium, i.e. the IFD, to determine how assessment uncertainty influences the ability of foragers to optimize their behaviour.

We model a continuous input system where food enters a patch at a set rate according to a Poisson process. Food is available to be consumed when it enters the patch, but does not accumulate in the patch. As foragers search for food, they use personal sample information to form an assessment of patch quality with uncertainty. Under these conditions, it is important for an individual to assess the rate at which food is acquired. Since food enters the patch according to a Poisson process, the important parameter to estimate is the rate of encounter with food (λ). To estimate the rate of encounter, it is sufficient to know the number of events (r), i.e. food items encountered, and the amount of time (t) to encounter those events (Pratt et al. 1995). Our modelled foragers use a Bayesian assessment approach, where a prior expectation of patch quality is

updated on the basis of current information to form a posterior expectation of patch quality. This posterior expectation can then be used as the prior expectation to form future assessments. Bayesian assessment uses updating rules to combine prior and current information. Mangel (1990) showed that assessment of the rate of encounter for a Poisson process can be updated according to the following rules:

$$\begin{aligned} r_i'' &= \psi r_i' + r_i + (1 - \psi)r_0 \\ t_i'' &= \psi t_i' + t_i + (1 - \psi)t_0 \end{aligned} \quad (5.1)$$

where the prior expectation of reward (r) and time (t) are denoted with a prime ($'$), the posterior, or updated, expectation by a double prime ($''$), and the current values with no prime. r_0 and t_0 represent the default values for r and t respectively (see Table 5.1 for parameter values). ψ is the memory parameter, representing the rate at which prior information is devalued. A ψ value of 0 represents no memory and 1 represents perfect memory. When a forager samples a patch, r_i and t_i are the number of food items encountered and time spent in the patch respectively. Assessments for unsampled patches are also updated, but with $r_i = t_i = 0$. When a patch is not sampled, the assessments of r_i and t_i'' decay towards r_0 and t_0 at a rate dependent on ψ .

The rate of encounter in a patch is assessed using the updating rules in equations (5.1) so that:

$$\bar{\lambda}_i = \frac{r_i''}{t_i''}. \quad (5.2)$$

Uncertainty about the assessed rate of encounter (Mangel 1990) is:

Table 5.1. Model parameters, values and descriptions.

| Parameter | Value | Description |
|-------------|---|--|
| r_0 | 1 | Default assessment of r |
| t_0 | 1 | Default assessment of t |
| r', r'' | ... | Prior & posterior assessment of r |
| t', t'' | ... | Prior & posterior assessment of t |
| r | ... | Rewards obtained in latest sample period |
| t | ... | Duration of latest sample period |
| T_s | 5 | Number of time steps per sample period |
| R | 0.20, 0.40, 0.50, 0.665, 0.75 | Proportion of food in patch 1 |
| ψ | 0.85, 0.90, 0.95, 0.99999 | Memory decay parameter |
| λ | 0.05, 0.10, 0.20, 0.40 | Total rate of food input |
| N | 5, 10, 20, 40 | Total number of foragers |
| λ/N | 0.00125, 0.0025, 0.005, 0.01, 0.02, 0.04, 0.08 | Total rate of food input per forager |
| c_j | ... | Randomly assigned competitive ability |
| T_T | 10 000 | Total number of time steps per model run |

$$s_i^2 = \frac{r_i''}{t_i''}. \quad (5.3)$$

Thus, an imperfectly informed forager need only remember r_i'' and t_i'' to maintain a current assessment of patch quality and their uncertainty about that assessment.

The modelled foragers choose among patches using the Z model of perceptual constraints as the decision rule (Koops unpubl. ms, chapter 4), where a forager chooses a patch according to the probability that it is better than another patch. This assumes that foragers have been selected to maximize their personal food intake rate, and that travel time and costs are negligible (*as per* Fretwell & Lucas 1970). The probability that patch A is better than patch B is based on the area under a normal distribution (Hogg & Tanis 1988), and is defined as:

$$P(\bar{\lambda}_A > \bar{\lambda}_B) = \Phi(Z) = \int_{-\infty}^Z \frac{1}{\sqrt{2\pi}} e^{-z^2/2} \quad (5.4)$$

where Z is the mean difference expressed in standard deviation units:

$$Z = \frac{\bar{\lambda}_A - \bar{\lambda}_B}{\bar{s}} \quad (5.5)$$

and:

$$\bar{s} = \sqrt{\frac{s_A^2}{t_A''} + \frac{s_B^2}{t_B''}}. \quad (5.6)$$

$\Phi(Z)$ is a monotonically increasing function over the range of Z and anything that increases the absolute value of Z will increase the perceptual ability of the forager (Koops unpubl. ms, chapter 4).

All foragers are assigned a competitive ability that determines their relative ability to acquire food in a patch. Each forager obtains a portion of the food entering a patch according to the proportion of competitive abilities they represent in that patch, i.e. food is infinitely divisible. The assigned competitive ability, c_j , is a random value greater than zero, from a normal distribution with $\bar{x} = 1$ and $s = 0.25$, with:

$$c_j = \bar{x} + s\left(\sqrt{-2\log z_1}\right)\cos(2\pi z_2) \quad (5.7)$$

where all z_1 and z_2 are uniform random numbers from the range 0 to 1 (Hilborn & Mangel 1997). These competitive abilities are assigned at the beginning and do not change over the course of the simulations.

To seed the simulations, we gave all foragers a prior expectation of $r_o = 1$ and $t_o = 1$, so that $\bar{\lambda}_i = 1$ and $s_i^2 = 1$ for each patch, and the default assessment is that all patches are equal. These values were chosen for three reasons. First, relatively large default values (see Table 5.1 for actual λ values) were used to encourage occasional re-sampling late in the simulations. If the defaults are small, unsampled patches decline in value and will never be re-sampled. Second, this ensures that assessment uncertainty of unsampled options is relatively high, again encouraging re-sampling. Finally, the initial prior expectation will carry little weight because $t_o = 1$. Since the initial prior is based on only one time unit of information, its effect on patch assessment will be quickly swamped by current information. However, the effect of the initial prior will also be influenced by

memory (ψ), exhibiting a greater effect at low memory values. Foragers are then randomly distributed among patches for time step 0. Every five time steps, all foragers simultaneously re-evaluate their assessment and assessment uncertainty of each patch quality according to the updating rules outlined by equations (5.1), (5.2) and (5.3), then choose a new patch according to the decision rule outlined by equation (5.4). Every forager chooses patches based on their own independent assessment of patch quality. The model assumes that foragers have been selected to maximize their personal food intake rate, and that travel time and sampling costs are negligible.

5.3.1 *Model Output*

Simulations were run for a total of 10 000 time steps (T_T), for each of five food ratios (R), four group sizes (N), four total food input rates (λ), and four memory values (ψ) (see Table 5.1). Thus, we have data from 320 simulations across the five food ratios, providing the slope of 64 group distribution versus food distribution regressions for each N - λ - ψ combination (see below). Each parameter combination was replicated 500 times, and the mean proportion of foragers and the mean proportion of competitive abilities in patch I were recorded every 30 time steps to generate group level dynamics for the mean of 500 replicates of each N - λ - ψ combination (Fig. 5.1).

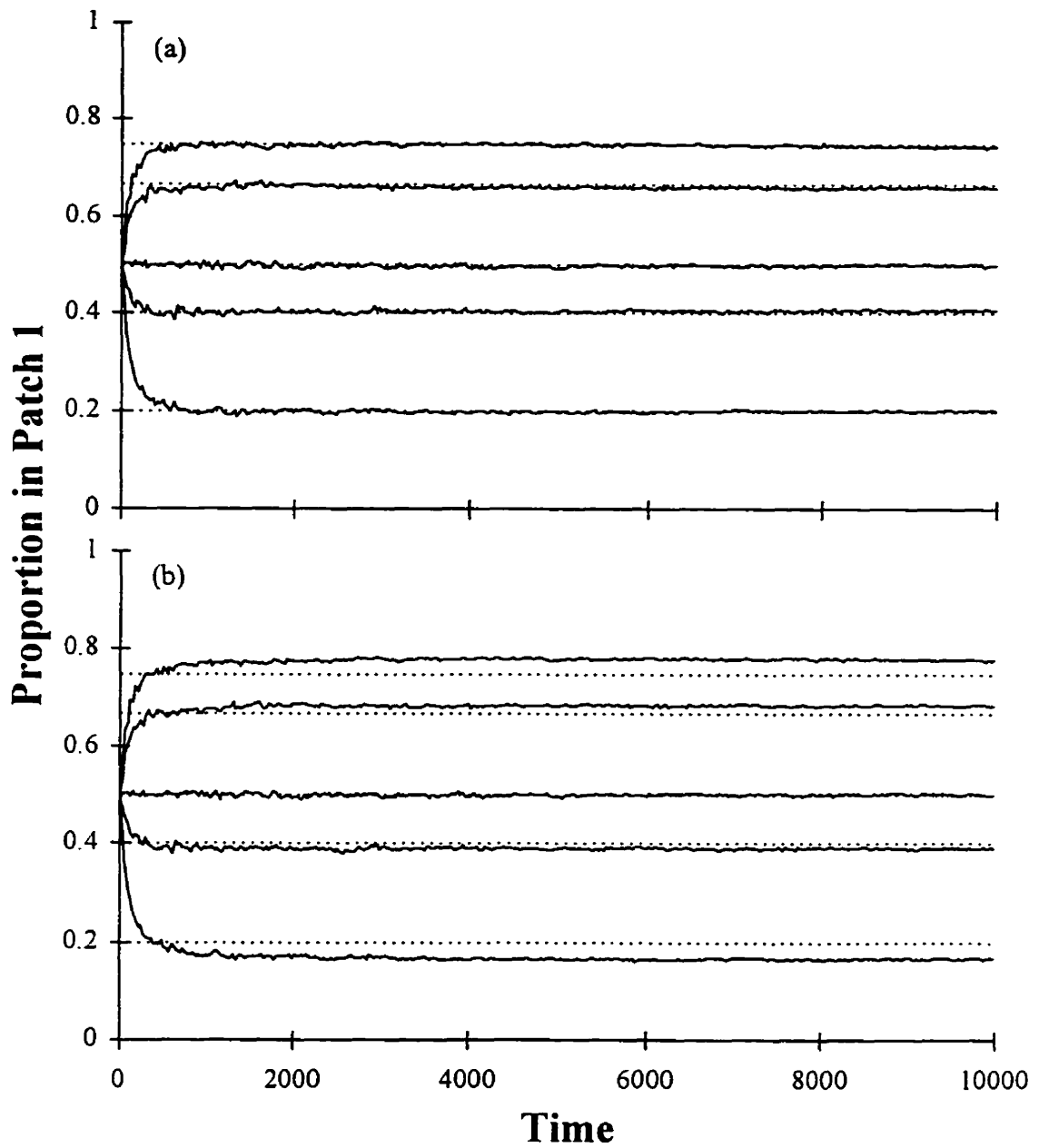


Figure 5.1. An example of the time series data for the distribution of (a) foragers and (b) competitive abilities for $N = 10$, $\lambda = 0.20$, and $\psi = 0.99999$. Reference lines represent the distribution of resources.

To obtain the equilibrium proportion of foragers (or competitive abilities), the final 1000 time steps of a run were used to calculate the mean proportion of foragers (or competitive abilities) in patch 1. Equilibrium was determined as being reached when the proportion settled at the mean of the last 1000 time steps ± 0.02 . Starting from $t = 0$, each data point was classified as being inside ($p_t = 1$) or outside ($p_t = 0$) of this tolerance zone. Ten consecutive p_t points were used to calculate the mean number of data points within the tolerance zone (\bar{p}), providing a number between 0 and 1. The time to equilibrium (t_{eq}) was reached when at least nine of ten observation points were inside the tolerance zone ($\bar{p} \geq 0.9$), as long as \bar{p} did not fall below 0.7 thereafter. These criteria, while arbitrary, ensure that t_{eq} is not established too soon, and that equilibrium is not lost when a forager samples.

To measure conformity to the IFD, we calculated the slope of the regression of the \log_{10} equilibrium proportion foragers (or competitive abilities) in patch 1 against the \log_{10} proportion of food in patch 1, for all 64 N - λ - ψ combination of parameters. Deviation from the IFD was calculated as this slope minus one (the IFD predicted slope). Negative deviations represent underuse of the good patch and overuse of the poor patch, i.e. undermatching. Positive deviations represent overmatching.

For the first 400 replicates of each combination of model parameters, data for each individual in each replicate were recorded, including: competitive ability, probability of switching (every 5 time steps), probability of occupying the better patch (every 5 time steps), total amount of food eaten, and the proportion of food eaten in patch 1.

5.3.2 *Data Analysis*

To determine the relative influence of each of the model parameters on the results, we used a forward stepwise multiple regression approach (Kleinbaum et al. 1988). The parameters or interactions that explained the most variance in the model results were included, allowing us to drop parameters and interactions that were not necessary to explain the results of the model. Criteria for inclusion in the regression model was an F value with a significance less than 0.05, and any parameter was subsequently dropped from the regression model if the significance of its F value exceeded 0.10.

5.3.3 *Meta-Analysis Methods*

We used the IFD literature to acquire data on how our model parameters influence conformity to the IFD. We limited our data collection to continuous input IFD studies that used at least three food ratios to allow calculation of a slope (but see Kennedy & Gray 1993). Only studies that held the total input rate constant across food ratios were included. Data from treatments that manipulated the presence of predators or refuges were excluded, since the presence of a predator (Abrahams & Dill 1989) or a refuge (Utne et al. 1993) will influence patch use, though any control treatments that fit our criteria were included (e.g. Utne et al. 1993). We ignored between treatment manipulations of prior information, sex (Abrahams 1989), travel distance (Kennedy & Gray 1997), input rate (Gray & Kennedy 1994), and food size (Kennedy & Gray 1994), even though any of these factors could influence the distribution of foragers and conformity to the IFD. For any studies that did not provide a slope, we used data available in the original paper to

calculate the slope of $\text{Log}(N_1/N_2)$ vs. $\text{Log}(R_1/R_2)$, where N_1 and N_2 are the number of foragers in patch 1 and 2 respectively and R_1 and R_2 are the amount of food in patch 1 and 2 respectively. Treatments within a study were included as independent data points.

5.4 Model Results

5.4.1 *Individual Behaviour*

In this model, we specified the decision rule foragers use to make patch choice decisions. Each individual is unique in their competitive ability, and we expect this to influence the behaviour of individuals. The key individual behaviours from this model are patch switching, used by foragers to acquire information and reduce uncertainty, and the probability that a forager occupies the absolute best patch, an indication of the ability of foragers to perceive differences in patch quality.

5.4.1.1 Patch Switching

The average probability of switching is 0.33 ($s = 0.216$), ranging from a minimum of 0 to a maximum of 0.63. The probability of switching is decreased by memory (ψ) and food input rate (λ), and increased by group size (N): $P(\text{Switch}) = 2.05 - 2.49 \psi - 0.29 \text{Log}_{10}(\lambda/N)$ ($r^2 = 0.83$, $F_{2, 317} = 745$, $p < 0.001$).

On an individual basis, the probability of switching is negatively related to an individual's competitive ability, with better competitors exhibiting a lower probability of switching. The mean slope of this relationship is -0.13 ($SD = 0.13$), however, the

observed slopes range from a low of -0.63 to a high of 0 (no effect of competitive ability on switching). The slope of this relationship is influenced by memory, food input rate and group size (Table 5.2), though not linearly for any of these parameters. The influence of competitive ability on the probability of switching (Fig. 5.2) is greatest at intermediate levels of λ/N .

5.4.1.2 Foraging Location

On average, the probability that a forager occupies the best patch is determined by the distribution of food, λ/N , and memory. Use of the better patch increases with increasing λ/N and memory (ψ). Individually, we find that the probability of occupying the better patch is influenced by an individual's competitive ability, with better competitors more likely to occupy the better patch. The mean slope of this relationship is 0.18 (SD = 0.18) ranging from a minimum of 0 to a maximum of 0.61. The main influence on the slope of this relationship is λ/N , with the magnitude of the slope increasing proportionally with λ/N . When foragers have near perfect memory, competitive ability always has an influence on the patch a forager is most likely to occupy.

Table 5.2. Regression analysis of the steepness of the relationship between an individual's probability of switching and competitive ability. For the final model: $r^2 = 0.23$, $F_{3,316} = 31.59$, $p < 0.001$.

| Variable | Coefficient (SE) | r^2 change | F | df | p-value |
|--|------------------|--------------|-------|--------|---------|
| Constant | -3.72 (0.45) | | | | |
| $\text{Log}_{10}(\lambda/N)$ | -1.92 (0.22) | 0.041 | 13.45 | 1, 318 | < 0.001 |
| ψ | 3.76 (0.49) | 0.144 | 59.04 | 1, 316 | < 0.001 |
| $\text{Log}_{10}(\lambda/N) \times \psi$ | 2.02 (0.24) | 0.046 | 16.10 | 1, 317 | < 0.001 |

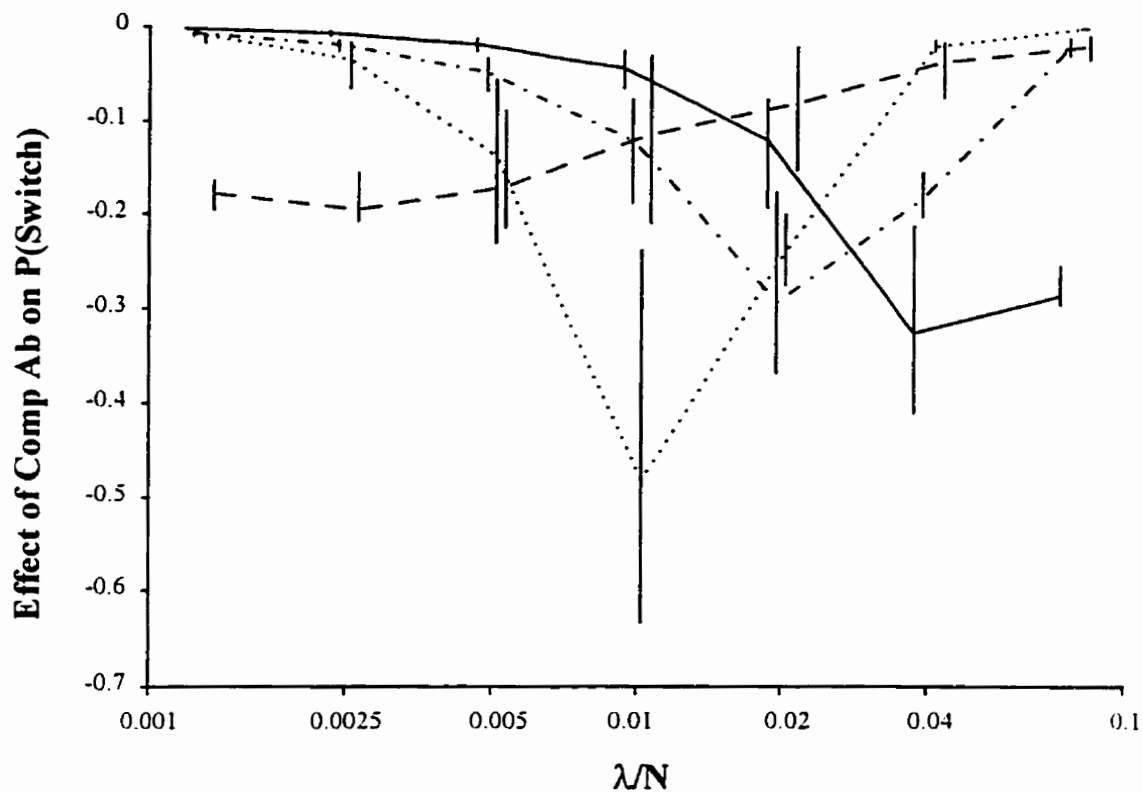


Figure 5.2. The influence of competitive ability (Comp Ab) on the probability of switching patches ($P(\text{Switch})$), as measured by the regression slope, as a function of food availability (λN), plotted on a log scale, and memory (ψ). Dashed line: $\psi = 0.99999$; dotted line: $\psi = 0.95$; dashed-dotted line: $\psi = 0.90$; and solid line: $\psi = 0.85$. All lines pass through the median, bars represent the range.

5.4.2 Group Dynamics

5.4.2.1 Conformity to the IFD

When food is limited, either due to a low total rate of food input (λ) or many competitors (N), deviations from an IFD are at their greatest. The majority of forager distributions undermatch the distribution of resources, with slopes as low as 0.03, i.e. random patch selection at all food ratios (Fig. 5.3a). At low λ/N levels, overmatching is only observed with near perfect memory ($\psi = 0.99999$). As λ/N increases, either due to increased rate of food input or decreased competitors, the distribution of both forager numbers (Fig. 5.3a) and competitive abilities (Fig. 5.3b) approaches the IFD, and this approach is faster for foragers with better memory. When λ/N is high, overmatching is common at all memory levels examined, and is more likely to occur in the distribution of competitive abilities (Fig. 5.3).

Deviation from an IFD is explained by λ/N (the rate of food input per forager) and the interaction between λ/N and ψ (Table 5.3) for both the distribution of foragers ($r^2 = 0.85$, $F_{2,61} = 177.83$, $p < 0.001$) and the distribution of competitive abilities ($r^2 = 0.86$, $F_{2,61} = 185.17$, $p < 0.001$). In both cases, conformity to the IFD was increased when the total food input rate (λ) was increased, the number of foragers (N) were decreased, or λ/N was increased (Fig. 5.3). Increased memory decreased deviation from the IFD, and foragers

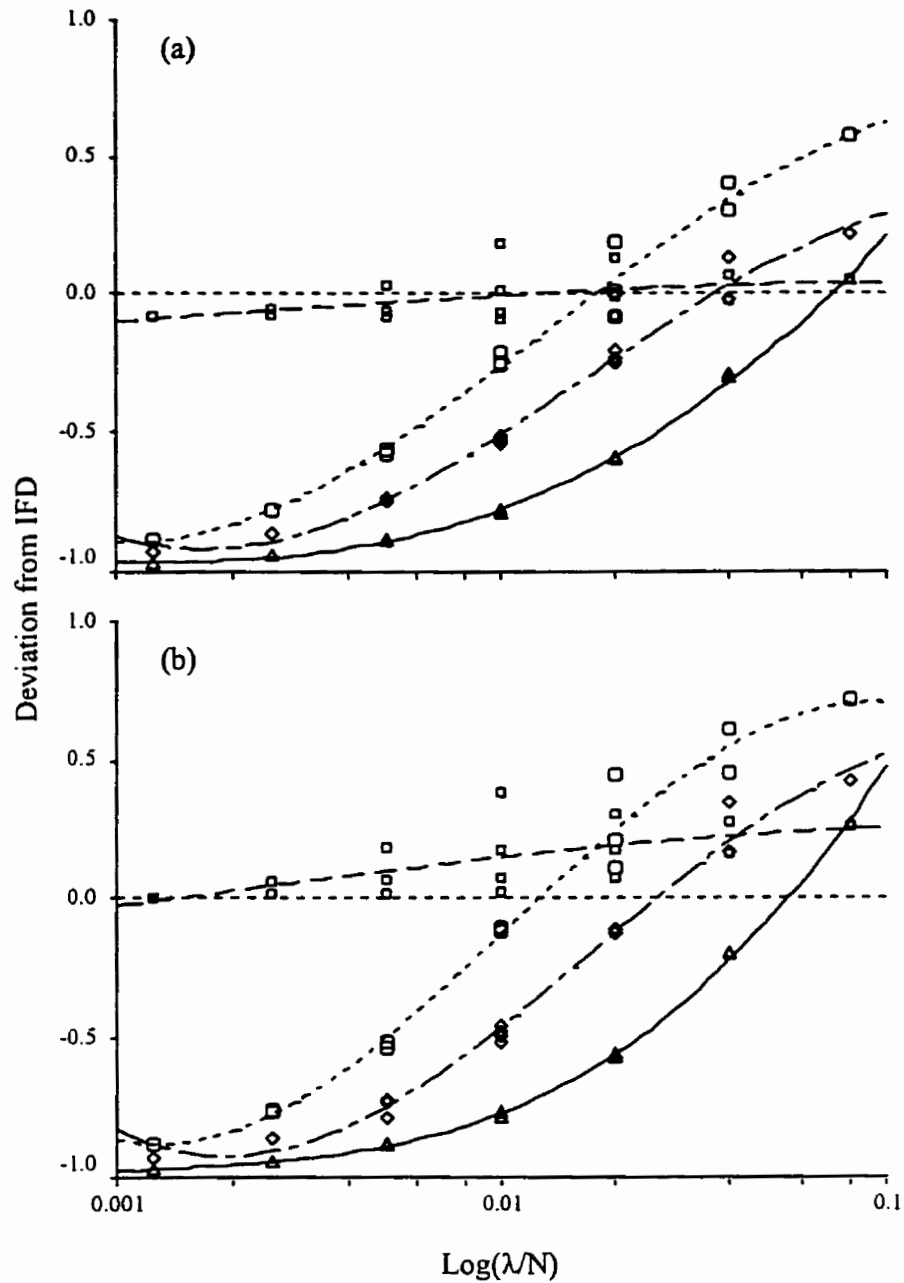


Figure 5.3. Deviation from the IFD predicted distribution of (a) forager numbers and (b) competitive abilities as a function of food availability (λ/N) for the four values of memory (ψ). Negative deviations represent undermatching, positive deviations represent overmatching. Dashed line & squares: $\psi = 0.99999$; dotted line & circles: $\psi = 0.95$; dashed-dotted line & diamonds: $\psi = 0.90$; and solid line & triangles: $\psi = 0.85$. Horizontal reference lines indicate perfect conformity to the IFD.

Table 5.3. Stepwise multiple regression results for deviation from an IFD.

| Variable | Coefficient (SE) | r^2 change | F | df | p-value |
|--|------------------|--------------|--------|-------|---------|
| (a) Foragers Numbers | | | | | |
| Constant | 0.77 (0.08) | | | | |
| $\text{Log}_{10}(\lambda/N)$ | 2.66 (0.16) | 0.43 | 47.58 | 1, 62 | < 0.001 |
| $\text{Log}_{10}(\lambda/N) \times \psi$ | -2.27 (0.17) | 0.42 | 174.75 | 1, 61 | < 0.001 |
| (b) Competitive Abilities | | | | | |
| Constant | 1.08 (0.10) | | | | |
| $\text{Log}_{10}(\lambda/N)$ | 3.11 (0.19) | 0.45 | 50.22 | 1, 62 | < 0.001 |
| $\text{Log}_{10}(\lambda/N) \times \psi$ | -2.64 (0.20) | 0.41 | 177.30 | 1, 61 | < 0.001 |

with near perfect memory ($\psi = 0.99999$) exhibited excellent conformity to the IFD at all λ/N levels. Thus, in an environment that does not change, conformity to the IFD will be increased whenever: (i) memory is increased; (ii) the rate of encounter with food is increased; or (iii) the number of competitors is decreased.

When competitors are unequal, the distribution of competitive abilities should conform to the distribution of resources. This model predicts that the slope of the distribution of foragers versus food is always less than the slope of the distribution of competitive abilities versus food (paired $t_{63} = 9.65$, $p < 0.001$). When both the distribution of foragers and competitive abilities undermatch the distribution of food, competitive abilities conform more closely to the IFD than foragers (Table 5.4). However, when the distribution of foragers and competitive abilities both overmatch the distribution of food, foragers conform more closely to the IFD than competitive abilities (Table 5.4). When foragers undermatch while competitive abilities overmatch, there is no difference in their conformity to the IFD, though in this case both conform very well to the IFD (Table 5.4). There are no cases where the foragers overmatch while their competitive abilities undermatch.

5.4.2.2 Meta-Analysis Results

From eight studies that fit our criteria, we obtained 15 data points with no more than three from any one study (Table 5.5). These IFD experiments were carried out on four species:

Table 5.4. Comparison of the regression slopes between the proportion of foragers and the proportion of competitive abilities against the proportion of food. These analyses are divided into situations where foragers undermatch or overmatch the resource distribution, and where competitive abilities undermatch or overmatch the resource distribution. m_F and m_C are the slopes of regressions with foragers and competitive abilities, respectively. Parenthetical values are standard deviations. All t-tests are paired.

| Competitive Abilities: | Foragers: | |
|-------------------------------|---|---|
| | Undermatch | Overmatch |
| Undermatch | $m_F = 0.37 (0.25)$ $m_C = 0.42 (0.29)$ $t_{37} = 5.57, p < 0.001$ | Not Observed |
| Overmatch | $m_F = 0.94 (0.029)$ $m_C = 1.08 (0.061)$ $t_{37} = 0.72, p = 0.49, \beta = 0.90$ | $m_F = 1.17 (0.17)$ $m_C = 1.36 (0.16)$ $t_{37} = 22.99, p < 0.001$ |

Table 5.5. Meta-analysis data on the influence of group size and total input rate on conformity to the IFD.

| Reference | Species | Food | Treatment | Ratios | Group Size ^a | Input Rate ^b | Slope |
|-------------------------------|-------------------------------|----------------|---------------|--------|-------------------------|-------------------------|-------|
| Abrahams (1989) | <i>Poecilia reticulata</i> | onion fly eggs | males PM | 5 | 10 | 11.42 | 0.48 |
| | | | females PM | 9 | 10 | 19.03 | 0.75 |
| Gray & Kennedy (1994) | <i>Anas platyrhynchos</i> | bread | low rate | 5 | 18.37 | 0.056 | 0.42 |
| | | | high rate | 5 | 22.91 | 0.6 | 0.65 |
| Kennedy & Gray (1994) | <i>Anas platyrhynchos</i> | bread | small pieces | 5 | 33.75 | 0.33 | 0.32 |
| | | | large pieces | 5 | 33.19 | 0.081 | 0.41 |
| Kennedy & Gray (1997) | <i>Anas platyrhynchos</i> | bread | 16m | 5 | 30.12 | 0.33 | 0.55 |
| | | | 45m | 5 | 29.12 | 0.33 | 0.42 |
| Kennedy et al. (1994) | <i>Gobiomorphus breviceps</i> | white worms | control | 5 | 12 | 0.083 | 0.42 |
| Koops & Abrahams ^c | <i>Poecilia reticulata</i> | brine shrimp | point rich | 5 | 10 | 0.19 | 0.98 |
| | | | bar rich | 5 | 10 | 0.19 | 1.16 |
| Utne et al. (1993) | <i>Gobiusculus flavescens</i> | zooplankton | control | 4 | 10 | 1 | 0.65 |
| Utne & Aksnes (1994) | <i>Gobiusculus flavescens</i> | copepods | juvenile ctrl | 4 | 10 | 0.83 | 0.82 |
| | | | male ctrl | 4 | 10 | 0.83 | 0.53 |
| | | | female ctrl | 4 | 10 | 0.83 | 0.42 |

^a Used reported mean group size for the mallard studies. ^b Input Rate measured in food items per second. ^c Unpublished data.

three fishes (guppies, bullies and gobies) and one bird (mallards). From these data, we can test two model predictions: (i) conformity to the IFD should decrease as group size (N) increases; and (ii) conformity to the IFD should increase as total food input rate (λ) increases. As predicted by the simulation results, increasing group size decreased conformity to the IFD (Fig. 5.4a). While increasing the total rate of food input tended to increase conformity to the IFD (Fig. 5.4b), this effect was weak.

5.4.2.3 Time to Equilibrium

The time to reach an equilibrium distribution of foragers is influenced by the initial deviation from the food distribution = $|R - 0.5|$, memory, and the food input rate per forager ($r^2 = 0.63$, $F_{5,314} = 107.43$, $p < 0.001$). As the initial deviation increases, time to equilibrium distribution of foragers increases, increased memory increases time to equilibrium, and less food per forager (due to decreased λ or increased N) increases time to equilibrium (Table 5.6a, Fig.5.5a). For competitive abilities, the time to reach equilibrium is mostly influenced by memory and the interaction between initial deviation and food input rate per forager (Table 5.6b, Fig. 5.5b, $r^2 = 0.54$, $F_{2,317} = 184.82$, $p < 0.001$). In both cases, increasing memory increases the time to reach the equilibrium.

Time to reach equilibrium was significantly longer (paired $t_{319} = 2.43$, $p = 0.019$) for the distribution of competitive abilities ($\bar{x} = 542.44$, $SD = 34.29$) than for the

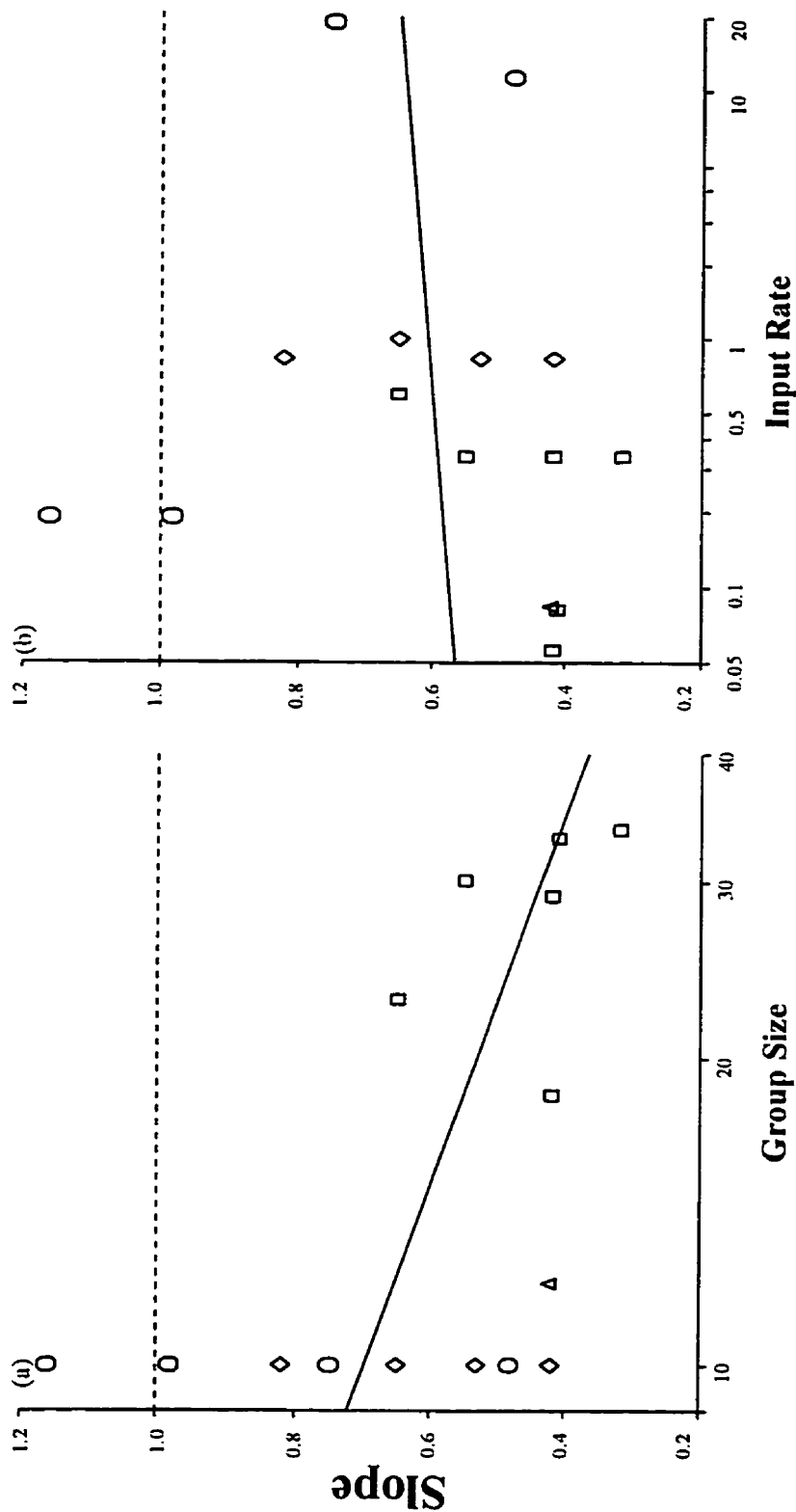


Figure 5.4. Meta-analysis of deviation from an IFD (dashed reference line) as a function of (a) group size and (b) total food input rate. Note that abscissae are plotted on a log scale. Square symbols are mallards, circles are guppies, diamonds are gobies, and the triangle is bullies.

Table 5.6. Stepwise multiple regression results for time to equilibrium, dependent variable is Log_{10} time to equilibrium.

| Variable | Coefficient (SE) | r^2 change | F | df | p-value |
|--|------------------|--------------|--------|--------|---------|
| (a) Forager Numbers | | | | | |
| Constant | 7.20 (0.63) | | | | |
| ψ^a | -5.19 (0.68) | 0.29 | 133.12 | 1, 318 | < 0.001 |
| | | -0.003 | 2.10 | 1, 317 | 0.148 |
| | | 0.068 | 57.74 | 1, 314 | < 0.001 |
| Init_Dev | -9.49 (1.29) | 0.063 | 42.41 | 1, 316 | < 0.001 |
| $\text{Log}_{10}(\lambda/N)$ | 2.62 (0.29) | 0.006 | 3.89 | 1, 315 | 0.049 |
| $\text{Log}_{10}(\lambda/N) \times \psi$ | -2.86 (0.31) | 0.031 | 22.17 | 1, 314 | < 0.001 |
| Init_Dev $\times \psi$ | 11.24 (1.40) | 0.17 | 102.08 | 1, 317 | < 0.001 |
| (b) Competitive Abilities | | | | | |
| Constant | -0.17 (0.16) | | | | |
| ψ | 2.87 (0.18) | 0.38 | 198.49 | 1, 318 | < 0.001 |
| $\text{Log}_{10}(\lambda/N) \times \psi$ | -0.44 (0.042) | 0.15 | 105.76 | 1, 317 | < 0.001 |

^a Initially, ψ entered the model, then was dropped, then picked up again.

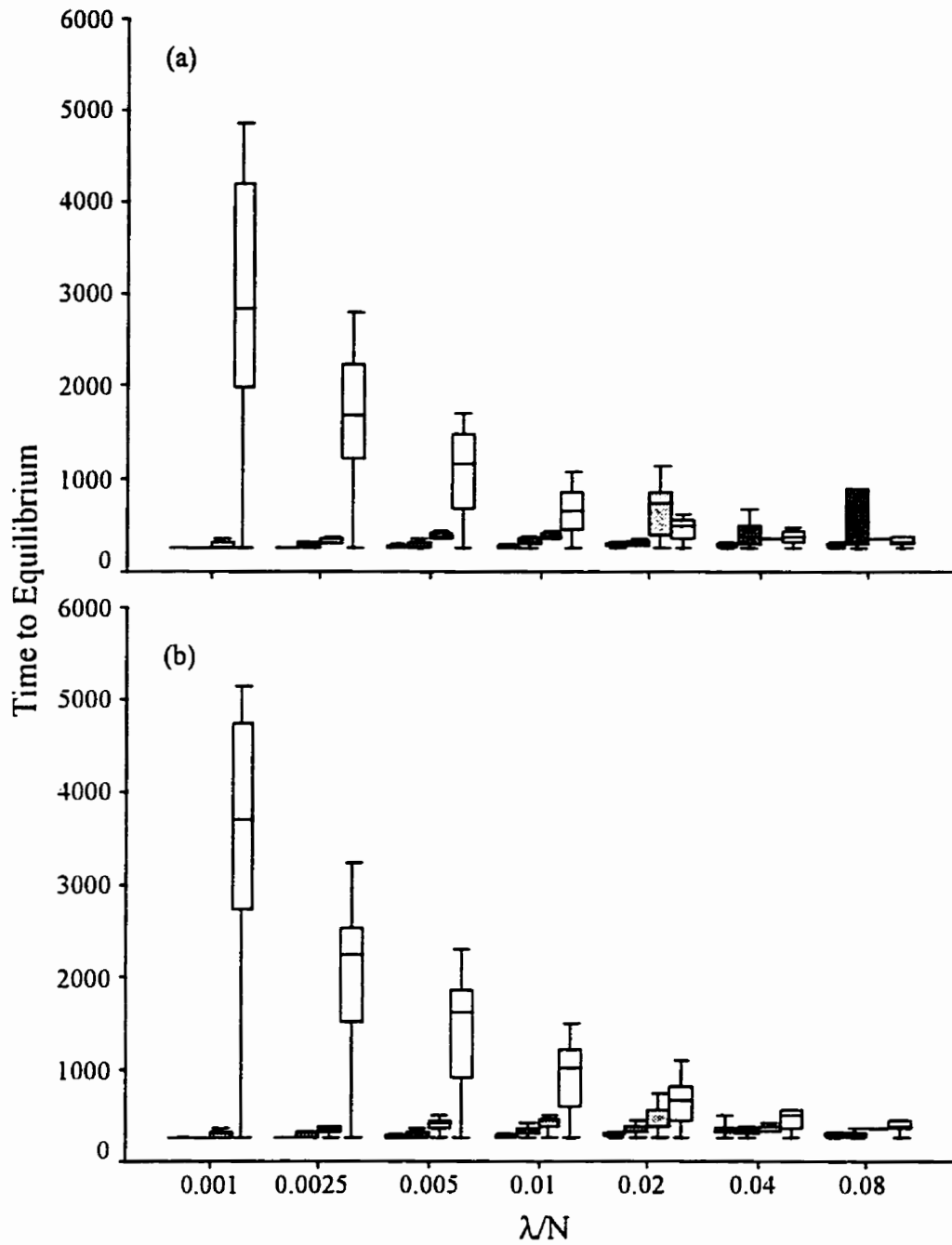


Figure 5.5. Boxplot of time to reach equilibrium for the distribution of (a) foragers and (b) competitive abilities as a function of food availability (λN) plotted on a log scale and memory (ψ). Empty boxes: $\psi = 0.99999$; light gray boxes: $\psi = 0.95$; dark gray: $\psi = 0.90$; and black boxes: $\psi = 0.85$.

distribution of foragers ($\bar{x} = 511.03$, $SD = 29.25$). Though the mean difference is small (31.41 time steps), this effect is consistent across most of the examined model parameters, with the time to equilibrium of foragers being longer than the time to equilibrium of competitive abilities in only 27 of 320 simulation runs (binomial test, $p < 0.001$).

5.4.3 *Sensitivity Analysis*

Since the group level dynamics depend on the behaviour of individuals, which in turn is influenced by the cognitive ability of individuals, it is worth investigating some of the assumptions that may influence cognition for a group level effect. First, the model assumes that all foragers have a unique competitive ability. While this is realistic, how important is this realism? So we start by assuming that all foragers are equal competitors. Second, the model assumes that food is infinitely divisible. However, food items are often indivisible, which means that foragers may get nothing. This could increase assessment uncertainty and constrain perception. Finally, we assumed that the foraging environment was stable. Memory plays an important role both in the ability of a group to conform to the IFD, and in the time it takes a group to reach equilibrium. Less than perfect memory is generally viewed as an adaptation to environmental variability. So we relax the assumption of environmental stability to investigate the role of temporal variability on optimal memory.

5.4.3.1 Equal Competitors

To assess the impact of unequal competitive abilities on the model results, we re-ran a subset of the simulations with equal competitors. Of all the parameter values, we chose to use $N = \{10, 20\}$, $\lambda = \{0.10, 0.20\}$ and $\psi = \{0.90, 0.95\}$ across all five food distributions. No difference was found between equal and unequal competitors in their time to reach an equilibrium distribution, probability of switching, or foraging location (Table 5.7). While the distribution of equal competitors exhibited significantly higher deviations from an IFD than the distribution of competitive abilities of unequal competitors (paired $t_{39} = 7.74$, $p < 0.001$), there were no differences in the deviation of equal and unequal competitors from an IFD (Fig. 5.6; paired $t_{39} = 1.26$, $p = 0.22$, $\beta = 0.77$).

5.4.3.2 Indivisible Food Items

We relax the assumption of infinitely divisible food items by foragers competing for each food item that enters a patch. Food is allocated through a lottery, with each food item going to one forager instead of being divided among all foragers. A forager's probability of winning the lottery and obtaining a given food item in a patch is defined as:

$$\pi_{f,j} = \frac{c_k}{\sum_{j=1}^n c_j} \quad (5.8)$$

Table 5.7. Comparison of the results of simulations with equal and unequal competitors when $\lambda = \{0.10, 0.20\}$, $N = \{10, 20\}$, $\psi = \{0.90, 0.85\}$ and $R = \{0.2, 0.4, 0.5, 0.665, 0.75\}$. All $n = 40$, all $\beta > 0.65$.

| Variable | Equal: \bar{x} (s) | Unequal: \bar{x} (s) | paired t | p-value |
|---------------------------------|----------------------|------------------------|----------|---------|
| 1. Food Eaten | 112.24 (54.99) | 112.29 (55.01) | 1.21 | 0.23 |
| 2. P(Occupy Best Patch) | 0.50 (0.15) | 0.50 (0.14) | 0.002 | 0.99 |
| 3. P(Switch Patches) | 0.35 (0.15) | 0.35 (0.14) | 1.53 | 0.13 |
| 4. Prop'n food eaten in patch 1 | 0.50 (0.20) | 0.50 (0.19) | 0.12 | 0.91 |
| 5. Slope of 2 vs 3 | 0.015 (1.72) | 0.045 (0.95) | 0.17 | 0.86 |
| 6. Slope of 4 vs 3 | 0.025 (1.84) | 0.058 (0.99) | 0.19 | 0.85 |
| 7. Time to equilibrium | 359.25 (66.73) | 378.75 (141.5) | 1.02 | 0.31 |

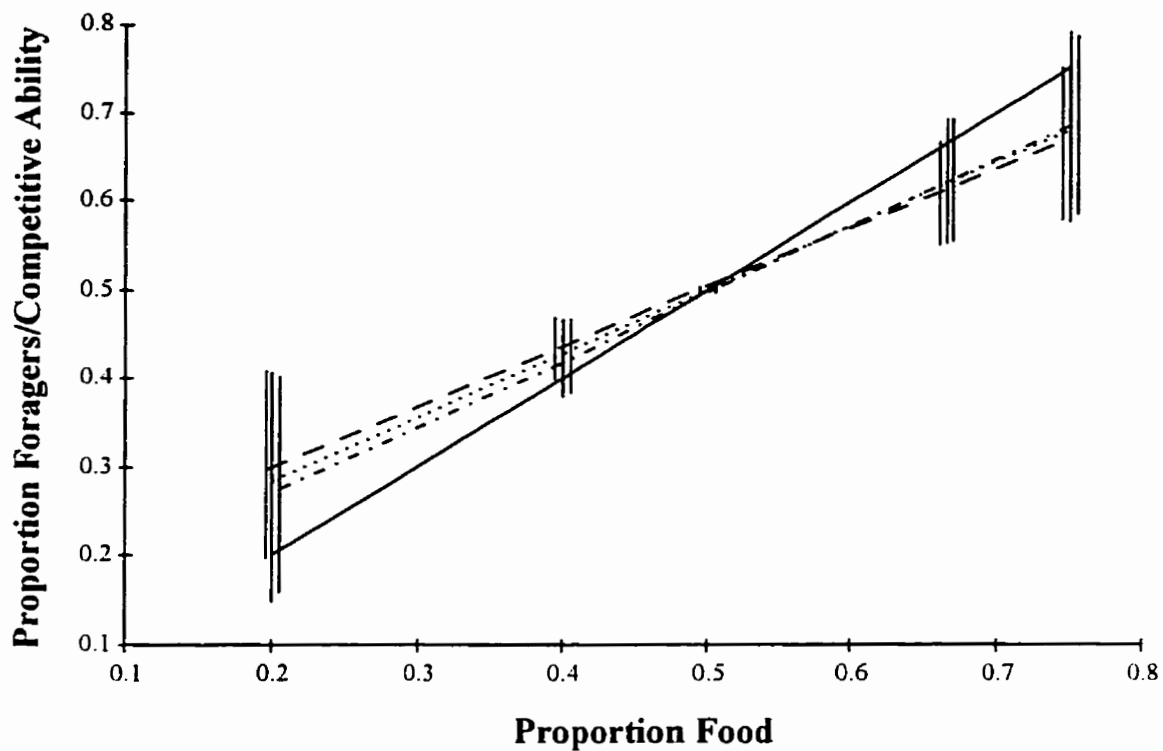


Figure 5.6. Distribution of equal competitors (dotted line), unequal competitors (dashed line) and competitive ability (dashed-dotted line) plotted against the distribution of food. Bars represent the range of values observed in simulation runs, and in each case a ordered left to right: equal competitors, unequal competitors, and competitive abilities. Solid line is the IFD. Data offset for clarity of presentation.

where π_{fi} is the probability of obtaining food item f in patch i and n_i is the number of competitors in patch i . Thus, we made food items indivisible, but put no limit on the consumption rate of foragers. The divisibility of food items had no effect on a forager's probability of occupying the best patch, the influence of competitive ability on foraging location or food eaten, or the time to equilibrium (all paired $t_{39} < 1.5$, $p > 0.1$, $\beta > 0.7$). When food was made indivisible, the average probability of switching patches decreased from 0.35 (SD = 0.14) to 0.32 (SD = 0.10; paired $t_{39} = 4.75$, $p < 0.001$). In addition, the influence of competitive ability on switching significantly decreased from -0.25 (SD = 0.16) to -0.17 (SD = 0.06; paired $t_{39} = 4.67$, $p < 0.001$). Finally, conformity to the IFD decreased in both the distribution of foragers (Fig. 5.7a, paired $t_{39} = 8.22$, $p < 0.001$) and competitive abilities (Fig. 5.7b, paired $t_{39} = 6.87$, $p < 0.001$).

5.4.3.3 Temporal Variability

To manipulate the temporal variability of the environment, we set patches to switch profitability (*sensu* Milinski 1979) during the computer simulation. All results presented to this point were run in a completely stable environment. Now we present results from simulations of groups of 40 competitors, 10 foragers with each of the four memory parameters. For each group, 10 competitive abilities were randomly generated, then assigned to an individual of each memory level. This allows us to look at the optimal memory for a given combination of parameters while controlling for the influence of

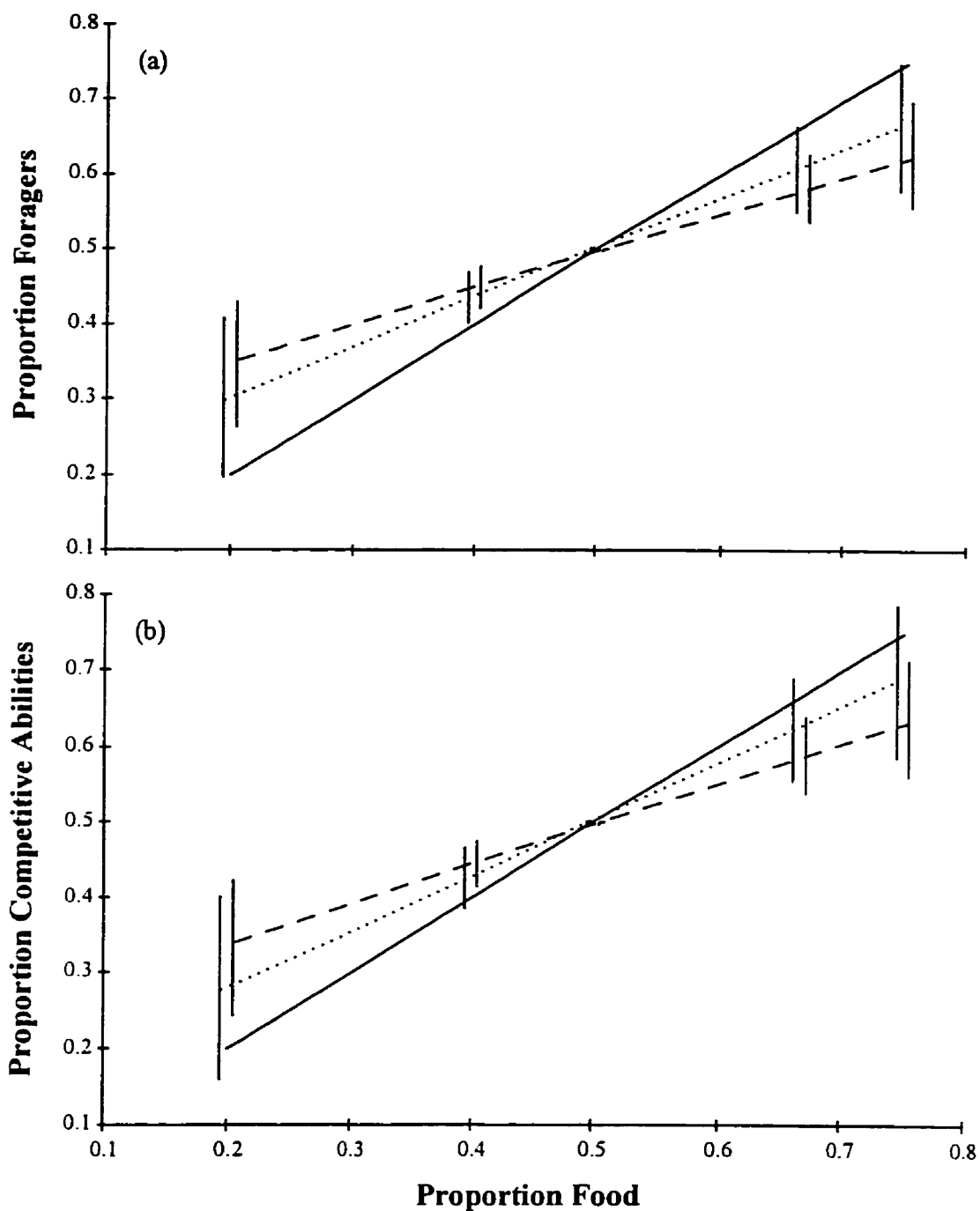


Figure 5.7. Distribution of (a) foragers and (b) competitive abilities when foraging on infinitely divisible (dotted line) and indivisible food items (dashed line), plotted against the distribution of resources. Bars represent the range of values observed in simulation runs. Solid line is the IFD. Data offset for clarity of presentation.

competitive ability. To measure the value of increased memory, we used the amount of food eaten by foragers of a given competitive ability relative to a forager with $\psi = 0.85$.

When resources are randomly distributed among patches ($R = 0.5$), increased memory provides no benefit to a forager (Fig. 5.8a). However, as the quality of patches diverges (increased R) and as the availability of food decreases (lower λ), the value of memory increases (Fig. 5.8). So, memory is of value whenever foragers are faced with a discrimination problem. In a stable environment, we find that near perfect memory is optimal. A forager can not do better than near perfect memory. As environmental stability declines, so does the optimal memory level (Fig. 5.9a). The environment eventually becomes so unstable that a forager does better by averaging across the environmental fluctuations, and optimal memory starts to increase.

Unequal competitors experience different levels of food acquisition. Better competitors acquire more food, decreasing the patch discrimination problem (see equations 5.4 and 5.5). Therefore, optimal memory may be a function of competitive ability. For simplicity, we consider the best competitors, defined as foragers with a competitive ability more than two standard deviations above the mean ($c_j > 1.5$), and the worst competitors, defined as foragers with a competitive ability more than two standard deviations below the mean ($c_j < 0.5$). Optimal memory differs between the best and worst competitors over many levels of environmental instability (Fig. 5.9b). When the environment is stable, both optimize memory at near perfect memory ($\psi = 0.99999$). As environmental stability decreases, optimal memory decreases quickly for the best

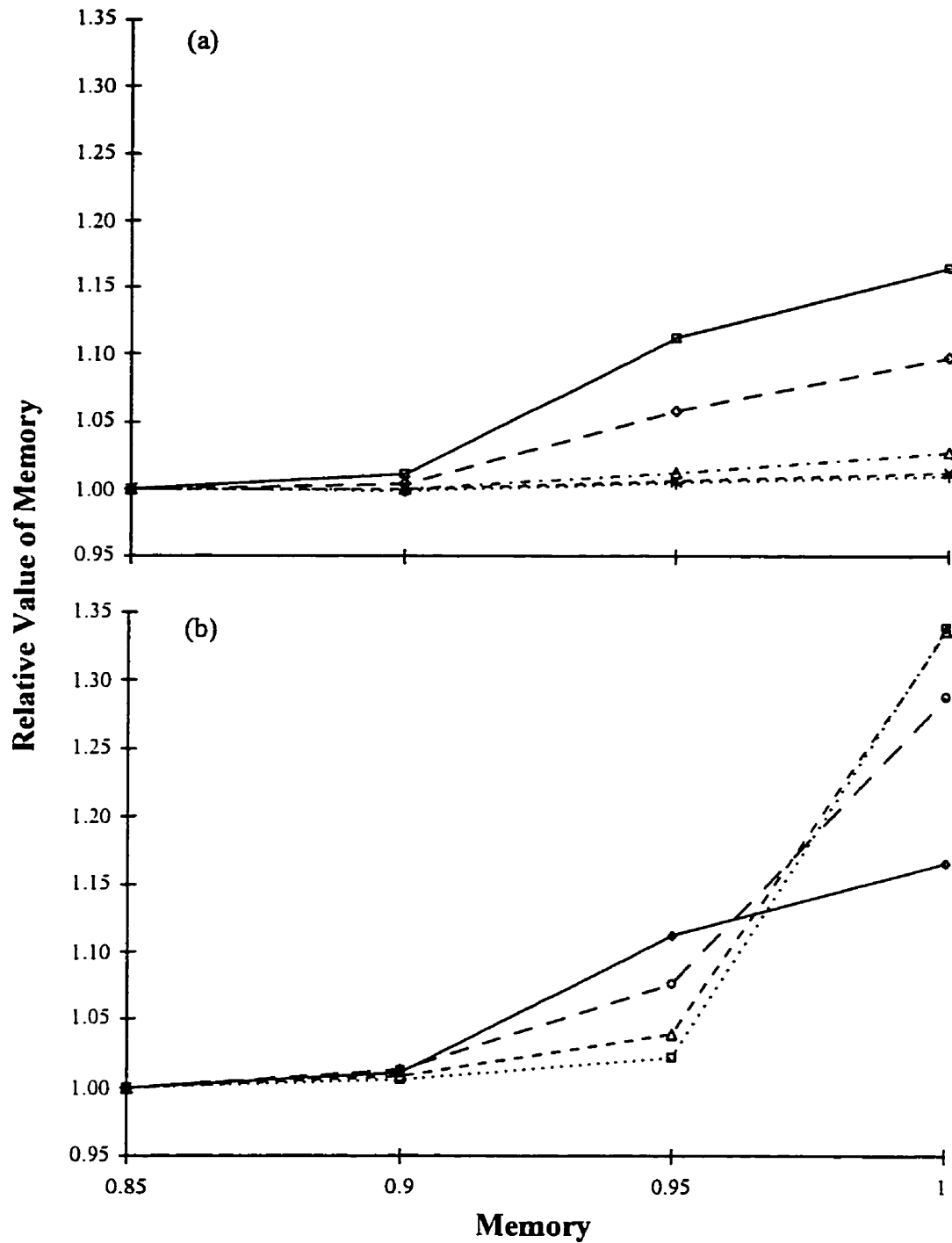


Figure 5.8. The relative value of memory (ψ) for (a) the five food ratios when $\lambda = 0.40$ (dotted line is $R = 0.5$; small dash is $R = 0.4$; dash-dotted line is $R = 0.665$; large dash is $R = 0.75$; solid line is $R = 0.2$), and (b) the four levels of food input when $R = 0.2$ (dotted line is $\lambda = 0.05$; small dash is $\lambda = 0.10$; large dash is $\lambda = 0.20$; solid line is $\lambda = 0.40$).

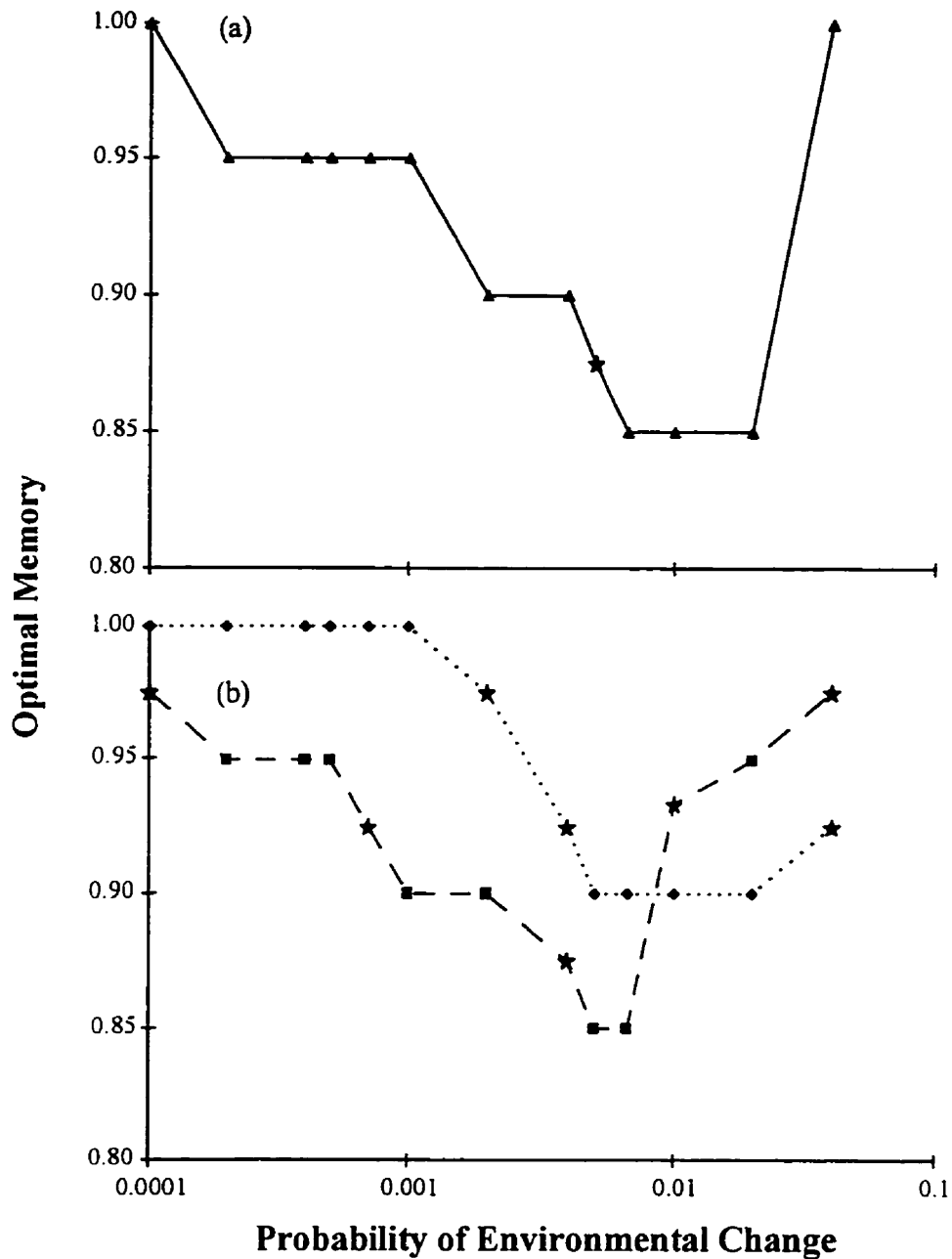


Figure 5.9. (a) Optimal memory for all foragers (solid line & triangles) and (b) optimal memory for the best (dashed line & squares) and worst (dotted line & diamonds) competitors as the probability of environmental change increases. Star symbols represent values where memory immediately above and below are both optimal. $\lambda = 0.40$, $N = 40$, $R = 0.2$.

competitors, while optimal memory for the worst competitors stays at near perfect. At low levels of environmental instability, i.e. low probability of change, optimal memory for the worst competitors is higher than for the best competitors. Optimal memory "bottoms out" when the probability of environmental change is about 0.005 (Fig. 5.9b), at $\psi = 0.85$ for the best competitors and $\psi = 0.90$ for the worst competitors. When the environment becomes very unstable (probability of change ≥ 0.01), optimal memory increases, and the optimal memory for the best competitors is greater than for the worst competitors.

5.5 Discussion

The dynamics of this model are driven by the cognitive ability of foragers to process information, as modelled by the decision rule. These foragers are using a stochastic decision rule where a patch is chosen for exploitation based on the probability that it provides the highest rate of resource acquisition. This probability is based on the information a forager acquires from two sources: food and time. Increased time spent foraging, i.e. increasing sample size, decreases assessment uncertainty (equation 5.3) leading to greater perceptual ability (equation 5.5). Thus, a forager acquires information about the quality of a patch regardless of the amount of food acquired. However, food is also an important source of information. The more food a forager acquires, the greater its assessed mean intake rate, and the greater its perceptual ability. We see this effect in the simulation results when a group is able to conform more closely to the distribution of resources when the food input rate (λ) is increased or the number of competitors (N) is decreased thereby increasing the amount of food and information each forager acquires.

Consequently, even under a constant input rate, unequal competitors occupy different information niches. Foragers that acquire more food acquire more information and face a simpler discrimination problem. The foragers that acquire more food are the better competitors, and hence, on average, better competitors will appear to be better perceivers because of the increased amount of food they acquire. This is apparent through the influence of competitive ability on the individual's probability of switching and the probability that the individual will occupy the better patch. As competitive ability increases, switching declines and the probability that the individual occupies the better patch increases.

Switching in this model is determined solely by uncertainty in patch assessment. As assessment uncertainty increases, the probability that one patch is better than another decreases (see equations 5.4 and 5.5), and the probability that a forager will switch patches increases. However, the influence of competitive ability on switching is not consistent. As food availability (λ/N) decreases, competitive abilities play a greater role in a forager's perceptual ability and the probability of switching (Fig. 5.2). This change is driven by the poorer competitors, not the better competitors. As food availability decreases, fewer foragers of lesser competitive ability obtain enough food to perceive a difference in patch profitability, leading to greater undermatching, and increased benefits to occupants of the better patch. As food availability declines further, competitive abilities lose their influence on switching as differences in patch profitability become imperceptible to even the best competitors. This process, however, is mediated by memory, since increasing memory increases the amount of prior information a forager has access to, and

thus increases a forager's perceptual ability. As the perceptual ability of all foragers increase, the importance of competitive ability on perceptual ability decreases, and the point of maximal influence of competitive ability on switching shifts to lower food availability levels (Fig. 5.2).

The probability that a forager occupies the better patch is also determined by its competitive ability. Since most of the deviations from an IFD are toward under use of the good patch, not only is the good patch better when empty, it is also better when the group is at equilibrium. For the same reasons discussed for switching, we see a decline in the importance of competitive abilities on foraging location as food availability (λ/N) decreases. When food availability is high, we expect all foragers to have the ability to accurately determine the better patch, and this does occur since we see closer conformity to the IFD (Fig. 5.3). So, why do the better competitors still occupy the better patch? The answer to this is a matter of history. Even though we did not build the system by sequentially adding individuals (*as per* Abrahams 1986, Spencer et al. 1995, 1996, Houston & Lang 1998), we still find that history is important (*as per* Spencer et al. 1995) because the better competitors realize and occupy the better patch earlier, thereby decreasing its value to the poorer competitors. Since good competitors make good perceivers, we observe the better competitors occupying the better patch.

5.5.1 *Unequal Competitors vs. Perceptual Constraints*

Deviations from the IFD have typically been explained as either violations of the assumption of equal competitors (Parker & Sutherland 1986) or ideal knowledge

(Abrahams 1986). However, these explanations are not mutually exclusive. For example, Houston and McNamara (1988) conclude by stating that the combined effects of unequal competitive abilities and perceptual constraints could produce greater undermatching, i.e. that the effects could be additive. Spencer et al. (1995) published the results of computer simulations of perceptually constrained unequal competitors that showed this result. When we removed unequal competitive abilities from our model, we were not able to show any significant change in the distribution of foragers. This suggests that, as Hughie and Grand (1998) concluded: "...competitive inequalities, which are usually difficult to quantify, may often be safely ignored" (p. 17). Though this may be true if we are only interested in predicting the distribution of organisms among resource patches (as stated by Hughie & Grand 1998), ignoring competitive abilities ignores the system dynamics, such as the influence of competitive ability on switching behaviour.

Another difference between previous models and ours is in the predicted distribution of competitive abilities. Models of unequal competitors (Parker & Sutherland 1986) predict that, while the distribution of foragers may undermatch the resources, the distribution of competitive abilities will conform to the distribution of resources. This is a result of assuming that foragers are perfectly informed, and as Spencer et al. (1995) showed, when unequal competitive abilities and perceptual constraints are combined, the distribution of competitive abilities will also deviate from the IFD. Spencer et al.'s (1995) model, however, only showed undermatching. We know that overmatching of foragers does occur (see review by Kennedy & Gray 1993), and our model predicts that the distribution of competitive abilities should be more likely to overmatch, especially when

the distribution of foragers conforms well to the IFD (Table 5.4). Coho salmon, *Oncorhynchus kisutch*, do appear to distribute themselves among resource patches according to their competitive abilities, exhibiting some undermatching of competitive abilities (Grand 1997, Grand & Dill 1997). However, measuring the distribution of competitive abilities is not commonly accomplished, so overmatching of competitive abilities has not been observed.

The phenotype-limited IFD of Parker and Sutherland (1986) predicts that better competitors should reside in the better quality patches. This same prediction can be generated by an historical model where competitors are added sequentially if the better competitors arrive first (Spencer et al. 1995, but see Houston & Lang 1998), and is likely to occur when foragers arrive sequentially and occupants get to reallocate after each arrival (Houston & Lang 1998). Our model makes the same prediction without assuming that better competitors arrive first, or that competitive abilities vary across resource patches, or that foragers arrive sequentially. Instead, this result arises from the differences in perceptual ability caused by differences in competitive ability. While differences in competitive abilities may not be necessary to predict the distribution of foragers (Hughie & Grand 1998), they may be necessary to predict differences in switching behaviour (Milinski 1984) and patch occupancy (Grand 1997).

5.5.2 *Optimal Memory*

The value of memory to a forager is influenced by the physical environment of the forager. As the environment possess tougher discrimination problems, memory becomes more

valuable (Fig. 5.8) due to the increase in available information associated with increased memory. Instability, however, devalues memory (Fig. 5.9), since the information provided by memory is information about the past, i.e. prior information. As the predictive power of prior information decreases, so does the value of memory. Not only does environmental stability increase the value of memory, it also increases the optimal memory level (Fig. 5.9). In addition to the physical environment, the social environment is also predicted to influence optimal memory (Fig. 5.9b). Competitively superior foragers should have a lower optimal memory than poor competitors, possibly due to the influence of competitive ability on the information niche occupied. Thus, better competitors are able to be more flexible to environmental change through lower memory because they are not confronted with the same information problems that confront a poor competitor.

In this model, memory refers to the devaluing of aging information. Initially, information gets full weight in the current assessment of patch quality. As time passes, the weight of a piece of information declines exponentially (see equation 5.1). However, this says nothing about the mechanism of memory. Coarsely, prior information could be devalued at a rate dependent on the amount of neural material available to store information. This possibility is suggested from work on spatial memory and hippocampus size in food caching animals (see review by Giraldeau 1997). If this is the case, then the influence of the social environment on optimal memory (Fig. 5.9b) predicts that poor competitors should make the best of a bad situation by diverting energy into the development and maintenance of memory. Alternatively, if the rate of devaluing prior information is sensitive to local conditions, then we should be able to manipulate an

animal's "memory" by changing its environment. To explain deviations from an IFD, the most recent foraging conditions (Abrahams 1989, Milinski pers. comm.) may not be sufficient, we may also need to consider the environmental stability foragers have experienced.

5.5.3 *Testing the Model*

This model's predictions can be tested through the effect of three parameters: memory (ψ), food input rate (λ), and group size (N). Memory would obviously be the most difficult to test, while food input rate and group size can be combined into a single variable: food availability (λ/N). We start by addressing the more difficult approach.

Testing the influence of memory on conformity to an IFD may be difficult, especially if memory is subject to stabilizing selection. There are two immediately apparent approaches that could be used to test the predictions that increasing memory should increase conformity to the IFD while also increasing the time it takes a group to reach equilibrium. The first is to use the approach of Mackney and Hughes (1995), who used groups from three different populations of sticklebacks to test for differences in memory. They found that the residential marine population had the shortest memory window (8 d, $\psi = 0.875$), followed by the anadromous population (10 d, $\psi = 0.90$), with the residential freshwater population exhibiting the longest memory window (> 25 d, $\psi > 0.96$). Our model would predict that the freshwater population should be able to conform more closely to the IFD than the marine population, though it would take longer to get there. Similarly, cross-species tests could be used to test this prediction between species

from relatively stable environments where memory should be high and species from relatively unstable environments that would select for lowered memory.

Alternatively, if memory is flexible to the local foraging conditions, groups of foragers could be held under predictable and unpredictable food conditions.

Unpredictable food conditions should select for a lower memory level than predictable food conditions, and hence, produce greater deviations from an IFD. This would also be interesting since foragers could dynamically adjust their use of prior information (Giraldeau 1997). This contrasts to a fixed memory that is a population specific character.

Food availability is definitely an easier way to test this model. As food availability increases, conformity to an IFD increases, and time to reach equilibrium decreases. An increase from low to medium food availability should increase the influence of competitive ability on switching behaviour. As food availability increases from medium to high, the influence of competitive ability will decrease. Food availability can be manipulated by changing food input rates or group size. When changing group size, however, one must be careful of the effect of interference (Gillis & Kramer 1987), which was not included in this model. Even though we ignored the potential influence of interference, our meta-analysis still found support for this model prediction (Fig. 5.4a).

Food availability can also be increased by increasing food input to the system. In the only experimental test of this prediction, Gray and Kennedy's (1994) mallard, *Anas platyrhynchos*, results (see Table 5.5) are consistent with this model prediction, even though our meta-analysis failed to find a significant effect (Fig. 5.4b). Gray and Kennedy

(1994), however, did not report on the competitive abilities of their foragers, nor the effect that competitive abilities may have had on patch occupation or switching behaviour.

5.5.4 Conclusions

Many of the environmental parameters included in the present model can be reduced to a single variable related to the amount of food a forager acquires. When foragers acquire more food, due to high input rates, small groups, or high competitive ability, habitat selection is an easy decision. Under these conditions, we can expect the distribution of foragers to accurately represent the distribution of resources. However, anything that limits the acquisition of food will limit habitat selection.

Obviously, food is not the only source of information that is important. Memory plays an important role as the source of prior information. In a stable environment, the more prior information, i.e. higher memory, the better a forager's ability to perceive differences. However, the use of this information source depends on environmental stability. When the environment becomes less predictable, we expect foragers to tradeoff their ability to conform to the current conditions with their ability to adapt to changing conditions. Thus, the ability of foragers to optimally select habitats will depend on the predictability of the environment in which they have evolved.

Acknowledgments - For discussion on this and related topics, we thank D. Gillis. MAK was supported by an NSERC PGS-B, and a University of Manitoba Graduate Fellowship. This research was funded by an NSERC Research Grant to MVA.

5.6 Appendix 5A - Computer Code

The following computer code for the basic model has been coded in Visual BASIC, and if typed in to a module in Microsoft Excel, will output data to a spreadsheet. Remark statements are in italics, all Visual BASIC keywords are in bold.

Option Explicit

Rem Declare user-defined types

Type PatchType

Lambda As Double *'To record assessments of lambda*
VarLambda As Double *'To record variance around lambda*
Food As Double *'To record remembered amount of food obtained*
SampleT As Integer *'To record remembered time spent in patch*
TotFood As Double *'To record total food obtained in patch*

End Type

Type FishType

Patch() As PatchType *'To track all subtypes for each patch*
Locale() As Integer *'To record the current patch*
CompAb As Double *'To record individual's competitive ability*
Switches As Integer *'To record the number of patch switches*
MeanLocale As Double *'To record mean patch location*

End Type

Rem Declare Constants

Public Const priorr As Single = 1, priort As Integer = 1
'priorr and priort are the prior expectations that all foragers start with,
'and all assessments decay back toward these two values.
Public Const pie As Double = 3.14159265358979
Public Const Tol As Double = 0.02

Sub Zsim()

Rem These simulations look at the predicted IFD if foragers are
Rem acquiring information from the beginning, and making patch
Rem choices on the basis of the Z model of perceptual constraints.

Rem i.e., patch types are not externally recognisable

Rem Initialisation

Dim rseed As Long

Dim Equal, Divisible As Boolean

Dim maxrns, maxr, rns, fgrs, numpatch, dt, totalt, watch, ro As Integer

Dim iters, reit, replicate, rep, N, i, dec, j, x, curi, t, A, B As Integer

Dim psi, TotAb, z1, z2, f, Pw, Px, rp, tp, TotLambda As Double

Dim initializing, rew, tim, PropNum, PropAb, xA, xB, md As Double

Dim seA, seB, ms, Z, pab, stdNum, stdAb As Double

Dim Comp(), R(), TotalSwitches(), PatchF(), k(), NewFood(), BestPatch() As Integer

Dim Lambda() As Single

Dim pbarNum(), TotCompAb(), tmppt(), tmpqual(), TallyNum(), TallyAb() As Double

Dim SumNum(), SumAb(), PatchCA() As Double

Dim forager() As FishType

rseed = -1 * Int(Timer)

initializing = ran1(rseed)

maxrns = 5

'number of food ratios

maxr = 500

'number of repetitions per food ratio

totalt = 10000

'time units per repetition

dt = 5

'sample period of foragers

numpatch = 2

'number of patches

iters = Int(totalt / dt)

'number of sample periods per repetition

watch = 30

'observation period

reit = Int(totalt / watch)

'number of observation periods per repetition

fgrs = 10

'group size

TotLambda = 0.2

'total rate of food input

psi = 0.95

'memory value

Equal = False

'False = unequal competitors; True = equal competitors

Divisible = True

'True = infinitely divisible food; False = indivisible food

Rem Run the simulation

For i = 1 To 5

'Clear the output sheets of previous output

Worksheets(i).Select

Range("A:Z").Select

Selection.Clear

Cells(1, 1).Select

Next i

For rns = 1 To maxrns

Worksheets(rns).Select

ReDim BestPatch(1 To numpatch)

ReDim Lambda(1 To numpatch)

Select Case rns

Case 1

 Lambda(1) = 0.2 * TotLambda

 Lambda(2) = 0.8 * TotLambda

 BestPatch(1) = 0

 BestPatch(2) = 1

Case 2

 Lambda(1) = 0.4 * TotLambda

 Lambda(2) = 0.6 * TotLambda

 BestPatch(1) = 0

 BestPatch(2) = 1

Case 3

 Lambda(1) = 0.5 * TotLambda

 Lambda(2) = 0.5 * TotLambda

'since neither patch is better, randomly choose one as "best"

If ran1(1) < 0.5 **Then**

 BestPatch(1) = 0

 BestPatch(2) = 1

Else

 BestPatch(1) = 1

 BestPatch(2) = 0

End If

Case 4

 Lambda(1) = 0.665 * TotLambda

 Lambda(2) = 0.335 * TotLambda

 BestPatch(1) = 1

 BestPatch(2) = 0

Case 5

 Lambda(1) = 0.75 * TotLambda

 Lambda(2) = 0.25 * TotLambda

 BestPatch(1) = 1

 BestPatch(2) = 0

End Select

Rem Output initial settings and initialise arrays. Housekeeping for each run

Worksheets(rns).Cells(1, 15) = "fgrs"

Worksheets(rns).Cells(1, 16) = fgrs

Worksheets(rns).Cells(2, 15) = "numpatch"

'assign 1 to best patch, 0 to others

'rate of encounter for each patch

'assign food ratio

'Number of foragers in the group

| | |
|--|--|
| Worksheets(rns).Cells(2, 16) = numpatch | <i>'Number of patches</i> |
| Worksheets(rns).Cells(3, 15) = "Lambda(i)" | |
| Worksheets(rns).Cells(3, 16) = Lambda(1) | <i>'rate of encounter with food items λ_1</i> |
| Worksheets(rns).Cells(3, 17) = Lambda(2) | |
| Worksheets(rns).Cells(4, 15) = "sample_t" | |
| Worksheets(rns).Cells(4, 16) = dt | <i>'Time between observations</i> |
| Worksheets(rns).Cells(5, 15) = "totalt" | |
| Worksheets(rns).Cells(5, 16) = totalt | <i>'Total time for "experiment"</i> |
| Worksheets(rns).Cells(6, 15) = "watch" | |
| Worksheets(rns).Cells(6, 16) = watch | <i>'Experimenter sample time</i> |
| Worksheets(rns).Cells(7, 15) = "psi" | |
| Worksheets(rns).Cells(7, 16) = psi | <i>'Memory parameter</i> |

```

ReDim pbarNum(0 To reit), pbarAb(0 To reit)
ReDim TallyNum(1 To maxr, 0 To reit), TallyAb(1 To maxr, 0 To reit)
ReDim TotalSwitches(0 To iters)
ReDim NewFood(1 To fgrs)
ReDim k(1 To numpatch)

```

```

For replicate = 1 To maxr
  Worksheets(rns).Cells(1, 7) = "reps = " + CStr(replicate)
  Rem Housekeeping for each replicate within a run
  ReDim forager(1 To fgrs) As FishType
  For N = 1 To fgrs
    ReDim forager(N).Patch(1 To numpatch)
    ReDim forager(N).Locale(0 To iters)
    forager(N).Switches = 0
    forager(N).MeanLocale = 0
  Next N

```

```

For N = 1 To fgrs
  For i = 1 To numpatch
    forager(N).Patch(i).Lambda = priorr / priort
    forager(N).Patch(i).VarLambda = priorr / (priort ^ 2)
    forager(N).Patch(i).Food = priorr
    forager(N).Patch(i).SampleT = priort
    forager(N).Patch(i).TotFood = 0
  Next i
Next N

```

| | |
|---------------------------------------|--|
| ReDim Comp(1 To numpatch) | <i>'Tracks the number of competitors in a patch</i> |
| ReDim TotCompAb(1 To numpatch) | <i>'Tracks total competitive ability in a patch</i> |
| ReDim R(1 To numpatch) | <i>'Records the number of food items that enter 'a patch during dt</i> |


```

ReDim tmpqual(1 To numpatch), tmppt(1 To numpatch)
    'tmpqual records forager's current assessment of lambda
    'tmppt will track patch numbers during sorting

Rem Randomly determine the competitive ability of each forager according
Rem to a distribution with mean = 1, SD = 0.25

TotAb = 0 'to record the sum total of all competitive abilities
For N = 1 To fgrs 'loop to assign competitive abilities
    If Equal = False Then
        Do
            z1 = ran1(2)
            z2 = ran1(3)
            forager(N).CompAb = 1# + 0.25 * ((-2 * Log(z1)) ^ 0.5) * Cos(2 * pie * z2)
            If forager(N).CompAb > 0 Then Exit Do
        Loop
    Else
        forager(N).CompAb = 1
    End If
    TotAb = TotAb + forager(N).CompAb
Next N

Rem Randomly assign foragers among the patches

For N = 1 To fgrs
    'randomly choose a patch number between 1 and numpatch
    i = Int(ran1(4) * numpatch) + 1
    If i > numpatch Then i = numpatch
    forager(N).Locale(0) = i
    forager(N).MeanLocale = BestPatch(i) / iters
    TotCompAb(i) = TotCompAb(i) + forager(N).CompAb
Next N

Rem Loop through iters decision steps

For dec = 1 To iters

    'allocate probabilities of getting a food item based on CompAb in patch
    ReDim PatchCA(1 To numpatch, 1 To fgrs), PatchF(1 To numpatch, 1 To fgrs)
    'PatchCA(i,j) partitions CompAb into j within patch i
    'PatchF(i,j) while keeps track of forager in PatchCA
    For j = 1 To numpatch
        k(j) = 0
    Next j

```

```

For N = 1 To fgrs
  i = forager(N).Locale(dec - 1)
  k(i) = k(i) + 1
  If k(i) = 1 Then
    PatchCA(i, k(i)) = forager(N).CompAb / TotCompAb(i)
  Else
    PatchCA(i, k(i)) = PatchCA(i, k(i) - 1) + forager(N).CompAb / TotCompAb(i)
  End If
  PatchF(i, k(i)) = N
Next N

'Determine amount of food to enter each patch

For i = 1 To numpatch
  x = 0
  Px = Application.Poisson(x, Lambda(i) * dt, True)           'Prob(0 food items)
  f = ran1(5)
  If f > Px Then
    Do
      Pw = Px           'set Pw = prob(x-1) to prob(x) for previous value
      x = x + 1         'new value of x
      Px = Application.Poisson(x, Lambda(i) * dt, True)       'Prob(x food items)
      If (Pw < f) And (f <= Px) Then           'x food items enter patch
        R(i) = x
      Exit Do
    End If
  Loop
  Else
    R(i) = x           '0 food items enter patch
  End If
Next i

ReDim NewFood(1 To fgrs)
If Divisible = False Then
  'allocate food indivisibly among foragers in the patch
  For i = 1 To numpatch
    If R(i) > 0 Then
      For x = 1 To R(i)
        f = ran1(6)
        j = 0
        Do
          j = j + 1
          If f <= PatchCA(i, j) Then
            NewFood(PatchF(i, j)) = NewFood(PatchF(i, j)) + 1

```

```

    Exit Do
  End If
  If j > k(i) Then Exit Do
    'if something goes wrong then the food item got away
  Loop
  Next x
Else
  For j = 1 To k(i)
    NewFood(PatchF(i, j)) = 0
  Next j
End If
Next i
Else
  'Determine amount of food obtained by each forager based on
  'forager's competitive ability, i.e. food infinitely divisible
  For N = 1 To fgrs
    i = forager(N).Locale(dec - 1)
    NewFood(N) = R(i) * forager(N).CompAb / TotCompAb(i)
  Next N
End If

For N = 1 To fgrs

  i = forager(N).Locale(dec - 1)
  For j = 1 To numpatch
    rp = forager(N).Patch(j).Food      'prior rewards
    tp = forager(N).Patch(j).SampleT  'prior sampling time
    If j = i Then
      'updating assessment of currently sampled patch
      forager(N).Patch(j).Food = psi * rp + NewFood(N) + (1 - psi) * priorr
      forager(N).Patch(j).SampleT = psi * tp + 1 + (1 - psi) * priort
      forager(N).Patch(j).TotFood = forager(N).Patch(j).TotFood + NewFood(N)
    Else
      'updating assessment of patches not sampled this time period
      forager(N).Patch(j).Food = psi * rp + (1 - psi) * priorr
      forager(N).Patch(j).SampleT = psi * tp + (1 - psi) * priort
    End If
    rew = forager(N).Patch(j).Food
    tim = forager(N).Patch(j).SampleT
    forager(N).Patch(j).Lambda = rew / tim
    forager(N).Patch(j).VarLambda = rew / (tim ^ 2)
  Next j
Next N

```

```

'Rank patches based on updated assessments,
'choose a new patch using Z model as decision rule
ReDim TotCompAb(1 To numpatch)
For N = 1 To fgrs
  For i = 1 To numpatch
    tmpqual(i) = forager(N).Patch(i).Lambda
    tmppt(i) = i
  Next i

  'Sort patches based on assessed quality
  Call Srt(numpatch, tmpqual(), tmppt())

  'Calculate mean difference and mean variance
  'of assessed top two patches
  A = tmppt(1)
  B = tmppt(2)
  xA = forager(N).Patch(A).Lambda
  xB = forager(N).Patch(B).Lambda
  md = xA - xB
  seA = forager(N).Patch(A).VarLambda / forager(N).Patch(A).SampleT
  seB = forager(N).Patch(B).VarLambda / forager(N).Patch(B).SampleT
  ms = (seA + seB) ^ 0.5

  'Calculate the Z score
  Z = md / ms

  'What is the probability that the patch with the highest estimated
  'mean lambda is better than the next patch? Prob(A>B)
  pab = Application.NormSDist(Z)

  'Choose patch based on the probability it is better
  If ranl(7) <= pab Then i = A Else i = B

  'update forager's location, comp & TotCompAb counters
  j = forager(N).Locale(dec - 1)
  TotCompAb(i) = TotCompAb(i) + forager(N).CompAb
  forager(N).Locale(dec) = i
  If j > i Then
    TotalSwitches(dec) = TotalSwitches(dec) + 1
    forager(N).Switches = forager(N).Switches + 1
  End If
  forager(N).MeanLocale = forager(N).MeanLocale + BestPatch(i) / iters
Next N

```

Next dec

Rem Output

'Column headers

If replicate = 1 Then

Cells(1, 1).Select

'Output column headers

Cells(1, 1) = "Time"

Cells(1, 2) = "Mean(Num)"

Cells(1, 3) = "SD(Num)"

Cells(1, 4) = "Mean(Ab)"

Cells(1, 5) = "SD(Ab)"

Cells(i, 6) = "Tot Switches"

Cells(1, 7) = "Run"

Cells(1, 8) = "Comp Ab"

Cells(1, 9) = "P(Switch)"

Cells(1, 10) = "P(Best Patch)"

Cells(1, 11) = "Food Eaten"

Cells(1, 12) = "Prop Food 1"

End If

For t = 0 To reit

'Reset competitor counter

ReDim Comp(1 To numpatch), TotCompAb(1 To numpatch)

'Count the number of competitors per patch at time t

For N = 1 To fgrs

curi = forager(N).Locale(t * watch / dt)

Comp(cur_i) = Comp(cur_i) + 1

TotCompAb(cur_i) = TotCompAb(cur_i) + forager(N).CompAb

Next N

'Output patch occupancy in proportion of total foragers

For i = 1 To numpatch

PropNum = Comp(i) / fgrs

'prop foragers in patch 1

PropAb = TotCompAb(i) / TotAb

'prop competitive abilities in patch 1

If i = 1 **Then**

TallyNum(replicate, t) = PropNum

TallyAb(replicate, t) = PropAb

pbarNum(t) = pbarNum(t) + (PropNum / maxr)

pbarAb(t) = pbarAb(t) + (PropAb / maxr)

If replicate = maxr **Then**

```

Cells(2 + t, 1) = t * watch
Cells(2 + t, 2) = pbarNum(t)
Cells(2 + t, 4) = pbarAb(t)
Cells(2 + t, 6) = TotalSwitches(t * watch / dt)
stdNum = 0
stdAb = 0
For rep = 1 To maxr
  stdNum = stdNum + ((TallyNum(rep, t) - pbarNum(t)) ^ 2) / (maxr - 1)
  stdAb = stdAb + ((TallyAb(rep, t) - pbarAb(t)) ^ 2) / (maxr - 1)
Next rep
Cells(2 + t, 3) = stdNum
Cells(2 + t, 5) = stdAb
End If
End If
Next i

Next t

ro = (replicate - 1) * fgrs + 1
For N = 1 To fgrs
  Cells(ro + N, 7) = replicate
  Cells(ro + N, 8) = forager(N).CompAb
  Cells(ro + N, 9) = forager(N).Switches / iters
  Cells(ro + N, 10) = forager(N).MeanLocale
  Cells(ro + N, 11) = forager(N).Patch(1).TotFood + forager(N).Patch(2).TotFood
  If (forager(N).Patch(1).TotFood + forager(N).Patch(2).TotFood) > 0 Then
    Cells(ro + N, 12) = forager(N).Patch(1).TotFood / (forager(N).Patch(1).TotFood
    + forager(N).Patch(2).TotFood)
  Else
    Cells(ro + N, 12) = "NA"
  End If
Next N

Next replicate

Next rns

Beep

End Sub

'This subroutine to sort arrays was taken from:
'Sprott, J.C. 1991. Numerical recipes, routines and examples in BASIC.
'Cambridge University Press, Cambridge.

```

Sub Srt(N, RA(), RB())

Rem declarations

Dim L, p, q, i, j As Integer

Dim IR, tempRA, tempRB As Double

Dim tempA(), tempB() As Double

Rem sorts the array RA with N elements in ascending order

Rem rearranges the array RB when sorting RA

ReDim tempA(N), tempB(N) As Double

L = Int(N / 2) + 1

IR = N

Do

If L > 1 Then

L = L - 1

tempRA = RA(L)

tempRB = RB(L)

Else

tempRA = RA(IR)

tempRB = RB(IR)

RA(IR) = RA(1)

RB(IR) = RB(1)

IR = IR - 1

If IR = 1 Then

RA(1) = tempRA

RB(1) = tempRB

Exit Do

End If

End If

i = L

j = L + L

While j <= IR

If j < IR Then

If RA(j) < RA(j + 1) Then j = j + 1

End If

If tempRA < RA(j) Then

RA(i) = RA(j)

RB(i) = RB(j)

i = j

j = j + j

Else

```

        j = IR + 1
    End If
Wend
RA(i) = tempRA
RB(i) = tempRB
Loop

Rem Reorganize the arrays RA and RB so they appear in descending order of RA
For p = 1 To N
    tempA(p) = RA(p)
    tempB(p) = RB(p)
Next p
For q = 1 To N
    RA(q) = tempA(N - q + 1)
    RB(q) = tempB(N - q + 1)
Next q

End Sub

' This subroutine to generate random numbers was taken from:
' Spratt, J.C. 1991. Numerical recipes, routines and examples in BASIC.
' Cambridge University Press, Cambridge.

```

Static Function ran1(IDUM&)

```

Rem Declarations
Dim R(97) As Double
Dim M1, IA1, IC1, M2, IA2, IC2, M3, IA3, IC3, IX1, IX2, IX3 As Long
Dim IFF, j As Integer
Dim RM1, RM2 As Double

Rem Sort
M1 = 259200
IA1 = 7141
IC1 = 54773
RM1 = 0.0000038580247
M2 = 134456
IA2 = 8121
IC2 = 28411
RM2 = 0.0000074373773
M3 = 243000
IA3 = 4561
IC3 = 51349
If IDUM& < 0 Or IFF = 0 Then

```



```

IFF = 1
IX1 = (IC1 - IDUM&) Mod M1
IX1 = (IA1 * IX1 + IC1) Mod M1
IX2 = IX1 Mod M2
IX1 = (IA1 * IX1 + IC1) Mod M1
IX3 = IX1 Mod M3
For j = 1 To 97
  IX1 = (IA1 * IX1 + IC1) Mod M1
  IX2 = (IA2 * IX2 + IC2) Mod M2
  R(j) = (CSng(IX1) + CSng(IX2) * RM2) * RM1
Next j
IDUM& = 1
End If
IX1 = (IA1 * IX1 + IC1) Mod M1
IX2 = (IA2 * IX2 + IC2) Mod M2
IX3 = (IA3 * IX3 + IC3) Mod M3
j = 1 + Int((97 * IX3) / M3)
If j > 97 Or j < 1 Then Debug.Print "Abnormal exit": Exit Function
ran1 = R(j)
If ran1 > 1 Then ran1 = 1
R(j) = (CSng(IX1) + CSng(IX2) * RM2) * RM1
End Function

```

5.7 References

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Chapter 6: Assessing the Ideal Free Distribution: Do Guppies Use Aggression as Public Information about Patch Quality?

6.1 Abstract

Aggression can be costly to foragers, yet some recent research suggests that foragers should use aggression as a cue to patch quality (the attractive aggression hypothesis). If aggression is predictive of patch quality, then the attractive aggression hypothesis predicts that the distribution of foragers should follow the distribution of aggression. If, instead, aggression is repulsive because it is costly, then the distribution of foragers should diverge from the distribution of aggression. We tested the attractive aggression hypothesis using female guppies, *Poecilia reticulata*, and found that the distribution of foragers followed the distribution of food, but was unaffected by the distribution of aggression. These data do not support the attractive aggression hypothesis, but instead suggest that the distribution of aggression is a consequence of the distribution of foragers, and aggression is not used as public information about patch quality by guppies.

6.2 Introduction

When faced with patches of unknown quality, social foragers have access to two sources of information: personal sample information and public information. Personal sample information, as the name suggests, is information acquired by personally sampling the patch. Public information is acquired from the behaviour of other animals (Valone 1989), and a forager can sample a patch by observing the behaviour of foragers in a patch (Templeton & Giraldeau 1996). The use of these two sources of information are not necessarily incompatible.

When resources are patchily distributed in the environment, Fretwell and Lucas (1970) predicted that animals would distribute themselves according to the resource distribution, in what they called an ideal free distribution (IFD). IFD theory assumes that foragers have perfect information, and that all foragers compete on an equal basis. However, even when these assumptions are known to be violated, foragers are still capable of conforming to the resource distribution (Milinski 1988, Milinski & Parker 1991), though not always (Kennedy & Gray 1993). The question is: why do foragers do so well? What information do foragers use to assess patch quality? The more information an animal has access to, the better its perceptual ability (Koops unpubl. ms, chapter 4). Thus, foragers that use public information can increase their ability to assess patch quality, and should be able to exhibit closer conformity to an IFD.

The idea that foragers can use public information to assess patch quality has a long history in the IFD literature. For example, Harper (1982) found that mallard ducks, *Anas platyrhynchos*, were initially misled by the rate of food input when he changed the size of

food items. This suggests that ducks foraging in one patch could acquire information about the rate of food input in the other patch, either from seeing the food enter the patch (thrown by the experimenter) or from the behaviour of other foraging ducks. Milinski (1984), finding no change in the time it took groups to reach the IFD when he changed the timing of food input, concluded that three-spined sticklebacks, *Gasterosteus aculeatus*, did not acquire information from one another. We know that foragers are attracted to the foraging (Krause 1992) and anticipatory (Reebs & Gallant 1997, Lachlan et al. 1998) activity of conspecifics, but this does not mean they use this information to assess the quality of patches. Gotceitas and Colgan (1991) found that three-spined sticklebacks prevented from personally sampling a patch failed to choose the more profitable patch, instead preferring the patch with more conspecifics.

Experimental results from Pitcher et al. (1982) and Pitcher and Magurran (1983) suggest that goldfish, *Carassius auratus*, and European minnows, *Phoxinus phoxinus*, can use information from other members of a foraging group. In these experiments, however, all members were able to forage freely. The ability to acquire personal sample information seems to be important. Pitcher and House (1987) found that when goldfish were able to acquire food in low quantity, they used information from successfully foraging conspecifics, but when no food was available, they ignored public information.

Kennedy and Gray (1994) proposed that foragers use aggressive interactions as information about the quality of patches. When the quality of a food patch increases, aggressive interactions tend to increase, therefore, aggression could be a reliable predictor of patch quality, and aggression would be attractive. They tested their hypothesis with

mallard ducks, manipulating the distribution of aggressive interactions by increasing the size of food items, while keeping the total food per trial constant. When food occurred in large items, the distribution of aggressive interactions were a better predictor of resource distribution, and the mallards exhibited closer conformity to the IFD.

Attraction to aggression is surprising, since aggression is generally considered to be costly, potentially lowering food discovery rates through interference, incurring time and energy costs, risking injury, and increasing predation risk. Given the potential costs of aggression, it is equally reasonable for foragers to avoid patches with more aggressive interactions, i.e. repulsive aggression. Alternatively, the distribution of aggression may be a result of the distribution of foragers, and have nothing to do with patch assessment, i.e. neutral aggression.

When testing the attractive aggression hypothesis, Kennedy and Gray (1994) used the distribution of aggressive interactions as the source of public information about patch quality. However, the distribution of aggressive interactions will be influenced by the distribution of foragers, and there is no way to tell whether aggressive interactions influence the distribution of foragers, or whether foragers influence the distribution of aggressive interactions. Therefore, there is no reason to expect the distribution of aggressive interactions to provide any more information about patch quality than the distribution of foragers. Alternatively, if aggression does provide public information about patch quality, the distribution of per capita aggression controls for the distribution of foragers. According to the attractive aggression hypothesis, a change in the distribution of per capita aggression, should change the distribution of foragers.

Here we present a test of Kennedy and Gray's (1994) attractive aggression hypothesis using female guppies, *Poecilia reticulata*. Female guppies have been shown to conform more closely to an IFD than males, refining their assessment of patch quality over time (Abrahams 1989). Male guppies, however, appear to be less concerned with the distribution of food than females. Female guppies have also been shown to socially learn foraging information from other female guppies (Laland 1997, Lachlan et al. 1998), suggesting that they could use public information for patch assessment.

To test the attractive aggression hypothesis, we need to manipulate the distribution of per capita aggression. We do this by providing food at two sources: one spatially dispersed and the other spatially concentrated. According to resource defense theory, concentrating food in space should increase aggressive interactions, while dispersing food in space should decrease aggressive interactions (see Grant 1993 for a review). When food is dispersed broadly at the rich site, while food is concentrated at the poor site, the distribution of per capita aggression should provide a poor indication of the distribution of food. When food is concentrated at the rich site and dispersed at the poor site, the distribution of per capita aggression should provide a good indication of the food distribution. By always providing food through both sources, but reversing their value, we attempt to manipulate the distribution of per capita aggression without affecting total aggression levels. If foragers use aggression as public information about patch quality, changing the distribution of per capita aggression should have a corresponding change in the distribution of foragers.

6.3 Methods

Seven groups of 10 female guppies (weight: $\bar{x} = 0.196$ g, $SD = 0.045$, $n = 4$; length: $\bar{x} = 21.57$ mm, $SD = 1.82$, $n = 4$), *Poecilia reticulata*, were placed in 38 L aquaria (50 cm L x 26.5 cm W x 29 cm H). Food was provided at two ends of the tank, approximately 40 cm apart, through feeders that passively drained into the tank [see Abrahams (1989) for a complete description of the feeders]. Each site provided freshly hatched, live brine shrimp, *Artemia salina*, nauplii and eggs. A total of 125 μ L (approximately 170) brine shrimp were divided between the two feeders each morning (AM trial) and afternoon (PM trial) in one of 5 food ratios: 5:1, 2:1, 1:1, 1:2, 1:5. Two different food delivery ends were attached to the feeders: a bar, spreading the food over 20 cm from five equidistant holes, and a point source, pushing the food up from the bottom of the tank through a single hole. We subjected each group to two different treatments. The bar rich treatment, where the rich patch provided food through the bar while the poor patch provided food through the point source. The point rich treatment, where the rich patch provided food through the point source while the poor patch provided food through the bar. When neither patch was richer, i.e. in the 1:1 food ratio, the location of the point and bar were randomly determined by a coin toss. Each group experienced all five food ratios in random order in each of the two treatments. The order of treatments was balanced across groups. Each food ratio was provided for one day, morning and afternoon, with each feeding lasting 15 min. Spatial distribution data were collected on each group every 30 s for 15 min. The total number of aggressive interactions (chase, bite, or threat) over the 15

min trial were recorded at each feeder. Data were collected live for the first three groups, then from videotape for groups four through seven.

To analyze the distribution of aggressive interactions, we used per capita aggression to remove any effect of forager distribution (as observed by Kennedy & Gray 1994) and the possibility that there are more aggressive interactions at a site simply because there are more foragers since fish can be attracted to a site based on the number of conspecifics (e.g. Gotceitas & Colgan 1991). By spatially concentrating food at the point source, we should be increasing the per capita aggression at this site creating a positive relationship between the distribution of per capita aggression and the distribution of food. When the bar source is rich, this relationship should be negative. We start our analysis by testing for this treatment effect.

Since we are interested in the ability of foragers to assess the distribution of resources, we limit our analysis of the spatial distribution of foragers to the last 5 minutes of the trial. The distribution of per capita aggression were calculated for the entire trial as the number of interactions in a patch (I) divided by the mean number of foragers at the patch (N). All seven groups experienced all five food ratios in both treatments, so data on the distribution of per capita aggression, $\text{Log}[(I_1/N_1)/(I_2/N_2)]$, and foragers, $\text{Log}(N_1/N_2)$, were analyzed using an analysis of variance with repeated measures (ANOVAR). If we observe the expected treatment effect, the attractive aggression hypothesis predicts: (i) a treatment effect on the distribution of foragers, and (ii) a higher slope of $\text{Log}(N_1/N_2)$ against $\text{Log}(R_1/R_2)$ in the point rich treatment.

6.4 Results

To test the attractive aggression hypothesis, we need to affect the distribution of per capita aggression without changing the overall aggression levels (Kennedy & Gray 1994). We observed no difference in the total aggression levels between the point rich ($\bar{x} = 61.46$, $SD = 17.29$) and the bar rich ($\bar{x} = 72.00$, $SD = 19.75$) treatments (paired $t_6 = 1.37$, $p = 0.22$, $\beta = 0.79$). The total number of foragers actively feeding during the trials did differ between the bar rich ($\bar{x} = 9.60$, $SD = 0.38$) and the point rich ($\bar{x} = 9.25$, $SD = 0.61$) treatments (paired $t_6 = 2.97$, $p = 0.025$), however, the per capita aggression levels did not differ (paired $t_6 = 1.10$, $p = 0.31$, $\beta = 0.85$; bar rich: $\bar{x} = 7.47$, $SD = 1.92$; point rich: $\bar{x} = 6.62$, $SD = 1.68$). Therefore, we conclude that our manipulation did not change aggression levels, and changes in the distribution of foragers can be due to changes in available information and not increased total aggression. There is also no evidence that the repeated-measures design led to any habituation or the formation of dominance hierarchies (Fig. 6.1), since either would have led to a decrease in aggression over the course of the experiment.

The distribution of per capita aggression during the AM trials was not influenced by treatment alone (ANOVAR: $F_{1,6} = 0.37$, $p = 0.57$, $\beta = 0.92$), nor was it influenced by food ratio alone (ANOVAR: $F_{4,24} = 1.41$, $p = 0.26$, $\beta = 0.63$). However, there was a

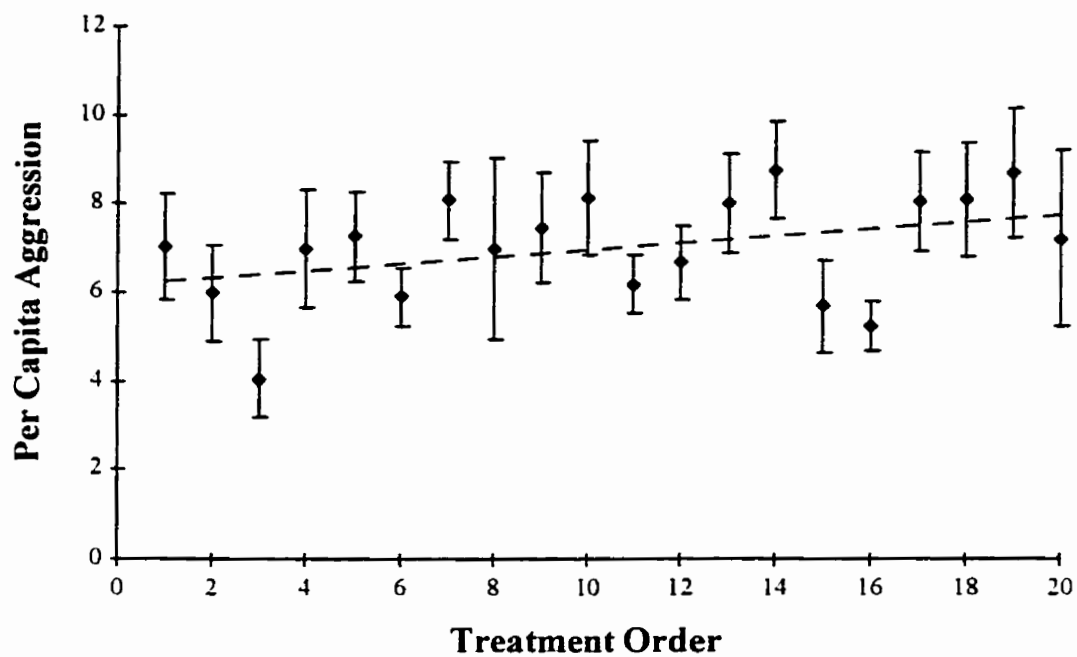


Figure 6.1. Mean (± 1 S.E.) per capita aggression in each of the 20 trials experienced by each group, showing no evidence of habituation and or the formation of dominance hierarchies. In each case $n = 7$.

significant interaction between treatment and food ratio (Fig. 6.2a, ANOVAR: $F_{4,24} = 3.84$, $p = 0.015$). Thus, our experimental manipulation had the desired effect on the distribution of per capita aggression during the AM trials. This effect was lost by the PM trials (ANOVAR: treatment: $F_{1,6} = 3.22$, $p = 0.12$, $\beta = 0.67$; food ratio: $F_{4,24} = 2.45$, $p = 0.07$, $\beta = 0.40$; treatment x food ratio: $F_{4,24} = 1.57$, $p = 0.21$, $\beta = 0.59$), so we restrict our analyses to the AM data only, since we are interested in foragers assessing the IFD.

The distribution of foragers was not significantly affected by the treatment (ANOVAR: $F_{1,6} = 0.054$, $p = 0.82$, $\beta = 0.95$), nor was there any treatment by food ratio interaction (ANOVAR: $F_{4,24} = 1.84$, $p = 0.15$, $\beta = 0.52$). However, the distribution of foragers was significantly affected by the distribution of food (Fig. 6.2b, ANOVAR: $F_{4,24} = 49.57$, $p < 0.001$) as predicted by the IFD. Furthermore, in complete opposition to the attractive aggression hypothesis, the distribution of foragers was more extreme in the point rich treatment than the bar rich treatment in only 1 of 7 groups (sign test: $p = 0.12$).

6.5 Discussion

Guppies do not appear to use the distribution of per capita aggression as public information about patch quality. Sites with a relatively higher level of aggression are not attractive. This suggests that female guppies ignore aggression when making patch choice decisions. By using per capita aggression as our measure, we removed the causation problem faced by Kennedy and Gray (1994), and the change in the distribution of

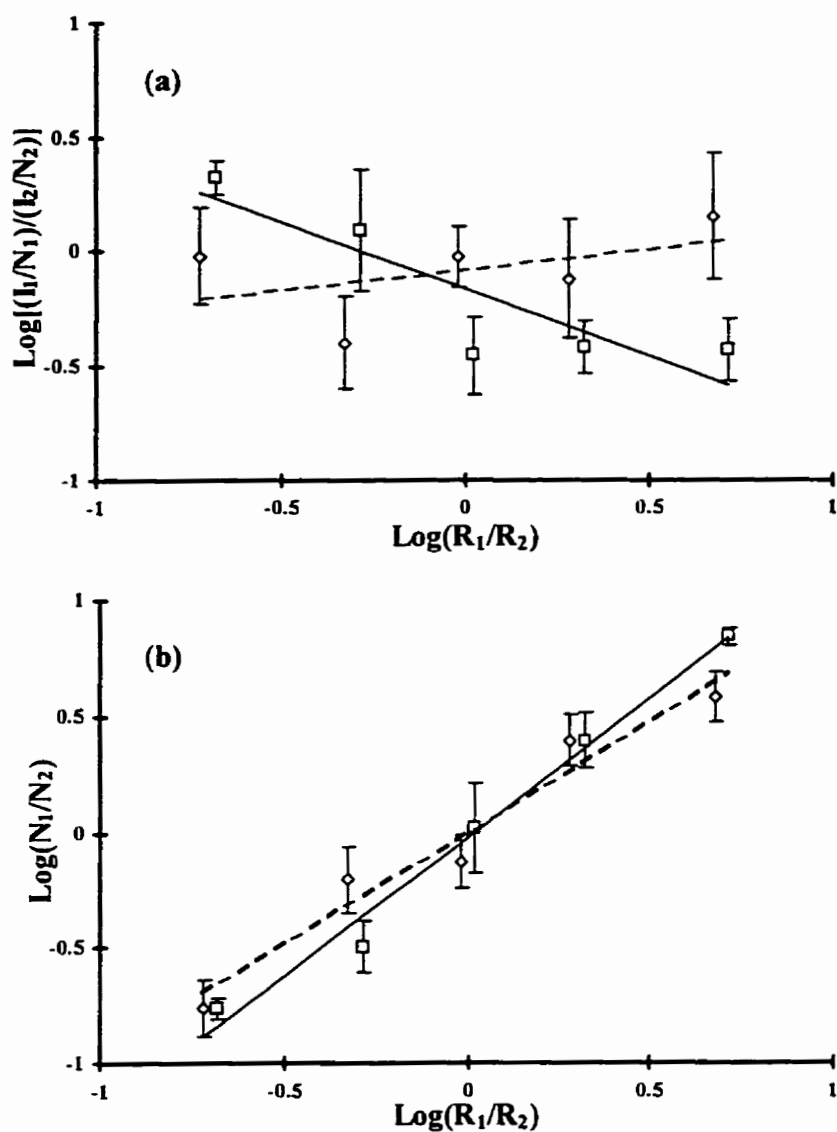


Figure 6.2. The distribution of (a) per capita aggression and (b) foragers as a function of the distribution of food in the bar rich and point rich treatments. The bar rich data are represented by a solid line and square symbols. The point rich data are represented by a dashed line and diamond symbols. The IFD predicts a slope of one for the distribution of foragers. The distribution of foragers in the bar rich treatment are described by the line: $y = -0.001 + 1.20x$, and in the point rich treatment by: $y = -0.02 + 0.97x$. All data were offset for clarity of presentation.

aggression could not have been caused by any change in forager distribution. Thus, this is the first true test of the attractive aggression hypothesis, and there is no evidence to support the idea that animals use aggression as public information.

A potential criticism of the current experiment is the low power. In our experiment, low power was caused by high variance (see Fig. 6.2a and analysis of per capita aggression levels, p.198). For the attractive aggression hypothesis to work, a strong correlation must exist between aggression levels and food availability. Due to high variance, our data demonstrate no such correlation, and further suggest that there is little information about resource availability associated with aggression.

It is possible that in manipulating the spatial distribution of food, we created a monopolizable resource at the point source, and this removed any effect of aggression as public information. While we did see greater per capita aggression at the point source as predicted by resource defense theory (Grant 1993), this did not translate itself into a change in the distribution of foragers. If the point source had been monopolized, we should have seen extreme undermatching in the point rich treatment, and overmatching in the bar rich treatment. This was not the case (Fig. 6.2b), though there was a trend in this direction in 6 of the 7 groups.

It is also possible that by using a repeated-measures design, groups had the opportunity to establish stable dominance hierarchies with low levels of aggression. We found no evidence that stable dominance hierarchies were established (Fig. 6.1), and the experimental design did not reduce aggression levels. Furthermore, Kennedy and Gray (1994) reported average aggression levels of 0.07 aggressive interactions per mallard per

minute. In our experiment, aggression levels were 6 times greater than this at 0.44 and 0.5 aggressive interactions per guppy per minute in the point rich and bar rich treatments respectively. So, the availability of public information through aggressive interactions was not limited in our experiment.

6.5.1 "*Guppies Aren't Ducks*"

Is it possible that mallards do use aggression as public information about patch quality and guppies do not? We expect life history to affect the value of information to an organism (Koops & Abrahams 1998, chapter 3), and information with the same reliability will sometimes be used or ignored based on the benefits and costs of information and misinformation (Koops unpubl ms, chapter 2). So, there may be a biological reason for differences between guppies and mallards in their use of aggression as public information.

Female guppies may not use aggression as information about food simply because it is a poor indicator of food. Guppies breed continuously throughout the year, and as such, males are continuously searching for and courting females. Male mating success has been positively correlated with aggressive behaviour and only socially dominant males engage in full copulation (Kodric-Brown 1993). Bruce and White (1995) showed that aggression among male guppies may be used by dominant males to suppress the sexual behaviour of subordinates, and even when there is no aggression, males still jockey for position when attempting to monopolize a female (Houde 1988). Thus, it is possible that aggression in guppies, while it is used in the context of competing for food (Magurran &

Seghers 1991), is continually present due to continuous breeding and courting, and as such is an unreliable indicator of the quality of food patches.

Mallards, however, have one breeding time per year, and exhibit peak aggression levels just before establishing territories (D'Eon et al. 1994). Kennedy and Gray (1994) did not specify the time of year when their study was conducted, but, if we assume it was not during this short period prior to establishing territories, aggression levels would not be elevated, so changes in aggression could be a reliable indicator of changes in patch quality.

Schooling in fish also provides anti-predator benefits through the confusion effect, however, the effectiveness of the confusion effect is reduced when individuals in the group stand out (Landeau & Terborgh 1986, Theodorakis 1989). Huntingford (1982) proposed that aggression levels should be reduced in schools that experience higher predation pressure, and Magurran and Seghers (1991) found support for this hypothesis in populations of wild guppies. If aggression is to be used to assess patch quality, it is presumably because it is easier to perceive a difference between patches based on aggression levels than intake rates. If aggression levels are reduced in guppy schools due to predation pressure, then the difference in aggression between patches may be insufficient for foragers to perceive a difference, and thus, aggression would fail to relieve the perceptual constraint faced by foraging guppies (Abrahams 1986, Koops unpubl. ms, chapter 4). However, as already discussed, aggression levels were not reduced in this experiment, so perceptual constraints do not explain the lack of evidence for the attractive aggression hypothesis.

6.5.2 Conclusions

While Kennedy and Gray (1994) concluded that mallards use aggression as a cue to patch quality, our study suggests that guppies do not. Biological differences between guppies and mallards suggest that there are very good reasons why guppies do not use aggression as public information about patch quality. This emphasizes previous conclusions that an organism's life history will be important in determining the sources of information used when making decisions (Koops & Abrahams 1998, chapter 3), and the idea that the use of information will be dependent on the ecology of the decision maker who will use information where and when it is beneficial (Giraldeau 1997). However, the present results, with Kennedy and Gray's (1994) use of aggressive interactions instead of per capita aggression, suggest that aggression is a consequence of the distribution of foragers, and there is no evidence of its use as public information about patch quality.

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Chapter 7: General Discussion

The acquisition and use of information will depend on many factors. Environmental variability, for example, will decrease the use of prior information as the environment becomes more variable and less predictable (chapter 1). The reason prior information is ignored is that an unpredictable environment makes prior information unreliable. In chapter 2 I explored the situation where information will sometimes be right and sometimes be wrong, and the decision maker cannot distinguish between these states. Given this inability to distinguish between correct and incorrect information, the decision maker is faced with either using or ignoring an information source. I demonstrated theoretically that partially reliable information will be ignored when the costs of being misinformed are greater than the benefits of being informed. Thus, information that is very valuable when correct, i.e. has high marginal costs, is susceptible to devaluation from unreliable sources. This implies that when forming assessments, the use of prior information will depend on the marginal costs of information. So, if information about patch quality has relatively low marginal costs while information about predation risk has relatively high marginal costs, prior information about patch quality should be excluded from an assessment sooner than prior information about predation risk.

The theoretical development in chapter 3 shows that the manner in which decisions map onto fitness will influence the value of information. Contrary to recent claims (Bouskila & Blumstein 1992), an animal's tolerance to imperfect information should be influenced by this relationship, which is defined by an animal's life history, and there will be no general bias in assessments. Whether an animal is more likely to overestimate or

underestimate will depend on its life history (Koops & Abrahams 1998, chapter 3). The steeper the relationship between energy reserves and fitness, the more tolerant an animal should be to imperfect information. As in chapter 2, when information has high marginal costs the decision maker will be more tolerant to unreliable information.

The result of using partially reliable or imperfect information will be increased uncertainty about the true state of the environment. Uncertainty also occurs when an animal must sequentially assess its environment. In chapter 4, I developed a model of decision making under uncertainty, showing how assessment uncertainty constrains the perceptual ability of a decision maker. The Z model of perceptual constraints predicts that animals will have poor perceptual ability when differences are small, when environmental variability is high, and when animals are limited in their ability to acquire information. In chapter 5, I investigated the emergent properties of the Z model by examining the influence of assessment uncertainty on the spatial distribution of a group of foragers. The same group dynamics observed in many IFD experiments emerged from the behaviour of individuals assessing patch quality with uncertainty. From these dynamics the model predicts the exploitation of information niches. Good competitors can invest less in cognitive processes, i.e. memory, and more in somatic material to maintain a competitive advantage. Poor competitors, however, can be better served by ceding the race for competitive advantage and diverting resources from somatic to cognitive processes. Thus, information can be viewed as a resource similar to any other ecological resource, with the potential for alternative strategies in the exploitation of that resource.

The need to understand the biology of the decision maker was demonstrated in chapter 6. Kennedy and Gray (1994) hypothesized that foragers use aggression as public information about patch quality. They concluded that mallard ducks, *Anas platyrhynchos*, do use aggression as a cue to patch quality. However, their experiment had causation problems, and it was not possible to tell if foragers followed the distribution of aggression, or if aggression followed the distribution of foragers. When I tested their hypothesis with guppies, *Poecilia reticulata*, I found that guppies were not attracted to aggression. High variance in aggression makes it unlikely that aggression serves as a reliable source of information about patch quality (c.f. chapters 2 and 4).

7.1 Future Directions

I think there are two future directions for the ecology of information use: one continuing to investigate individual information use, the other to investigate the emergent properties of information use. At the individual level, there are many questions to be answered about how and why animals use information. At this level, there are interactions between behavioural ecology, psychology, and neurophysiology (e.g. Real 1994, Dukas 1998), and there are still many unanswered questions. For example, as I demonstrated in chapter 5, optimal memory can vary depending on environmental stability and the animal's social environment. Yet, it is unknown whether an animal's memory is static or dynamic. By static I mean a set rate of memory decay, possibly constrained by neural decay rates. By dynamic, I mean that the animal is able to assess the reliability of prior information. With a dynamic memory, an animal can choose when to use and when to ignore prior

information, as suggested by the work of Valone and Brown (1989) and Valone (1991, 1992). As seen in chapter 5, knowing the flexibility of an animal's memory will determine how well the behaviour of groups of animals can be predicted.

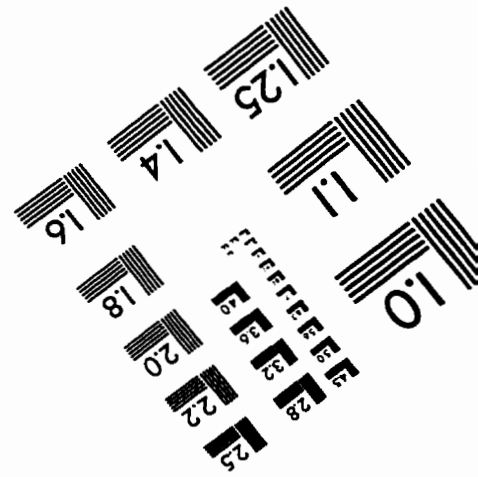
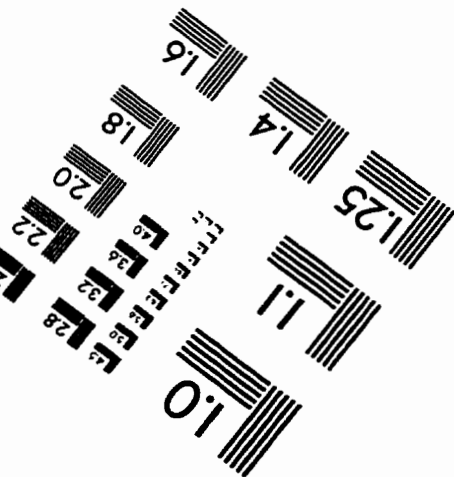
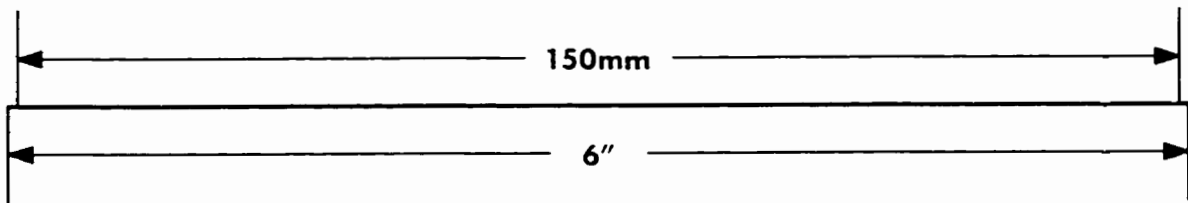
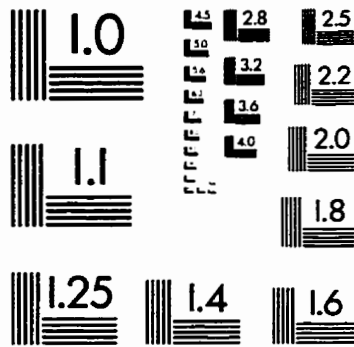
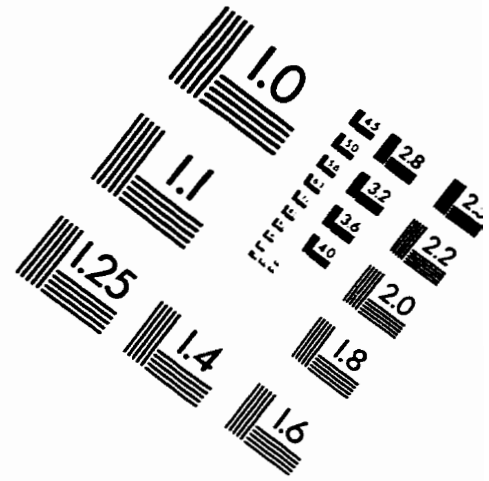
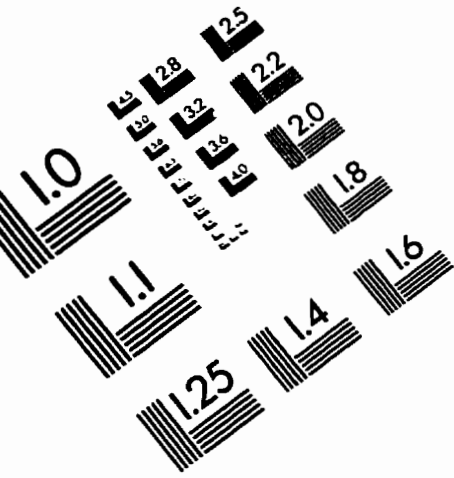
Active research at the individual level is fundamental to investigating the emergent properties of information use. Behavioural ecology was originally started by ecologists who realized that the behaviour of individuals can affect the dynamics of populations, communities and species interactions (e.g. Brown 1964, MacArthur & Pianka 1966, Fretwell & Lucas 1970). Recently, there has been a trend in behavioural ecology toward applying knowledge of individual behaviour to broader ecological problems (e.g. Dall & Cuthill 1997, Anholt 1997, Berrigan & Seger 1998, Kamil & Bond 1998). This is known as emergentism (Mayr 1982), and involves the system level dynamics emerging from the behaviour of its components. This was demonstrated on a smaller scale in chapter 5 when the behaviour of a group of foragers emerged from the behaviour of individual foragers. This same approach can be used at the population level, and allows behavioural ecologists to apply their knowledge of individual behaviour to populations and communities. For the ecology of information use, this approach allows investigation of questions about how the cognitive abilities of individuals influence the growth and decline of populations, and the influence of populations on the communities they inhabit (e.g. Kamil & Bond 1998).

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IMAGE EVALUATION TEST TARGET (QA-3)



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