BEHAVIOURAL DECISIONS OF GUPPIES (POECILIA RETICULATA): A QUANTIFICATION OF FORAGING TRADE-OFFS USING THE IDEAL FREE DISTRIBUTION

by

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Behavioural decisions of guppies (*Poecilia reticulata*): a quantification of foraging trade-offs using the ideal free distribution.

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ABSTRACT

In this thesis I use the ideal free distribution (IFD) theory to quantify trade-offs made by guppies (*Poecilia reticulata*) between various behavioural activities important to their fitness. IFD theory predicts that animals will distribute themselves within their environment such that each receives equal benefits. Thus, if animals conform to an IFD, net benefits received by those at one site (e.g., a food patch) should equal the net benefits received by others faced with a trade-off (e.g., between food and the risk of predation) at another site.

I used an apparatus which allowed groups of ten male or ten female guppies to conform to an IFD while feeding from two separate feeders. I then measured the influence that risk of predation had on foraging decisions by making one feeder risky while providing equal amounts of food from both feeders. I could then determine how much food had to be added to the risky feeder to offset the risk of predation; this represented the energetic equivalent of the risk of predation. This manipulation completely offset the effect of risk for females, but not for males, suggesting that the relation of food intake to fitness is different for the two sexes.

I also measured the "food value" of different courtship opportunities (represented by females of different size) to a group of ten males. Faced with this trade-off, the males did not adopt a stable distribution between the two resources, but fed first and then courted the female. The males switched to courting earlier when more food was available, suggesting that their behaviour was influenced by their energetic state, and more individuals switched to courting as the size of the female increased.

Finally, I examined the value of food to male and female guppies. Growth rate increased with diet level for both sexes, but females grew more rapidly than males on the same diet. Male size was less influenced by food supply, and their courtship success was unaffected by their diet level. These results suggest that additional food provides a greater incremental fitness benefit to females than to males. Thus, when faced with a trade-off, females should be prepared to incur greater costs than males to gain additional food. Knowledge of the relationship between resources and fitness is therefore needed to predict how animals behave when faced with trade-offs.

ACKNOWLEDGEMENTS

At the end of each research chapter I have acknowledged the contribution of various individuals specific to that project. Here, I would like to thank those people that assisted me in a more general way and contributed to my enjoyment and memories of life as a graduate student at SFU.

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DEDICATION

To my parents

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CHAPTER I

GENERAL INTRODUCTION

In their recent book on foraging theory, Stephens & Krebs (1986) make the analogy between the study of foraging behaviour and how an engineer might understand how a machine operates. Their point is that the function of the machine must be known before its mechanism can be understood. Foraging theorists have typically assumed that animals make foraging decisions which function to maximize their average net rate of energy intake.

However, a growing body of literature has demonstrated that these models often cannot explain decisions made by animals forced to trade-off one resource for another (see Lima & Dill, submitted, for a review). Previous attempts to understand how animals make such choices relied on dynamic optimization theory to predict optimal sequences of behaviour (McFarland 1977). However, this approach has been of limited value since many dynamic optimization problems are difficult to solve (Stephens & Krebs 1986).

To understand how animals make decisions involving trade-offs, it must be recognized that the function of the decision should be to maximize the fitness of the animal. Thus, the animal must weigh the various alternatives available to it and select that which maximizes its fitness. The goal of this thesis was to examine quantitatively the trade-offs made by groups of foraging guppies (*Poecilia reticulata*) forced to choose between 2 resources; one was always food, the other was either security (reduced risk of predation) or, in the case of males, access to females.

To quantify trade-offs, both resources must be expressed in a common currency. To do this, I used the ideal free distribution (IFD) theory (Fretwell & Lucas 1970, Fretwell 1972) as a tool. IFD theory predicts that if animals are 'ideal', in that they have perfect knowledge of the distribution of resources in their environment, and 'free' to use these resources on an equal basis with other animals, they will distribute themselves such that all individuals receive equal net benefits. Thus, in an environment which contains only one resource (e.g., food), all individuals will receive the same amount of that resource. However, in an environment in which areas (patches) contain different resources, the amount of resource obtained by one individual at one area will be equal in value to the amount of a different resource obtained by another individual somewhere else. Thus, IFD theory can be used to convert the value of one resource to another, representing them in a common currency.

Chapter II of this thesis introduces the concept of IFD theory by reviewing previous studies using it to explain animal distributions. A model is then developed which demonstrates how limited abilities to perceive differences in patch quality can generate a characteristic deviation from the distribution predicted by IFD theory. Chapter III presents an experimental apparatus which allows groups of ten male or ten female guppies to conform to the assumptions of the IFD. This system is then used in Chapter IV to quantify the influence of risk of predation on guppy foraging decisions. A simple rule is also tested describing how the guppies incorporate risk of predation into their foraging decisions. Chapter V examines how male guppies trade-off food intake against courtship opportunities. Finally, Chapter VI examines the relationship between food and fitness in both male and female guppies, in an attempt to understand how life history characteristics influence foraging decisions involving trade-offs.

LITERATURE CITED

Fretwell, S.D. 1972. Populations in a seasonal environment. Princeton University Press, Princeton, NJ

Fretwell, S.D., & H.L. Lucas. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheoretica 19: 16-36.

Lima, S.L., & L.M. Dill. submitted. Behavioural decisions made under the risk of predation: a review and prospectus. Q. Rev. Biol.

McFarland, D.J. 1977. Decision making in animals. Nature 269: 15-21.

Stephens, D.W. & J.R. Krebs. 1986. Foraging theory. Princeton University Press, Princeton, NJ

CHAPTER II

PATCH CHOICE UNDER PERCEPTUAL CONSTRAINTS: A CAUSE FOR DEPARTURES FROM AN IDEAL FREE DISTRIBUTION

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SUMMARY

A review of tests of ideal free distribution (IFD) theory reveals a characteristic bias: patches with a small proportion of the resources are relatively overused and patches with a larger proportion of the resources are relatively underused. A model is developed to examine how animals with limited abilities to perceive differences in patch quality affect an IFD by foragers. This constraint produces the observed bias, a bias that is exaggerated as the number of patches increases. Sutherland (1983) has developed a model based on interference which can also explain the observed bias. The two models can be differentiated in that only the perception limit model (this paper) is sensitive to absolute changes in overall resource availability and to increases in the number of animals. Additionally, Sutherland's model predicts that when deviations away from an IFD occur there will be no differences in intake rates, while the perception limit model predicts that intake rates should vary between patches.

INTRODUCTION

The ideal free distribution (IFD) theory was developed by Fretwell & Lucas (1970) and Fretwell (1972) to describe how animals should distribute themselves within an environment between patches of varying suitability. If patch suitability declines as the density of animals in that patch increases, the IFD predicts that the proportion of animals in a patch will equal the proportion of resources available in that patch. For such a situation to occur, all animals must be 'ideal' in their ability to select a patch which maximizes fitness (they must have perfect information about the environment) and be 'free' to enter and use any patch on an equal basis with other residents (all animals must be identical with respect to their competitive abilities).

In systems where patch suitability can be determined, IFD theory can be used to predict animal distributions. Published studies have fallen into two major categories: animals competing for breeding opportunities (Parker 1978; Davies & Halliday 1979; Sargent et al. 1986) and animals competing for food (Milinski 1979, 1984; Zwarts & Drent 1981; Harper 1982; Sutherland 1982; Talbot & Kramer 1986; Godin & Keenleyside 1984; Power 1984; Gillis 1985). These experiments record data in either spatial or temporal form. The spatial experiments record the proportion of resources in a patch and the proportion of animals using those patches. In these studies a characteristic bias has been observed: patches which have a small proportion of the resources have disproportionately more individuals using them and conversely, patches with a large proportion of the resources are underused (Table 2.1). In addition, Sutherland (1982) noted in his field observations of oystercatchers (*Haematopus ostralegus*) that more individuals used poor patches than would be predicted by an IFD.

Table 2.1. Departures from an IFD for spatial data, which illustrate the characteristic overuse of poor patches and underuse of good patches. A good patch contains an above average proportion of resources, and a bad patch contains a below average proportion of the resources. A study is considered to show evidence of a bias when greater than one half of the observations deviate in one direction from the predicted result. Numbers in parentheses represent the sample size

Data source and species	Proportion of observations greater than expected on poor patches	Proportion of observations less than expected on good patches
Courtney & Parker (1985)	0.76 (37)	0.77 (35)
Figs. 5, 9 and raw data		
Tarucus theophrastus		
Davies & Halliday (1979)		
Fig. 13	0.60 (5)	0.75 (4)
Bufo bufo		
Gillis (1985)		
Fig. 3 30 fish	0.33 (6)	0.33 (3)
Fig. 3 60 fish	0.83 (6)	0.67 (3)
Fig. 3 120 fish	1.00 (6)	1.00 (3)
Fig. 3 240 fish	0.67 (6)	1.00 (3)
Brachydanio rerio		
Parker (1978)		
Fig. 8.3	1.00 (2)	1.00 (3)
Scatophaga stercoraria		
Sargent et al. (1986)		
Fig. 2a 1981 data	0.80 (10)	0.73 (11)
Fig. 2b 1982 data	0.67 (6)	0.50 (6)
Oncorhyncus kisutch		
Talbot & Kramer (1986)		
Fig. 2	0.73 (15)	1.00 (10)
Poecilia reticulata		
Zwarts & Drent (1981)		
Fig. 6 Low density	0.86 (7)	0.88 (8)
Fig. 6 High density	0.83 (6)	0.88 (8)
Haematopus ostralegus		
Total greater than 0.5	11	10
Total	12	12
Proportion	0.92	0.83

The temporal experiments record the distribution of animals through time between two non-depleting patches. The animals in these experiments also indicated a bias towards overuse of poor patches (Table 2.2). Further, since all experiments contained only two patches the most profitable patches had fewer animals than predicted.

Some authors have observed that their animals were not all of equal competitive ability and hypothesized that the observed deviation resulted from a violation of the 'free' assumption (called an ideal despotic distribution, Fretwell 1972). However, Milinski (1984) could find no effect of unequal competitive abilities on an IFD in sticklebacks (*Gasterosteus aculeatus*). Godin & Keenleyside (1984) also observed no significant differences in intake rates of animals within a patch which might have indicated despotic behaviour and a violation of the 'free' assumption. Therefore, basing explanations of deviations from an IFD upon despotic behaviours may not always be warranted.

Unequal competitive abilities may cause deviations from an IFD by a mechanism other than despotic behaviour. Sutherland and Parker (1985) and Parker and Sutherland (1986) argue that in experiments with a continuous-input of resources, unequal competitive abilities will result in animals distributing themselves such that the sum of competitive abilities will conform to the predicted distribution of an IFD. If the animals are not all of equal competitive ability, the distribution of animals will not necessarily conform to an IFD. This mechanism does not predict a specific deviation from an IFD and as such would not predict the consistent overbias observed in the literature.

Sutherland (1983) has suggested that in situations where there is no continuous-input, as in most field observations, deviations from an IFD could be

Table 2.2 Departures from an IFD for temporal data, which illustrate overuse of poor patches. These studies examine single distributions with multiple observations at predetermined points in time. Again, an overbias occurs when greater than one half of the observations are greater than predicted by an IFD. Data represent the mean results of multiple observations taken only when the distribution reached an equilibrium. If a dynamic stage existed in the process leading to the equilibrium distribution, it was excluded by fitting a straight line to the initial points of the distribution. The point at which observations ceased conforming to this line was considered to be the beginning of the equilibrium distribution.

	Data from least profitable patch		
Data source and species	Ratio	Proportion of observations greater than expected	N
Godin & Keenleyside (1984)			
Fig. 2	2:1	0.61	28
Fig. 2	5:1	1.00	25
Aequidens curviceps			
Harper (1982)			
Fig. 2	2:1	0.50	12
Anas platyrhynchos			
Milinski (1979)			
Fig. 1	5:1	0.71	28
Fig. 2	2:1	1.00	15
Fig. 2	2:1	1.00	13
Gasterosteus aculeatus			
Milinski (1984)			
Fig. 3	2:1	0.44	16
Fig. 3	2:1	0.38	16
Gasterosteus aculeatus			
Total greater than 0.5		5	
Total		8	
Proportion		0.625	

due to interference. In Sutherland's model, interference is considered to be any kind of interaction between predators which reduces searching efficiency. This is distinct from despotic behaviour in that all animals within a patch are affected equally; despotic behaviour results in unequal use of resources by individuals within a patch. Sutherland's (1983) model assumes that interference will cause patch suitability to decline more rapidly with increases in animal density than would be predicted by an IFD. Therefore, the deviation from an IFD may be due solely to errors in perspective, with the observer overestimating patch suitabilities at high densities in comparison to their actual value to the animal. What appears to the observer as a departure from an IFD may actually be a perfect IFD from the animals' perspective.

This paper presents an alternative model to examine departures from IFD's based on limited perceptual abilities. It examines the predicted results of an IFD experiment when animals have a limited ability to resolve differences in patch suitability while foraging for food.

METHODS

In designing this model I assumed that animals assess patch suitability from perceived individual intake rates, not from the total amount of food available in the patch (see Harper 1982; Milinski 1984). Hence, the quality of a patch is equal to the total amount of food available (F) divided by the total number of animals in the patch (N) plus the animal which is making the decision whether or not to enter or stay in that patch, i.e. patch suitability equals $F/(N+1)$.

A consequence of animals assessing patch suitability in this manner is that the difference between any two patches will be greatest at the lowest total densities of predators. The effect of animals preferentially going to the best patches, thereby reducing their suitability, will lower the absolute difference between patches. As a result, with a fixed food supply the differences between patches will decrease asymptotically as the number of animals in the environment increases (Fig. 2.1).

If animals are 'ideal' they will be unaffected by this decay function. However, if there is some finite level beyond which they cannot resolve differences in patch suitability (a perception limit), then those animals entering after this point will be unable to gain sufficient information to choose the most profitable patch (Fig. 2.1).

The initial condition of the model (Fig. 2.2) was an environment containing an undepletable food supply available at a rate of 20 food units per unit time, distributed between two, three, or four patches. Simulations were performed in situations where the food was divided between patches in such a way that no patch contained less than two food units.

The model operated by sequentially entering 10 animals into the environment. Every animal was identical, i.e., they were each capable of consuming all the food by themselves, they had the same perception limit (they were able to perceive differences in patch quality of one, two, or three units of food per unit time per individual), and they all used the same decision rule. The decision rule was simply to go to the best patch when that could be perceived. If the best patch could not be resolved from the next best patch due to the difference in suitability being less than the perception limit, one of the indistinguishable patches was chosen at random. In a multi-patch system, as the perception limit increases, or patch suitabilities become more similar, the animal must choose randomly between an increasing number of patches. This decision rule can most easily be explained by

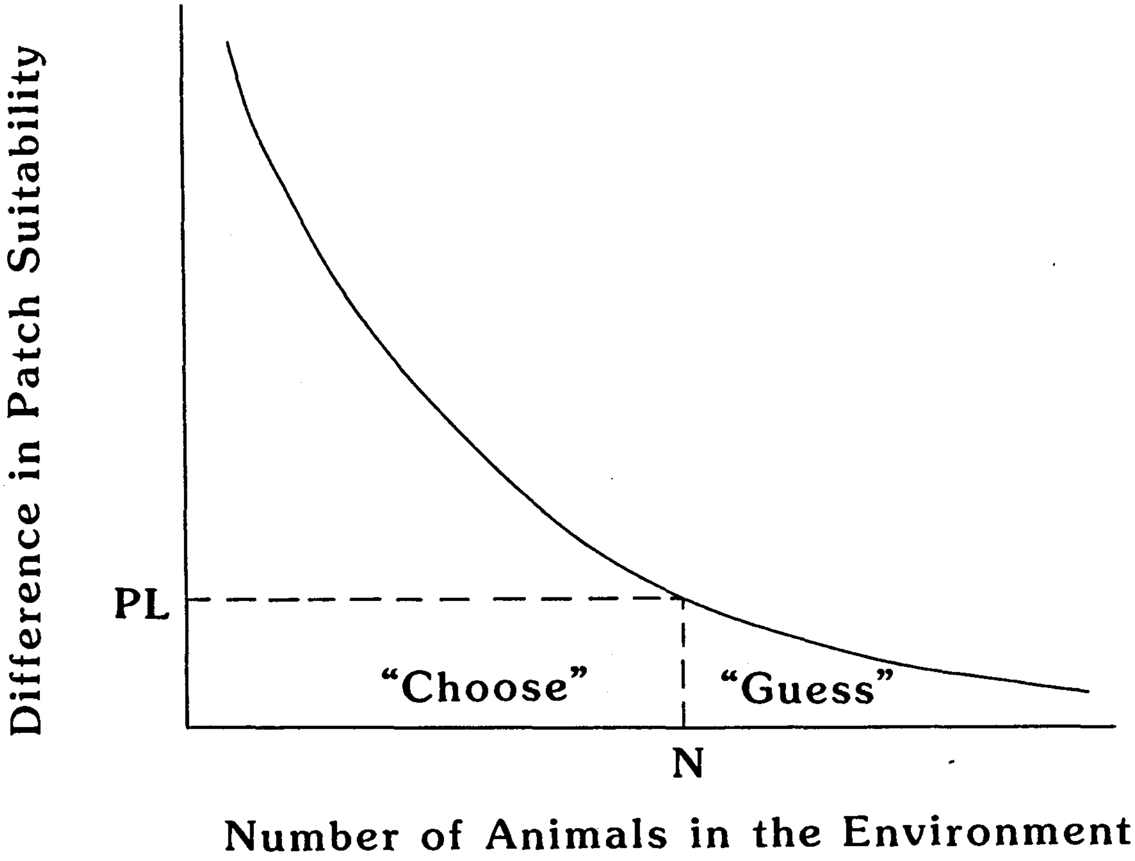

Figure 2.1. The relationship between the difference in patch suitability and the number of animals in the environment. If a limited ability exists to resolve differences between patch suitabilities (PL) then only a limited number of animals (N) will be able to choose which patch to enter. All animals beyond this point will be unable to resolve differences in patch suitability and will have to choose a patch at random ("guess").

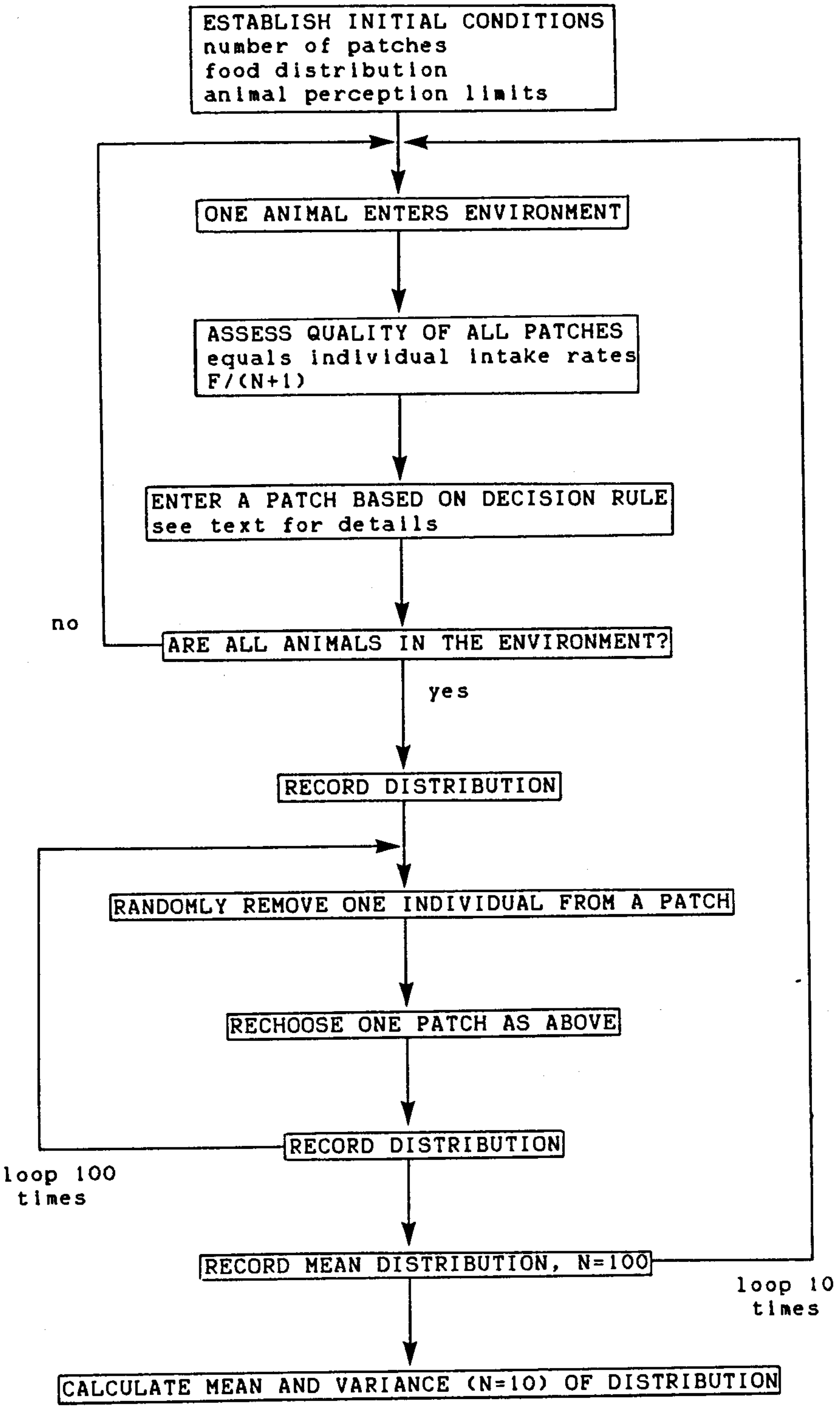

Figure 2.2. Flowchart illustrating model operation. See text for details.

a numerical example. Consider an animal entering an environment with four patches which have patch suitabilities of 3.5, 2, 1.4 and 1. If the animal has a perception limit of 1 it will correctly enter the patch with the highest suitability. However, if the perception limit is two the animal will be unable to perceive differences between 3.5 and anything greater than 1.5 and will have to choose randomly between the two best patches. As the perception limit increases the probability increases that an animal will have to choose a patch randomly (henceforth referred to as guessing).

After an initial distribution was determined, the animals were allowed to redistribute. This is analogous to switching, which has been observed in IFD experiments (Milinski 1979; pers. obs.). Individuals were chosen randomly to vacate a patch (causing an adjustment in the rate of food availability) and to rechoose a patch using the original decision rule. One hundred resamplings were allowed.

Data were recorded on the position of the animals for each of the 100 resampling periods and the final result obtained was the overall average. The simulation was run 10 times for each distribution of food and perception limit and the mean and variance of the distributions was recorded.

The deviations from an IFD produced by this model were compared to the predictions of Sutherland's (1983) model to determine if they could be distinguished quantitatively. The predicted IFD distributions from Sutherland's model are generated by the equation $B_i = ca_i^{1/m}$ where B_i is the proportion of animals in the ith patch, a_i is the proportion of resources in the ith patch, m is the degree of interference and c is a normalizing constant such that the B_i values sum to unity.

RESULTS

The results of the simulation are illustrated in Fig. 2.3. The most striking result of this simulation is that any deviation from perfect information will produce only one type of bias, an underuse of good patches and an overuse of poor patches.

The size of the deviation is affected by the perception limit. As the deviation from an IFD increases, so do the differences in individual intake rates. Since animals choose patches upon the basis of individual intake rates, any deviation which exceeds their perception limit will provide enough information for the next animal to choose the correct patch. Therefore the perception limits provide feedback which limit the difference in individual intake rates and the magnitude of the deviation from an IFD.

Two opposing forces affect the shape of the distribution. As the environment becomes less uniform, the initial differences in patch suitability increase and the number of animals which must guess is reduced. This provides a force limiting the deviation from an IFD at extreme resource distributions. However, since guessing distributes the animals in a uniform manner, guessing animals are "more wrong" at less uniform resource distributions. This provides a force producing less deviation at a uniform resource distribution. A consequence of these conflicting forces is a smaller deviation from an IFD at extreme resource distributions with good perception limits (PL=1, Fig. 2.4). However, this trend does not continue as PL increases (PL=2 and 3, Fig. 2.4), because the large differences in patch suitability are no longer great enough to be perceived and the number of guessers is no longer reduced. Therefore the inefficiency of guessing causes the deviation to increase at extreme resource distributions.

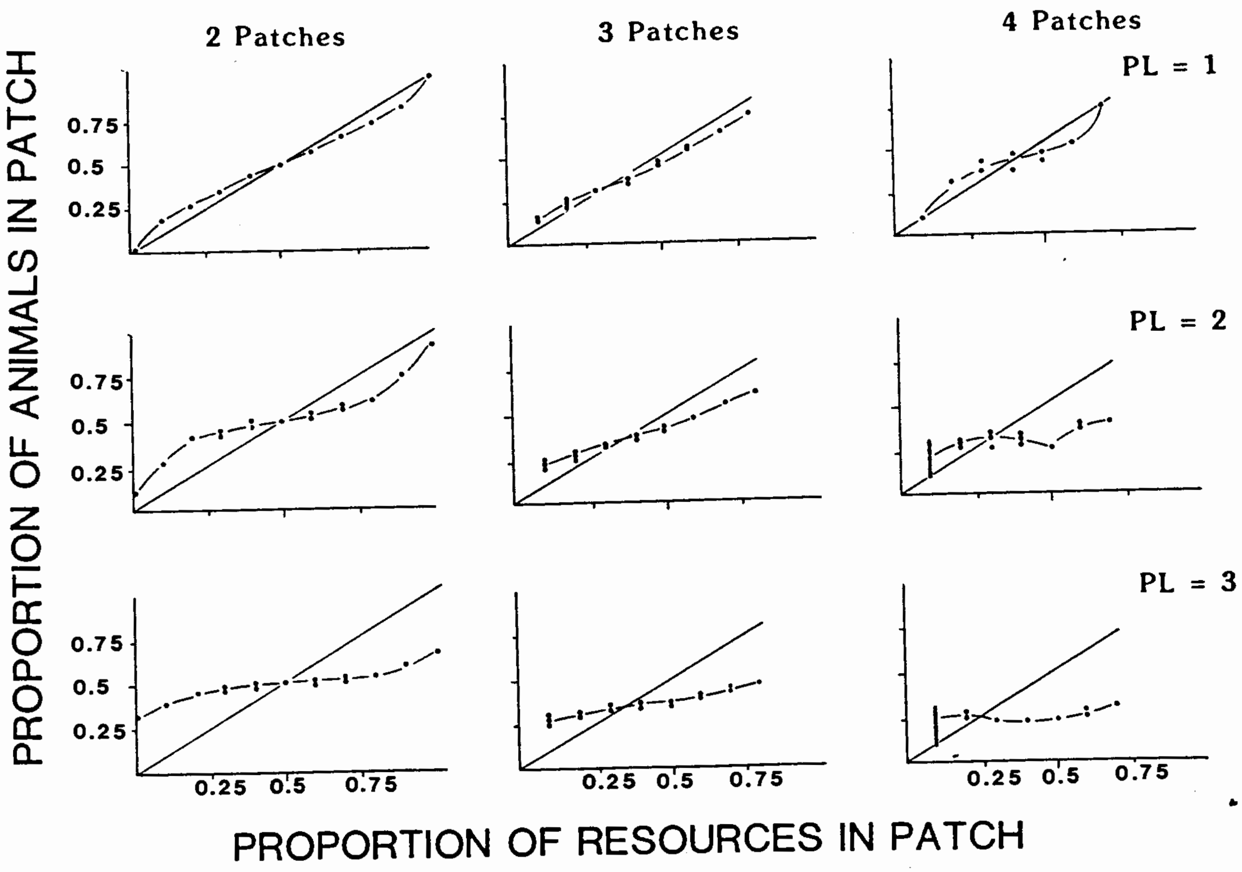

Figure 2.3. Results of simulations for three different perception limits (PL) of animals in an environment with the resources distributed between two, three or four patches. The diagonal lines represent the distribution predicted by IFD, the curved lines are interpolations of the simulated distributions.

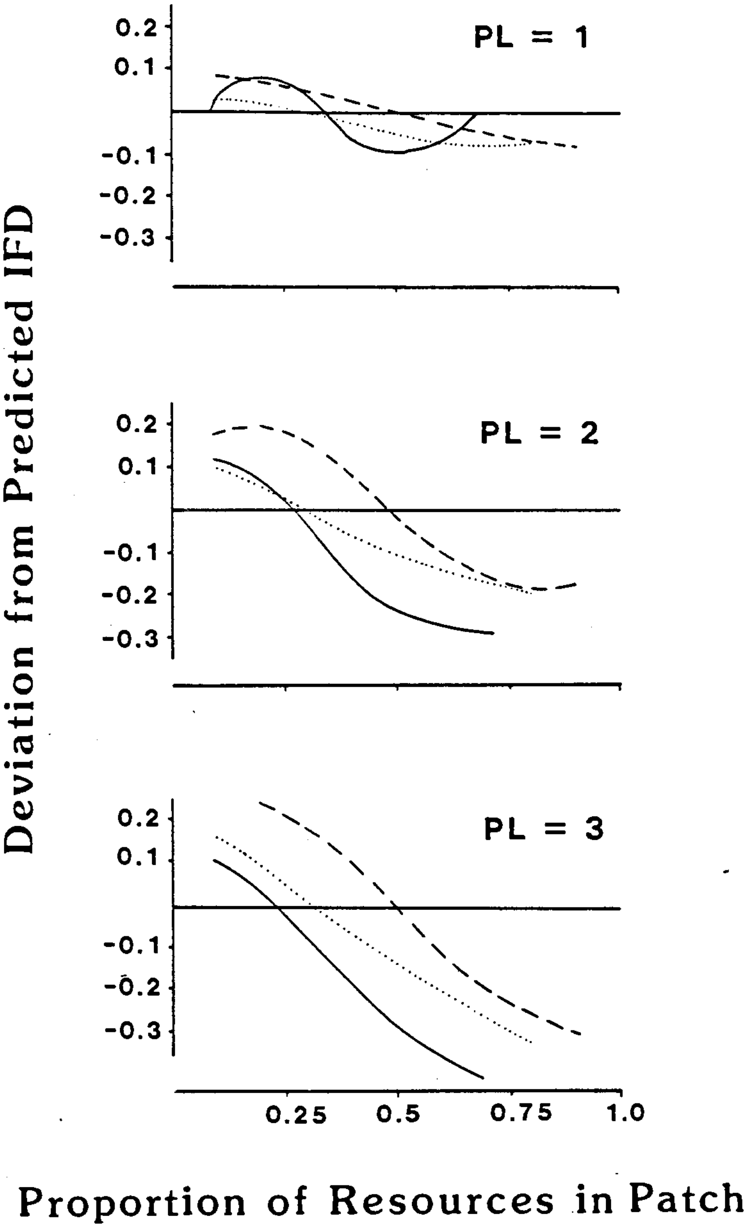

Figure 2.4 The biases produced from an IFD as a result of the combined effects of varying abilities to perceive differences in patch suitability (PL) and the number of available patches. The deviation corresponds to the observed distribution minus the predicted distribution. Solid lines represent four patch systems, dotted lines three patch systems and dashed lines two patch systems.

Perception limit model vs Sutherland's model

Sutherland's (1983) interference model produces approximately similar dynamics to this model when large m values (levels of interference) are used (maximum m value from the literature is 1.13) (Fig. 2.5). However, there are some subtle differences between the models. Sutherland's model predicts an increasing deviation away from the IFD at extreme differences in patch suitability. In addition, the inflection point (by definition the point which divides patches into good and bad) is constant for all levels of interference: in all cases it is equal to the reciprocal of the number of patches in the environment. The inflection point in the perception limit model is affected both by the number of patches in the environment and the perception limit, and ranges between 1/2 and the reciprocal of the number of patches. This is because the type of guess an animal makes is a function both of the number of patches available and the number which are indistinguishable as the 'best' patch. For example, when there are four patches in the environment, the inflection point shifts towards the origin (Fig. 2.4). At low perception limits an animal may only have to guess between between two indistinguishable patches, but as the perception limit increases more patches will become indistinguishable from the best patch.

Another distinction which is inherent in the assumptions of the two models is that net intake rates will not differ between patches when the bias is produced by interference. However, the perception limit model predicts that the resource will be used inefficiently such that individuals in a high quality patch will have a greater intake rate than those in the poor patches, the degree of this difference not exceeding individual perception limits.

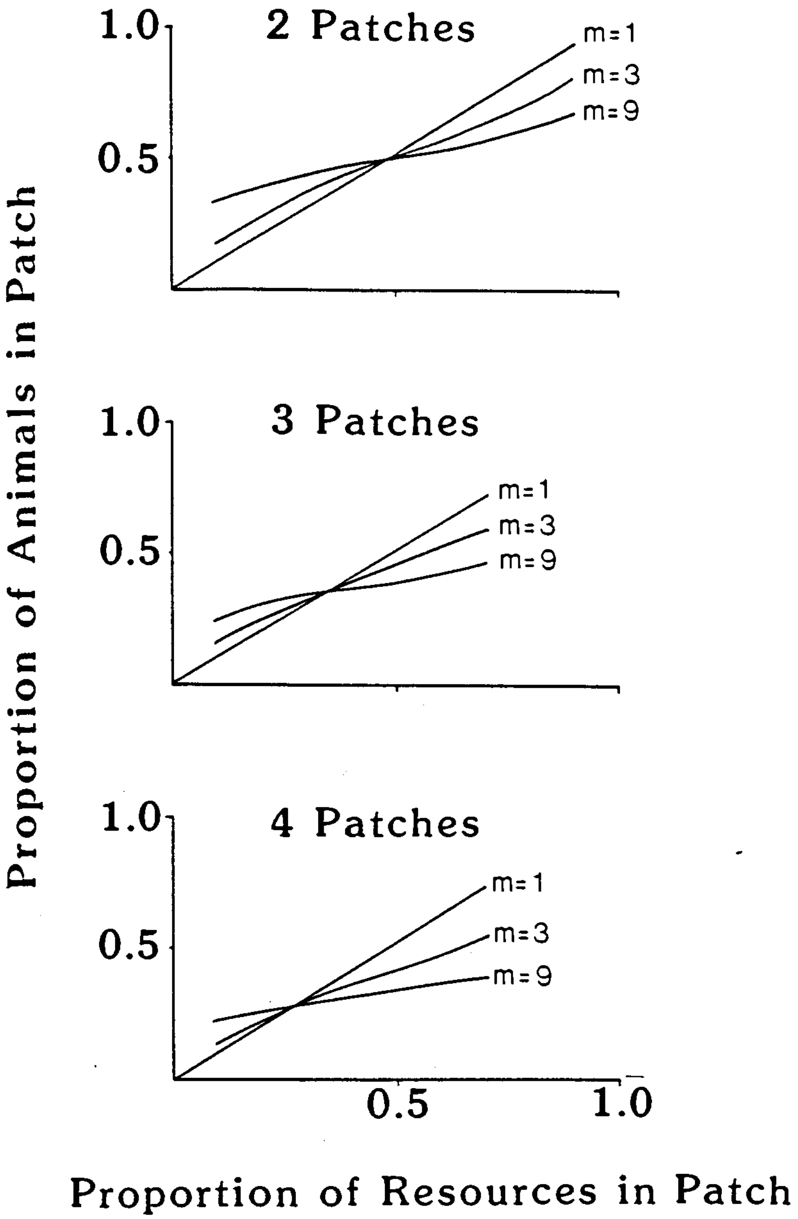

Figure 2.5. Predicted distributions from Sutherland's (1983) interference model for three different interference levels.

DISCUSSION

The simple and reasonable assumption that animals are constrained by some finite level at which differences in patch suitability can be perceived produces a characteristic bias from an IFD. This bias is a result of the random patch choice rule used when differences cannot be perceived between patches. Since the rule states that any indistinguishable patch is chosen with equal probability, too many animals will go to a poor patch and too few to a good patch. However, the extent of this bias will be regulated by the perception limit. If the deviation from an IFD becomes very large, the difference in patch suitability will again become perceptible resulting in those animals who enter the environment later (or those who resample) choosing the best patch and reducing the deviation. As a result, deviations from an IFD by a perception limit should produce a stable, characteristic distribution.

Since the shape of the deviation from an IFD with a random decision rule closely resembles the results of Sutherland's (1983) interference model, distinguishing the cause of the bias would not be possible solely from the results of field observations on distributions. Indeed, since the two models violate different assumptions of the IFD (the interference model affects availability of resources while the perception limit model affects abilities to perceive relative levels of availability of these resources) it is possible for both to operate simultaneously.

However, the two hypotheses can be distinguished by experimental manipulation. The perception limit model predicts that any manipulation which increases the proportion of animals which must guess which patch to use will increase the deviation away from an IFD; Sutherland's model predicts that deviations are solely dependent upon the interference level. Therefore, the perception limit model predicts that decreasing the overall resource density without changing proportions available in each patch will increase the deviation from an IFD whereas Sutherland's model predicts no change. The perception limit model also predicts that increasing the number of animals in the environment will increase the deviation from an IFD whereas Sutherland's model predicts no change with a constant interference level.

The two hypotheses may also be distinguished *a posteriori* if data are available on net individual intake rates. If a deviation from an IFD is observed, the perception limit model would predict that individuals in good patches will have greater net intake rates than individuals in poor patches. Sutherland's model would predict no differences in net individual intake rates between patches assuming all animals are identical.

In this model, the environment was assumed to be deterministic such that no new information was required once the distribution was known. However, recent attention has been given to the cost of acquiring information in a stochastic environment (see Kacelnik & Krebs 1985 for a brief review). For example, Regelmann (1982) used a learning rule which generated a similar effect to my model. Rather than examining the population, as in the present model, Regelmann's learning rule was used to describe decisions made by each individual at a given point in time. Each individual chooses a patch based upon the ratio of patch profitabilities incorporating both current and past rewards with either a cost or no cost to switching patches. Regelmann's model resulted in more individuals in the poor patch than predicted by an IFD and was attributed to all individuals having an equal probability of resampling the environment. Since there are more individuals in the better patch, the probability of more individuals moving from the best to the worst patch are greater than vice versa. This effect was more profound when a cost was associated with switching patches.

The mechanism which results in the overuse of the poor patch in this model results from the random nature by which animals make decisions when there is no perceived difference in only the current value of the patches. If patches are not perceived to be different it is assumed that they are of equal value. Thus, too many animals appear in the poor patch because the random decision rule distributes animals in a characteristic deviation from an IFD. This is distinct from patch choice by animals in Sutherland's model since interference produces real differences in patch quality to animals which must compete for food.

Since deviations from an IFD increase with the number of simultaneous choices an animal must make, the effect of a finite perception limit will become more obvious in complex environments. The result will be an inefficient use of the available resources. Rules of thumb used by animals to benefit from this deviation (e.g., if patch difference is not perceptible, go to the patch with the greatest number of competitors) will not spread as their benefits are inversely proportional to their frequency in the population. From a game theory point of view, the population is not displaying an evolutionarily stable state (Maynard Smith 1973) and therefore should be susceptible to invasion by a mutant with a greater ability to resolve patch differences. If perception limits cause the observed deviations from the IFD, this suggests either that the population is still evolving improved perception limits, or that the benefit gained from improved perception limits would be offset by the increased cost of gaining information. If the latter is the case, deviations from an IFD in the absence of interference represent the equilibrium point between the benefits of improved information and the cost of achieving these benefits.

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REFERENCES

Courtney SP, Parker GA (1985) Mating behaviour of the tiger blue butterfly (*Tarucus theophrastus*): competitive mate-searching when not all females are captured. Behav Ecol Sociobiol 17: 213-221

Davies NB, Halliday TR (1979) Competitive mate searching in male common toads, *Bufo bufo*. Anim Behav 27: 1253-1267

Fretwell SD (1972) Populations In A Seasonal Environment. Princeton Univ Press, Princeton

Fretwell SD, Lucas Jr. HL (1970) On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheoretica 19: 16-36

Gillis DM (1985) Animal aggregation, interference and the ideal free distribution. M.Sc. Thesis, McGill University, Montreal P.Q., 60p

Godin J-GJ, Keenleyside MH (1984) Foraging on patchily distributed prey by a cichlid fish (Teleostei, Cichlidae): a test of the ideal free distribution. Anim Behav 32: 120-131

Harper DGC (1982) Competitive foraging in mallards: 'ideal free ducks'. Anim Behav 30: 575-584

Kacelnik A, Krebs JR (1985) Learning to exploit patchily distributed food. In: Sibly RM, Smith RH (eds) Behavioural Ecology: Ecological consequences of adaptive behaviour. Blackwell Scientific Publications, Oxford, pp 189-205

Maynard Smith J (1973) The theory of games and the evolution of animal conflict. J Theor Biol 47: 209-221

Milinski M (1979) An evolutionarily stable feeding strategy in sticklebacks. Z Tierpsychol 51: 36-40

Milinski M (1984) Competitive resource sharing: an experimental test of a learning rule for ESSs. Anim Behav 32: 233-242

Parker GA (1978) Searching for mates. In: Krebs JR, Davies NB (eds) Behavioural ecology: an evolutionary approach. Blackwell Scientific Publications, Oxford, pp 214-244

Parker GA, Sutherland WJ (1986) Ideal free distributions when individuals differ in competitive ability: phenotype-limited ideal free models. Anim Behav 34: 1222-1242

Power ME (1984) Habitat quality and the distribution of algae-grazing catfish in a Panamanian canal. J Anim Ecol 53: 357-374

Regelmann K (1984) Competitive resource sharing: a simulation model. Anim Behav 32: 226-232

Sargent RC, Gross MR, van den Berghe EP (1986) Male mate choice in fishes. Anim Behav 34: 545-550

Sutherland WJ (1982) Spatial variation in the predation of cockles by oystercatchers at Traeth Melynog. Anglesey. II. The pattern of mortality. J Anim Ecol 51: 491-500

Sutherland WJ (1983) Aggregation and the 'ideal free' distribution. J Anim Ecol 52: 821-828

Sutherland WJ, Parker GA (1985) Distribution of unequal competitors. In: Sibly RM, Smith RH (eds) Behavioural ecology: Ecological consequences of adaptive behaviour. Blackwell Scientific Publications, Oxford, pp 255-273

Talbot AJ, Kramer DL (1986) Effects of food and oxygen availability on habitat selection by guppies. Can J Zool 64: 88-93

Zwarts L, Drent RH (1981) Prey depletion and the regulation of predator density: oystercatchers (*Haematopus ostralegus*) feeding on mussels (*Mytilus edulis*). In: Jones NV, Wolff WJ (eds) Feeding and survival strategies of estuarine organisms Plenum Publishing Corp, London, pp 193-216

CHAPTER III

FORAGING GUPPIES AND THE IDEAL FREE DISTRIBUTION: THE INFLUENCE OF INFORMATION ON PATCH CHOICE

INTRODUCTION

Foraging theory generally assumes that animals have perfect knowledge of their environment. Whether the environment is deterministic or stochastic, theory assumes that animals know the parameters which describe the availability of food. Although this assumption is unlikely to be true, the question of how animals obtain information to make decisions was ignored until KREBS *et al.* (1978) examined models of optimal information acquisition in great tits (*Parus major*). Since that time, a variety of models have been presented suggesting simple mechanisms whereby animals may gain information about their environment (for a review see KACELNIK & KREBS 1985). In these models, information is viewed as a commodity, and as with other commodities, there are costs and benefits associated with its acquisition. The benefit of information is that it allows the animal to increase its probability of making a correct decision; as such it is subject to diminishing returns. The cost of information is of two kinds. The first is the opportunity cost associated with sampling: when an animal is sampling, this reduces the rate at which it can forage. The second cost is the physiological cost of storing and processing information. As the animal gains more information, we assume that more neural material is required to store and process it.

The ideal free distribution (IFD) theory (FRETWELL & LUCAS, 1970; FRETWELL 1972) can be used to measure how information is acquired while foraging. It describes how a group of animals should distribute themselves between feeding patches which provide food at a constant rate, such that each animal maximizes its energy intake rate. The IFD predicts that they will distribute themselves between food patches such that the proportion of animals in a patch equals the proportion of food available. To achieve this distribution the animals must be 'free' to enter and use resources on an equal basis with patch residents, and 'ideal' in that they have perfect knowledge of the food distribution. When the 'free' assumption is satisfied, deviations from the IFD reflect an inability to learn or respond to the energy-maximizing distribution. Further, the extent of any deviation should be inversely related to the ability to learn, because progressively larger deviations result in increasing reductions in intake for some animals.

The IFD also provides an experimental system for examining how information is used in making foraging decisions. HARLEY (1981), REGELMANN (1984), and McNAMARA & HOUSTON (1985) have developed linear operator models which examine how current and past information are used to achieve an IFD. Their models assume that individuals decide where to forage based on their own intake rate rather than assessing patch quality based on the total amount of food available there. (This assumption has been confirmed by HARPER (1982) for mallard ducks (*Anas platyrhynchos*) and MILINSKI (1984) for sticklebacks (*Gasterosteus aculeatus*).) In an environment which has a stable distribution of food, increasing use of past information increases conformity with an IFD. In this situation, animals which are capable of using more past information will be able to achieve a distribution which is closer to an IFD.

The IFD can therefore be used to measure several characteristics of animals' foraging behaviour. Deviation from an IFD can be used as an indicator of the ability to gather information, and detailed analysis of the distribution of animals within an experiment can reveal the relative contributions of past and current information used by animals.

METHODS

Guppies (*Poecilia reticulata*) are a strongly sexually dimorphic species of fish. Females are relatively large, drab, indeterminate growers, while males are small, brightly coloured (and likely conspicuous; ENDLER 1978), determinate growers (REZNICK 1983). In these experiments fish were tested in groups of ten similar-sized males (0.109 g ± 0.017 SD) or ten similar-sized females (0.182 g ± 0.027 SD). Similar-sized individuals were used to prevent dominance hierarchies developing within the apparatus (BROWNE 1981) ensuring that individuals would have similar competitive abilities. The same two groups of fish were used in all experiments, any who died (3 males and 1 female) being replaced with equal sized individuals.

All experiments were performed in two 90-l aquaria. The fish lived in the aquaria throughout the experimental period so that no daily acclimation periods were required. They were maintained on a 12-h light/dark cycle and fed NutraFin (TM) and brine shrimp *ad lib* daily between experiments. During experiments the fish were maintained exclusively on the food provided during experimentation (see below) except for a weekly supplement of NutraFin flakes for essential nutrients.

Tap water was used in the experiments and was hardened by the presence of oyster shells in the corner filters. Each aquarium contained a 3-cm layer of aquarium gravel. The ends of the aquaria had black plexiglas attached to the inside to prevent reflection, and the backs of the aquaria were covered with black plastic. They were completely surrounded by a black plastic blind, from behind which observations were made.

Feeders were located at opposite ends of the aquaria. Each feeder consisted of a 2-l Erlenmeyer flask with a glass tube attached to its lower side (see Fig. 3.1 for details). The feeders contained 2-l of water and a pre-weighed amount of food (see below) which drained into the aquarium through a plastic dispenser. This was a submerged tube which extended over the width of the aquarium; food entered through five uniformly spaced holes. Presenting the food over this large area rendered the patch indefensible and provided the fish with 'free' access to the food.

Eggs of the onion fly (*Delia antigua*) were used as the food in the experiments because, (i) they are small enough for guppies to easily consume and, (ii) they are slightly negatively buoyant when fresh, allowing them to slowly fall through the water column. Eggs in the feeders were kept in suspension via a stir bar constantly rotated by a magnetic stir plate. This ensured that over time they left the flask at a uniform rate (as determinined in preliminary experiments).

The feeders could be operated remotely from behind the blind. Each feeder was sealed by a rubber stopper through which a glass tube passed. The glass tube extended to the bottom of the feeder just above the stir bar. This maintained a constant drain rate while the feeders were dispensing eggs. A piece of tygon tubing attached to this glass tube led behind the blind. The end of the tygon was sealed by a hypodermic needle embedded in a cork, and the entire system was sealed by a syringe attached to the needle. The feeder could be turned on remotely simply by removing the syringe plunger. Once this was removed, water (and eggs) drained from the feeders at the same rate that air entered. Removing the plungers from both feeders allowed them to start simultaneously without disturbing the fish.

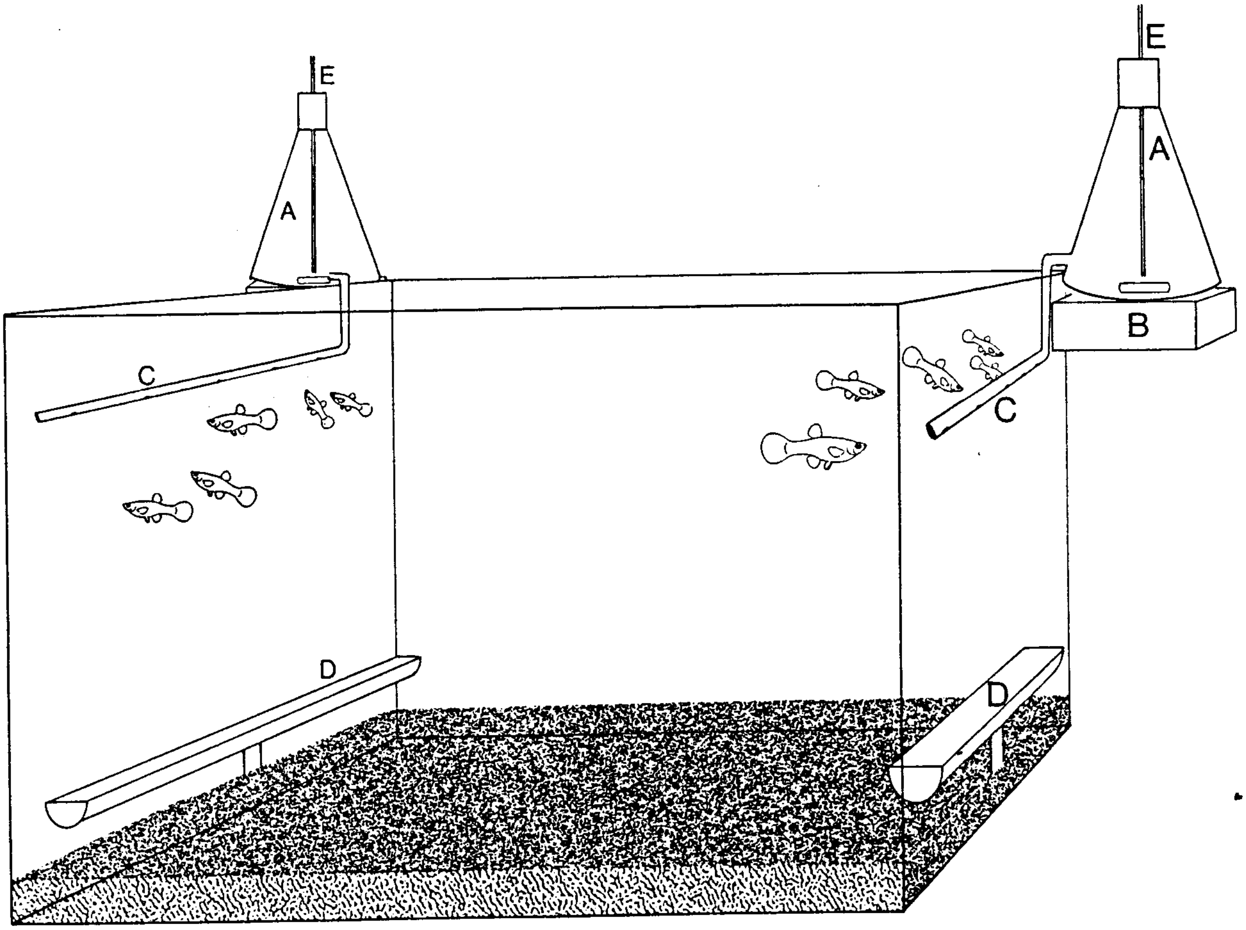

Fig. 3.1. Apparatus for examining IFD for male and female guppies. An onion fly and water mixture is held in 2 litre Erlenmeyer flasks (A) at the ends of the aquarium and kept in suspension by stir plates (B). The onion fly eggs and water drain from the flask and into feeder bars (C), which spread the food over the width of the aquarium. The eggs then fall through the water column and, if not consumed, are removed from the aquarium by food traps (D). The drain rate of the flasks is kept constant by a glass tube (E) which controls the rate at which air enters the system.

Spatial distribution of fish

The distribution of guppies was recorded using a metronome sampling technique. The guppies were divided into three categories: those feeding at the left hand feeder (patch A), the right hand feeder (patch B), or not feeding at all. Positions were recorded every 30-sec for 24-min after food delivery commenced, providing 48 observations for each trial. From these data a single value was obtained to describe the stable distribution of guppies in that trial. The time over which the distribution of guppies was stable was determined by plotting the proportion of guppies at the left hand feeder against time for each trial. A horizontal line (representing a stable distribution) was fitted by eye to these data to determine if there was an initial deviation. Data were considered to deviate from a stable distribution if four or more consecutive points increasingly departed from the horizontal line. If no deviation was observed, the mean for all 48 observations was used to describe the results. If a deviation was observed, only the data after the deviation were used.

The distribution of food was altered in these experiments while keeping the overall amount of food constant. Twenty mg of food was provided to the females in 9 different distributions, while 12 mg was provided in 5 different distributions for the males. (Different amounts of food were used to compensate partially for differences in body size between the sexes.) Since the feeders drained at a constant rate, altering the amount of food in a feeder changed the rate at which food was provided. The experiments were randomized over days and between sides so that a different distribution was encountered each day. However, the same distribution was provided three times a day. Within a day, at least 3 hours separated experiments to prevent satiation effects. These experiments were replicated 6 times for the females and 5 times for the males for a total of 162 trials for the females, and 75 for the males.

Individual intake rates

To check that individual fish maintained equal intake rates at the feeders, I videotaped a group of 6 male guppies at a feeder in a 20-l aquarium. In order to obtain the resolution necessary to distinguish individuals, the fish were filmed under two high intensity movie lights with a Panasonic studio video camera. The fish were provided 7.2-mg of onion fly eggs from one feeder, three times a day for five days, and were filmed for the first four minutes of each trial. From the videotapes I counted the number of eggs individual male guppies obtained within each trial. ANOVA was used to determine whether individuals had consistently different capture rates. A similar experiment could not be performed with females, due to the difficulty of distinguishing individuals.

RESULTS

Conformity with the IFD

A. Individual Intake Rates

For male guppies there were no differences in individual intake rates between six individuals over the five trials (ANOVA, p = 0.385). Analysis of individual intake rates for females was impossible for the reason noted above. However, from videotape of females and many hours of observation during the IFD experiments, no exclusion from the feeders was observed. Therefore, the feeding system rendered the food indefensible and provided an environment in which the 'free' assumption of an IFD applied.

B. Spatial Distribution

The spatial distribution of both the male (Fig. 3.2) and female (Fig. 3.3) guppies was strongly affected by the distribution of food ($p \leq 0.001$, see Table 3.1). However, the results of the AM experiments for the males and the AM and Noon experiments for the females had slopes which were significantly different (Table 3.2) from the slope of 1 predicted by IFD theory. In these cases, the calculated slopes were less than 1, indicating that too few animals used the feeder with the most food (and consequently too many used the feeder with the least food). The other experiments all resulted in distributions which were not significantly different from that predicted by an IFD (Table 3.2).

Comparison of the groups

A. Behavioural Differences

Examination of focal animals during the above experiments indicated that there were behavioural differences between the two groups. When food was presented to the male group, they continued to shuttle between patches. However, individuals in the female group were generally faithful to a feeding patch after a stable population distribution had been reached, and little movement was observed. Most of the movement by the female guppies occurred during nonfeeding intervals, and did not involve movement to the other patch.

B. Effects of Experience

The female group (but not the male group) conformed more closely to an IFD in successive exposures (i.e., AM, Noon, PM) to the same food distribution (compare Figs. 3.2 and 3.3). This effect was quantified by calculating the average sum of squares of the deviations of the observed distribution from the IFD.

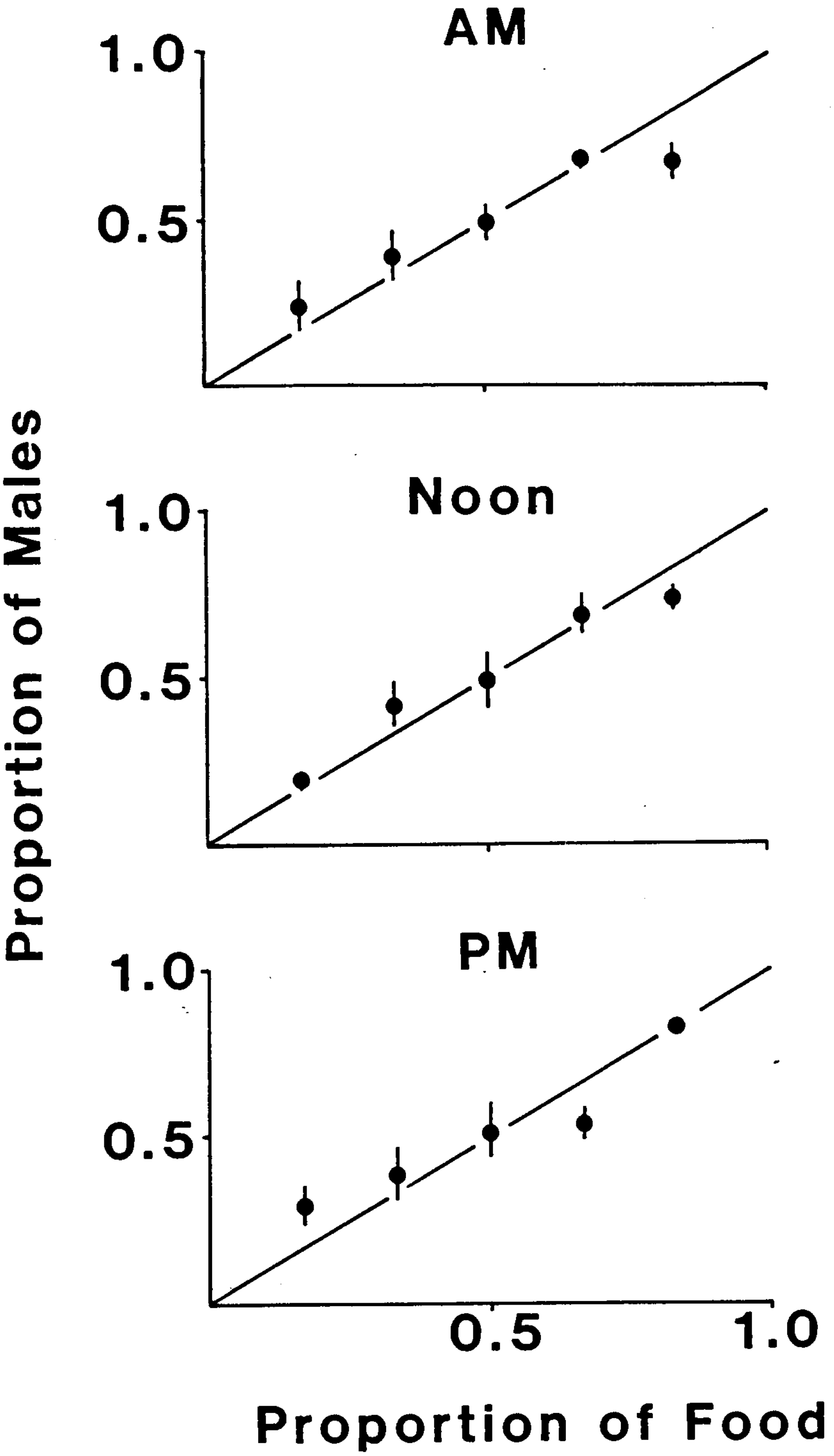

Fig. 3.2. The proportion of male guppies at the left hand feeder (designated patch A) versus the proportion of food available there. AM, Noon, and PM correspond both to the time of day the experiments were performed, and the experience with that distribution on that day (AM is the first exposure, PM is the third). The straight line through the data corresponds to the predicted IFD. Bars indicate one standard error. N = 25 for each graph.

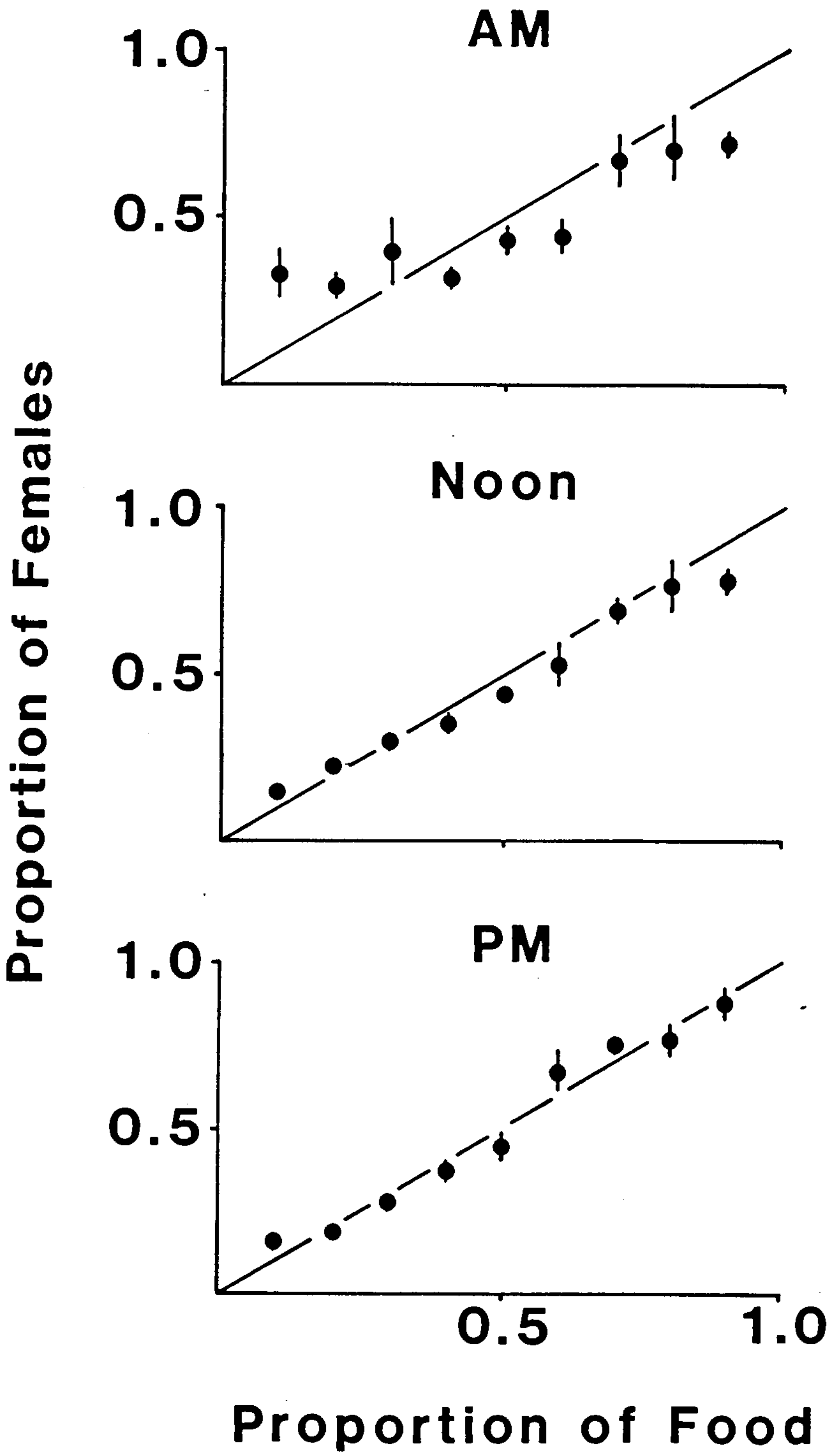

Fig. 3.3. The proportion of female guppies at one patch versus the proportion of food available there. Format as for Fig. 2. N = 54 for each graph.

Table 3.1. Summary of ANOVA statistics for the influence of food on the distribution of male and female guppies. Data were arcsin square-root transformed for this analysis.

Sex	Time	N	Calculated F	p
Male	AM	25	7.52	.001
	Noon	25	11.08	<.001
	PM	25	7.67	.001
Female	AM	54	7.66	<.001
	Noon	54	35.62	<.001
	PM	54	51.82	<.001

Table 3.2. Comparison of the distribution of female and male guppies to that predicted by an IFD. Note that an IFD predicts that the relation between the proportion of food in a patch and the proportion of animals using that patch should be a straight line of slope 1 passing through the origin.

		Regression Statistics			Probability	
Sex	Time	Slope	Y-Intercept	r^2	Slope=0	Slope=1
Male	AM	0.695	0.14	0.571	<.001	.023
	Noon	0.818	0.09	0.653	<.001	.155
	PM	0.733	0.14	0.561	<.001	.058
Female	AM	0.589	0.19	0.507	<.001	<.001
	Noon	0.853	0.04	0.834	<.001	.007
	PM	0.979	0.00	0.878	<.001	.662

Plotting these data for the two groups in the successive trials within a day confirmed that the female group significantly improved their conformity with an IFD with more exposure whereas the male group showed no apparent trend (Fig. 3.4); test time was a significant factor in the conformity of the female group to an IFD (ANOVA; $p < 0.001$) whereas it was nonsignificant for the male group (ANOVA; $p = 0.455$). With this successive improvement by the female group, they eventually fitted an IFD better than the male group (Fig. 3.4, Table 3.2).

To determine whether the improved conformity by the female group was due to experience or to a time-of-day effect, they were exposed to the same distribution of food (70% of the food at patch A) for nine consecutive trials (three times a day for three days). The experiment yielded no effect of time of day on conformity with an IFD (ANOVA; $p = 0.282$). Thus, the improvement observed with time by the female group in their ability to conform to an IFD must have been due to increased experience *per se*.

The influence of information

The linear operator rules which various authors have proposed to describe patch choice suggest that the influence of experience progressively declines with time, with the rate of decline being inversely related to the animal's memory. The relative effect of experience on patch choice should be most apparent when patch profitability suddenly changes. If animals weight past experience heavily, then it should account for much of the distribution of fish immediately following the change. Conversely, if experience is not used to a great extent, then it should not account for much of the new distribution.

The role of experience was examined by analyzing the relative amount of variation explained by experience (PD--their previous assessment of patch quality,

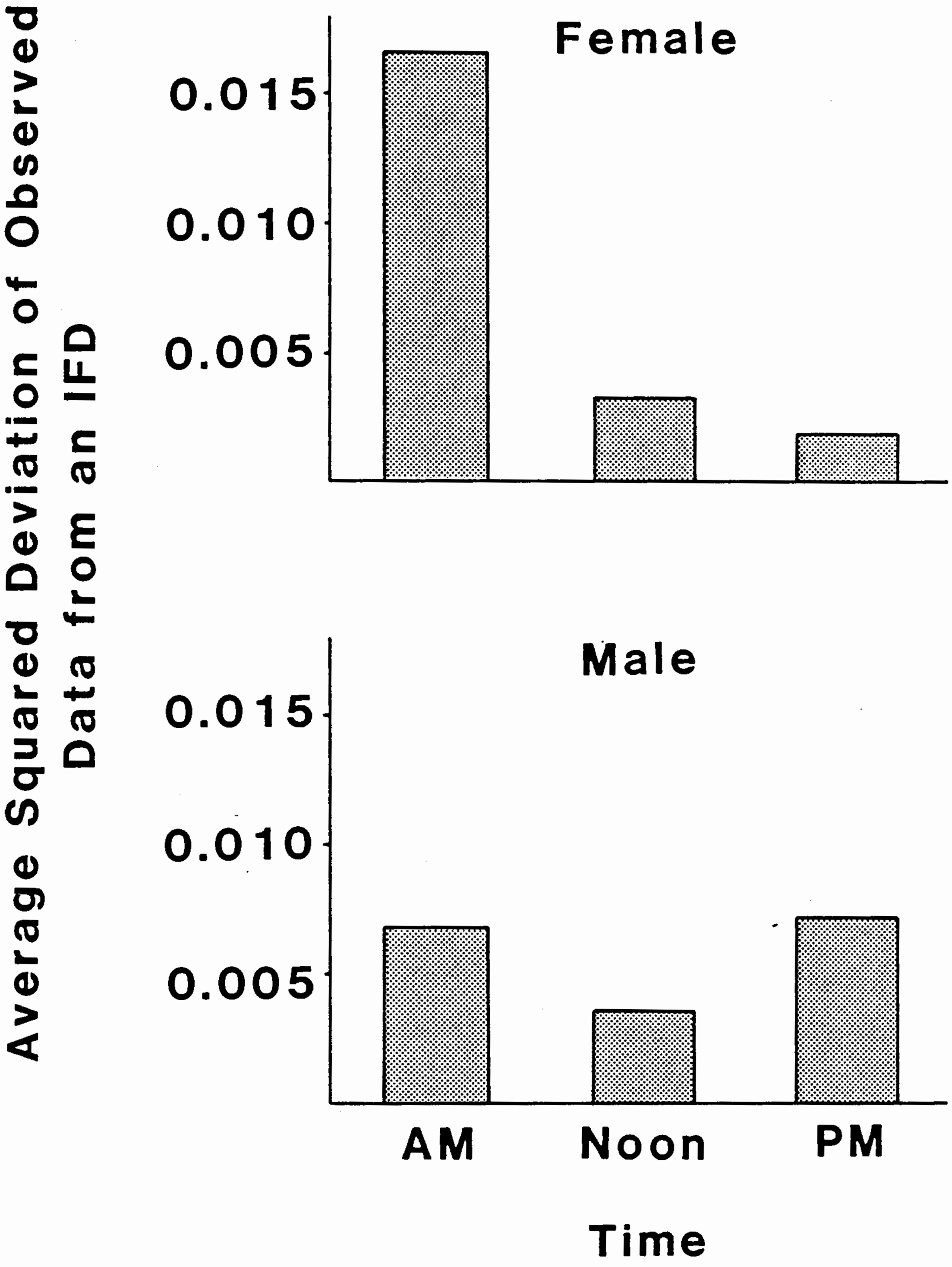

Fig. 3.4. The influence of experience on the mean sum of squared deviation from an IFD for male and female guppies. N = 54 for each female bar, 25 for each male bar.

which was estimated by their distribution in the last trial of the *previous day*) and current information (CF--the *current* distribution of *food*) for the first fifteen observations (7.5 min) of each AM experiment. To do this, sixty separate regressions were performed. Each regression used either PD or CF as the independent variable and the proportion (arcsin square-root transformed) of male or female guppies at patch A at one time interval as the dependent variable. Fifty three data points were used in each regression for the female group, and 24 points for the male group (there was no PD on day 1). The relative power of CF and PD to explain the observed variation in the data was determined as the ratio of their calculated coefficients of determination.

This analysis demonstrated that the relative amount of variation explained by PD declined progressively with time for both groups (Fig. 3.5). However, the relative influence of PD was substantially different between groups. The calculated ratio was very large for the first three observations for the female group, due to very low initial correlation coefficients for CF. Thus, initial decisions were almost completely unaffected by the current distribution of food, resulting in a greater influence of previous distribution. This result was not observed with the male group (Fig. 3.5).

If guppies use a linear operator rule for making patch choice decisions, then the female group used more stored than current information for their initial decisions. Thus, their previous experience with a patch exerted a strong influence on subsequent decisions. This effect could be observed by examining the initial distribution of the female group in the context of their previous day's experience. Their deviation from an IFD was significantly less when the previous distribution differed 20% or less from the current distribution (therefore, their memory provided relatively accurate information), compared to situations where their memory would

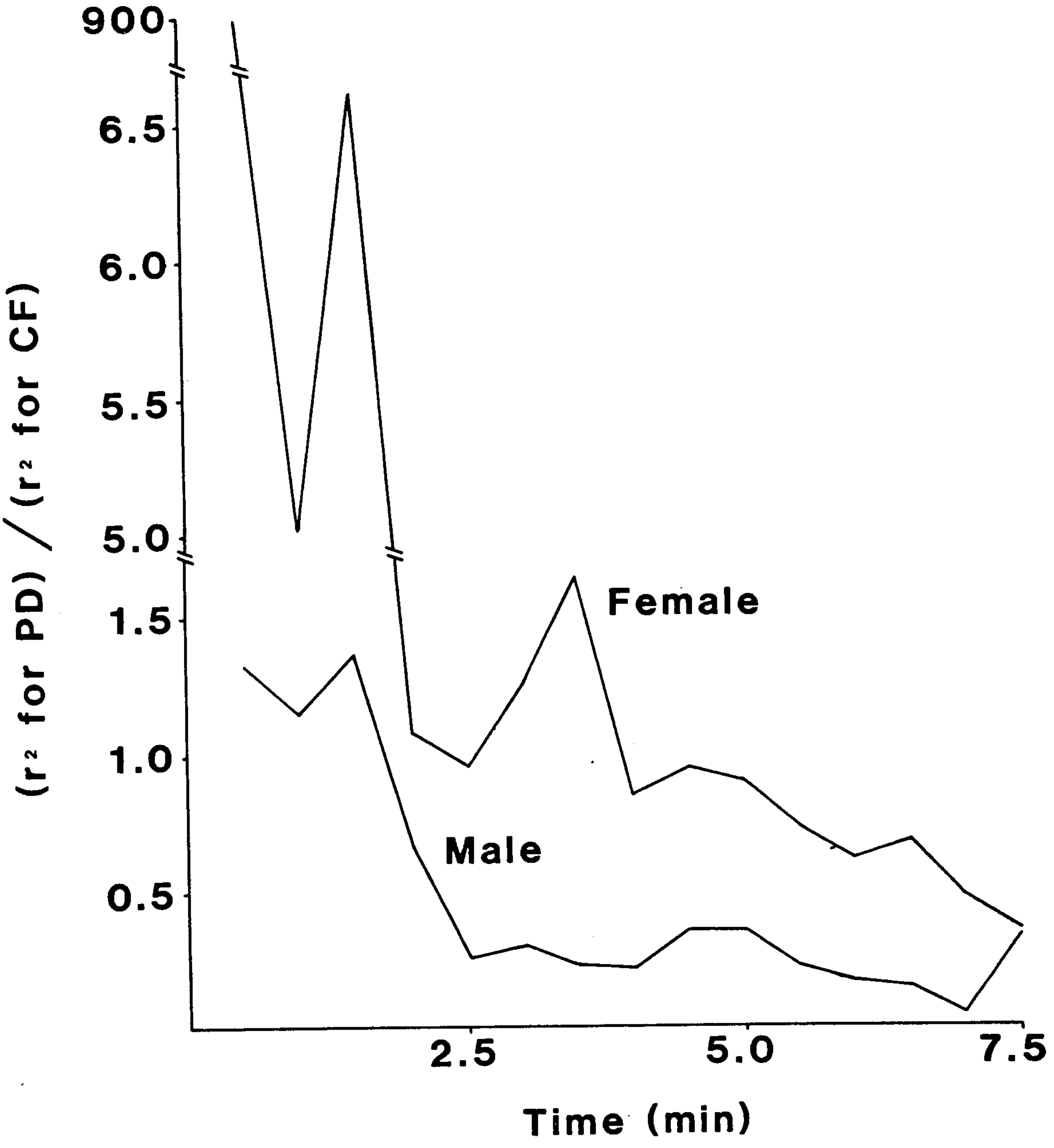

Fig. 3.5. The ratio of coefficients of determination for PD (the distribution of guppies on the final exposure of the previous day) and CF (the current distribution of food) for the first fifteen observations of the AM trial. See text for details of the calculation.

be misleading (where the previous distribution differed by 80% or more -- t-test of average sum of squared deviations, p = 0.005). This result was not observed for the male group (t-test, p = 0.276).

DISCUSSION

These experiments demonstrate that guppies conform closely to the spatial distribution predicted by an IFD. Previous experiments by HARPER (1982), GODIN & KEENLEYSIDE (1984), MILINSKI (1979, 1984), and TALBOT & KRAMER (1986) have examined the distribution of animals with respect to an IFD. All these experiments resulted in a distribution which was similar, but not identical, to an IFD. These authors argued that the deviation was due to differences in competitive ability, violating the assumption of 'free' access to the resource by all individuals. This was likely due to the method by which food was presented. In all of the above experiments, food was provided within each patch at a point source, making it an easy resource to defend. In this paper, by contrast, food was provided over a wide area, providing equal access for all individuals. Consequently, unlike previous experiments, deviations from the predicted IFD should not be due to violations of the 'free' assumption but to the guppies' inability to correctly perceive or respond to the distribution of food (a violation of the 'ideal' assumption).

The IFD theory can be used to quantify the influence of limited information on foraging behaviour. In situations where attainment of an IFD is limited only by the forager's ability to choose the correct patch, the deviation should represent a stable equilibrium between the costs and benefits of additional information (ABRAHAMS 1986). If the deviation from an IFD is large enough, animals will be able to perceive discrepencies in patch quality and move to more profitable patches, thus reducing the deviation. However, this process will continue only until differences in patch quality can no longer be perceived. The limit on the ability to perceive patch differences should occur when the benefits of additional information (eg., the ability to capitalize on deviations from an IFD) equal the costs of gaining this information.

The two groups of guppies differed in their response to repeated exposures to the same distribution of food. The female group deviated most during their initial exposure (AM trial) to a new distribution of food. With further exposure to the same distribution (Noon and PM trials), they progressively increased their conformity to an IFD. The male group did not change their deviation from an IFD with increasing experience with the same distribution of food and, upon initial exposure to a new distribution, conformed more closely than the female group to an IFD.

A possible mechanism to explain these results would be that guppies make foraging decisions based on both current and past information (as predicted by linear operator models). The difference between the male and female groups would reflect differences in the relative weight given past information for making decisions. Analysis of the relative power of current and past information to explain the distribution of fish indicated that the female group used relatively more past information than the male group for making decisions. Thus, the initial poor performance by females exposed to a new distribution (the AM trial) would be caused by their memory no longer reflecting the current distribution of food. However, with repeated exposure to the same distribution, they continuously improved their assessment of patch quality, reducing their deviation from an IFD. The lack of improvement by males could be due to their inability to retain information between experiments. However, it also results in a rapid conformity to an IFD upon first exposure to a new distribution, because they are not misled by their memory.

DUSSAULT & KRAMER (1981) have also noted behavioural differences between male and female guppies. Over a 12 h period, they observed that females fed at about six times the rate of males, while the males spent much of their time courting females. Since I used single groups of males and females, the influence of sex on these results cannot be statistically tested. It is possible that behavioural differences between the two groups resulted from uncontrolled individual variation within the guppy population. However, I believe it more likely that the differences observed reflect biological differences between the sexes. Guppies are a sexually dimorphic species with mature females being larger than mature males. Females give birth to litters of live young and are capable of storing sperm for up to eight broods. Their litter size is limited by their body size and food intake (HESTER 1964), so that their fecundity (and hence fitness) is limited by the amount of energy they can obtain. As guppies have a promiscuous mating system, male fitness is not so much influenced by energy as by access to females (FARR 1980, BAERENDS *et al.* 1955).

The relation between energy and fitness can account for the amount of information a foraging guppy should be selected to acquire. As guppies obtain more information, their foraging rate (and hence their fitness) should increase due to a reduced number of mistakes (e.g., not foraging at the most profitable patch). However, obtaining this information will also have a cost. Guppies should be selected to gather information up to the point where the marginal benefits of information equal the marginal costs of obtaining it. Presumably, the cost of obtaining information should be similar for both sexes of guppy. However, since the fitness benefits from additional energy intake are greater for females than for males, females should be selected to obtain relatively more information than males, ultimately resulting in differences in their foraging behaviour.

SUMMARY

1. The performance of a group of ten male and a group of ten female guppies foraging for food at 2 separate feeders was examined. No differences were observed in individual intake rates by males feeding at a single feeder.

2. As the proportion of food at a feeder was altered, the proportion of fish using that feeder changed to match the availability of food. From this, I concluded that both groups of fish conformed to the predictions of the ideal free distribution (IFD) theory.

3. During these experiments, males continued to shuttle between these patches whereas females tended to remain at a patch.

4. The female group conformed more closely to an IFD in successive exposures to the same food distribution. The male group exhibited no improvement with increasing experience.

5. For both groups, the relative influence of experience on foraging decisions declined progressively with time. However, unlike the male group, the female group appeared to rely heavily on experience for their initial foraging decisions.

6. The relative influence of experience on foraging decisions was further illustrated by examining the initial distribution of the female group in the context of the previous day's experience. Their deviation from an IFD was significantly less when the previous distribution differed 20% or less from the current distribution, compared to situations where the previous distribution differed by 80% or more. This result was not observed for the male group.

7. The differences between the male and female groups are likely due to differences in selective pressure. As fitness benefits from additional energy are greater for females than they are for males, females should be selected to obtain relatively more information than males, ultimately resulting in differences in their foraging behaviour.

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LITERATURE CITED

ABRAHAMS, M.V. (1986). Patch choice under perceptual constraints: a cause for departures from an ideal free distribution.--Behav. Ecol. Sociobiol. 19, p. 409-415.

BAERENDS, G.P., BROUWER, R. & WATERBOLK, H.TJ. (1955). Ethological studies on *Lebistes reticulatus* (Peters) I. An analysis of the male courtship patterns.--Behaviour 8, p. 249-334.

BROWNE, K.D. (1981). Aggressive behaviour and social structure in the guppy (*Poecilia reticulata*), a teleost.-- Ph.D. Thesis (C.N.A.A.), Polytechnic of Central London.

DUSSAULT, G.V. & KRAMER, D.L. (1981). Food and feeding behaviour of the guppy *Poecilia reticulata*, (Pisces: Poeciliidae).--Can. J. Zool. 59, p. 684-701.

ENDLER, J.A. (1978). A predator's view of animal colour patterns. Pp. 319-364.-- In: Evolutionary biology, Vol. II (HECHT, M.K., W.C. STEERE & B. WALLACE, eds). Plenum Press, New York.

FARR, J.A. (1980). Social behaviour patterns as determinants of reproductive success in the guppy *Poecilia reticulata* Peters (Pisces: Poeciliidae): an experimental study of the effects of intermale competition, female choice, and sexual selection.-- Behaviour 74, p. 38-91.

FRETWELL, S.D. (1972). Populations in a seasonal environment Princeton Univ. Press, Princeton.

---------, ---. & LUCAS Jr., H.L. (1970). On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development.--Acta Biotheoretica 19, p. 16-36.

GODIN, J-G.J. & KEENLEYSIDE, M.H.A. (1984). Foraging on patchily distributed prey by a cichlid fish (Teleostei, Cichlidae): a test of the ideal free distribution theory.--Anim. Behav. 32, p. 120-131.

HARLEY, C.B. (1981). Learning the evolutionary stable strategy.- Theor. Biol. 89, p. 611-633.

HARPER, D.G.C. (1982). Competitive foraging in mallards: 'ideal free ducks'.--Anim. Behav. 30, p. 575-584.

HESTER, F.J. (1964). Effects of food supply on fecundity in the female guppy, *Lebistes reticulatus* (Peters).--J. Fish. Res. Board Can. 21, p. 757-764.

KACELNIK, A. & KREBS, J.R. (1985). Learning to exploit patchily distributed food. Pp. 189-205.-- In. Behavioural ecology: ecological consequences of adaptive behaviour (Sibly, R.M. & R.H. Smith, eds). Blackwell Scientific Publications, Oxford.

KREBS, J.R., KACELNIK, A. & TAYLOR, P. (1978). Tests of optimal sampling by foraging great tits.--Nature 275, p. 27-31.

McNAMARA, J. & HOUSTON, A.I. (1985). A simple model of information use in the exploitation of patchily distributed food.--Anim. Behav. 33, p. 553-560.

MILINSKI, M. (1979). An evolutionary stable feeding strategy for sticklebacks.--Z. Tierpsychol. 51, p. 36-40.

--------, -- (1984). Competitive resource sharing: an experimental test of a learning rule for ESSs.--Anim. Behav. 32, p. 233-242

REGELMANN, R. (1984). Competitive resource sharing: a simulation model.--Anim. Behav. 32, p. 226-232.

REZNICK, D. (1983). The structure of guppy life histories: the tradeoff between growth and reproduction.--Ecology 64, p. 862-873.

TALBOT, A.J. & KRAMER, D.L. (1986). Effects of food and oxygen availability on habitat selection by guppies in a laboratory environment.--Can. J. Zool. 64, p. 88-93.

Résumé

1. La performance de 10 guppys mâles et 10 guppys femelles fut examinée alors que ceux-ci s'alimentaient à deux mangeoires séparées. Aucune différence ne fut observée entre les taux d'alimentation individuels des mâles se nourrisant à une mangeoile particulière.

2. La proportion des poissons se nourrissant à une mangeoile changeait de façon à équivaloir l'abondance de nourriture à mesure que la proportion de nourriture était altérée entre les deux mangeoires. J'en conclus que les deux groupes de poissons suivent les prédictions émises par la théorie de "distribution libre idéale" (DLI).

3. Les mâles se promenaient constamment entre les mangeoires durant les expériences, tandis que les femelles avaient tendance à demeurer à une mangeoile.

4. Après des expositions répétées à une même distribution de nourriture, la distribution des femelles s'approchait de plus en plus de celle de la DLI, tandis que celle des mâles ne montrait aucune amélioration avec le temps.

5. L'influence relative de l'expérience sur les décisions portant sur l'aquisition de nourriture peut expliquer les différences entre les deux groupes. Cette influence relative déclinait graduellement dans le temps pour les deux groupes, bien qu'elle demeurait plus forte pour les femelles que pour les mâles.

6. Cette même influence relative de l'expérience sur les décisions d'alimentation devint plus apparente quand la distribution des femelles fut examinée dans le contexte de l'expérience acquise la journée précédente. Comparée aux situations où la distribution précédente différait par 80% ou plus de la distribution actuelle, la déviation de la distribution des groupes à partir de la DLI était significativernent

moindre quand la différence entre les deux distribution (précédente et actuelle) était de 20% ou moins.

7. Les différences observées entre le groupe mâle et le groupe femelle sont probablement dues à des différences d'intensité de sélection. Comme les bénéfices de reproduction différentielle dérivés de sources additionnelles alimentaires sont plus grands pour les femelles que pour les mâles, les femelles devaient être sélectionnées de façon à obtenir plus d'information que les mâles, ce qui se traduit par des différences dans leur comportement alimentaire.

CHAPTER IV

A DETERMINATION OF THE ENERGETIC EQUIVALENCE OF THE RISK OF PREDATION

ABSTRACT

The influence of predation risk on patch choice was measured by examining the spatial distribution of ten guppies (*Poecilia reticulata*) between two feeders, at one of which there was a risk of predation. The distribution was assumed to be ideal free. Nine unique situations were examined using all possible combinations of three risk levels and three diet levels, for each sex of guppy separately. Both sex and diet level influenced the effect of predation risk on patch choice. For the females, the effect of risk was highest at the intermediate diet level. However, the males exhibited the opposite response; the effect of risk of predation was least at the intermediate diet level. A simple equation was then used to predict how much extra food (representing the energetic equivalent of risk) must be added to the risky patch for the guppies to become indifferent between the safe and risky patches. This manipulation caused a similar number of guppies to use both the risky and safe feeders, reducing or offsetting the influence of risk of predation. However, the male guppies were less influenced by this manipulation than were the females. The different results for the two sexes are consistent with known differences in their life histories, indicating that a knowledge of an animal's life history is necessary to understand how it makes trade-offs when choosing where to forage.

Keywords: habitat selection; foraging; risk of predation; predator-prey; trade-off; ideal free distribution; guppies; *Poecilia reticulata*

10-year index: habitat selection by fish; foraging under a trade-off of foraging rate and risk of predation; use of the ideal free distribution theory to quantify risk of predation

INTRODUCTION

For over a decade, the approach of assuming that animals decide when, where, and how to forage with the goal of maximizing their net rate of energy intake has enjoyed considerable success in predicting foraging behaviour in both the laboratory and the field (Stephens & Krebs 1986). However, recent experiments have demonstrated that exposing foraging animals to risk of predation can profoundly alter their decisions (reviewed by Lima & Dill, submitted). Several studies reviewed by Lima & Dill have demonstrated that both energy intake and risk of predation influence behaviour in a manner that appears adaptive, yet few attempts have been made to describe quantitatively the trade-off between energy and risk of predation. To be able to predict how these factors combine to influence behaviour, each should be expressed as its contribution to the fitness of the animal. For most species, this measure is difficult. Alternatively, risk of predation can be expressed in units of energy, providing a common currency for these two factors. The relationship between energy and fitness will be determined in large part by the animal's life history, and is crucial to predictions concerning the effect of predation risk on foraging behaviour.

Behavioural decisions made from strictly energetic concerns would not be affected by the shape of this relationship: as long as there was some increasing relation between energy and fitness, animals would be predicted to behave so as to maximize their net rate of energy intake. However, this relationship can profoundly influence the behaviour of animals faced with a trade-off between energy intake and predation risk. Consider an animal which must choose between two patches. One patch is free of risk but provides food at a relatively low rate. The other provides food at a greater rate, but with an associated risk of death. The choice of patch will depend upon the relation between energy and fitness. If the difference in extra fitness from additional energy more than offsets the fitness cost of predation risk, then the animal should use the risky patch; otherwise, it should use the safe patch. Thus, the adaptiveness of risking death is dependent upon the precise form of the relation between energy and fitness.

We performed a series of experiments using separate groups of ten male and ten female guppies (*Poecilia reticulata*) to examine how their foraging behaviour was influenced by risk of predation. Female guppies are typical of an animal whose fitness is energy limited. They mate promiscuously and give birth to litters of live young. Litter size is positively correlated with female size and also influenced by the caloric quality of the diet (Hester 1964). In contrast, male fitness is limited by access to females (Farr 1980, Baerends et al. 1955), a factor that is not determined by the availability of energy (Abrahams & Reynolds, in prep.).

We measured the energetic equivalence of risk with two series of experiments. In the first series, groups of guppies were allowed to choose between two patches providing food at equal rates. One patch was safe, but the other required the guppies to feed in the presence of a predator. As the guppies shared the food equally at both patches, their spatial distribution was used to measure the energetic equivalence of risk, taken to be the difference in intake rate between individuals at the risky feeder and those at the safe feeder. The second series of experiments used these data to determine how much additional food must be added to a patch to offset the effect of risk, i.e., that amount necessary to achieve equal numbers of guppies using the safe and risky patches. Having measured the energetic equivalent of risk, we could also determine the relative influence that risk has on animals with different life histories. Specifically, we could determine whether risk has a relatively greater effect on animals which receive fewer benefits from additional energy (i.e., males).

METHODS

Experiment 1

We used the ideal free distribution (Fretwell & Lucas 1970; Fretwell 1972) as a tool to determine the caloric equivalence of risk. Ideal free distribution (IFD) theory predicts that animals should distribute themselves in a habitat such that all individuals benefit equally from the available resources. This will occur if the animals satisfy two assumptions: they are 'ideal', in that they have perfect knowledge of their environment, and 'free' to enter and use resources in any patch on an equal basis with residents. In an environment in which there is only one type of resource available, the animals will distribute themselves such that their spatial distribution equals that of the resource (i.e., the proportion of animals in a patch will equal the proportion of total resources available in that patch). This type of distribution is considered to be an example of a spatial evolutionarily stable strategy because no animal could improve its situation by moving to another patch (Parker 1984).

The method by which the IFD can be used to quantify the energy equivalence of risk of predation can best be explained by way of an example. Consider an environment in which 10 individuals compete for 20 units of food divided evenly between 2 patches. The IFD predicts that if food is the only variable, there should be an equal number of individuals in each patch. However, if one patch has an associated risk of predation whereas the other does not, fewer individuals will use the risky patch than the safe patch and consequently those individuals which risk attack by a predator will receive more food than will individuals in the safe patch.

In such a situation, animals conforming to an IFD will have equal fitness in both the safe and risky patches, not necessarily equal energy intake rates. Therefore, the energetic equivalent of the imposed risk per individual (ER_i) can be calculated as the intake of those individuals in the risky patch in excess of that in the safe patch:

$$ER_i = F/NR_i - F/NS \qquad (1)$$

where: F = the amount of food available in either patch

NR_i = the number of foragers in the risky patch at risk level i

NS = the number of foragers in the safe patch

In our example, if 7 individuals used the safe patch, then ER_i would be 10/3 - 10/7, or 1.90 food units.

This approach was used to quantify risk with two separate groups of ten similar-sized male (average mass of 0.110 g) and female (average mass of 0.414 g) guppies. Experiments were performed in a 90-l aquarium maintained at 27° C and illuminated at 350 lux. Feeders placed at each end of the aquarium (for details of the apparatus, see Fig. 4.1 and Abrahams, submitted) provided food (eggs of the onion fly, *Delia antigua*) at a constant rate for 24 min, and distributed it over a large area, making it an indefensible resource. A screen placed down the middle of the aquarium separated the feeders, and by placing a predator on one side a patch could be made the risky one. Note, however, that the mesh size was large enough so that the guppies could travel easily between the patches.

When the spatial distribution of food was varied between the two feeders, and no risk was associated with either of them, male and female guppies adjusted their distribution in conformity with an IFD (Abrahams, submitted). In addition, analysis of videotaped sequences of guppies using the feeders demonstrated that

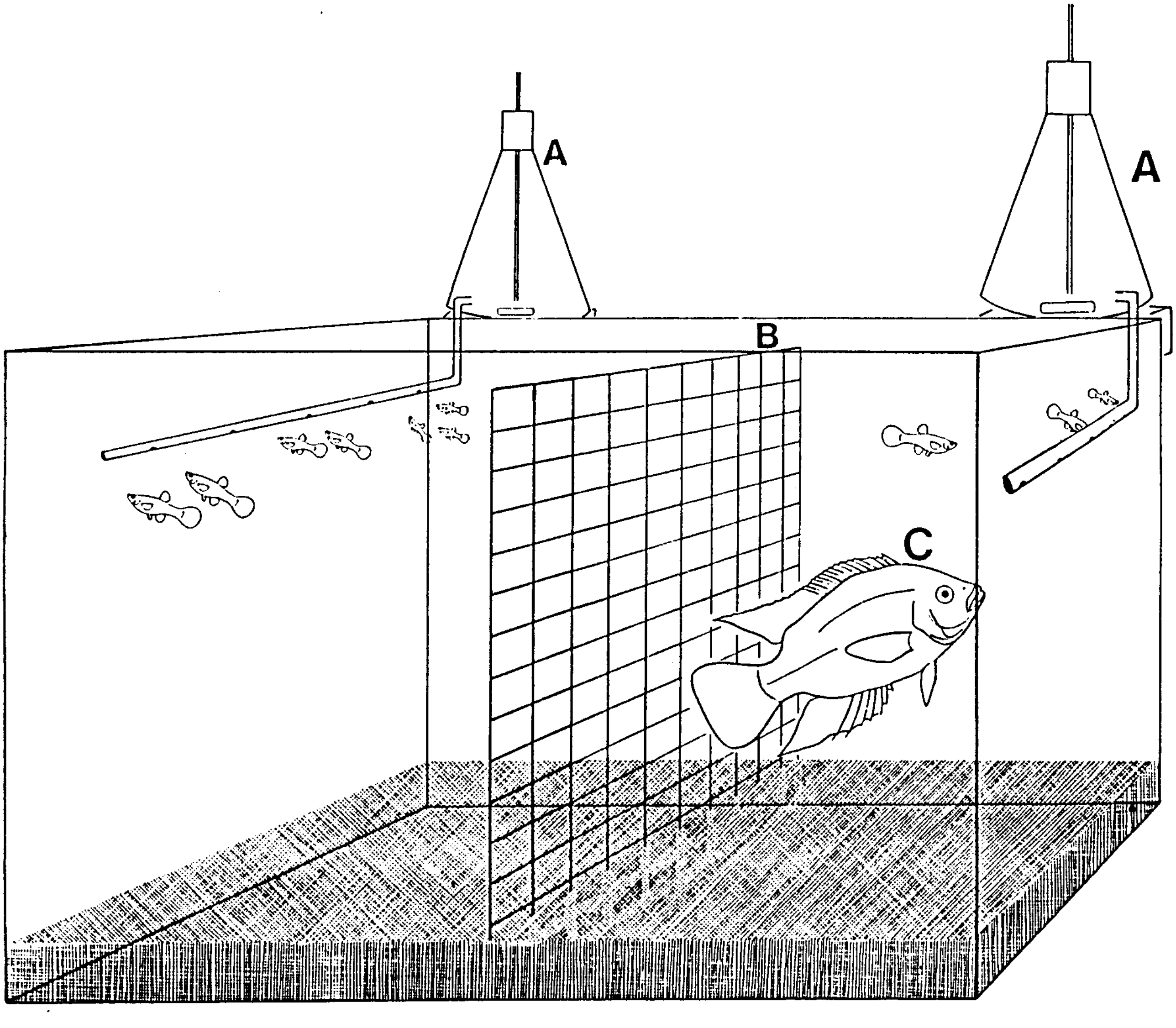

Fig. 4.1. Apparatus used for experiments 1 and 2. Food is provided by feeders (A) located on either side of the screen (B). The feeder on the right could be placed 2, 16, or 32 cm from the screen. The mesh size of the screen restricted the predator (C) to the right side of the aquarium while allowing the guppies to move freely between sides.

intake rates were not significantly different between individuals (Abrahams, submitted). Thus, with this apparatus, the IFD is a valid tool for determining the equivalence between energy and risk of predation.

A 150 g cichlid (*Cichlasoma* sp.) was used as the predator for the females and 2 - 20 g gouramis (*Trichogaster leeri*) for the males. Different predators were used for the females and males because of differences in size and susceptibility to predators between the two sexes. The appropriateness of these fish as predators was determined through a series of pilot studies. The criteria for selecting a predator were that the guppies would tend to avoid it if approached (i.e., they treated it as a threat) yet still would be willing to use the risky feeder. The predators were encouraged to stay at the far end of their side of the aquarium by digging a hole in the gravel for the cichlid and providing a flower pot for the gouramis. These different predators represented a similar threat to the males and females. The cichlid killed 5 females in 162 experiments and the gouramis killed 3 males in 153 experiments. When a guppy was killed, it was replaced in the next trial by a similar-sized individual.

Two factors were varied in these experiments for each sex: risk and diet level. Risk was varied by moving the "risky" feeder 2, 16, or 32 cm from the dividing screen (corresponding to low, medium, and high risk levels, respectively). Moving the feeder varied risk by changing the distance the guppies had to move to escape predatory attacks. Three diet levels (10, 20, and 40 mg in total for the females; 6, 12, and 24 mg for the males) were provided, divided equally between the two feeders. (Different amounts of food were used for each sex to compensate partially for differences in body size.) Thus, each sex was exposed to 9 unique combinations of risk and diet level. During experiments the fish were maintained exclusively on the food provided during experimentation except for a weekly supplement of NutraFin flakes for essential nutrients.

Experiments were first performed using the intermediate diet level, then the lowest and finally the highest one. Within a diet level, the risk level was randomly chosen and the feeder placed in the appropriate position. Once food began to enter the system, the proportions of guppies using the two feeders was recorded every 30 sec for 24 min, providing 48 pairs of observations for each trial. The mean of the 48 observations per feeder was calculated and used to describe the distribution of the guppies. Each risk–diet combination was repeated three times in one day, with at least three hours separating trials. A different risk level was selected randomly (without replacement) for each day until all three risk levels had been tested for three days *each* at a given diet level (nine observations per risk level). After all risk levels had been examined at all diet levels, the entire procedure was repeated as above, except that the predators were removed. This served as a control to determine whether feeder location influenced the results.

Experiment 2

Experiment 1 provided data to predict how much food must be added to the risky patch to make the guppies indifferent when choosing between the risky and safe patches. The calculation was based upon the IFD prediction that if the two patches are of equal value then an equal number of individuals (5 in this case) should be in each patch. We assumed that risk of predation reduces the fitness of each individual by a fixed amount. Thus, the fitness equivalent of risk in experiment 1 (R_i) can be described by the following equation:

$$R_i = a(F_R/NR)^x - a(F_S/NS)^x \qquad (2)$$

where: $a(F/N)^x$ = a general expression relating individual energy intake (F/N) to fitness, in the safe (F_S) and risky (F_R) patches

In order to encourage five individuals to use the risky feeder, sufficient additional food must be provided to offset the fitness loss due to risk of predation in that patch. The energetic equivalent of risk (ER_i) was determined in experiment 1. The amount of food necessary to offset the effect of risk should equal five times (i.e., NR) this value. Consequently, the amounts of food in the two feeders must be related as:

$$F_R = F_S + (5 \times ER_i) \qquad (3)$$

where: F_R = the amount of food in the risky patch

F_S = the amount of food in the safe patch

The amount of extra food required was calculated for each of the nine situations previously described, for both sexes. Note that this manipulation will increase the intake rates of *all* individuals by a constant amount (I). We assume that R_i is independent of this manipulation, such that the following relationship must hold:

$$a((F_R/NR) + I)^x - a((F_S/NS) + I)^x = a(F_R/NR)^x - a(F_S/NS)^x \qquad (4)$$

If the relation between fitness and energy increases at a greater than linear rate ($x > 1$), then we will have added more food than necessary to offset the fitness loss due to the risk of predation. Consequently, the risky patch with additional food will be of greater value than the safe patch so more individuals than predicted will use the risky feeder. Conversely, if the true relation between fitness and energy increases at a less than linear rate ($x < 1$), insufficient food will have been added to offset the fitness loss from risk, resulting in too few individuals using the risky feeder. Thus, deviations from an equal distribution of animals can be used to infer the shape of the energy–fitness relationship.

The order of these experiments was determined by the same method as the previous experiments. The intermediate diet level was examined first, then the low and finally the high diet level. Within a diet level, risk levels were randomly chosen and each combination was repeated 9 times (3 times on each of 3 days), except for the males at the high diet level where experiments were repeated only 6 times (3 times on each of 2 days). The same group of male and female guppies were used as in Experiment 1.

RESULTS

Experiment 1: The caloric equivalence of risk

A. Effects of a Predator

When food was distributed equally between the two feeders, fewer guppies used the risky feeder than would be predicted by the IFD based only on the distribution of food. This was true for both sexes (Figs. 4.2 and 4.3). The proportion that used the risky feeder decreased significantly as it was moved moved further from refuge (Table 4.1). This result is consistent with our assumption that risk increases as the feeder is moved further from- the screen, and demonstrates that both male and female guppies are capable of detecting and responding to a variable risk of predation. Since equal amounts of food were available at both feeders, and the guppies captured virtually all of it, the difference in individual intake rates between the two patches also increased as the feeder was moved further from cover.

B. Effect of Diet Levels

Although equal amounts of food were available at both feeders, diet level significantly influenced the proportion of guppies which used the risky feeder (Table 4.1). A larger proportion of the females used the risky feeder at the low and high

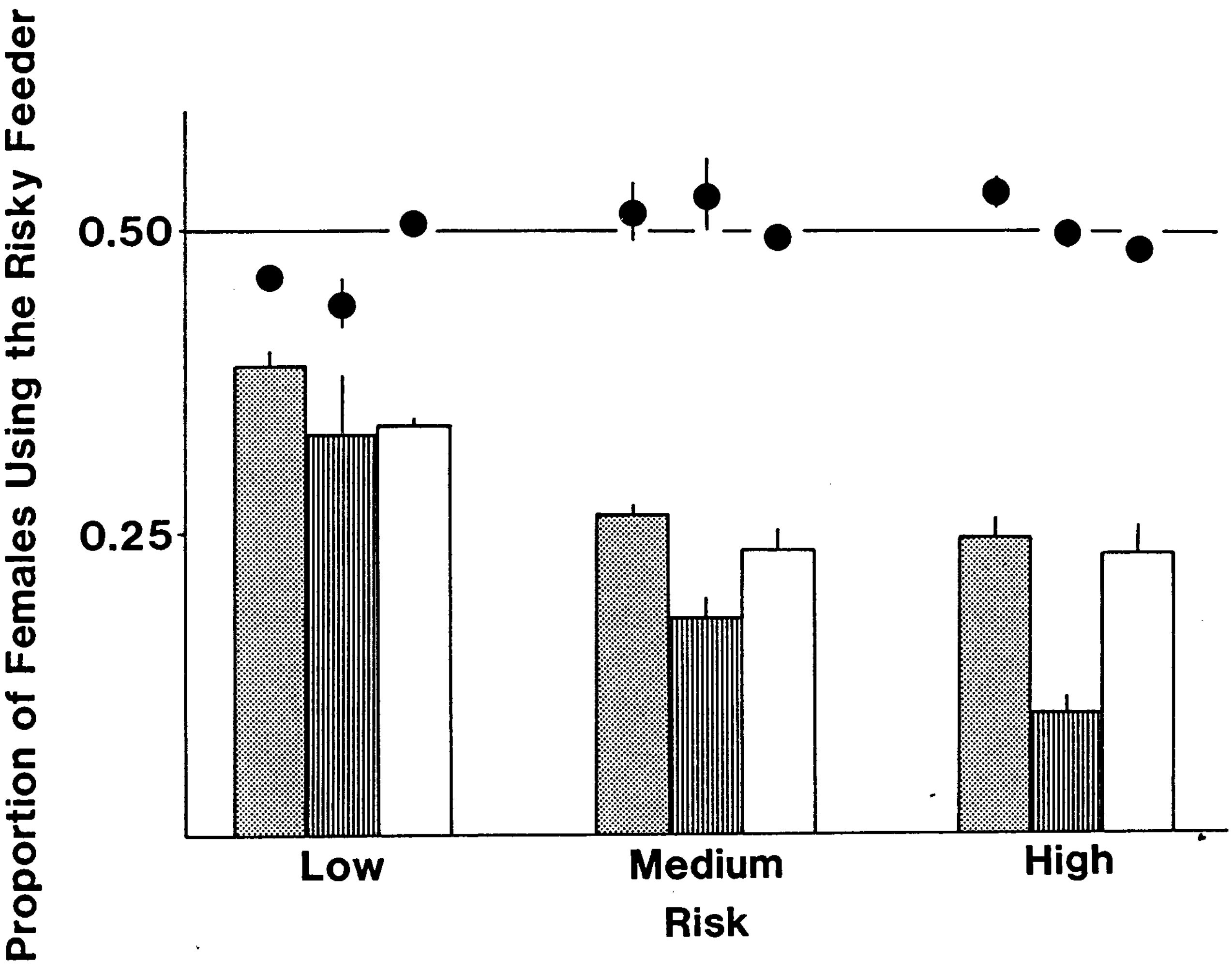

Fig. 4.2. The proportion of females using the risky feeder as a function of different risk and diet levels when equal amounts of food were available at both feeders. Dots represent the result in the absence of a predator (controls) and the bars are the result with the predator present. Stippled bars represent the result for the low diet level, striped bars for the intermediate diet level, and open bars for the high diet level. The error bars for both control and treatment data represent one standard error.

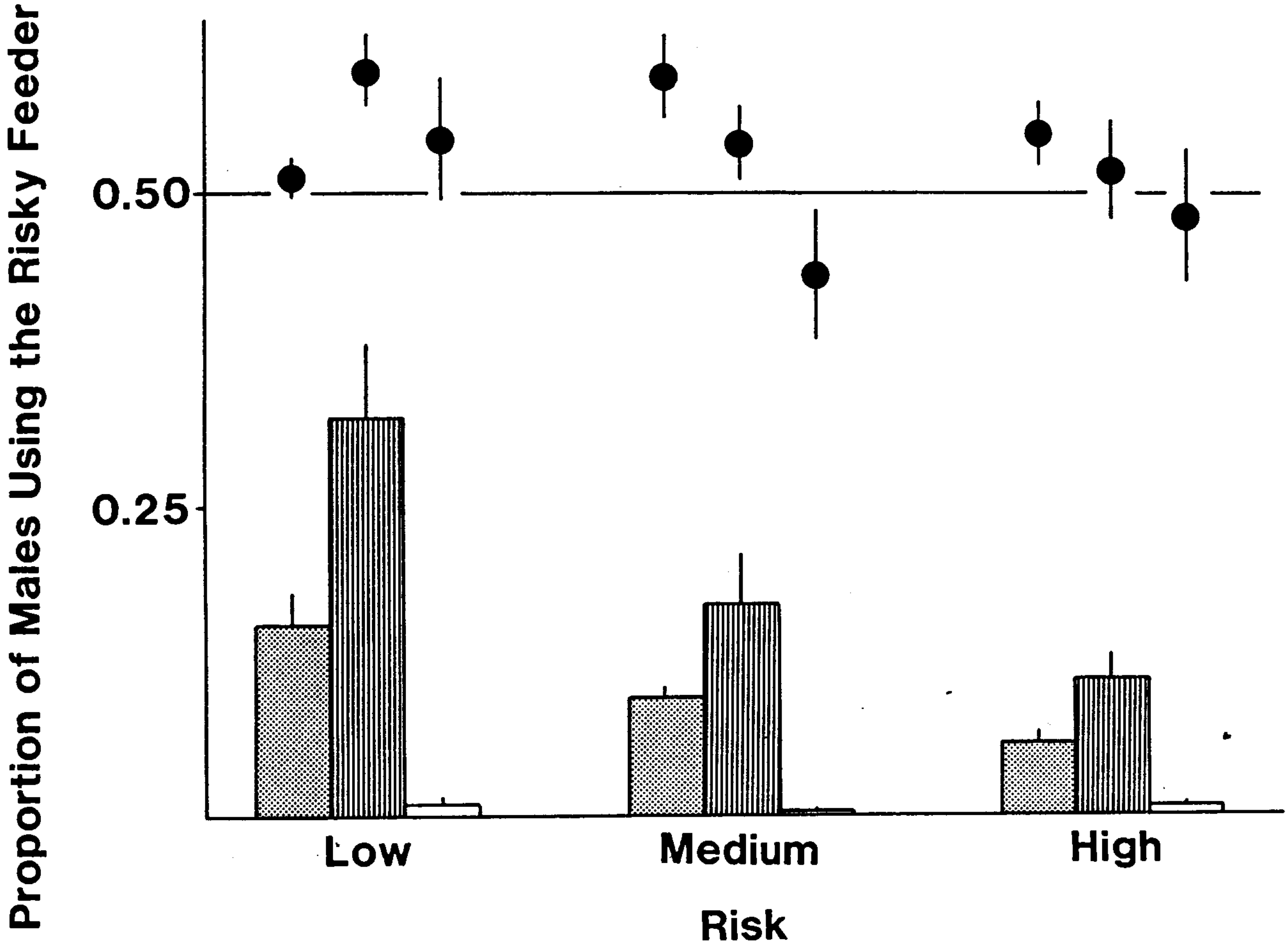

Fig. 4.3. The proportion of males using the risky feeder as a function of different risk and diet levels when equal amounts of food were available at both feeders. Key as in Fig. 2.

Table 4.1. The influence of feeder position and diet level on the proportion of male and female guppies using the risky feeder in the presence or absence of a predator. Probabilities were calculated by two-way ANOVA using arcsin square-root transformed data. The degrees of freedom for the effects of feeder position and diet level were 2, 72; for the interaction they were 4, 72.

		Predator Absent		Predator Present	
Sex	Effect	F	p	F	p
FEMALES	Feeder Position	3.561	0.051	80.851	<0.001
	Diet Level	1.365	0.283	25.443	<0.001
	Interaction	2.000	0.117	3.671	0.014
MALES	Feeder Position	0.786	0.400	7.451	0.005
	Diet Level	2.983	0.078	110.659	<0.001
	Interaction	1.504	0.223	2.349	0.074

diet levels (Fig. 4.2) than at the intermediate diet level. At these extreme diet levels, the females appeared to become less sensitive to risk, showing little change in their use of the risky feeder between the medium and high risk levels. There was thus a significant interaction between risk and diet level (Table 4.1).

There was no significant interaction between risk and diet level for the males (Table 4.1). They also differed from the females in their response to changes in diet level. The largest proportion of males used the risky feeder at the intermediate diet level, less at the lowest diet level, and almost none at the highest diet level. At the highest diet level, the males completely avoided the risky feeder except for brief visits by one or two individuals.

The difference in response between the male and female guppies at the highest food level may have been due to differences in their ability to consume food. The highest diet level for the males may have provided food at the safe feeder at a rate which exceeded their ability to consume it, a level not experienced by the females. Thus, using the risky feeder would not provide a significant energetic benefit to males. If this explained the males' avoidance of the risky feeder at the highest diet level, then increasing the absolute amount of food available to the females should generate a similar result. We did this by providing the females with 60 mg of food at each feeder, and placing the risky feeder 32 cm from the screen. Providing food at this rate far exceeded the females' ability to consume it, yet a significant proportion (35%) continued to use the risky feeder. Thus, even if food were provided to the males at a rate in excess of their ability to consume it, their response was different from the females in a comparable situation.

C. Control Experiments

Repeating these experiments in the absence of a predator revealed that neither the position of the feeder nor diet level significantly altered the distribution of the guppies. However, it should be noted that the feeder position did have a marginally significant effect on the spatial distribution of the females in the absence of predators (Table 4.1). This position effect slightly increased their use of the risky feeder as it was moved farther from the screen (Fig. 4.2; top); this would act to reduce the observed effect of a predator.

Experiment 2: Offsetting the influence of risk

The combinations of food and risk used in these experiments are summarized in Table 4.2. The amount of food in the risky feeder was determined using equation (3) except for the high (12 mg in the safe feeder) diet level for males. At this diet level, the males almost completely avoided the risky feeder; the average number of males using the feeder was less than one. As a result, the amount of food consumed by individuals in the presence of the predator was overestimated. Consequently, the amount of food used for this trial was estimated from the results of the other two diet levels. We observed that, for the males, the ratio of food in the risky feeder (as determined by equation (3)) to food in the safe feeder approximately doubled with each increase in risk level. Furthermore, the ratios at the low diet were approximately twice that at the intermediate diet level. The amount of food used at the high diet level was determined by using ratios that were double those calculated at the low diet level (because the males' avoidance of the risky feeder was most extreme at the high diet level). These ratios were then used to calculate the absolute amount of food to be used in the risky feeder.

Table 4.2. The amounts of food (mg) predicted to offset the influence of risk, for the different combinations of risk and diet level. One mg (wet weight) of onion fly eggs contains 1.93 calories.

Sex	Food in Safe Feeder	Low Risk	Intermediate Risk	High Risk
FEMALES	5	6.1	9.5	10.4
	10	13.8	23.8	50.0
	20	29.7	42.0	42.7
MALES	3	9.8	16.1	26.6
	6	10.4	18.4	27.5
	12	81.1	127.2	213.0

The most striking result of this experiment was the difference between the sexes. The additional food resulted in the females returning to or exceeding their control level (Fig. 4.4 and Table 4.3). Conversely, the males returned to their control level in only one case, and in all others were below it (Fig. 4.4 and Table 4.3). At the high diet level, the males continued to avoid completely the risky feeder.

The influence that risk and diet level had on the deviation of this result from the control distribution was determined by a two-way ANOVA. For analysis, this deviation was calculated as the absolute difference between the experimental and control distribution (after each had been arcsin square-root transformed). No significant difference between risk levels was observed, either for males ($F_{(2, 63)} = 0.852$, $p = 0.40$) or females ($F_{(2, 72)} = 2.655$, $p = 0.75$). However, there was a significant difference between diet levels (males and females, $p < 0.001$).

There was a significant interaction between risk and diet level for females ($F_{(4, 72)} = 4.36$, $p < 0.003$) that was not observed for males ($F_{(4, 63)} = 1.55$, $p = 0.199$). This was a result of the females exceeding the control distribution at the low and high diet levels but not at the intermediate diet level. The males were below the control distribution at every diet level, with the deviation from the control distribution increasing with diet level.

Within both experiments 1 and 2, the intermediate diet level was examined first, then the low and finally the high diet level. As such, it was possible that the results attributed to diet manipulations could also have been an order effect. This interpretation is unlikely since the order of presentation was identical for both sexes, yet they exhibited opposite responses to diet manipulations.

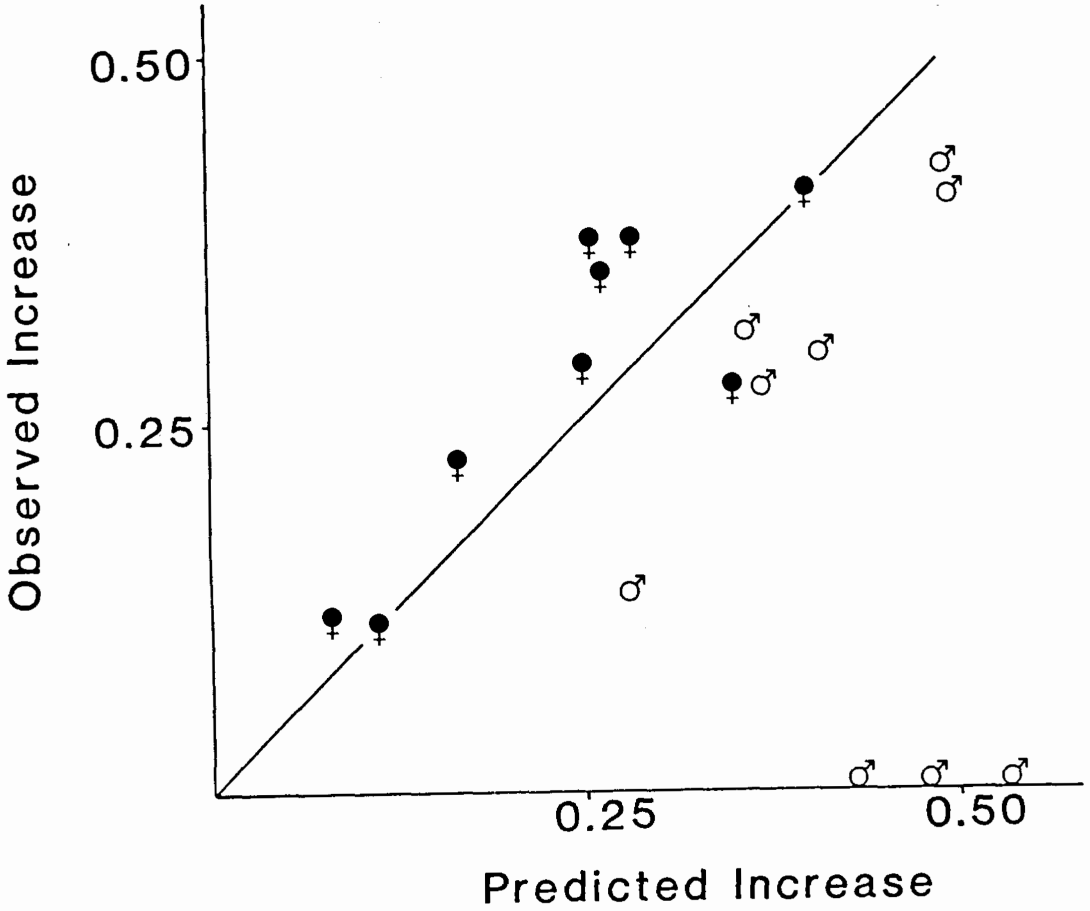

Fig. 4.4. Summary of the results of the experiment to offset the influence of risk. The abcissa represents the initial avoidance of the risky patch when the amount of food in both feeders was equal (proportion using "risky" feeder in the absence of a predator minus proportion using risky feeder (with predator) in experiment 1), and thus the predicted increase in its use after the addition of extra food. The ordinate represents the avoidance of the risky patch after additional food was added (proportion using risky feeder in experiment 2 minus proportion using risky feeder in experiment 1). If the additional food offsets the risk, then the results of experiment 2 should return to the control distribution of experiment 1, i.e., fall along the diagonal. Symbols denote results for the two sexes.

Table 4.3. Summary of t-tests comparing the distribution of guppies between control experiments and experiments with additional food added to offset the effect of risk. = denotes no significant difference, + (treatment > control), or - (treatment < control). Data were arcsin square-root transformed before analysis. Significant p-values are given in parentheses. The results for each cell were repeated 9 times, except for the results for the males at the high (12 mg of food in the safe feeder) which were repeated 6 times.

		Risk Level		
	Food in Safe Feeder	Low	Medium	High
FEMALES	5	+ (0.006)	=	+ (0.020)
	10	=	=	=
	20	+ (0.004)	+ (<0.001)	+ (<0.001)
MALES	3	- (0.0160)	=	- (0.030)
	6	- (0.001)	- (0.016)	- (0.008)
	12	- (<0.001)	- (<0.001)	- (<0.001)

DISCUSSION

These results demonstrate that risk of predation can be expressed in units of energy, and therefore that sufficient food can offset the effect of risk. By determining the energetic equivalence of risk, we quantitatively described its influence on foraging behaviour at different diet levels. For females, risk had its greatest measured energetic equivalent at the intermediate diet level. For males, the greatest energetic equivalent of risk occurred at the highest diet level. At this diet level, males continued to avoid the risky feeder even when more than 17 times as much food was available there than at the other feeder. In addition, the measured value of risk was less for females than for males, consistent with the prediction that risk should have a greater influence on animals which receive relatively less fitness advantage from equivalent additional amounts of energy.

When we calculated how much food was necessary to offset risk, we assumed that the amount of energy delivered to guppies was equal to the amount of food they consumed. However, the net intake rate may be affected by risk. When animals are in the presence of a predator, it is possible that the threat increases their standard metabolic rate. Furthermore, foraging efficiency in the presence of a predator may be reduced owing to the need for vigilance (Caraco et al. 1980, Milinski & Heller 1978). Thus, the absolute energetic value of risk determined in these experiments probably overestimates somewhat the true energetic equivalent of risk. Male guppies may also obtain non-energetic benefits from foraging: if they consume food which contains carotenes, this may alter body coloration, providing a mating advantage (Endler 1982). However, the onion fly eggs used in these experiments do not contain carotene (Richards & Davies 1977) so this should not have affected the results of the experiments.

Equation (3) assumes a linear relation between energy intake and fitness. Violations of this assumption generate a characteristic result: an accelerating relation will result in additional food exceeding the influence of risk so that more guppies than predicted will use the risky feeder. Conversely, a decelerating relation will result in the additional food being insufficient to offset risk and fewer guppies than predicted using the risky feeder. Thus, the value of additional food gained by taking a risk depends on the absolute amount of food which can be obtained in safety (see Sih 1982b for a further discussion of this idea). When male and female guppies are placed on identical controlled caloric diets, females always grow more rapidly than males; they also change their growth rate more rapidly than males when their diet is changed (Abrahams & Reynolds in prep.). These results suggest that the relation between energy intake and fitness is different between the sexes: females appear to benefit more than males from increased energy, a difference consistent with their responses to extra food in Experiment 2.

Since single groups of males and females were used, the influence of sex on these results cannot be statistically tested. It is possible that behavioural differences between the two groups resulted from uncontrolled individual variation within the guppy population. However, we believe it more likely that these differences reflect biological differences between the sexes.

Previous studies have found other factors to be important in determining the response of animals to risk of predation. Sih (1982a, 1982b) found that notonectids (*Notonecta hoffmani*) were more willing to risk exposure to their predator (larger instars) when they had been starved than when they were well fed. Dill and Fraser (1984) also observed this phenomenon with juvenile coho salmon (*Oncorhynchus kisutch*). House sparrows (*Passer domesticus*) were also more likely to exploit riskier habitats in cold weather because of their increased energy requirements

(Elgar 1986). Thus, animals appear to be more willing to risk exposure to a predator when the immediate benefits of energy (e.g., minimizing the probability of starvation) are increased. This present study suggests that the response of animals to a risk of predation was a function of the potential benefits which can be derived from additional food -- a characteristic of the animal's life history.

In a similar study, Gilliam and Fraser (in press) were able to predict successfully how much additional food was necessary to induce juvenile creek chub (*Semotilus atromaculatus*) to forage in areas of greater risk. They developed a model which predicted that, in the presence of an absolute refuge containing no food, animals should use the refuge and forage in the habitat that has the minimum ratio of mortality rate to feeding rate (a special case of a general model derived by Gilliam 1982; see also Werner and Gilliam 1984). The major difference between their experiments and ours was the method by which risk was incorporated into foraging decisions. We assume that habitat quality is determined by the additive effects of energy and risk whereas Gilliam and Fraser (in press) assume that it is determined by the *ratio* of mortality rate to feeding rate. These models can be distinguished experimentally. The ratio approach of Gilliam and Fraser predicts that habitat use decisions are affected only by relative differences in habitat quality. Manipulating an environment such that food levels in all habitats are multiplied by a constant factor should not alter habitat use, as the relative differences in habitat quality remain unchanged. Our model would predict that this manipulation should alter habitat use since habitat quality is measured by the absolute difference between the benefits of food and the costs of risk.

Risk of predation is not only an important factor influencing foraging behaviour, but also a potentially important determinant of community structure (Dill 1987). Kotler (1984), for example, demonstrated that species of desert rodents least vulnerable to predators tend to forage in open areas whereas the most vulnerable species are restricted to areas under bushes. Thus, risk of predation can influence community structure by allowing animals specializing in predator escape to exploit risky environments, reducing their interactions with superior competitors. Mittelbach (1984) and Werner et al. (1983) have suggested that predation risk is important in structuring aquatic communities. Development of models to describe adequately the influence of risk of predation on habitat choice therefore would not only benefit foraging theory, but contribute to our understanding of community structure as well.

Given that animals choose patches on the basis of trade-offs between the availability of food and the associated risk of predation, the following scenario can be imagined. Animals will find a range of habitats in which food availability and risk are positively correlated. (Any patches which are relatively safe and have readily available food will be preferentially used, lowering food availability to conform to the correlation; any patches which are very risky but have a low food availability will be ignored, and predators will be expected to move to more profitable patches as a consequence.) Faced with this situation, there are a number of potential strategies which foragers could adopt. Animals could avoid patches which risk exposure to a predator, spending their lives in energetically poor habitats. There they would grow slowly, and produce offspring at a slow rate, but live a long time. Others could use the richest habitats, grow and reproduce rapidly, but live a relatively short life. If these two alternative strategies (and perhaps others which involve time spent in a range of habitats) produce the same number of offspring over their lifetime, they should have equal fitness and persist in the population. Since individuals were not marked in our experiments, the possibility of alternative strategies could not be tested. However, it could be an important consideration in the development of habitat use models which incorporate risk of predation.

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LITERATURE CITED

Abrahams, M.V. (in review) Foraging guppies and the ideal free distribution: the influence of information on patch choice.

Abrahams, M.V. & J.D. Reynolds (in prep.) Relationships between energy and fitness: sex differences in guppies.

Baerends, G.P., R. Brouwer & H.TJ. Waterbolk. 1955. Ethological studies on *Lebistes reticulatus* (Peters). I. An analysis of the male courtship patterns. Behaviour 8: 249–334

Caraco, T., S. Martindale & H.R. Pulliam. 1980. Avian flocking in the presence of a predator. Nature 285: 400–401

Dill, L.M. 1987. Animal decision making and its ecological consequences: the future of aquatic ecology and behaviour. Canadian Journal of Zoology 65: 803–811

Dill, L.M. & A.H.G. Fraser. 1984. Risk of predation and the feeding behaviour of juvenile coho salmon (*Oncorhynchus kisutch*). Behavioural Ecology and Sociobiology 16: 65–71

Elgar, M.A. 1986. The establishment of foraging flocks in house sparrows: risk of predation and daily temperature. Behavioural Ecology and Sociobiology 19: 433–438

Endler, J.A. 1982. Convergent and divergent effects of natural selection on color patterns in two fish faunas. Evolution 36: 178–188

Farr, J.A. 1980. Social behaviour patterns as determinants of reproductive success in the guppy *Poecilia reticulata* Peters (Pisces: Poeciliidae): an experimental study of the effects of intermale competition, female choice, and sexual selection. Behaviour 74: 38–91

Fretwell, S.D. 1972. Populations in a seasonal environment. Princeton University Press

Fretwell, S.D. & H.L. Lucas. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheoretica 19: 16–36

Gilliam, J.F. 1982. Habitat use and competitive bottlenecks in size-structured fish populations. Ph.D. thesis. Michigan State University, East Lansing. 107pp.

Gilliam, J.F. & D.F. Fraser. (in press). Habitat selection under predation hazard: test of a model with foraging minnows. Ecology

Hester, F.J. 1964. Effects of food supply on fecundity in the female guppy, *Lebistes reticulatus* (Peters). Journal of the Fisheries Research Board of Canada 21: 757–764

Kotler, B.P. 1984. Risk of predation and the structure of desert rodent communities. Ecology 65: 689–701

Lima, S.L. & L.M. Dill. (in review). Behavioural decisions made under the risk of predation: a review and prospectus

Milinski, M. & R. Heller. 1978. Influence of a predator on the optimal foraging behaviour of sticklebacks (*Gasterosteus aculeatus* L.). Nature 275: 642–644

Mittelbach, G.G. 1984. Predation and resource partitioning in two sunfishes (Centrarchidae). Ecology 65: 499–513

Parker, G.A. 1984. Evolutionarily stable strategies. In: Behavioural Ecology, 2nd ed. (eds. J.R. Krebs & N.B. Davies). Sinauer, Sunderland, Mass. pp. 30–61

Richards, O.W. & R.G. Davies. 1977. Imm's general textbook of entomology. Vol. 1. (10th ed.). Chapman & Hall, London

Sih, A. 1982a. Foraging strategies and the avoidance of predation by an aquatic insect. Ecology 63: 786–796

Sih, A. 1982b. Optimal patch use: variation in selective pressure for efficient foraging. American Naturalist 120: 666–685

Stephens, D.W. & J.R. Krebs. 1986. Foraging theory. Princeton University Press.

Werner, E.E. & J.F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics 15: 393–425

Werner, E.E., J.F. Gilliam, D.J. Hall & G.G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology 64: 1540–1548

CHAPTER V

THE TRADE-OFF BETWEEN FORAGING AND COURTING IN MALE GUPPIES (*POECILIA RETICULATA*)

ABSTRACT

Experiments were performed to determine the energetic equivalence of courtship opportunities to male guppies (*Poecilia reticulata*). I assumed that under certain conditions, animals will distribute themselves within an environment such that all will receive equal fitness benefits (i.e., conform to an ideal free distribution). I provided a group of ten male guppies with an environment containing two resources which they had to choose between: food, and access to a female. If all the males are to receive equal benefits from this environment, then those which court the female must receive the same benefit as those which feed. Thus the food consumed by the feeding males should equal the caloric equivalent of access to the female. My results demonstrate that males did not adopt a stable distribution between these two resources. Instead, all the males began by feeding and then a certain proportion switched to courting the female. The more food that was available, the earlier was the switch, and the proportion which eventually courted the female was positively correlated with her size. These data suggest that courtship and feeding decisions made by male guppies incorporate the costs and benefits associated with present and expected future reproductive success.

INTRODUCTION

Faced with a choice between two habitat patches containing resources important to fitness (e.g., food and mates), an animal has two options for exploiting them. In one case, the animal could choose at each point in time that resource patch which provides the greatest fitness benefit. If a group of animals make their choices (near-) simultaneously, the result should be an ideal free distribution, the number of animals in a patch being proportional to the fitness to be gained there. This is explained more fully below. Alternatively, the animals could choose that patch providing the resource of greatest immediate benefit to fitness, switching to the other patch (and resource) once their immediate needs for the first resource had been met. If the first resource were food, such animals would behave as typical foraging time minimizers (Schoener 1971; Hixon 1982).

Male guppies (*Poecilia reticulata*) are expected to be most like time-minimizers. Guppies are strongly sexually dimorphic; females are relatively large and drab while males are smaller and more brightly coloured. Unlike most fish, males stop growing (or grow very slowly) after they mature (Reznick 1983). The mating system is promiscuous, with the fitness of males being limited by their ability to gain access to females. Males expend considerable time locating and displaying to females (Farr 1977), and females are sensitive to male colour (Endler 1980, 1983; Kodric-Brown 1985; Houde 1987) and courtship intensity (Farr 1980; Bischoff et al. 1985) when selecting mates. In this study, a group of male guppies was offered a choice between feeding and courting a female.

I used ideal free distribution (IFD) theory (Fretwell & Lucas 1970; Fretwell 1972) to determine the energetic equivalence of courtship opportunities. The animals must satisfy two assumptions for this distribution to arise. First, they must be 'ideal' in that they have perfect knowledge of the distribution of resources; second, they must be 'free' to use these resources equally with other animals. In an environment which contains only one type of resource, the spatial distribution of animals should be the same as the spatial distribution of that resource. When several different types of resources are available, the distribution of animals should also result in all animals receiving equal benefits, regardless of which resource(s) they are using. Abrahams & Dill (submitted) develop this argument more completely for the resources "food" and "safety".

The IFD can be used to test the two hypotheses regarding how males should allocate their time between feeding and courting a female. The first hypothesis assumes that at the stable IFD, the energetic intake rate of the feeding guppies should provide the same long term benefit to fitness as courting the female. Thus, this hypothesis predicts that increasing the amount of food available should reduce the number of males which court a female of a given size (due to the increased benefits of feeding). Similarly, increasing the size of the female should reduce the number of males feeding due to the increased benefits of courting (due to female fecundity increasing with size; Hester 1964).

The alternate hypothesis predicts that males will feed to capacity in the least amount of time and then switch to other activities. As for the first hypothesis the benefits from feeding and courtship are independent, but the method by which males allocate their time to these activities differs. This hypothesis predicts that the relative amount of time spent feeding should be inversely proportional to food availability. For example, if the food availability is doubled, males should spend exactly half as much time feeding.

METHODS

A group of 10 similar-sized male guppies (average mass 0.105 g ± 0.015 SD) were placed in a 90-l aquarium. Similar sized individuals were used to ensure that they had similar competitive abilities. The same ten males were used in all experiments.

The males lived in the aquarium throughout the experimental period so that no daily acclimation periods were required. They were maintained on a 12-h light/dark cycle and fed NutraFin (TM) and brine shrimp *ad lib* daily between experiments. During experiments the fish were maintained exclusively on the food provided during experimentation (see below) except for a weekly supplement of NutraFin flakes for essential nutrients.

The aquarium contained a 3-cm layer of aquarium gravel. The ends had black plexiglas attached to the inside to prevent reflection, and the back was covered with black plastic. Observations were made from behind a black plastic curtain completely surrounding the tank.

The males were provided with a choice of courting a female or feeding. Because males are not capable of simultaneously courting and feeding (Dussault & Kramer 1981), and the two choices were presented at opposite ends of the aquarium (Fig. 5.1), the males could choose only one option at any time.

Eggs of the onion fly (*Delia antigua*) were used as the food in these experiments. They were provided by a feeder which presented them at a constant rate over a wide area throughout the experiment (see Abrahams (submitted) for details), ensuring that all males had equal access to the food (Abrahams, submitted). Eggs that were not consumed were removed from the aquarium by a food trap.

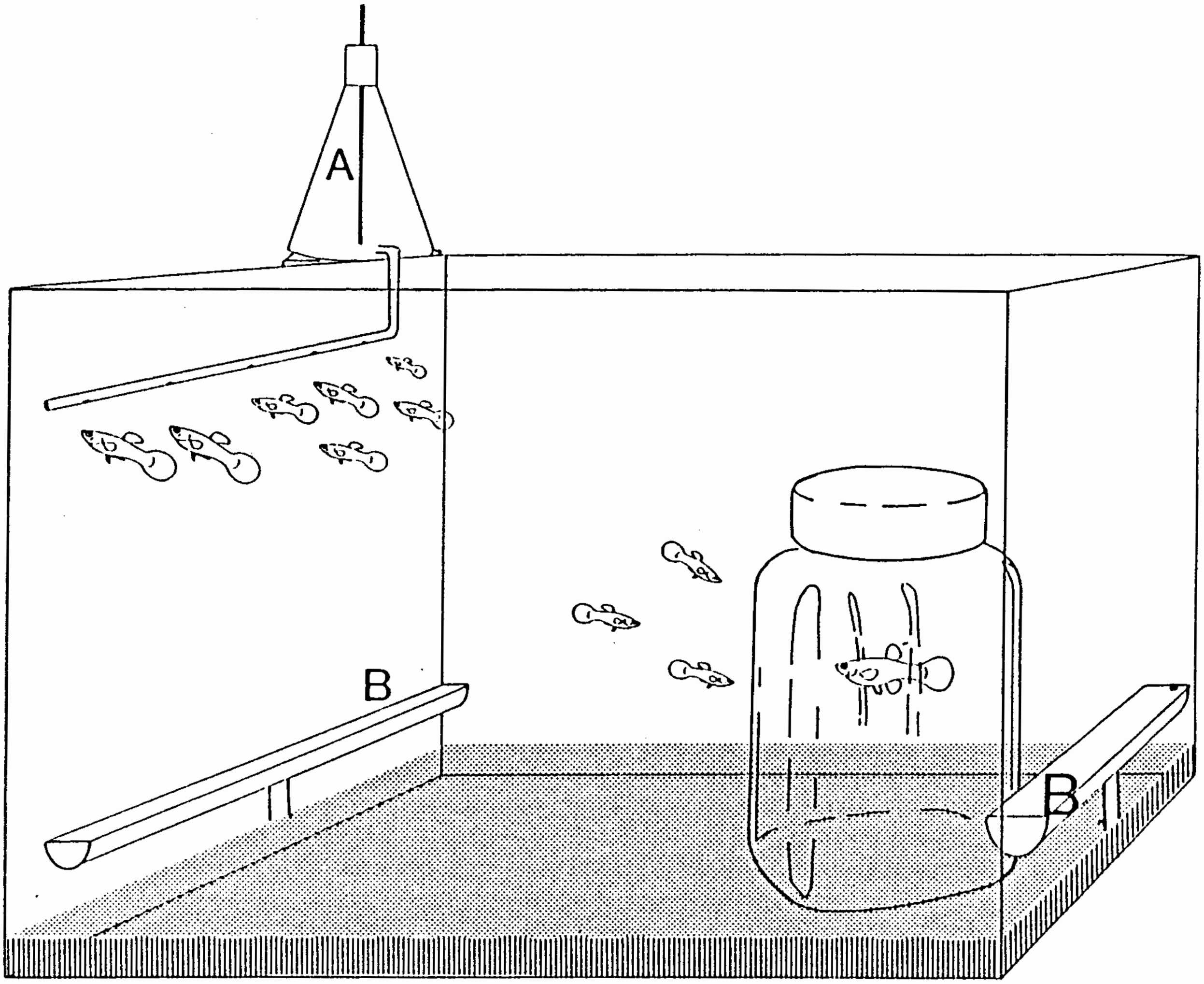

Figure 5.1. Apparatus used for the experiments. Note that the positions of the feeder and the female can be reversed in this apparatus. Food is provided by the feeder bar (A) and removed from the apparatus by the food trap (B).

The females were presented to the males in square 4-l glass jars. The females lived in these jars thoughout the experiment and were fed NutraFin *ad lib* daily. The jars contained a 3-cm layer of gravel with some pieces of oyster shell. The water was aerated by an air stone and unconsumed food was removed daily.

When a female's jar was added to the aquarium, the lid was removed and the jar filled with water from the aquarium. The lid of the jar contained holes covered with a fine mesh screen, providing both visual and chemical contact between the males and the female. The jar was placed in the aquarium 5-cm from the end opposite the feeder and rotated so that the sides of the jar were at 45^{o} to the sides of the aquarium. This allowed the males to court the female from any side of the jar, increasing their access to her.

In these experiments, 3 different diet levels (6, 12 and 24 mg of food per 24 min) and 5 different sizes of female (0.073, 0.126, 0.207, 0.895 and 1.170 g wet weight) were used. Including the two ends of the aquarium as a third factor, there were 30 unique combinations provided to the males. Experiments were performed using the medium diet level first, then the low and finally the high diet level. Within each diet level, female size and end of tank for presentation were chosen randomly. The selected combination was provided to the males 3 times in one day, with each trial being separated by at least 3 hours to prevent satiation. Each combination of diet level, female size, and female position was repeated 6 times (3 times on each of 2 days).

Experiments were performed by first placing the feeder at one end of the aquarium and then placing the female at the opposite end. As soon as the female was in the aquarium, the observer moved behind the blind and started the flow of food from the feeder. The activities of the males were recorded every 30 sec for

24 min using a metronome sampling technique. The males' activities were divided into three categories: feeding, courting the female, or neither. From these data, temporal changes in male activity within an experiment could be detected, and the overall result of the experiment summarized as the mean of all 48 observations of the proportion engaged in different activities.

RESULTS

The position of the female within the aquarium had no significant influence on the mean proportion of courting males within an experiment (t-test of arcsin square-root transformed data, $p = 0.62$). Thus, data were pooled between sides so that each combination of female size and diet level had 12 repeated observations.

Both diet level and female size had a significant influence on the mean proportion of males courting (Table 5.1, Fig. 5.2). However, there was also a significant interaction between these two main effects. The nature of this interaction was such that the influence of female size was reduced at the low and high diet levels. The overall effect of female size was to increase the mean proportion of guppies courting, as predicted by the first hypothesis. However, increasing diet levels increased the proportion of males courting a female of any given size, rather than decreasing it as predicted by the first hypothesis.

The first hypothesis also predicts that males should achieve a stable distribution between the food and the female throughout an experiment. However, the distribution of males varied distinctly over time. In all experiments, males would use the feeder initially, then switch to courting the female (Fig. 5.3). The first hypothesis therefore must be rejected.

Table 5.1. Summary of the statistics for these experiments, all by two-way ANOVA. Because all treatment parameters were constrained, the data were arcsin square-root transformed before analysis. Numbers in parentheses indicate degrees of freedom for each column.

Dependent Variable		Female Size (4,165)	Diet Level (2,165)	Interaction (8,165)
Mean Proportion Courting	F	28.46	182.78	6.58
	p	<.001	<.001	<.001
Switch Time	F	11.84	135.08	5.16
	p	<.001	<.001	<.001
Number Courting After Switch	F	37.88	46.36	3.75
	p	<.001	<.001	<.001

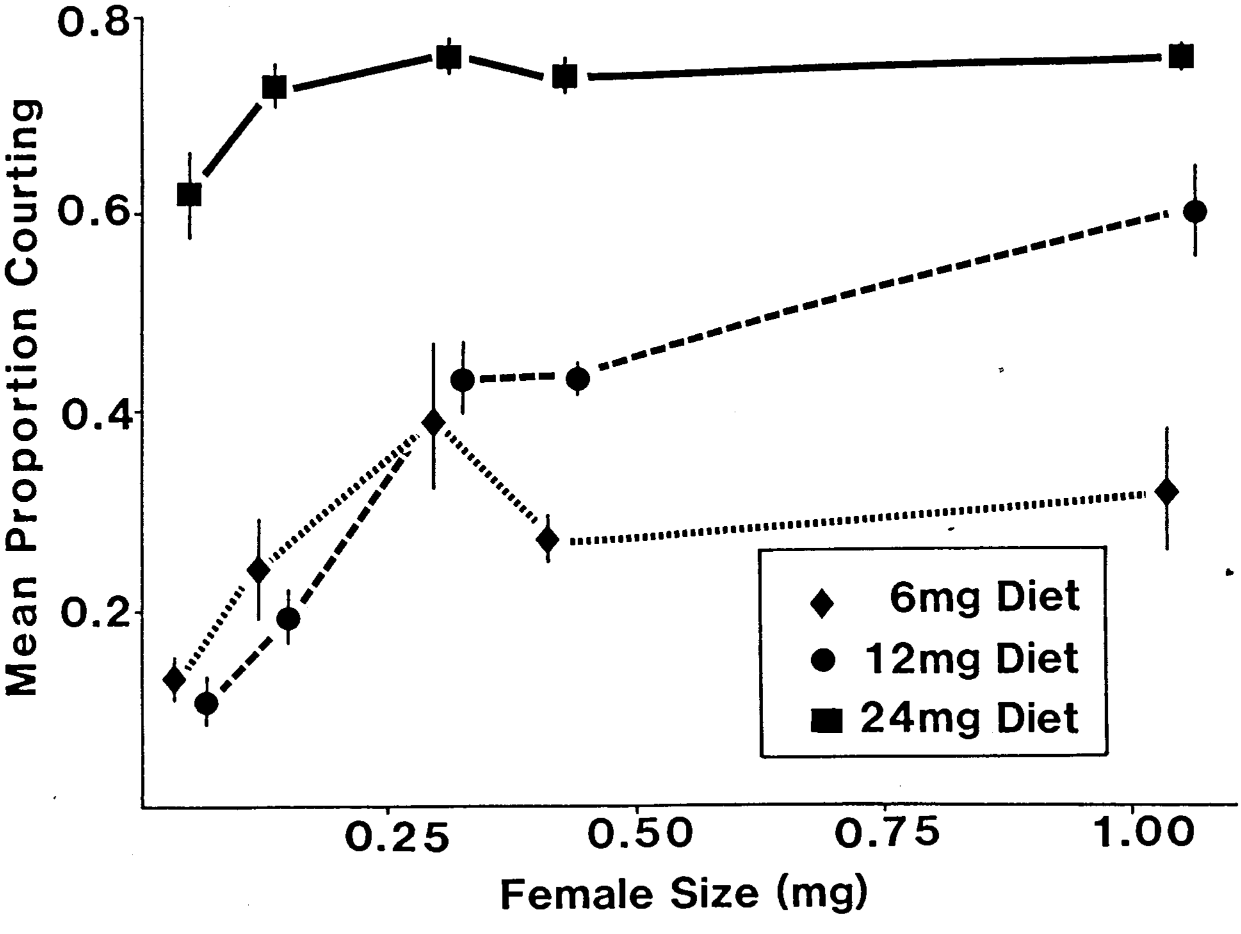

Figure 5.2. The overall mean proportion of males courting the female as a function of female size and diet level. Error bars correspond to one standard error.

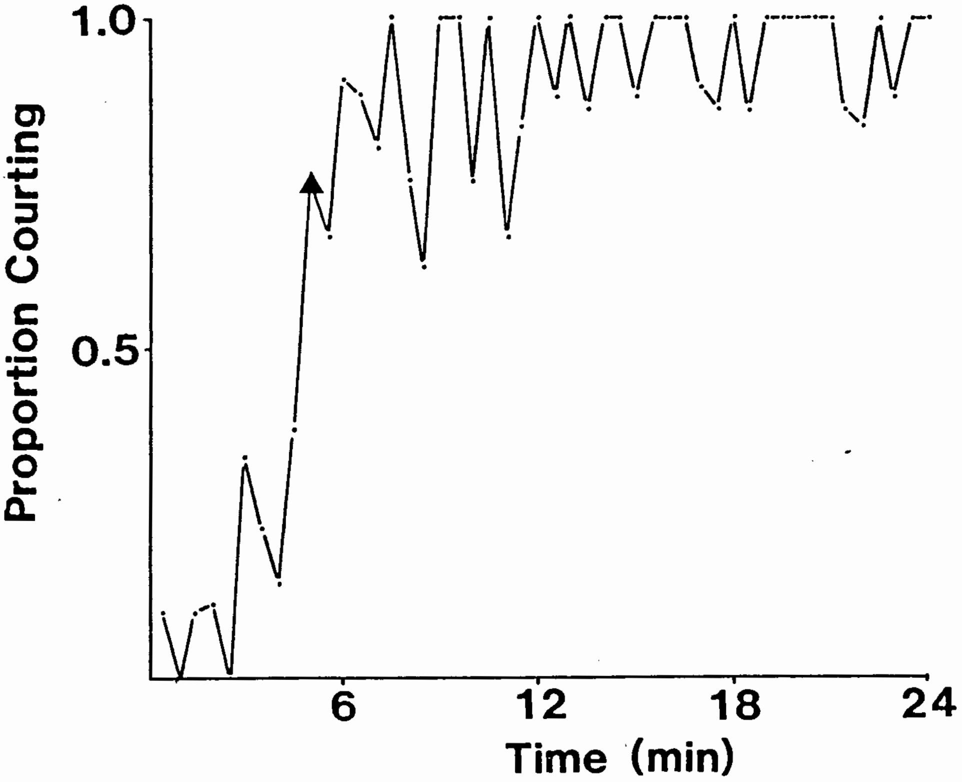

Figure 5.3. The results of a single experiment illustrating the change in male behaviour with time. Initially the males fed, but then switched to courting the female. The triangle indicates the switch point, as defined in the text.

The second hypothesis is based on the assumption that males allocate the minimum foraging time necessary to obtain a fixed amount of food. As the feeder provided food at a constant rate, and all the food was consumed (at least prior to the switch point), the amount of food consumed by the males increased linearly with time. Thus, males should spend the least time feeding at the highest diet level, twice this time feeding at the medium diet level and four times as much time feeding at the lowest diet level.

The time spent foraging was defined as the time from the beginning of the experiment to the point at which more than 50% of the males had switched to courting the female for at least the three subsequent observations (see example in Fig. 5.3). If no switch point was observed, it was designated to occur at 24 min (the end of the experimental period).

The switch points occurred at times which were significantly influenced both by diet level and female size (Table 5.1 and Fig. 5.4). There was also a significant interaction between these two main effects. The influence of female size was most extreme at the medium diet level causing switching to occur earlier as female size increased. There was no obvious trend at the other diet levels (Fig. 5.4). At the lowest diet level, switch points were probably constrained by the limited time in the experiment, obscuring the influence of female size. Pooling the data for all female sizes at the 24 mg diet level, the males switched from feeding to courting after 5.9 min. If the guppies switched after consuming the same amount of food at the other diet levels, they should have stopped feeding at 11.8 min at the 12 mg diet level and 23.7 min at the 6 mg diet level. At the 12 mg diet level they spent significantly more time feeding (16.05 min) than predicted ($p < 0.001$, Mann Whitney U-test). Comparison with the switch time predicted by the hypothesis could not be made conclusively at the 6 mg diet level as 53% of the trials never resulted in a

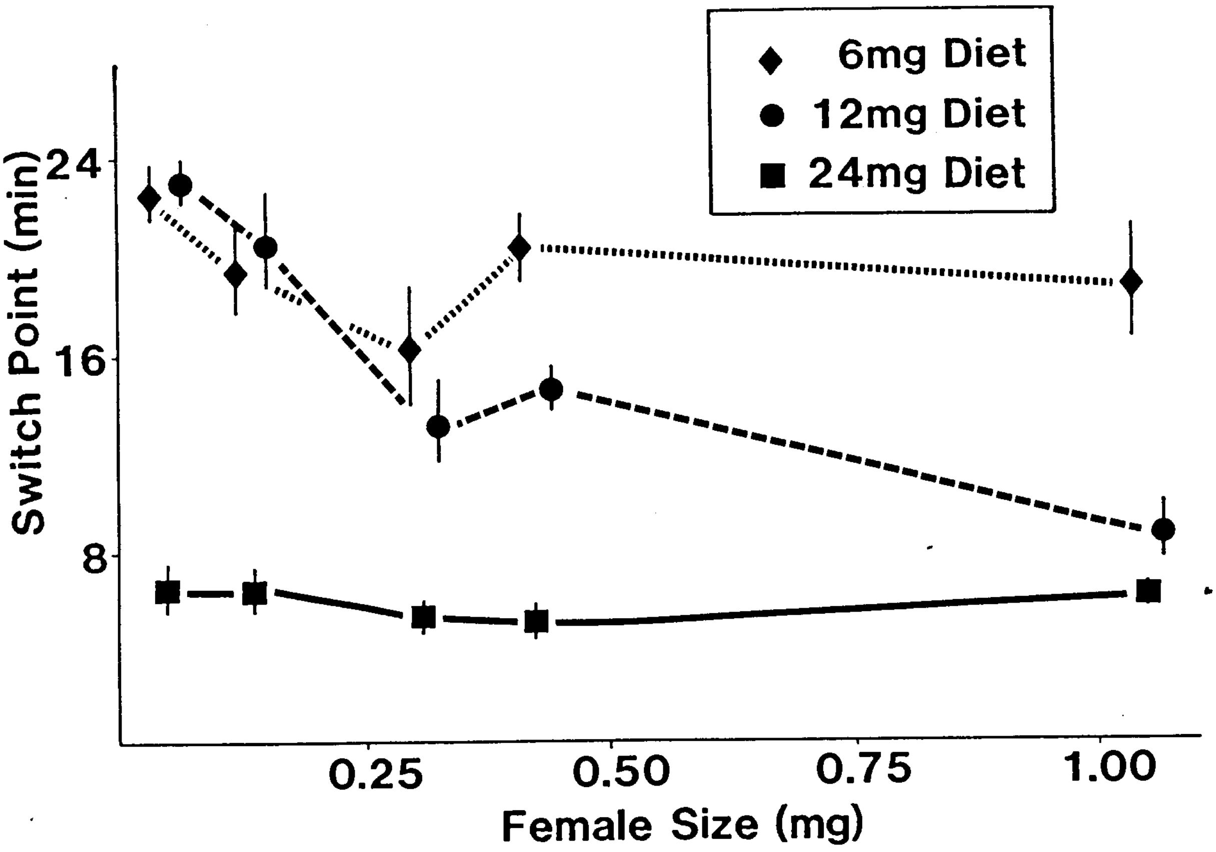

Figure 5.4. The mean times at which the switch points occurred for different diet levels and female sizes. Error bars correspond to one standard error.

switch (as defined above) by the end of 24 min. However, if the switch times were normally distributed with a mean of 23.7 min, this pattern would be expected.

The number of males which courted the females after the switch point continued to be significantly influenced by female size and diet level (Fig. 5.5 and Table 5.1). (If no switch point was observed, the mean number courting the female for the last half of the experiment was used). Again, there was a significant interaction. Increasing numbers of males courted larger females, with this influence being most pronounced at the medium diet level. At the two smallest female sizes, the low and medium diet levels produced a similar result, while substantially more males courted these females at the highest diet level (Fig. 5.5). The medium and high diet levels produced a similar result for the 3 largest female sizes, while fewer males courted these females at the lowest diet level.

The number of males which were classified as neither using the feeder nor courting the female increased significantly after the switch point (t-test, $p < 0.001$). Prior to the switch point, an average of 1.2 males were observed neither feeding nor courting, compared to 3.3 males after the switch point.

DISCUSSION

Male guppies did not follow an IFD when trading-off feeding and courtship opportunities. More males courted larger females when a constant amount of food was provided (as predicted by the IFD) but decreasing the amount of food available *decreased* the number of courting males, contrary to the predictions of the IFD. There was limited support for the second hypothesis that males behave as stereotypical time minimizers, consuming the same amount of food at all diet levels and then switching to other activities, but they ate more food at the lower

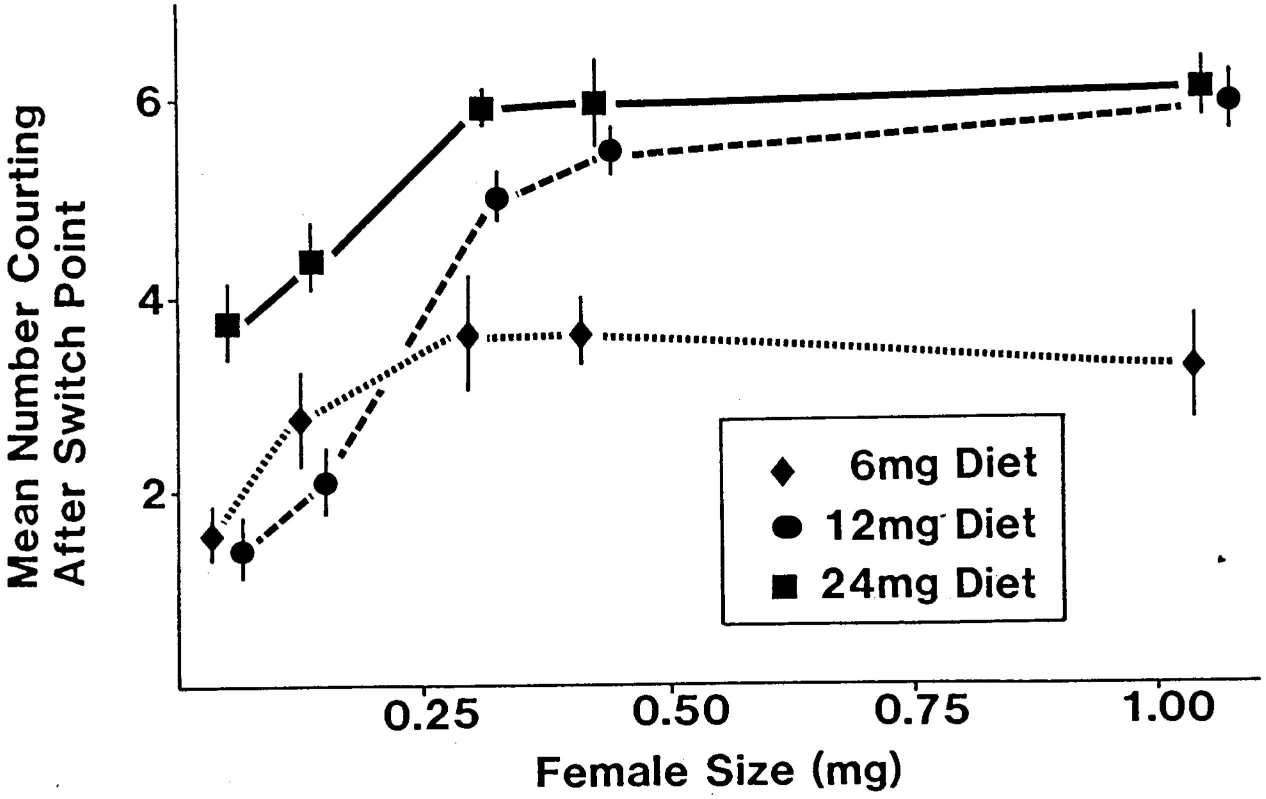

Figure 5.5. The mean number of males courting females after the switch point as a function of diet level and female size. Error bars correspond to one standard error.

diet levels than expected. Further, the amount of food available continued to influence the males' behaviour after they had stopped feeding, resulting in more males courting the same female at higher diet levels.

A possible explanation for these results was that the assumption of equal access to the resources did not apply in this apparatus. I have previously confirmed that male guppies have equal access to the food dispensed from these feeders (Abrahams, submitted), but I could not confirm this assumption for access to the females. Previous experiments have suggested that males differ markedly in their ability to attract females. Endler (1980, 1983) and Kodric-Brown (1985) have demonstrated that male coloration can significantly influence male reproductive success, and Farr (1977) has suggested that there may be negative frequency dependent mate choice (based on coloration) by females. Males may also be able to increase access to females by increasing their courtship intensity (Farr 1980).

These differences in potential competitive abilities for females can influence the spatial distribution of animals (Parker & Sutherland 1986). In this experiment it should result in fewer males courting a female than predicted. This is because the value of a courtship opportunity to a male should be the product of the fecundity of the female (a function of her size) and the probability of success. Those males which are best at competing for females should be the most likely to attempt to court her.

This may explain a potential bias in the data, but it does not explain why the males change their behaviour over time. As the benefits from courting and feeding were both negatively affected by density, and the resources could not be depleted, an animal that reversed its behaviour (i.e., courted and then fed) would have a substantial competitive advantage. That this type of behaviour was not observed suggests that energy has a greater immediate benefit than courtship, at least to a hungry male guppy.

Recent models employing dynamic optimization techniques to describe animal behaviour (e.g., Mangel & Clark 1986) have suggested that the relative benefits associated with different activities depend upon the animal's state. That is, different activities have associated with them, different costs and benefits, and the animal's state reflects differing susceptibilities to costs.

This may explain the results of the present experiments. Given that male guppies should be selected to maximize their fitness, they should engage in activities which provide the greatest net benefits to their fitness. In this experiment, the two activities were feeding and courting. The net benefit from courting is the potential number of eggs which can be fertilized minus the energetic costs of courtship. Although the energetic cost of courtship may be constant, the male's ability to pay is not. As the male's energetic state worsens, losing a fixed amount of energy will increasingly reduce the male's expected lifetime. Thus, the net benefit of courting is the potential benefits from a current courtship minus the reduced benefits from all future courtships.

The net benefit from feeding is that it will increase the male's expected lifetime. This increases the potential number of females a male will encounter, increasing his fitness. Again, the benefits from feeding should be state-dependent. They will be highest when the male is at a low energetic state, eventually diminishing towards zero as the male's gut becomes full.

Figure 5.6 illustrates how the changing benefits associated with these activities can account for the results of these experiments. At the beginning of an experiment, the male's energetic state is low, and the potential benefits of feeding

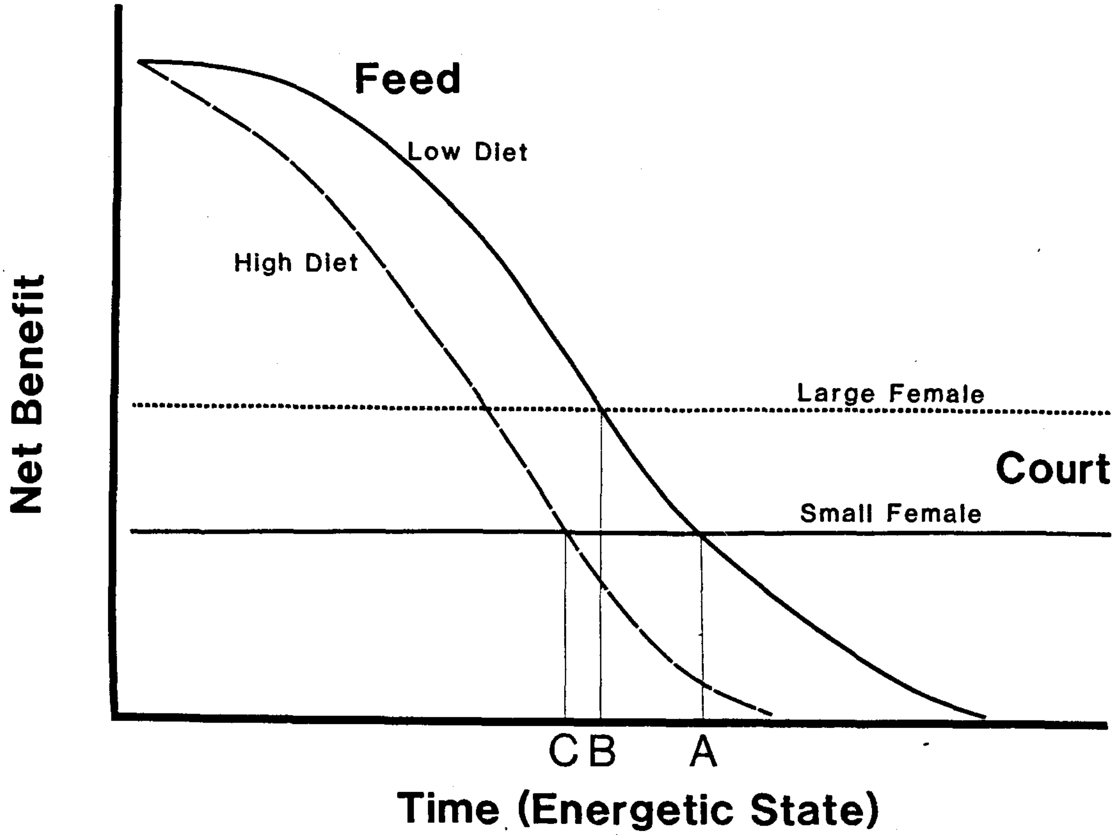

Figure 5.6. A model consistent with the results of these experiments. The ordinate represents the hypothetical net fitness benefits of either feeding or courting and the abcissa corresponds to time within an experiment (which is linearly related to energetic state). In this model the males on a low diet should switch from feeding to courting at time A. Increasing the size of the female will reduce the switch time to B. Increasing the amount of available food will reduce the switch time to courting a small female to C. Both effects were observed in the experiments. Although the courtship benefit lines are drawn horizontally, they could have a slight positive slope if males with low energy states are less attractive to female or less able to compete successfully for them. However, this will not alter the qualitative predictions of the model.

will be at their highest. As the male's energetic state improves, the potential benefits of feeding will diminish until they eventually fall below the benefits of courtship. At this time, the males should switch activities from feeding to courting (point A in Fig. 5.6). Increasing diet level will increase the rate of change in the male's energetic state. This will result in the net benefits of feeding declining more rapidly, resulting in an earlier switch from feeding to courting (cf. A and C in Fig. 5.6). The switch time from feeding to courting can also be reduced by increasing the benefits of courtship (e.g., by providing a larger female; cf. A and B in Fig. 5.6).

At present this model represents a *post hoc* explanation of the data. However, it makes some testable predictions. Males at higher food levels should consume less food than at lower diet levels before switching to courting. This should occur because males will experience ongoing metabolic costs while they are feeding. By obtaining food at a faster rate, they will require less food to acquire comparable net benefits from feeding and thus for it to become profitable to switch to courting. Furthermore, if males trade-off food against courtship as predicted, then males which are constantly exposed to larger females should feed less than males exposed to smaller females. As a result, these males should tend to grow more slowly and die sooner than males with smaller females. Their fitnesses, however, should be equal.

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LITERATURE CITED

Abrahams, M.V. (in review). Foraging guppies and the ideal free distribution: the influence of information on patch choice. Behaviour

Abrahams, M.V. & L.M. Dill (in review). A determination of the energetic equivalence of the risk of predation. Ecology

Bischoff, R.J., J.L. Gould & D.J. Rubenstein 1985. Tail size and female choice in the guppy. Behav. Ecol. Sociobiol. 17: 253 255

Dussault, G.V. & D.L. Kramer 1981. Food and feeding behaviour of the guppy, *Poecilia reticulata* (Pisces: Poeciliidae). Can. J. Zool. 59: 684-701

Endler, J.A. 1980. Natural selection on color patterns in *Poecilia reticulata.* Evolution 34: 76-91

Endler, J.A. 1983. Natural and sexual selection on color patterns in Poeciliid fishes. Env. Biol. Fishes 9: 173-190

Farr, J.A. 1977. Male rarity or novelty, female choice behaviour, and sexual selection in the guppy, *Poecilia reticulata* (Pisces, Poeciliidae). Evolution 31: 162-168

Farr, J.A. 1980. Social behaviour patterns as determinants of reproductive success in the guppy *Poecilia reticulata* Peters (Pisces: Poeciliidae): an experimental study of the effects of intermale competition, female choice, and sexual selection. Behaviour 74: 38-91

Fretwell, S.D. 1972. Populations in a seasonal environment. Princeton Univ. Press. 217 pp.

Fretwell, S.D. & H.L. Lucas. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheor. 19: 16-36

Hester, F.J. 1964. Effects of food supply on fecundity in the female guppy, *Lebistes reticulatus* (Peters). J. Fish Res. Board Can. 21: 757-764

Hixon, M. 1982. Energy maximizers and time minimizers: theory and reality. Am. Nat. 119: 596–599

Houde, A.E. 1987. Mate choice based upon naturally occurring color pattern variation in a guppy population. Evolution 41: 1–10

Kodric–Brown, A. 1985. Female preference and sexual selection for male coloration in the guppy (*Poecilia reticulata*). Behav. Ecol. Sociobiol. 17: 199–205

Mangel, M. & C.W. Clark 1986. Towards a unified foraging theory. Ecology 67: 1127–1138

Parker, G.A. & W.J. Sutherland. 1986. Ideal free distributions when individuals differ in competitive ability: phenotype limited ideal free models. Anim. Behav. 34: 1222–1242

Reznick, D. 1983. The structure of guppy life histories: the tradeoff between growth and reproduction. Ecology 64: 862–873

Schoener, T.W. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst. 2: 369–404

CHAPTER VI

RELATIONSHIPS OF ENERGY TO GROWTH AND COURTSHIP IN GUPPIES

ABSTRACT

Two experiments were performed to examine the relative value of food energy to male and female guppies. First, we provided diets of different energetic quality to groups of newborn male and female guppies. Female growth was more rapid than that of males at every diet level, and their growth rate increased more rapidly with increases in diet level than did that of males. Second, we tested the influence of diet on the males' courtship behaviour and attractiveness to females. Although there was considerable variation among males in courtship intensity and ability to attract females, these differences were not related to a four-fold variation in diet levels experienced for seven days prior to each trial. These results suggest that energy intake will have a greater influence on female fitness than on male fitness, and are consistent with the behavioural responses of the two sexes in energy-predation risk trade off experiments (Chapter IV).

INTRODUCTION

Well adapted animals are assumed to make foraging decisions which maximize their fitness, and therefore must consider both the fitness benefits and costs associated with each foraging decision. The costs involved will be both direct (i.e., the time and energy required to obtain food) and indirect (e.g., the risk of predation associated with obtaining that food, lost opportunities to spend time on other activities, etc.) and will be primarily determined by features of the environment in which the animal forages. The benefits of foraging will be determined by the animal's ability to convert food energy to fitness and therefore will be an intrinsic characteristic of the animal (i.e., a part of its life history strategy).

Sexual selection can produce dramatically different life history strategies between males and females within a species. In many species, differences in conspicuousness to predators or in parental investment patterns might be expected to exert different selective pressures on the foraging behaviour of each sex. One such species is the guppy (*Poecilia reticulata*). This fish exhibits strong sexual dimorphism, females attaining a larger size than males. They are fertilized internally, and give birth to litters of live young. After they mature (at approximately two months of age), they give birth year-round with a gestation period of 23-30 days. Males mature at approximately the same age as females, but their growth slows markedly at this time or stops altogether (Liley & Seghers 1975, Reznick 1983). The males are brightly coloured and compete for access to females. The species is highly promiscuous, with males neither defending territories nor providing parental care (Baerends et al. 1955).

The significance of energy to the fecundity of female guppies has been well documented (Hester 1964, Dahlgren 1980, Dussault & Kramer 1981, Reznick 1983). Because litter size is constrained by the size of the female (Reznick 1982, 1983), increased energy intake can increase fecundity by allowing the female to grow to a larger size. Furthermore, energy can also affect litter size directly: females on reduced diets may resorb oocytes to compensate for starvation stress (Hester 1964).

The relationship between food and fitness for male guppies is more complicated. Males obtain carotenoid pigments through their diets (Endler 1983). These pigments, which produce yellow, orange, and red colouration, increase their attractiveness to females (Endler 1983, Kodric-Brown 1985, Houde 1987). Thus, if aspects of foraging ability signalled by these colours have a heritable component, females that choose males on this basis may produce offspring of both sexes bearing the male's "good genes" (Endler 1980, Kodric-Brown 1985).

One potential connection between energy and male fitness concerns male display rate. Working with aquarium strains, Farr (1980) and Bischoff et al. (1985) demonstrated that male guppies can increase their access to females by more vigorous and frequent courtship (sigmoid) displays. (Sigmoid displays involve the male making an S-shape with the body, while raising the dorsal fin and spreading the caudal fin.) Presumably, males that obtain more food energy are able to display more vigorously than less well fed males.

Considering these sex differences in life history, we compare growth rates of male and female guppies fed various diets, and we examine the influence of diet level upon male courtship success. Combined with existing information concerning female reproductive output, our aim is to present a composite view of the value of food to each sex from a life history perspective, and examine the implications of this relationship for sexual selection and sex differences in foraging decisions.

METHODS

Experiment 1: Growth

This experiment examined how the growth rates of juvenile guppies are affected by different energetic diet levels. We used a food which varied in caloric quality but not gross bulk, so that the same amount could be fed to all guppies regardless of energetic content.

The food consisted of beef liver and non-nutritive bulk (alpha cellulose). Raw beef liver was ground to a paste-like consistency in a blender and strained through cheese cloth to remove fibrous material. Cellulose powder was converted to a paste of similar consistency by adding 4.7 ml of water per gram of cellulose. Five different diet levels (20, 40, 60, 80, and 100 percent liver) were created using different volumetric combinations of the liver and cellulose pastes.

The food thus prepared was freeze-dried, then crumbled and seived to produce two categories of even-sized particles that floated without breaking-up. The small particles, which could be consumed easily by young guppies, were between 0.59 and 0.85 mm in diameter; the larger particles were between 0.85 and 1.00 mm in diameter.

We used guppies from a stock obtained about 10 years ago from a lowland section of the Guayamare river in Trinidad. Newborn young were obtained from isolated females and reared on a diet of live brine shrimp nauplii (*Artemia* sp.) and ground NutraFin (TM) flakes. When they were between 0.02 and 0.04 g in body mass (2 - 3 weeks of age), individuals were placed in isolation in one half of a 20-l aquarium and randomly assigned to one of the experimental diets. All tanks were maintained on a 12 h photoperiod at 25° C and pH 7.

Each fish was fed twice per day and maintained on this diet for a minimum period of 10 weeks. They received a ration equal to 10% of their body weight per day using combinations of the two particle sizes. This provided slightly more food than each guppy could consume, so excess food was removed daily, prior to the first feeding of the day.

The length and weight of each fish was measured every 2 weeks. The fish were not anaesthetized and were weighed on moist paper towel on an electronic Mettler balance. The amount of food they received subsequently was adjusted to their new weight unless a fish lost weight, in which case its diet was maintained at the previous level. Fish that died during this experiment were replaced with new individuals between 0.02 and 0.04 g in body mass.

Data were used only for fish that grew on each diet for a minimum of 10 weeks; some were maintained as long as 34 weeks. Twelve fish that died or progressively lost weight during the initial 10 week period were excluded from the analysis. Thus, the growth rate for each fish was described by the line of best fit through the measured weights. In no case did growth appear asymptotic.

Experiment 2: Mate Choice

This experiment determined how different amounts of energy available for metabolic activities influence the ability of male guppies to display to and attract females. Three groups of mature males were provided three different diet levels and then competed for females. By rotating these males through all diet levels, we could compare their courtship success at the different diet levels. Therefore, variation between males in attractiveness within diet levels was attributable to all male characteristics (except diet) that contribute to mate choice, and variation among diet levels was due only to differences in available energy.

Ten mature male (average length 19.78 mm ± 1.53 SD) and nine mature female guppies (34 mm ± 14 SD) were removed from a common holding tank and separated 6 weeks prior to the start of the experiment. They received a 12 h photoperiod and were kept at 25^{o} C. The females were maintained together in a 100-l aquarium, while each male was maintained in isolation in one half of a 20-l aquarium. Each male was individually photographed on both sides. From enlarged photographs, the number of colour spots on each male was recorded and the areas of these spots calculated from sketches with a computer digitizer (Apple II with Graphics Tablet). Nearly all carotenoid spots were orange; occasional yellow and pink spots were combined with orange for analysis. Males were assigned randomly to one of three groups; one group contained 4 individuals, the other groups contained 3 individuals each. Each group was maintained on one of three different caloric diets: 0.18, 0.36 or 0.72 mg of onion fly eggs (*Delia antigua*) per individual per day, provided over two feedings per day. All individuals were capable of consuming all the food at every diet level.

After the males had been maintained on their diets for 7 days, we measured their ability to attract females. (Seven days was chosen so as to avoid the effect of diet level on growth, which would confound the interpretation of our results). The males were transferred to an aquarium divided into ten equal-sized peripheral chambers and one central chamber (Fig. 6.1). The bottom and sides of the aquarium, and the partitions between peripheral chambers were opaque (sand-coloured). Each peripheral chamber was separated from the central chamber

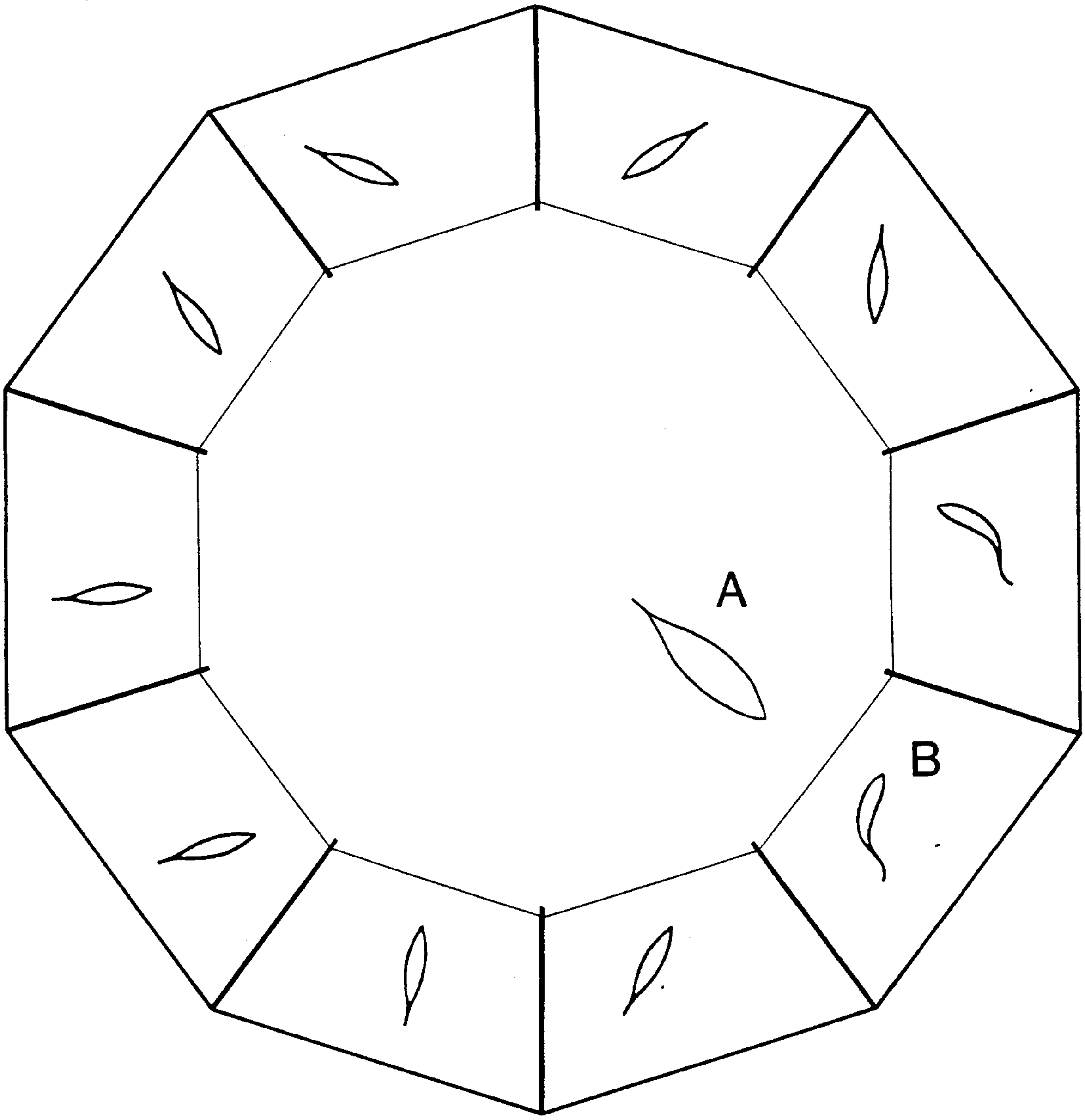

Figure 6.1. Overhead view of apparatus used for measuring mate choice by female guppies. A single female was placed in the center chamber (A) and each male was randomly placed in one of the 10 peripheral chambers (B) separated from her by a clear partition. The entire apparatus was covered by a wire and paper cone (not shown) and the behaviour of the guppies was recorded with a video camera.

by a transparent plexiglas partition.

Each of the ten male guppies was randomly assigned to one of these chambers. The aquarium was covered by an opaque white cone made of paper on a wire support and illuminated by three 150 watt flood lights located equidistant, 30 cm from the cone. This arrangement generated a diffuse light (1300 lux) with no shadows within the apparatus. A video camera mounted 150 cm directly above the chamber recorded the behaviour of all fish simultaneously.

To examine the males' relative ability to attract a female, a single female guppy was randomly selected and placed in the center chamber. The males were able to see the female, and since the partitions were not water tight, olfaction was also possible. As the males courted her, the female swam by each chamber. We recorded the number of times the female 'visited' each male's partition, as well as the total amount of time she spent with each male. The female was considered to have visited a male when she stopped and faced him directly in front of his partition, usually touching the plexiglas. Females were tested sequentially for 20 min each, with 9 used in two trials, and 8 in the third. Four criteria were used to measure each male's ability to attract females: the average number of visits received, the average duration of time the females spent with that male, and the male's average rank based on the relative number of visits or the relative total duration of visits per female. From these experiments we also recorded the number and duration of the males' sigmoid displays. We combined this information with the females' behaviour to determine the average number of sigmoid displays per visit and the average display duration per visit.

After testing, all males were returned to their holding tanks and fed NutraFin (TM) flakes *ad lib* for 7 days after testing (to prevent any influence from previous diet levels in subsequent trials). At the end of that time, each group of males was placed on the next highest diet level, with that group previously on the highest diet level rotated to the lowest one. They were maintained on their new controlled diets for 7 days, after which female preference was examined as described above. This entire sequence was conducted three times, such that each male was tested at each of the 3 diets.

Data from all three rotations were combined to determine the influence of diet level and morphological characters of the males on their ability to attract females. Male courtship and female choice data were log-transformed to compensate for skewness.

RESULTS

Experiment 1: Growth

The growth rates of each fish could be described by a straight line, fitted by least squares. The average proportion of variation explained (r^2) was 0.767 (SD = 0.198) for the male data and 0.891 (SD = 0.119) for the female data. Fish could not be sexed prior to being used in this experiment and this resulted in an unequal number of males and females (23 males and 11 females). Due to the low number of females, none were tested at the 60% diet level and only one was tested at the 20% diet level.

The growth rates of both sexes varied significantly among diet levels (regression analysis, $F_{4,18} = 3.522$, $p = 0.027$ for the males; $F_{3,7} = 4.517$, $p = 0.046$ for the females). At every diet level females grew more rapidly than males (Fig. 6.2), and their growth rates increased more than did the males' as the diet level increased (comparison of slopes and intercepts simultaneously, $F_{2,30} = 9.762$, p =

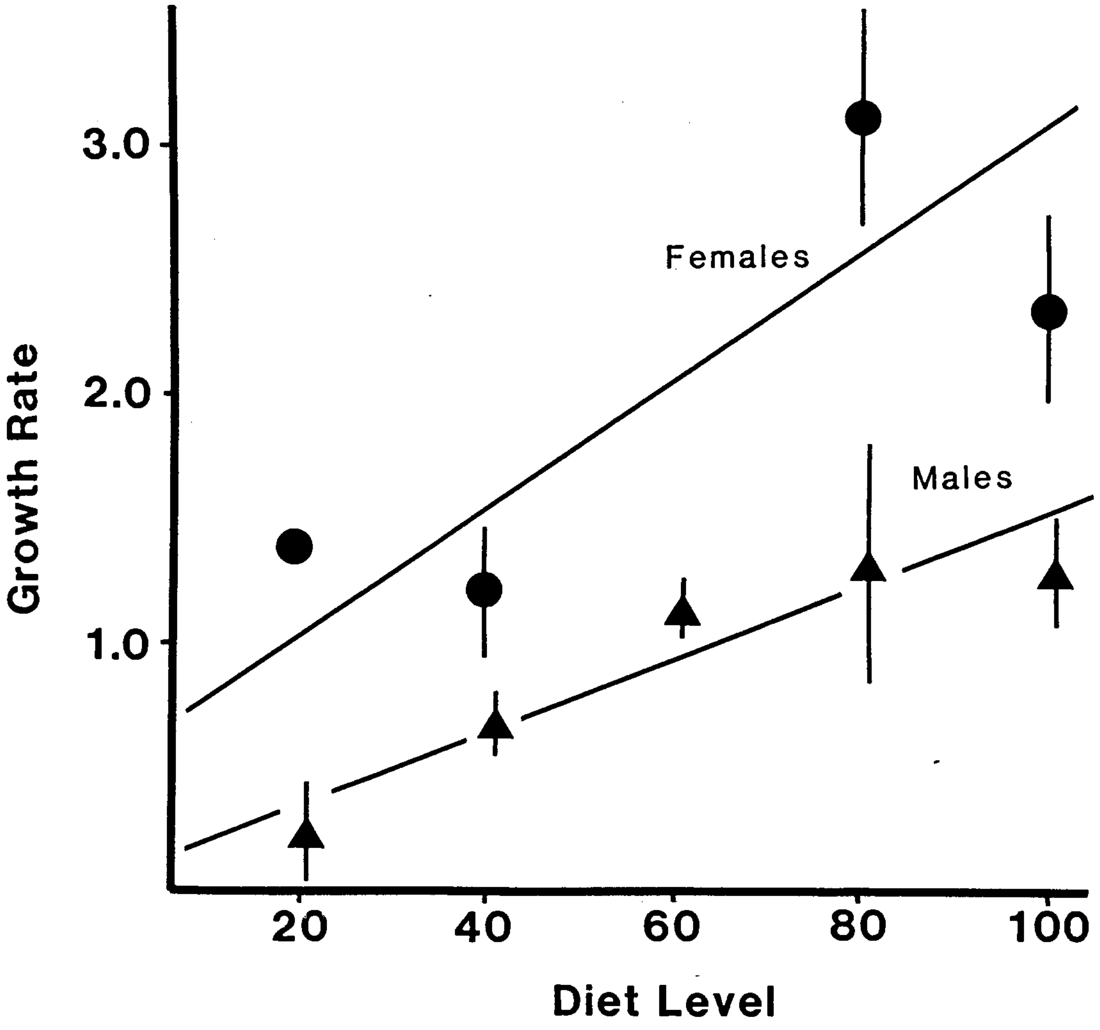

Figure 6.2. Growth rates of male (triangles) and female guppies (circles) placed on the five different diets. The growth rate was the slope of the line of best fit to the bi-weekly weights (mg) of individual fish. The diet levels correspond to percent liver in the food. Bars indicate one standard error. The lines were fitted by least squares method.

0.00054).

At the 100% diet level the growth rates of the females appeared to decline, though not significantly. This may suggest that although this diet provided more energy and protein, liver was suboptimal when presented in the absence of cellulose. In the wild, guppy's diets include algae and other plant material (Dussault & Kramer 1981). Although guppies are not known to be capable of digesting cellulose, its presence in the diet may improve assimilation efficiency, thus accounting for the observed result. The male growth rates were not significantly different at the top 3 diet levels (one-way ANOVA, $F_{2,12} = 0.322$, $p = 0.744$), suggesting that their growth was no longer constrained by available energy.

Males and females appeared to reach sexual maturity at every diet level, although males at the 20% diet level grew very little during this experiment. These males also differed from males at higher diet levels by failing to develop the substantial coloration typical of a mature male.

Experiment 2: Mate Choice

The behaviour of the females in the apparatus changed with time during an experiment. Initially, they appeared to sample the males as they swam past them in broad circles, but they did not visit any particular male. They then appeared to engage in active choice by visiting (as defined above) various males. Male diet level did not influence female choice as measured by our four criteria (Table 6.1). Three experiments in which the female spent less than 10% of her time (2 min) visiting males were omitted from the analyses.

Two-way ANOVA revealed significant differences among males in both display number ($F_{9,200} = 9.207$, $p < 0.001$) and duration ($F_{9,200} = 6.955$, $p < 0.001$)

Table 6.1 Female mate choice and courtship by male guppies fed at three different diet levels. The experiment was performed in 3 stages, with 4 males at one diet level and 3 males each at the other 2 diet levels. Due to the exclusion of 3 trials from the analysis (see text), 8 females were tested at 2 stages and 7 females at the third. The sample size for the per visit data was further reduced as males which received no visits from a specific female were removed from the analysis. All tests of significance were performed with one-way ANOVA.

	MALE DIET			
	Low (n = 76)	Medium (n = 77)	High (n = 77)	p
MALE COURTSHIP				
No. displays	4.2	3.9	4.4	0.995
No. displays/visit*	0.4	0.6	0.6	0.676
Display duration (sec)	11.3	7.6	9.2	0.747
Display duration/visit*	1.4	1.1	1.2	0.789
FEMALE CHOICE				
No. visits	9.0	8.2	8.3	0.989
Male rank	5.0	5.2	4.9	0.754
Mean visit duration (sec)	67.6	53.5	67.5	0.953
Male rank	5.2	5.9	5.3	0.290

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* For low, medium, and high diet, n = 73, 76, and 76 respectively

but no significant influence of diet level on either measure (Table 6.1). There was a significant interaction between diet level and males for both measures of male behaviour ($F_{18,200} = 5.571$, $p < 0.001$ and $F_{18,200} = 5.343$, $p < 0.001$ for number and duration respectively). This was a result of 4 males increasing their displays with increasing diet levels while others exhibited no influence of diet level. It may be possible that these 4 males appeared competitively inferior (e.g., less carotenoid and irridescent coloration). To compensate for this, they may have relied on more intense sigmoid displays to attract females, and hence their display rate was more sensitive to diet level manipulation. However, these males did not differ significantly in body length, nor in area of black, orange or blue pigmentation (one-way ANOVA's, all $p > 0.25$), indicating no obvious morphological differences which may account for their different response to varying levels of food.

It is possible that any effect of diet level on female choice might only be evident after the males had depleted their energy reserves by engaging in a large number of displays. When the three trials were split into the first, second and third hours, with three females per hour, the number and duration of male sigmoid displays decreased significantly as time progressed (Table 6.2). However, there was no significant interaction between diet level and time on the number ($F_{18,200}$ = 0.456, $p = 0.768$) or duration of visits ($F_{18,200} = 0.797$, $p = 0.528$), or on male rank based on number of visits ($F_{18,200} = 1.309$, $p = 0.268$) or duration of visits ($F_{18,200} = 1.464$, $p = 0.214$). We also tested for a time effect by examining female choice in the last third of the experiment. Again, diet level had no influence on either the number ($F_{2,40} = 0.112$, $p = 0.895$) or duration of displays ($F_{2,40} = 0.009$, $p = 0.992$), or on the number ($F_{2,40} = 0.356$, $p = 0.702$) and duration of female visits ($F_{2,40} = 0.431$, $p = 0.652$).

Table 6.2. The effect of time in the trial on courtship by male guppies. Two of the females excluded from analysis were from the first hour of the trial and the third excluded female was from the third hour. Note that one rotation used only 8 females so that a total of 7 females were examined in the first hour, 9 in the second and 7 in the third. The sample size for the per visit data was further reduced as males which received no visits were removed from the analysis. Tests of significance were performed with one-way ANOVAs.

	TIME				
Behaviour	Hour 1	Hour 2	Hour 3	F	p
No. displays*	4.9	4.4	3.1	3.557	0.030
No. displays/visit**	0.7	0.5	0.3	5.277	0.006
Display dur. (sec)*	12.1	9.9	5.8	3.496	0.032
Display dur./visit**	1.6	1.2	0.7	4.585	0.011

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* For Hour 1, 2, and 3, n = 70, 90, and 70 respectively.

** For Hour 1, 2, and 3, n = 68, 88, and 69 respectively.

DISCUSSION

Our results demonstrating faster growth rates by females than males on every diet level (Fig. 6.2) are consistent with the direction of size dimorphism of adults, and previous demonstrations of a close relationship between energy and fecundity in females (Hester 1964, Dahlgren 1980, Reznick 1983). A higher net benefit of food to adult females was also suggested by previous experiments demonstrating that females require less food to be induced to risk exposure to a predator than do males (Abrahams & Dill, submitted). Other components of fitness, such as the ability to outgrow small predators (Liley & Seghers 1975, Reznick & Endler 1982) and age at maturity, should be affected similarly by diet level in juveniles of both sexes.

Male poeciliids normally stop growing when they reach maturity, or their growth slows markedly (Constanz 1984). The lack of this pattern and the slow growth rate in our experiment suggests that the diet was not complete. However, our conclusions concern relative differences between the sexes. Given determinate growth for male guppies, a lack of direct male-male competition in the wild (Endler 1983, Luyten & Liley 1985), and the importance of female choice (Houde 1987), our second experiment sought to elucidate what we considered the most likely value of food energy to adult males, namely courtship success. Although female guppies chose specific males, these males were not chosen on the basis of diet level (Tables 6.1 and 6.2). Abrahams & Dill (submitted) demonstrated that this same variation in diet level significantly influences the willingness of males to obtain food when simultaneously exposed to a predator. Furthermore, this diet level variation significantly affects how males resolve trade-offs between foraging and courtship opportunities (Abrahams, submitted). Therefore, although the diet levels used in Experiment 2 significantly alter other forms of male behaviour, this manipulation apparently has no influence on their ability to attract females over a three hour period.

Toft & Shea (1983) have raised concerns that biologists often accept null hypotheses without consideration of the power of their statistical design (i.e., the probability of failing to reject a false null hypothesis, or committing a Type II error). However, as Rotenberry & Wiens (1985) note, there is no established methodology for determining one of the parameters necessary to calculate power, namely the magnitude of the expected effect (ES). As noted above, the diet levels used in this experiment were previously found to alter significantly other aspects of male behaviour (Abrahams submitted, Abrahams & Dill submitted); thus our *a priori* ES was substantial. If these diet levels actually generated 60% of the variation in male reproductive success, the experimental design would have a 0.75 probability of correctly rejecting the null hypothesis when $\alpha = 0.05$ (Cohen 1969). At this sample size, the probability of making a type II error is very sensitive to changes in ES. However, as Rotenberry & Wiens (1985) note, if this manipulation could generate only a small ES, it would be of little biological relevance anyway (i.e., there would be little biological difference between the null and alternate hypotheses).

Previous experiments have demonstrated that female guppies choose males based upon the amount of male carotenoid coloration (Endler 1983, Kodric-Brown 1985, Houde 1987) and the size of the male's tail (at least in aquarium strains, Bischoff et al. 1985). Endler (1980) and Kodric-Brown & Brown (1984) have suggested that females choose males on the basis of carotenoid coloration because males can obtain this colour only through their diet. Thus, it may be an honest signal of foraging ability.

But why do males engage in the apparently energetically demanding sigmoid display? Farr (1980) and Bischoff et al. (1985) have demonstrated that female mate choice can be influenced by sigmoid displays, suggesting that it may be an additional cue to the quality of the male. Presumably, a male that has had poor foraging success will be in poor condition and consequently unable to provide an intense sigmoid display. Our experiments attempted to alter male energetic state through diet level manipulations. That they did not influence courtship display suggests that males may be able to bluff this signal, at least over a three hour period. A fundamental reason why honest signalling might be an evolutionarily stable strategy is that males are selected to maximize *lifetime* reproductive success. Thus, males in any sexually selected species should not always court maximally because of the risks of depleting their energy reserves or exposing themselves to predation. The greater a male's overall quality, the more he can afford to court intensely, and the greater the benefit to a female of mating with him. The fact that male guppies did reduce the frequency and duration of sigmoid displays over the course of each trial independently of diet level suggests that the males' assessments of probability of mating success decreased with time. We are unable, however, to account for the lack of diet effect on the degree of reduction, unless energetic costs are not the main price of display. Predation risk may be important to males, and independent of the four-fold variation in diet level (Endler 1987).

In summary, it appears that energy is very important to the reproductive success of female guppies. Males grow more rapidly when they are able to obtain more food as juveniles, but they are less sensitive to variations in diet level than are females, and it is unclear whether this increased size provides a mating advantage. Furthermore, a four-fold variation in available energy for metabolic activities does not influence male attractiveness to females. Thus, sex differences in life histories mean that energy has different value to males and females. It appears that males are willing to take fewer risks than females to obtain extra energy (Abrahams & Dill, submitted) because the marginal increment to reproductive success, and thus fitness, is lower.

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LITERATURE CITED

Abrahams, M.V. (submitted). The trade-off between foraging and courting in male guppies (*Poecilia reticulata*).

Abrahams, M.V. & L.M. Dill (submitted). A determination of the energetic equivalence of the risk of predation.

Baerends, G.P., R. Brouwer & H.Tj. Waterbolk. 1955. Ethological studies on *Lebistes reticulatus* (Peters). I. An analysis of the male courtship patterns. Behaviour 8: 249-334

Bischoff, R.J., J.L. Gould & D.J. Rubenstein. 1985. Tail size and female choice in the guppy. Behav. Ecol. Sociobiol. 17: 253-255

Cohen, J. 1969. Statistical power analysis for the behavioural sciences. Academic Press, New York.

Constanz, G.D. 1984. Sperm competition in Poeciliid fishes. In: Sperm competition and the evolution of animal mating systems (ed. R.L. Smith). Academic Press, Orlando Fl. pp 465-485

Dahlgren, B.T. 1980. The effects of three different dietary protein levels on the fecundity in the guppy, *Poecilia reticulata* (Peters). J. Fish Biol. 16: 83-97

Dussault, G.V. & D.L. Kramer. 1981. Food and feeding behaviour of the guppy, *Poecilia reticulata* (Pisces: Poeciliidae). Can. J. Zool. 59: 684-701

Endler, J.A. 1980. Natural selection on color patterns in *Poecilia reticulata*. Evolution 34: 76-91

Endler, J.A. 1983. Natural and sexual selection on color patterns in Poeciliid fishes. Env. Biol. Fishes 9: 173-190

Endler, J.A. (1987). Predation, light intensity and courtship behaviour in *Poecilia reticulata* (Pisces: Poeciliidae). Anim. Behav. 35: 1376-1385

Farr, J.A. 1980. Social behaviour patterns as determinants of reproductive success in the guppy, *Poecilia reticulata* Peters (Pisces: Poeciliidae): an experimental study on the effects of intermale competition, female choice, and sexual selection. Behaviour 74: 38-91

Hester, F.J. 1964. Effects of food supply on fecundity in the female guppy, *Lebistes reticulatus* (Peters). J. Fish. Res. Board Can. 21: 757-764

Houde, A.E. 1987. Mate choice based upon naturally occurring color pattern variation in a guppy population. Evolution 41: 1-10

Kodric-Brown, A. 1985. Female preference and sexual selection for male coloration in the guppy (*Poecilia reticulata*). Behav. Ecol. Sociobiol. 17: 199-205

Kodric-Brown, A. & J.H. Brown. 1984. Truth in advertising: the kinds of traits favoured by sexual selection. Am. Nat. 124: 309-323

Liley, N.R. & B.H. Seghers. 1975. Factors affecting the morphology and behaviour of guppies in Trinidad. In: Function and evolution in behaviour (eds. G. Baerends, C. Beer and A. Manning). Clarendon Press, Oxford. pp. 92-118

Luyten, P.H. & N.R. Liley. 1985. Geographic variation in the sexual behaviour of the guppy, *Poecilia reticulata* (Peters). Behaviour 95: 164-197

Reznick, D. 1982. The impact of predation on life history evolution in Trinidadian guppies: genetic basis of observed life history patterns. Evolution 36: 1236-1250

Reznick, D. 1983. The structure of guppy life histories: the tradeoff between growth and reproduction. Ecology 64: 862-873

Reznick, D. & J.A. Endler. 1982. The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*). Evolution 36: 160-177

Rotenberry, J.T. & J.A. Wiens. 1985. Statistical power analysis and community wide patterns. Am. Nat. 125: 164-168

Toft, C.A. & P.J. Shea. 1983. Detecting community-wide patterns: estimating power strengthens statistical inference. Am. Nat. 122: 618-625

CHAPTER VII

GENERAL DISCUSSION

The experiments reported in this thesis demonstrate how a theory of spatial distribution (the ideal free distribution) can be employed to quantify how animals make decisions involving trade-offs. The second chapter of this thesis reviewed previous experiments which tested the assumptions and predictions of ideal free distribution (IFD) theory, and demonstrated theoretically how a simple perceptual constraint could cause the characteristic deviations from IFD theory observed in the literature.

The third chapter described an experimental system which allowed a group of ten male or ten female guppies to conform to the assumptions and predictions of IFD theory. Correlation analysis of the ability of past and current information to explain the distribution of fish with time revealed differences between male and female guppies in this regard. Female guppies appeared to make greater use of past information, and were able to conform more closely to the predicted IFD, suggesting that they were better adapted than males to feed on patchily distributed food.

The fourth chapter of the thesis used IFD theory to quantify how guppies trade-off risk of predation against energy when making decisions about where to forage. By quantifying risk of predation, this experiment demonstrated that guppies responded to risk differently when the absolute amount of food varied, i.e. as more food was made available at both the safe and risky feeders, their response to the predator changed. The form and magnitude of this effect depended on the sex of the group being tested. Foraging decisions of the female group were least affected by the predator at both the lowest and the highest diet levels. However, the males exhibited the reverse response, being most affected by the predator at the extreme low and high diet levels (at the highest diet levels males completely avoided the risky feeder). Not only did the two sexes exhibit different responses to diet level manipulations, but the males appeared to be more greatly influenced by the presence of a predator, as fewer males than females used the risky feeder.

Chapter V examined the behaviour of males confronted with the trade-off between access to food and courtship opportunities. The results of this experiment differed from the previous trade-off experiment in that the decisions of the male guppies changed with time: initially the males fed and then they courted the female. They switched from feeding to courting earlier as more food was available, and more males courted large females than courted small ones. The results of this experiment suggest that behavioural decisions made by male guppies are state dependent, i.e., the probability of a male choosing foraging over courtship behaviour depends upon the potential benefits to be obtained, which in turn depends upon the male's energetic state.

The final chapter of this thesis examined the relationship between energy and fitness for both male and female guppies. Based on the natural history of guppies, I assumed that the relation between energy and fitness for female guppies would be determined primarily by their ability to convert food to growth. However, the relationship might be more complicated for males: their fitness depends not only upon their ability to convert energy to growth, but also upon their ability to find and successfully court females. The results of these experiments demonstrated that females grew more rapidly than males at every diet level, and that additional energy intake did not influence male courtship success. Thus, I concluded that additional energy is of greater importance to female fitness than to male fitness.

The significance of this result is that it provides an explanation for the observed behavioural differences between the sexes (Chapts. III and IV). If animals make foraging decisions with no associated costs, the precise form of the relation between food and fitness should not influence their behaviour (i.e., all animals should attempt to obtain energy at the highest rate). However, when costs are involved, animals should pursue strategies which maximize their net benefit, a result which depends upon the relation between food and fitness. For example, consider a situation in which an animal can use a patch which contains 5 food units at a cost of 3 fitness units. An animal should use that patch only if it can obtain at least 3 fitness units from the 5 food units. Extending this analogy, it should be apparent that animals who receive greater fitness benefits from a resource should be prepared to incur greater costs to obtain it.

All the foraging experiments in this thesis required individuals to pay a cost for acquiring food, either by obtaining information (Chapter III), risking exposure to a predator (Chapter IV), or foregoing courtship opportunities (Chapter V). In Chapters III and IV, females were willing to incur greater costs than males, a result consistent with the different relationship between food and fitness in the two sexes. However, the result of Chapter V demonstrates that selected life-history relationships are not sufficient to completely understand decisions involving trade-offs. In this experiment, the behaviour of the males changed with time, suggesting that the costs or benefits associated with access to the food or female also changed with time, and probably with the male's state. Thus, a complete understanding of trade-off decisions must also consider dynamics.

The results of this thesis have implications for both foraging theory and community ecology. Foraging theory attempts to understand the decision rules of foraging animals (Krebs et al. 1983), yet most models describing the foraging behaviour of animals consider energy as the only variable. However, a growing body of literature has demonstrated that other factors, notably the risk of predation, can significantly affect foraging decisions (see Lima and Dill, submitted, for a review). Gilliam (1982) and Werner & Gilliam (1984) have predicted theoretically how animals should respond to risk of predation. However, there has been little empirical research to measure the exact influence that trade-offs exert on foraging decisions (but see Werner et al. 1983, Gilliam & Fraser, in press). The results of this thesis have helped to fill that void. My results confirm theoretical predictions that knowledge of the life history of an animal is important for understanding how it should trade off risk of predation against energy intake. However, by empirically examining courtship trade-offs, it becomes apparent that foraging theory must incorporate the ideas of decision theory (as described by McFarland 1977) to understand how animals make other sorts of trade-offs.

It is becoming increasingly apparent that understanding individual behaviour is necessary to understand community ecology (Dill 1987). Indeed, the behavioural interactions between predators and their prey (the risk of predation) may sometimes be of greater ecological importance than the number of prey actually consumed (the act of predation; Zaret 1980). Mittelbach & Chesson (1987) have suggested that an important indirect effect of predation is that risk of predation reduces intraspecific competition by forcing the more vulnerable age groups to stay in refuges. However, this can intensify interspecific competition if vulnerable age classes from different species use a common refuge. Thus, species that apparently do not compete as adults can suffer from intense interspecific competition as juveniles. Sih (1987) has suggested that risk of predation may be a sufficiently powerful ecological force as to explain prey life-styles often attributed to competition, and Power (1987) has provided evidence that the community structuring effects of predators extend beyond adjacent trophic levels. Clearly, the risk of predation is of major ecological importance, and other trade-offs are likely to be as well. Increasing our understanding of how animals make decisions involving trade-offs will increase our understanding of the determinants of community structure.

LITERATURE CITED

Dill, L.M. 1987. Animal decision making and its ecological consequences: the future of aquatic ecology and behaviour. Can. J. Zool. 65: 803-811

Gilliam, J.F. 1982. Habitat use and competitive bottlenecks in size-structured fish populations. Ph.D. thesis, Michigan State University, East Lansing

Gilliam, J.F. & D.F. Fraser. (in press). Habitat selection under predation hazard: test of a model with foraging minnows. Ecology

Krebs, J.R., D.W. Stephens & W.J. Sutherland. 1983. Perspectives in optimal foraging. In: Perspectives in Ornithology (eds., A.H.Brush & G.A. Clark, Jr.), Cambridge University Press, New York, pp. 165-216

Lima, S.L. & L.M. Dill (submitted). Behavioural decisions made under the risk of predation: a review and prospectus. Q.Rev. Biol.

McFarland, D.J. 1977. Decision making in animals. Nature 269: 15-21

Mittelbach, G.G. & P.L. Chesson. 1987. Predation risk: indirect effects on fish populations. In: Predation: Direct and Indirect Impacts on Aquatic Communities (eds., W.C. Kerfoot & A. Sih), University Press of New England, Hanover, NH, pp. 315-332

Power, M.E. 1987. Predator avoidance by grazing fishes in temperate and tropical streams: the importance of stream depth and prey size. In: Predation: Direct and Indirect Impacts on Aquatic Communities (eds., W.C. Kerfoot & A. Sih), University Press of New England, Hanover, NH, pp. 333-351

Sih, A. 1987. Predators and prey lifestyles: an evolutionary and ecological overview. In: Predation: Direct and Indirect Impacts on Aquatic Communities (eds., W.C. Kerfoot & A. Sih), University Press of New England, Hanover, NH, pp. 203-224

Werner, E.E. & J.F. Gilliam 1984. The ontogenetic niche and species interactions in size-structured populations. Ann. Rev. Ecol. Syst. 15: 393-425

Werner, E.E., J.F. Gilliam, D.J. Hall & G.G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology 64: 1540-1548

Zaret, T.M. 1980. Predation and freshwater communities. Yale University Press, New Haven, CT