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Foraging Guppies and the Ideal Free Distribution: The Influence of Information on Patch Choice

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With 5 figures

Abstract

10 male and 10 female guppies were each examined foraging for food at 2 separate feeders. The feeders provided food over a wide area so that individuals had equal access to the food. As the proportion of food at a feeder was altered, the proportion of fish using that feeder changed to match the availability of food. Thus, both groups of fish conformed to the predictions of the ideal free distribution (IFD) theory.

However, the behaviour of the two groups differed. During these experiments, males continued to shuttle between these feeders whereas females tended to remain at a feeder. Also, the female group conformed less well to an IFD on the first trial of each day but conformed more closely to an IFD in successive exposures to the same food distribution. The male group exhibited no improvement with increasing experience. For both groups, the relative influence of the previous day's experience on foraging decisions declined with time. However, unlike the male group, the female group relied on experience for their initial foraging decisions. It is possible that sampling by males provides the additional benefit of increasing their probability of encountering receptive females. This may account for the difference in information use by the male and female group.

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 that describe the availability of food. Although this assumption is unlikely to be true, the question of how animals obtain information to make decisions was not formally addressed until KREBS et al. (1978) examined models of optimal acquisition of information in great tits (*Parus major*). Since that time, a variety of models have suggested 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 which, as with other commodities, has 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. There are two kinds of costs: First, when an animal is sampling it reduces the rate at which it can forage. Second 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 that provide food at a constant rate, such that each animal maximizes its energy-intake rate. The IFD predicts 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 that 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 that has a stable distribution of food, increasing use of past information increases conformity with an IFD. In this situation, animals that are capable of using more past information will be able to achieve a distribution that 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, and exhibit indeterminate growth, while males are small, brightly coloured (and likely conspicuous; ENDLER 1978), and exhibit determinate growth (REZNICK 1983). I used guppies from a stock obtained about 10 years ago from a lowland section of the Guayamare river in Trinidad. In these experiments fish were tested in groups of 10 similar-sized males (0.109 g ± 0.017 SD) or 10

similar-sized females (0.182 g ± 0.027 SD). Similar-sized individuals were used to prevent dominance hierarchies developing within the apparatus (BROWNE 1981). This ensured that individuals within a group would have similar competitive abilities. The same two groups of fish were used in all experiments, any that died (3 males and 1 female) were 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 was 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. 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 that 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, (1) they are small enough for guppies to easily consume and, (2) 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 determined in preliminary experiments).
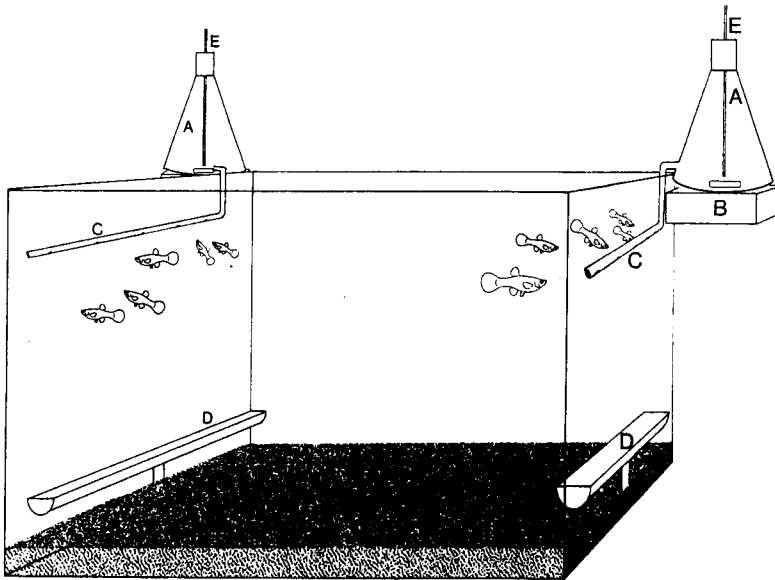

Fig. 1:   Apparatus for examining IFD for male and female guppies. A mixture of onion fly and water is held in 2-l Erlenmeyer flasks (A) at the ends of the aquarium and kept in suspension by stir plates (B). The onion-fly eggs and water drain from the flask and into feeder bars (C), which spread the 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

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.

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 s 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. 20 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 because of 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 h 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 test if 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 4 min 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 h of observation of both sexes during the IFD experiments, no exclusion from the
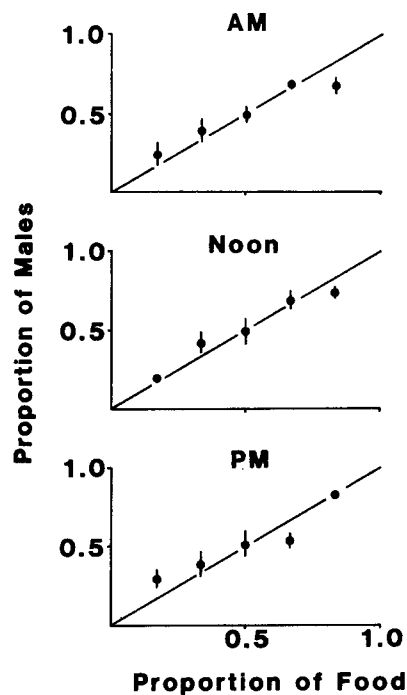
Fig. 2: Proportion of male guppies at the left-hand feeder (designated patch A) versus proportion of food available there. AM, Noon, and PM correspond both to the time of day the experiments were performed, and the experience with that distribution on that day (AM: first exposure, PM: third). Line corresponds to the predicted IFD. Bars: 1 SE; N = 25 for each graph

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. 2) and female (Fig. 3) guppies was strongly affected by the distribution of food (p ≤ 0.001, see Table 1). However, the results of the AM experiments for the males and the AM and Noon experiments for the females had slopes that were significantly different (Table 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

Table 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

Fig. 3: Proportion of female guppies at the left-hand feeder versus proportion of food available there. Format as for Fig. 2; N = 54 for each graph
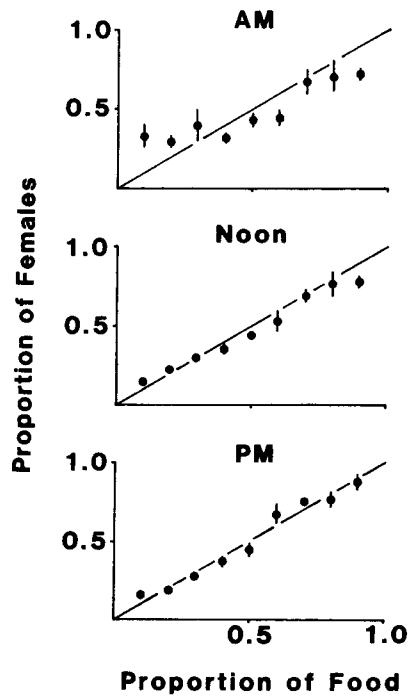
with the least food). The other experiments all resulted in distributions that were not significantly different from that predicted by an IFD (Table 2).

Comparison of the Groups

a. *Behavioural differences.* On average, 2.37 (SD = 1.02) males did not feed during these experiments, whereas an average of 1.89 (SD = 1.32) females did not feed. Examination of focal animals during the above experiments indicated that behavioural differences existed between the two groups which may account for

Table 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

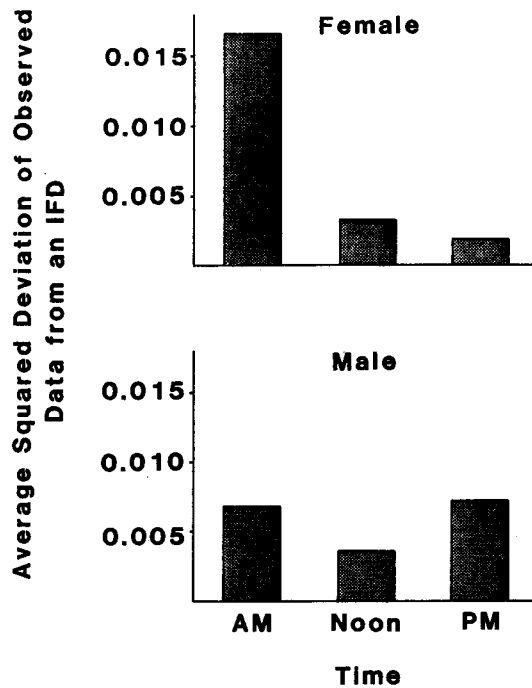| Sex	Time	Regression statistics			Probability	
		Slope	Y-intercept	r^2	Slope = 0	Slope = 1
Male	AM	0.695	0.14	0.571	<.001	.023
	Noon	0.818	0.09	0.653	<.001	.155
	PM	0.733	0.14	0.561	<.001	.058
Female	AM	0.589	0.19	0.507	<.001	<.001
	Noon	0.853	0.04	0.834	<.001	.007
	PM	0.979	0.00	0.878	<.001	.662

Fig. 4: 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

this difference. When food was presented to the male group, they continued to shuttle between patches. Thus, when observations were taken at 30-s intervals, some males were observed travelling between the two feeders and were recorded as not feeding. 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 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. 2 and 3). This effect was quantified by calculating the average sum of squares of the deviations of the observed distribution from the IFD. 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. 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. 4, Table 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 9 consecutive trials (three times a day for three days). The experiment yielded no effect of time of day on

Fig. 5: Ratio of partial correlation coefficients for PD (distribution of guppies on the final exposure of the previous day) and CF (current distribution of food) for the first 15 observations of the AM trial. Upper curve: females, lower: males. See text for details of the calculation
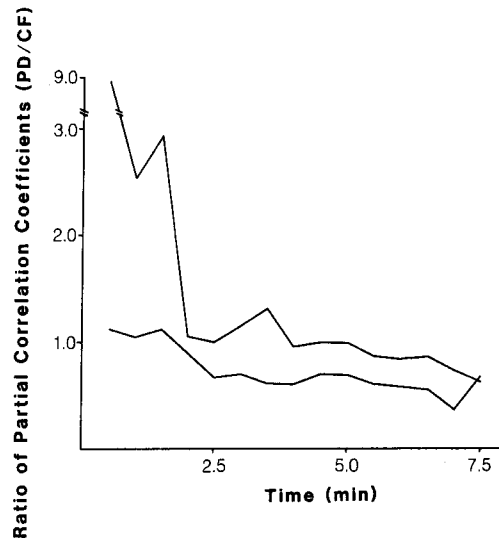
conformity with an IFD (ANOVA; $p = 0.282$). Thus, the improvement observed with time by the female group in their ability to conform to an IFD must have been due to increased experience per se.

The Influence of Information

The linear operator rules that various authors have proposed to describe patch choice suggest that the influence of experience progressively declines with time; the rate of decline is 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, 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, 60 separate partial correlations were calculated. Each calculation measured the partial correlation of either PD or CF with the proportion (arcsin square-root transformed) of male or female guppies at patch A at one time interval. 53 data points were used in each correlation for the female group, and 24 points for the male group (there was no PD on day 1).

This analysis demonstrated that the correlation of PD with the observed distribution of fish declined progressively with time for both groups (Fig. 5). However, the magnitude of this correlation 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 partial 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. 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 was detected 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 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 that 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 for presenting food. 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 instead 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 can perceive discrepancies 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 (e.g., 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 is 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 for making decisions. Thus, the initially 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, the differences observed probably reflect biological differences between the sexes. Guppies are sexually dimorphic 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. Because 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 results of this experiment present a paradox. While males appear to sample more frequently, females have a greater ability to retain information that ultimately allows them to conform more closely to an IFD. This paradox may be explained by differences in the cost of time spent sampling. Both males and females pay an opportunity cost for sampling; they spend time that could otherwise be used for feeding. However, males receive the additional benefit that time spent sampling increases the probability of encountering receptive females. Thus for males, the act of sampling may be of greater benefit to their fitness than the information acquired.

Acknowledgements

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