

Habitat Quality and the Distribution of Fish: Are Fish ‘Ideal Free’?

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Abstract: The purpose of this behavioral ecology laboratory experiment is to test two predictions of the ideal free distribution theory. In this laboratory exercise, students will expose a group of fish to two prey patches that differ in profitability. Students will test the predictions that competitors will distribute themselves such that: 1) the number of individuals per patch is proportional to the fraction of resources in that patch, and 2) the intake per individual is equal across all patches. Students can design their own experiment, set up the equipment, collect the data, and analyze and interpret the results. This project is appropriate for ecology and animal behavior courses as well as for introductory biology courses with a component providing students with experience designing and conducting scientific experiments.

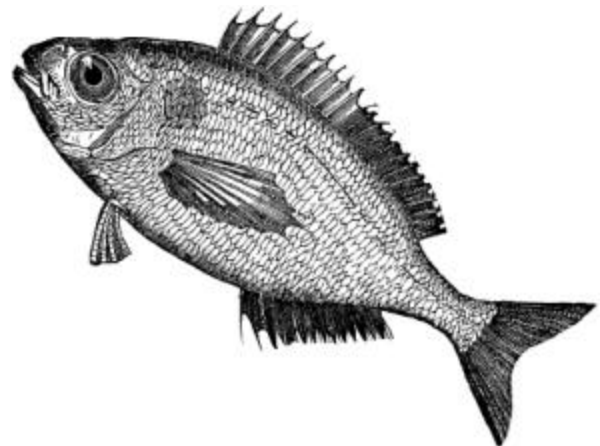
Key words: fish foraging, ideal free distribution theory, patchy resources, habitat quality

Introduction

The ideal free distribution (IFD) theory was developed by Fretwell and Lucas (1970) and Fretwell (1972) in an attempt to describe how animals would distribute themselves within an environment containing patches of varying suitability. The ideal free distribution theory can be applied whenever there is competition over a resource which is patchily distributed (e.g. food or mates) and the following conditions are met: 1) individuals are ‘ideal’ in assessing patch quality (i.e. they have complete information about the availability of resources), 2) individuals are ‘free’ to enter or leave any patch of their choice (there is no resource defense), 3) patch quality declines with increasing competitor density, 4) all individuals select the instantaneously most profitable patch compensating for existing competitors in the patch, and 5) all individuals are of equal competitive ability. If these conditions are met, the IFD theory predicts that competitors will distribute themselves such that: 1) the number of individuals per patch is proportional to the fraction of resources in that patch, and 2) the intake per individual is equal across all patches.

For example, if there is a group of six birds feeding in a field that has seeds distributed in two patches, and one patch has twice as many seeds as the

other patch, how should the birds distribute themselves so that each gets the most food? According to the IFD theory, it would be expected that there would be two birds in the poor patch and four birds in the rich patch. The food intake is predicted to be equal in both the rich and poor patches. A number of studies have tested the ideal free distribution theory in a variety of species and have found that animals tend to distribute themselves as predicted (Milinski 1979; Harper 1982; Power 1984; Godin and Keenleyside 1984; Gillis and Kramer 1987).



This study is designed to test the IFD theory. In this exercise, students will present fish with food distributed into two patches (a rich patch and a poor patch). Students will test the predictions that competitors will distribute themselves such that: 1) the number of individuals per patch is proportional to the fraction of resources in that patch, and 2) the intake per individual is equal across both patches. This exercise enables students to test one of the major theories in animal behavior at a modest expenditure of time and money.

Methods

Experimental Tanks

At least a week before the fish are brought into the lab, set up eight to ten experimental tanks (e.g. 10 gallon fish tanks). Cover the back, sides and bottom of each tank with white paper to prevent fish from viewing each other and to provide a uniform background. 'Divide' experimental tanks into left and right halves by using an erasable grease pencil to draw a line midway down the glass front of the tank, thus giving two halves of the tank that will be considered distinct prey patches. Fill each tank with water and condition the water to remove chlorine (appropriate chemicals for removing chlorine can be purchased from pet stores or from Biological Supply Houses). Heaters will not be required if you chose a fish species that does well at room temperature (see suggestions below). You may also want to set up a large holding tank (for example a 20 gallon tank) to house extra fish that can be used to replace experimental fish that become sick or die.

Foragers

Depending on your resources, and the time of year, a number of different species of fish can be chosen for this experiment. I have conducted this experiment with either goldfish or zebra fish (zebra danios) purchased from local fish stores. Both of these fish are hardy, inexpensive, and can be kept in tanks at room temperature. Alternatively, field collected fish may be used (e.g. sunfish) if you want to coordinate this lab with a field collection lab scheduled earlier in the term. Choose similarly sized fish, and obtain sufficient numbers for replicates. The number of fish needed will depend upon the patch densities chosen (see below). Bring the fish into the lab and allow them several weeks to acclimate to the laboratory.

Fish should be housed in the experimental tanks to allow them to become accustomed to the tanks. A conditioning period of approximately two weeks will allow the fish to become accustomed to the lab and to the people feeding them. During this period, feed fish flake food daily. It depends on the number of fish and how much you are feeding them, but generally, siphon out approximately 15% of the water from the tank and

replace it with conditioned water every 2 or 3 days. During the siphoning process, remove any debris that has accumulated in the tank.

Prey

A number of different food types can be used for this experiment. Suitable prey types for this experiment include commercially purchased goldfish food pellets or field collected prey such as *Daphnia*. Select equally sized individual prey items for experimentation.



Experimental Design and Procedures

The instructor can engage students in a discussion about the experimental design, and the class can determine the exact experimental design to be used. Points students should discuss include: What patch profitability ratio(s) will be tested? What prey type and prey densities will be used? How long will foraging trials be run? What data will be collected?

Students can begin experimental trials once fish are acclimated to the laboratory. Students can choose the patch profitability ratio(s) they wish to test. For example, students could test 1:1, 2:1, 3:1 or 4:1 ratios. Once patch profitability ratio(s) are chosen, students should determine how many fish would be needed. For example, if a 2:1 ratio is tested, groups of three fish per tank can be used. Students should perform eight to ten replicates of each patch profitability ratio that they choose to test. If the class is testing a 2:1 ratio, then twenty-four to thirty fish would be needed to give eight to ten replicates. Students should also decide what prey density will be added to each side of the tank. Prey densities should be chosen such that there is sufficient food to avoid prey depletion. For example, I have conducted this experiment using fifteen pellets for the poor patch, and thirty pellets for the rich patch. Prey densities can be determined by numbers, weight or volume depending on the prey type.

It is important to prevent foragers from becoming satiated during the experimental trials as the ideal free distribution model only applies in cases where the resource in question is actually limiting. To prevent satiation during the feeding trials, students can deprive fish of food for 24 hours before each trial, and limit the length of time of the feeding trials to periods that do not seem to satiate the fish (e.g. five minute feeding periods). As a control, each feeding period can be preceded by a non-feeding period. For example, each trial might consist of a 5-minute non-feeding (control) period followed by a 5-minute feeding period.

At the start of the feeding portion of the trials, students can manually drop prey into the two different sides (patches) of the tank. At the end of each feeding period, fish should be fed to satiation, and excess food should be removed with a net.

Data Collection and Analyses

The instructor can lead students through a discussion of what data should be collected to test the two predictions of the IFD theory. Students should periodically (e.g. every ten seconds) record the number of fish in both the rich and poor patch during both the control and feeding periods. Students should also record the number of prey items consumed on each side of the tank for individual fish. It may not be possible for students to record food intake for every fish in the tank, therefore students may chose to randomly select one 'target fish' from each tank that will be observed throughout the trial. For each 'target fish' students should record the number of prey items consumed on each side of the tank.

Results and Discussion

This experiment provides students with an opportunity to statistically analyze data. I've

conducted this lab in my class after students have been introduced to statistical analyses. The instructor can lead the students through a discussion of what results are expected.

Graphing the data will help the students visualize whether the fish are distributing themselves according to the predictions of the IFD theory. Students can graph the results to examine whether:

- 1) Fish were equally distributed on both sides of the tank during the control period as expected.
- 2) The number of individuals per patch is proportional to the fraction of resources in that patch.

To address these two predications, students can plot the mean (mean \pm SE) number of fish in the less profitable patch (on the y-axis) versus time (on the x-axis). Students can draw lines on the graph that corresponds with the expected number of fish based on IFD theory (see Figure 1). This figure should be the reverse of that plotted for the more profitable patch.

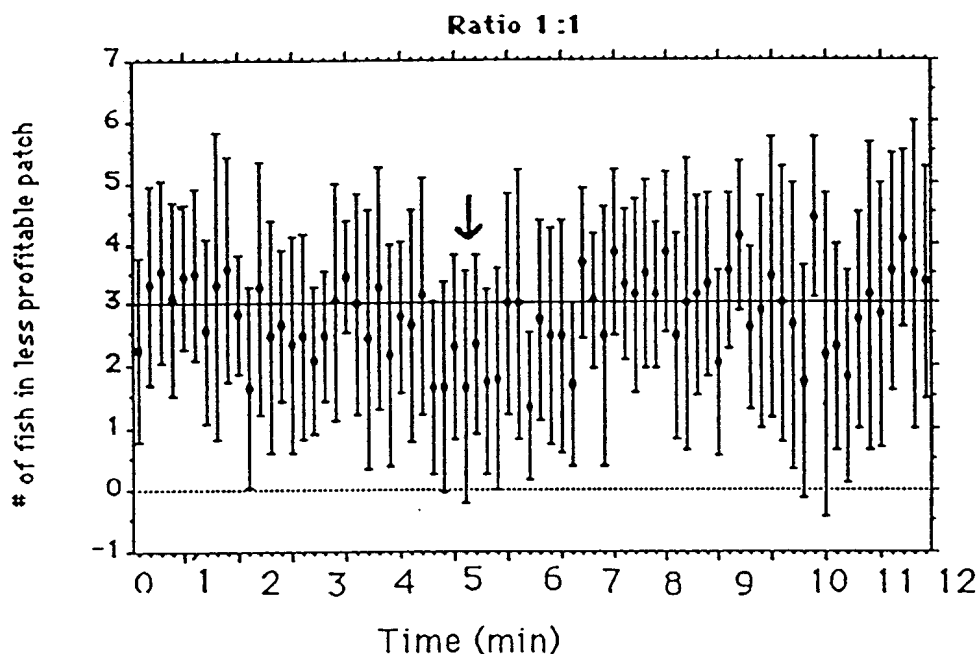


Figure 1. Mean number of fish observed per 10 s in the less profitable patch plotted against time elapsed since the start of the trial for the 1:1 treatment. The vertical bars are the 95% confidence intervals. Means are represented by dots and are based on observations of 6 different trials. Each trial consisted of 6 fish and the same fish were used for all trials. The arrow indicates the onset of the feeding period, and the solid line indicates the number of fish predicted by the ideal free distribution theory.

Students can statistically analyze the data to determine whether:

- 1) Fish were equally distributed on both sides of the tank during the control period as expected. To test this expectation, students can calculate the mean (mean \pm SE) number of fish on each side of the tank during the control period. The means can be compared statistically by performing a t-test.
- 2) The number of individuals per patch is proportional to the fraction of resources in that patch. To test this expectation, students can calculate the mean (mean \pm SE) number of fish on each side of the tank during the experimental period. The mean number of fish can be compared to the expected number by performing a t-test.
- 3) The food intake per individual is equal across all patches. To test this expectation, students can calculate the mean (mean \pm SE) number of prey items consumed on each side of the tank during

the feeding period. The means can be compared statistically by performing a t-test.

Questions students can address include: Did the fish distribute themselves according to the predictions of the IFD theory? If the fish did not distribute themselves according to the IFD theory, what explanations may account for the deviations from the predicted distribution? Were the assumptions of the IFD theory met? Were all fish equal in their competitive ability or were some fish superior competitors?

In my classes, I have students write laboratory reports (in scientific format) and/or orally present their experiments. However, for lower division courses, if the instructor prefers, students could write a shorter report by answering a series of questions provided by the instructor.

In conclusion, this laboratory exercise provides students with an opportunity to be involved with designing and conducting an experiment and analyzing and summarizing their results.

Literature Cited

- Fretwell SD, 1972. Populations in a seasonal environment. Princeton, N.J.: Princeton University Press.
- Fretwell SD, Lucas HL, 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biother* 19: 16-36.
- Gillis DM, Kramer DL, 1987. Ideal interference distributions: population density and patch use by zebra fish. *Anim Behav* 35:1875-82.
- Godin J-G J, Keenleyside MHA, 1984. Foraging on patchily distributed prey by a cichlid fish (*Teleostei: cichlidae*): a test of the ideal free distribution theory. *Anim Behav* 32:120-31.
- Harper DC, 1982. Competitive foraging in mallards: 'ideal free' ducks. *Anim Behav* 30:575-84.
- Milinski M, 1979. An evolutionary stable feeding strategy in sticklebacks. *Z Tierpsychol* 51:36-40.
- Power ME, 1984. Habitat quality and the distribution of algae-grazing catfish in a Panamanian stream. *J Anim Ecol* 53:357-74.

Call For Resolutions

The Steering Committee of ACUBE requests that the membership submit resolutions for consideration at the 2000 Annual meeting to the Chair of the Resolutions Committee. The proposed resolutions will be published in the August 2000 issue of *Bioscene*. Submit proposed resolutions to:

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