Chapter 1

Testing Issues of Foraging and Flocking Behavior

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Introduction

Students often have trouble understanding the problems that animals face when looking for food while trying to avoid predation in natural environments. I have developed field exercises in which students take the roles of foragers and predators so that they can have first-hand experience in simulating those problems.   Time, space, and food requirements are condensed to allow the simulations to occur in two 3-hour laboratory periods, but the results are usually consistent with theories supported by empirical evidence from field studies of other animals. Foraging data can be averaged from many students for statistical tests and to show the variation that results from differences in ability and motivation in a population of animals. Theoretical issues that can be attacked are: (1) why neither predators nor prey go extinct when there is a long period of nonrenewal of the prey population (i.e., winter), (2) the effects of habitat on foraging speed, (3) the advantages foragers can gain from experience in foraging, (4) the advantage of exclusive use of an area (territory) for foragers, (5) the effects of food density on foraging speed, (6) the advantages of camouflage for prey, (7) The effect of experience in forming search images, and (8) the advantages of foraging in mixed-species flocks for avoiding predation. The selective factors influencing each of these issues can be simulated by varying appropriate conditions affecting the foraging students. All exercises are developed by modifying one basic foraging design.

General Laboratory Set-up

Before the laboratory period the instructors need to do two things: (1) measure out macaroni or other foraging items into groups of 100 and place them in bags, and (2) go to the field site and place surveyor flags in grids of the appropriate dimensions for the experiments. Bagging foraging items can be done quickly by counting out 100 items once and placing them in a 250-ml graduated cylinder to determine their volume. From then on the cylinder can be filled to the same height to get approximately 100 items to fill other bags. Alternately, the 100 items can be weighed on a top-loading balance and other bags filled with the same weight of the items. Of course, 100 items must be counted for each different type of foraging item used (i.e., macaroni, navy bean, etc.).

Making grids of surveyor flags requires some method of making a right angle so that the grids are square. The right angles can be made by a 3-4-5 right triangle using a 120 foot rope marked at 30 and 70 feet or by 3 tapes making a 3-4-5 right triangle. Another method is to make one side of a 100-foot square, placing flags at 10-foot intervals and then use a sextant or sighting compass set at 90° to sight other sides of the square. Once three sides of a square are made with flags at 10- foot intervals, the tape used to make the middle side can be moved down between the other two sides to finish the grid (Figure 1.1). The grid should include twice as many squares as the number of foraging areas needed for the students. The grid should be used like a checker board with students only using the alternate (or black) squares to forage in (Figure 1.1). The student returns to a red square after each foraging bout. By placing the foraging items only in alternate squares there is no confusion arising from students foraging on adjacent squares. By making squares in grids, large numbers can be made quickly.
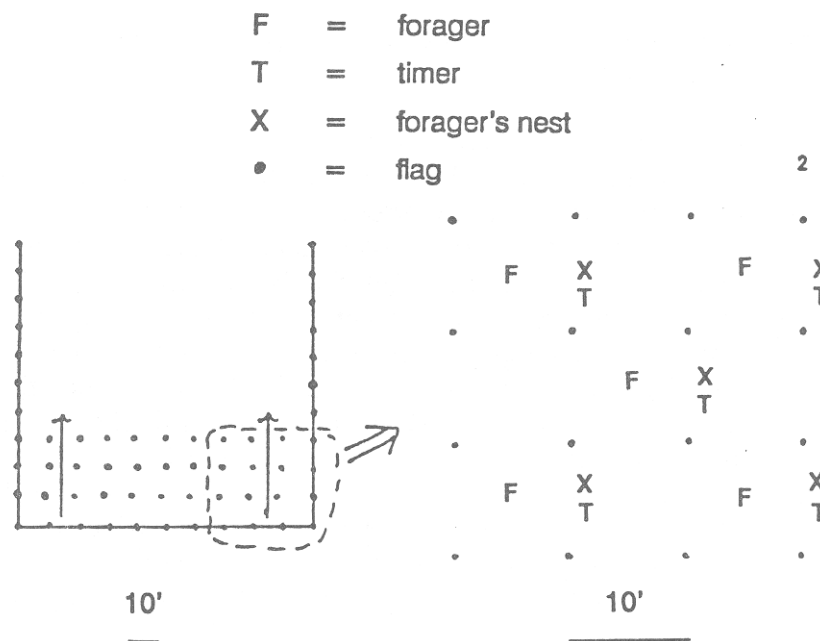
Figure 1.1. Outline of grid construction and use of the grid by student foragers. A grid of surveyor flags at 10-foot intervals can be made by using three 100-foot tapes to make three sides of a square and then move the middle tape up between the other two to complete the grid. Students use alternate squares within the grid for foraging so that there will not be food in adjacent squares.

During the actual laboratory period students are taken to the field site, asked to work in groups of two, and assigned squares of the grid to work in. One of each pair acts as a timer and the other as a forager. The timer is then given a bag of 100 food items and she or he scatters it throughout the 100 square feet of the 10- × 10-foot square. The forager then starts at the edge of the square and on cue from the timer enters the square and searches until five food items are found and picked up. The forager returns to the starting point and the timer records how many seconds it took the forager to find its daily requirement on this the first day of "winter." The activity is repeated until the day the forager cannot find five pieces of food in 60 seconds at which time she or he has starved to death. The students are told that the winter is 12 days long so that they will be motivated to survive until they have found at least 60% of the food, but the foraging continues until they starve even if they survive past day 12. The timer will end up with a list of days and the number of seconds needed for foraging on each day. Once the first forager has died the pair can be assigned a new square and their roles reversed. This is the basic procedure for all experiments, but the size of the squares, the nature of the habitat, the nature of the food items, the number of students foraging in a square, and the presence of other students acting as predators can be modified to illustrate a number of concepts in behavioral ecology. The participation of students in the actual foraging gives them an appreciation of the nature of selective pressures experienced by wild animals and their food. The daily food requirement, the length of the winter, or the size of the foraging area can be changed to fit different habitats so that the experiments can be run almost anywhere.

Specific Issues

1. How can both predator and prey populations survive a prolonged period like winter when the prey population is not being renewed?

When all members of a class have foraged for the first time, the range in numbers of days survived is usually large (Table 1.1) and an arbitrary length of winter chosen before the class will usually lead to some deaths and some survivors. With experience in a habitat an instructor can choose a length for winter that will allow better than half the class to survive and thus help encourage the students to work hard on later exercises. Unless the vegetation is very sparse, there will be an appreciable amount of the prey undiscovered when all the students have starved (approximately 1/3 of the food for Table 1.1). The data can be plotted in at least three patterns: (1) only using the times for the days individuals find their five pieces of macaroni to calculate mean foraging time for each day (Figure 1.2, circles), (2) including 60 seconds for all days after an individual dies (Figure 1.2, dots), or (3) including 60 seconds for the one day an individual dies (Figure 1.3, dots). The contrast of the first two patterns (Figure 1.2) demonstrates that the foraging times of the students that are skilled foragers and are surviving do not rise very fast compared to the less skilled foragers. Using 60 seconds only on the day of death is a compromise between the first two methods.

If the students are thinking about improving their survival they will want to cache food or eat more than their daily needs in order to store fat. I tell them that it is dangerous to be out foraging away from their nest and they must return as soon as food is found as they will learn when we add hawks to their environment. Students may also question the arbitrary length of winter in reaching the conclusion that both predator and prey populations will survive. That can lead to interesting discussions about how density-dependent population regulation and selective trade-offs between summer and winter foraging ability can lead to patterns of winter survival on nonrenewed food supplies in natural populations. Andrewartha and Birch (1954) and Weins (1977) have generated controversies

Table 1.1. Forage times (in seconds) for 22 students to find five pieces of macaroni in 100 ft^2 of grazed Kansas tallgrass prairie where the starting food supply was 100 pieces of macaroni. Students foraged on successive days until the day they could not find five pieces of macaroni within 60 seconds and were assumed to have starved to death. The winter period of no food renewal is assumed to be 12 days long.

Day	Students

| Day	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	$\bar{x}$
1	22	11	13	14	12	7	17	14	7	5	8	9	30	12	8	9	13	20	18	14	9	2	12.5
2	14	16	13	12	10	8	11	30	25	15	18	10	20	10	12	14	10	25	10	7	14	14	14.5
3	24	9	15	13	10	9	22	20	20	11	10	15	45	13	12	13	17	15	8	8	11	13	15.1
4	16	12	25	14	12	9	17	16	20	27	13	12	30	17	14	14	23	42	11	9	12	15	17.3
5	13	17	12	17	11	15	16	36	12	6	8	13	25	18	17	12	45	30	15	20	25	15	18.1
6	15	13	13	15	8	18	24	55	13	8	14	17	60	9	16	16	15	14	13	12	8	14	17.7
7	17	18	20	16	19	9	19	13	30	20	13	35		23	15	17	27	13	19	10	14	9	17.9
8	50	10	25	18	7	17	21	40	45	12	8	30		19	18	18	20	53	15	18	22	10	22.7
9	49	14	25	23	18	19	24	60	25	18	14	16		13	21	12	43	43	15	22	12	18	24.0
10	46	18	60	8	20	23	27		20	13	11	15		15	18	14	60	53	20	18	14	33	25.3
11	60	13		14	40	11	60		40	15	19	55		40	13	25		23	14	20	27	15	28.0
12		60		18	15	11			50	12	23	46		21	15	15		30	30	40	40	15	27.6
13				19	26	14			60	15	60	60		10	19	17		41	25	55	37	13	31.4
14				37	25	23				16				13	22	17		60	60	38	37	16	30.3
15				60	58	45				12				15	36	18				60	60	21	38.5
16				34	60	45				60				60	35	20						26	48.6
17				60		60									60	60						60	60

by assuming that relatively large prey populations are a good argument against food limitation for predators. These conclusions might be questioned on the basis of the students' data. The students should always analyze how the condensation of time, space, and energy requirements in the experiment lead to erroneous conclusions about natural populations.
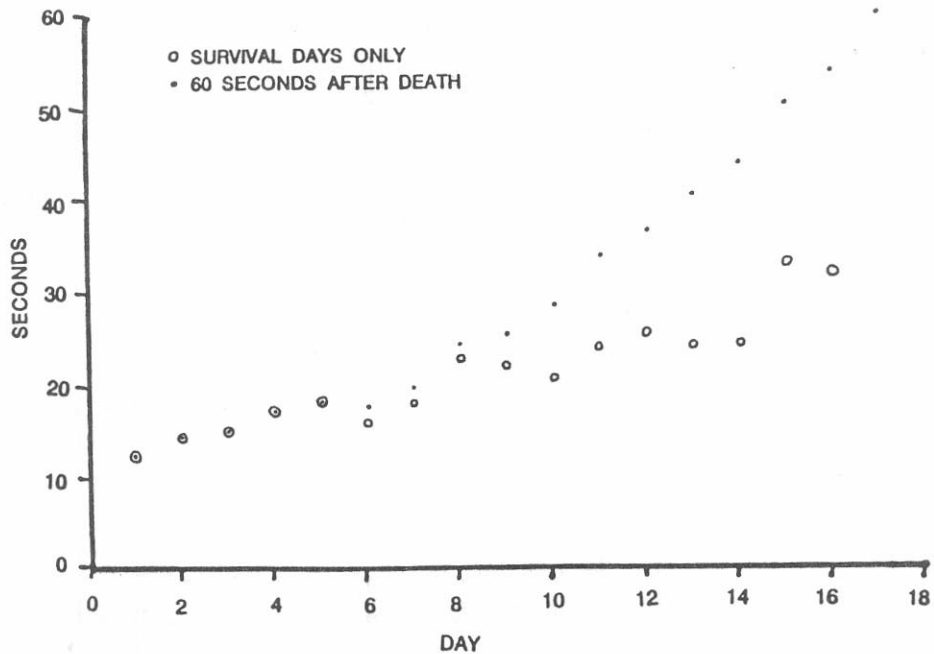
Figure 1.2. Plot of mean number of seconds students used to find five pieces of macaroni on successive days. Circles are means for days in which students survived by finding five pieces of macaroni and dots are means calculated by using 60 seconds for the day a student "died" and all successive days until all students were dead.

2. How does habitat affect ease of finding food and the forager's choice of habitat?

Four to six students repeat the foraging experiment in a different habitat with higher or denser vegetation (Figure 1.3). I often choose markedly denser vegetation to make the effect obvious and to counteract the improvement in foraging that students gain from experience. When the difference in foraging is less marked than in Figure 1.3, it allows students to think about the consequences of the interaction between population density and habitat quality (Fretwell and Lucas, 1970). The preferred habitat can have such a high population density of predators that an immigrating predator can form a territory large enough to allow it a faster feeding rate in the poorer quality habitat with fewer competitors.
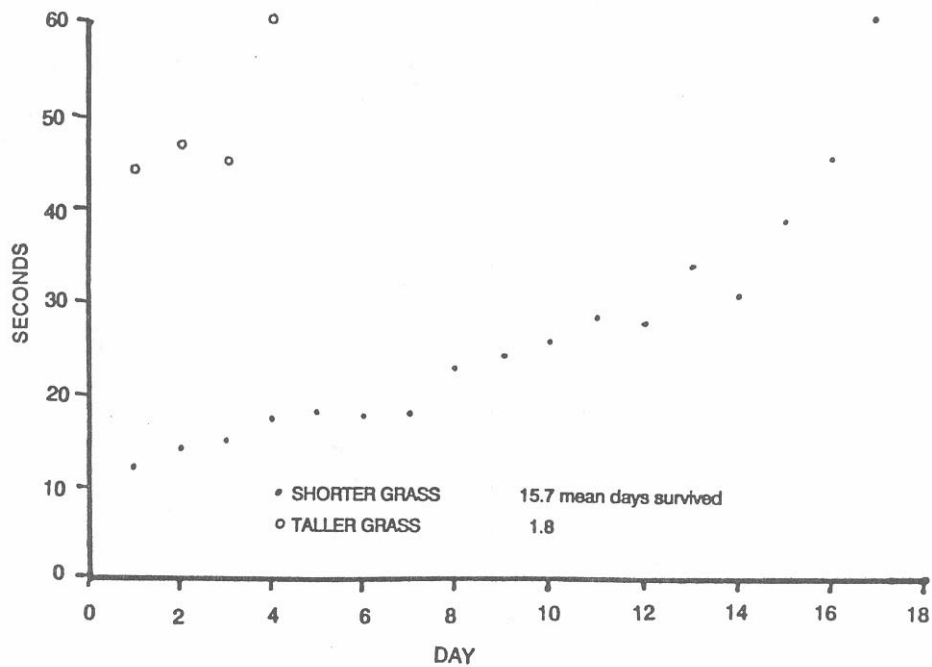
Figure 1.3. Plot of mean number of seconds students used to find five pieces of macaroni on successive days in short, grazed and tall, ungrazed prairie vegetation. Sixty seconds was used as the time on the day a student died, but not on following days.

3. Do animals learn to forage more effectively by repeating the same foraging activity?

Four to six students repeat the foraging experiment in the same habitat to determine if their previous experience allows them to learn to be more efficient foragers. In the past 2 years the students lived 1.9 and 5.8 days longer on the average during their second foraging trial. The average time it takes them to find food each day does not, however, decrease appreciably. Students actually learn to search their 100 ft^2 more systematically and often return to the nest slowly while scouting for the next day's food which is cheating on safety. Because the students are usually about the same age they are not a good example of the ontogeny of foraging ability. It should help them to think about the effect of age on foraging by asking them to speculate on the relative success in this exercise of humans aged 2, 5, 10, 20, 50, and 80. The critical importance of timing mating so that offspring are born at the time that allows them to become independent foragers when food is easiest to find is demonstrated in Sullivan (1989) and Geist (1971). This experiment seems to be one of the poorest for humans to simulate what goes on in natural populations and it is good to get students to be critical.

4. Does the exclusive use of an area give any advantage to an individual that would compensate for the time and energy needed to defend that territory?

Two or three groups of four students and their timers are separated for this experiment. Each group of four students forages together in a square 20 feet on a side (400 ft^2) in which one of the timers scatters 400 pieces of macaroni (Figure 1.4). Thus, the density of food and number of food items per student is the same as in the original experiment. One timer starts all four foragers together for each day and each of the four timers determines how long it takes his or her forager to find five pieces of macaroni. When a student finds five pieces and leaves them in the nest, she or he can return to the foraging area and mildly harass the remaining students until all have found their food. My experience has been that students are reasonable in their level of harassment without specific instructions and yet still effective in slowing their competitors. The experiment continues until all four foragers die. The mean day of death was 9.1 days sooner under this system of interference competition than in the original experiment on exclusive territories for 12 students in 1991. In only one of three groups did the last surviving student live longer than in the original experiment in spite of there being over 240 pieces of macaroni undiscovered. When foraging together the students can not be as systematic in covering the area and when they harass each other, often by stepping where a student is foraging, they push the macaroni deeper into the vegetation.
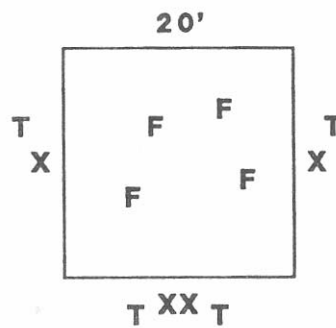
Figure 1.4. Positions of timers (T), foragers (F), and foragers' nests (X) for experiments on the effect of interference competition.

Two of the four nests for student foragers are beside each other and two are more isolated (Figure 1.4). This was designed to get the students to think about position effects on competition, but the distances are too small to have a significant effect.

Theoretical considerations of central place foraging (Orians and Pearson, 1979; Smith, 1968) and the costs and benefits of territorial defense (Carpenter, 1987 [and other papers that follow in the symposium]; Davies, 1978; Seastedt and MacLean, 1979) are extensive in the literature. Because aggression is involved in the experiment, students will often discuss what is the most effective level of aggression. The chapter on aggression in Dawkins (1989) is at a level that will generate student thought.

5. How does the density of food affect the foraging rate and longevity of a predator?

   Four to six students each forage individually in squares 14 feet and 2 inches on a side (200 ft^2), 17 feet and 4 inches on a side (300 ft^2), and 20 feet on a side (400 ft^2). The habitat and foraging rules are kept the same as in the original experiments. The results are compared with the results of students foraging in 100-ft^2 areas for the second time so that all students are foraging with some previous experience (Figure 1.5). There is always a tendency for foraging time to increase and survival time to decrease with decreasing food density. The change in foraging time is not, however, proportional to the area in which the macaroni is dispersed. Considerations of how travelling speed of foragers, field of vision of foragers, cryptic coloration of prey, and density of prey affect foraging speed are discussed in Gendron and Staddon (1983).
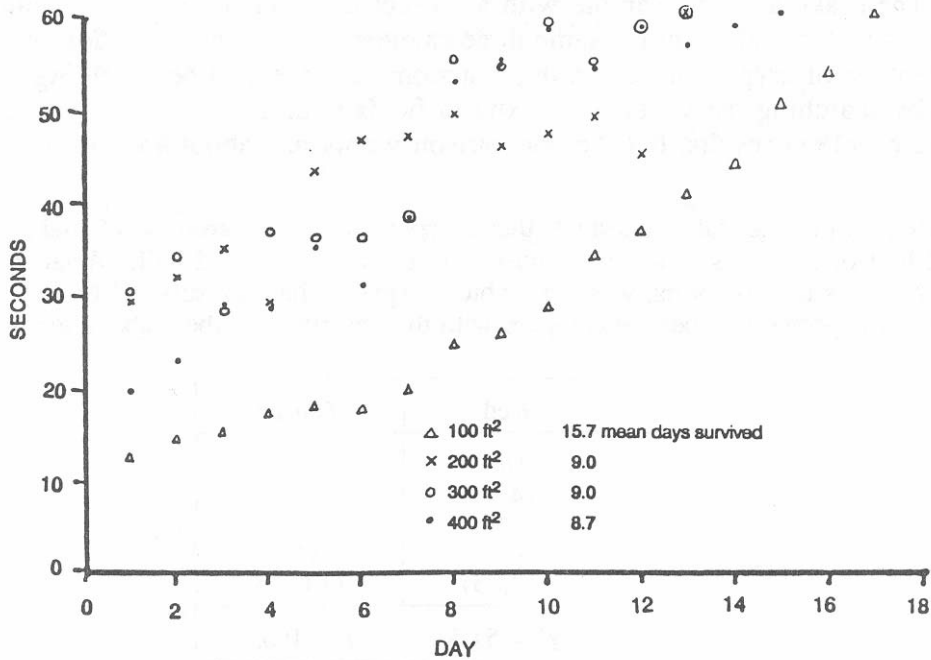
Figure 1.5. Plot of mean number of seconds students used to find five pieces of macaroni on successive days in areas with different food density. Sixty seconds was used on the day a student died, but not on following days.

6. Does matching the background color of the vegetation give prey an advantage in escaping predation?

   Four to six students forage on 50 pieces of macaroni matching the vegetation in color and 50 pieces contrasting in color to the vegetation in 100 ft^2. The number of each type of food found each day is recorded along with the number of seconds it takes to find five pieces of any kind. Usually some form of pasta can be found in shades of yellow, green, and red. Using larger pasta is not a problem as this experiment does not depend on comparison with earlier experiments. The red serves as a contrasting color and green or yellow the matching color depending on whether the vegetation is alive or dead. Because the food is not renewed the frequency of the conspicuous color will decrease during the experiment and make the more cryptic color more common, thus increasing its probability of being found. A test for advantage of matching coloration under these circumstances can be done by determining whether the matching color is more common in the first half of the food found than in the latter half of the food found during the whole experiment for the four to six students (Table 1.2). There is almost always a tendency for the cryptic color to be found

less frequently than the nonmatching color in the first half of the food items found, but the difference is statistically significant less than half of the time. The food items are too densely spaced and too different in shape from vegetation to be very cryptic. If colored pasta cannot be found in stores, macaroni can be dipped quickly in food coloring and dried individually on waxed paper so they will not stick to each other or become brittle when dried. In the growing season this experiment can be supplemented with a quick test using insects in vegetation. Have students look closely at the vegetation and yell out for each insect they see whether it is cryptic (matching the background it is on), aposematic (bright colors contrasting with the background), or neutral (uniform browns, grays, and blacks that probably have thermal functions). Continue until 100 insects have been observed to get the percent seen for the three categories. Then take a sweep sample with an insect net over the same vegetation, dump it in a flat pan or tray of water, and count the same three categories of insect coloration from the sweep sample. The percentage of cryptic insects in this "random" sample will be much higher than what the student found by searching the vegetation. Alfalfa fields with aposematic ladybird beetles and cryptic aphids give excellent results, but the comparison works just about anywhere.

Table 1.2. A 2 × 2 contingency table to test whether conspicuous red macaroni was found more often during the first half of student's foraging exercise than during the second half. A larger type of macaroni, which comes in two colors, was used which explains the long survival time. Values in parentheses are the expected numbers to compare with the observed numbers above them.

	Red	Yellow
First 10 days	163 (149.5)	137 (150.5)
After 10 days	125 (138.5)	153 (139.5)
	$\chi^2 = 5.05$	$P < 0.05$

The comparison of aposematic and cryptic color patterns is not a realistic representation of the evolution of cryptic coloration because aposematic colors are selected to be conspicuous to warn predators that potential prey are distasteful and not usable as food (Fisher, 1958 [Chapter 7]). In order to get a quick demonstration that some colors are easier to see than others in a laboratory period the comparisons are useful. Aposematic coloration is also the basis of convergent evolution of color patterns in mimicry complexes (Brower, 1969, 1988; Wickler 1968). The evolution and diversity of protective coloration are discussed in Cott (1940), Edmunds (1974), Kettlewell (1956), and Sumner (1935).

7. Among different types of prey, do predators find the type with which they are most familiar more often than the types which they have not seen as often?

Each student in a class is assigned to be a specialist on one of four kinds of food (macaroni, kidney beans, pinto beans, and navy beans). Each student forages in a 100-ft^2 area on 100 pieces of his or her special food. Then each student forages a second time in the same situation except that there are 25 pieces of each of the four kinds of food in the foraging area. The number of each type of food found each day is recorded along with the number of seconds it takes to find five pieces of any kind. Again there is the same problem with nonrenewed food supplies that applied to protective coloration; as the more easily found food is taken it becomes a smaller fraction of the remaining food. To determine if previous experience gives an advantage in finding one type of food over another, only the first half of the food found by each student is considered as the tendency is more likely to show up there. There is a second problem: because of size and color differences, some types of food are easier to find than others (Figure 1.6). To factor these differences out from consideration of the influence of experience, we ask the question, Is a type of food more likely to be found among the four types by a person who previously experienced looking for the food or by someone with no such experience? (Table 1.3). The results tend more often to show an advantage for experience, but the difference has never been statistically significant. Again, the items are too densely spaced and too dissimilar to the vegetation for a learned search image to be important in the result. This experiment gets students to think about this issue and it also sets up the next experiment which usually gives good results. Some of the considerations for learned search images are found in Gendron (1983) and Pietrewicz and Kamil (1981).
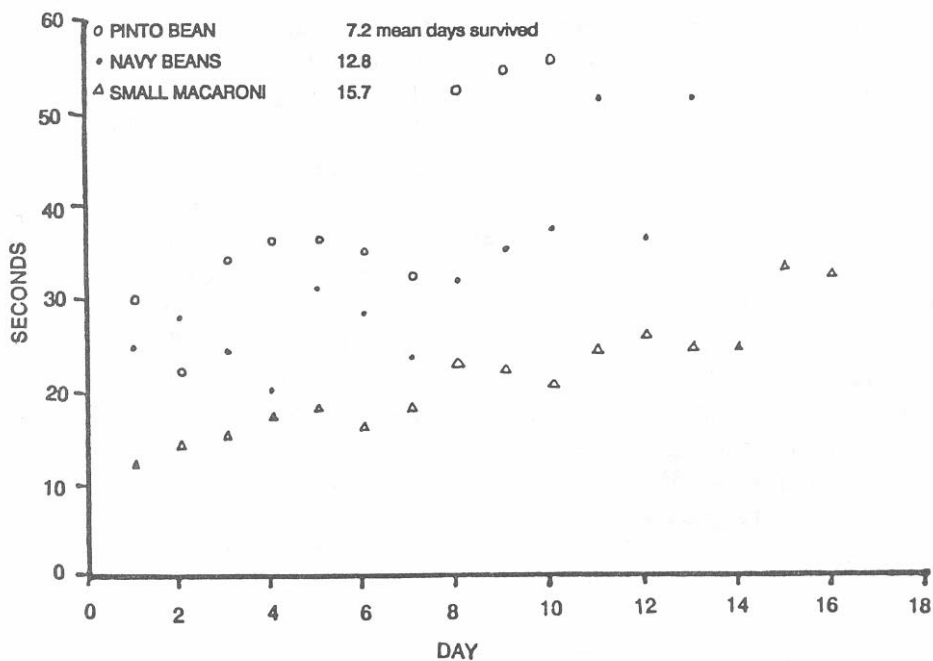

Figure 1.6. Plot of mean number of seconds students used to find five pieces of their food specialty on successive days in a 100-ft^2 area. The plot for kidney beans is not shown because it was so close to small macaroni used in all other experiments except protective coloration. Only the times for days in which foragers found five units of food were used to calculate the means in order to show that even among successful foragers the time it took to find some types of food was longer.

Table 1.3. A 2×2 contingency table to test whether food for which foragers have more experience is taken more often than food for which foragers have less experience. Values in parentheses are the expected numbers to compare with the observed numbers above them.

	Experienced forager	Other foragers
Experienced food	313 (296.3)	872 (888.7)
Other foods	872 (888.7)	2683 (2666.3)
	$\chi^2 = 1.67$	$P = 0.20$

8. What advantages do animals of the same or different species gain from foraging together that compensate for the interference competition that can occur?

Two rows of four 400-ft^2 foraging areas are marked out parallel to each other (Figure 1.7). Rows of flags are laid out at about 30 and 60 m from each of these rows of foraging areas. One end of the rows of foraging areas should be about 30 m from a gully or a row of trees or shrubs and a row of flags should be placed about 15 m from the gully. Four hundred pieces of each of the four types of food from the previous experiment are scattered in each square in one row. Four students, each one specializing in a different food type, forage together in one square. They can only forage on their species of food as if they were four different species specialized to eat different types of food. This is unlike the previous experiment where they were considered to be in one species that could feed on each of the four types of food. Each day one timer starts all four foragers and each timer records the time it takes his or her forager to find five pieces of food that day. Each day the groups of four foragers rotates to the next square until all four squares have been used and then they return to the original square to continue the pattern. A group of students hides in the gully as slow hawks and another group acting as fast hawks waits in the open behind the line 60 m from the row of foraging squares. Each group of hawks can have an average of one attack a day, but can have more than one attack on a given day if there has been no attack on some previous days. An attack is initiated when a slow hawk leaves the gully or a fast hawk crosses the 60-m line. An attack is successful if a slow hawk crosses the 15-m line of flags or the fast hawk crosses the 30-m line of flags before any of the foragers give an alarm call. A judge stands at each line and yells "kill" when a hawk crosses it. A hawk can kill only one forager at a time and that forager cannot give alarm calls the rest of that day. If any one of the foragers gives an alarm call by yelling "hawk" all other foragers are assumed to be saved by the warning. If a forager is killed or starves, she or he is allowed to be revived for the next day. The activity goes on for a prescribed number of days and then the second row of squares is used. Everything is the same for the second row of squares except that each of the four students forages in a different square. The students rotate to a new square each day so that the same amount of food depletion and movement will occur in each square as in the previous row of squares. These students in isolation do not give alarm calls, but instead give hand signals to their timers to indicate they have seen the hawk. The hawk should have one forager in mind when attacking and only register a kill if that forager has not signalled. To make the simulation realistic I ask the students in the flock to keep foraging and looking up for predators at the same rate after they have found five pieces of food so that they cannot act as a sentinel for the students still foraging. In the past I have allowed the hawk to kill any isolated forager that has not signalled (Table 1.4), but that is not realistic because the hawk would only have a chance to kill one isolated prey. Table 1.4 does represent selection for giving an alarm call within the hearing of close kin.
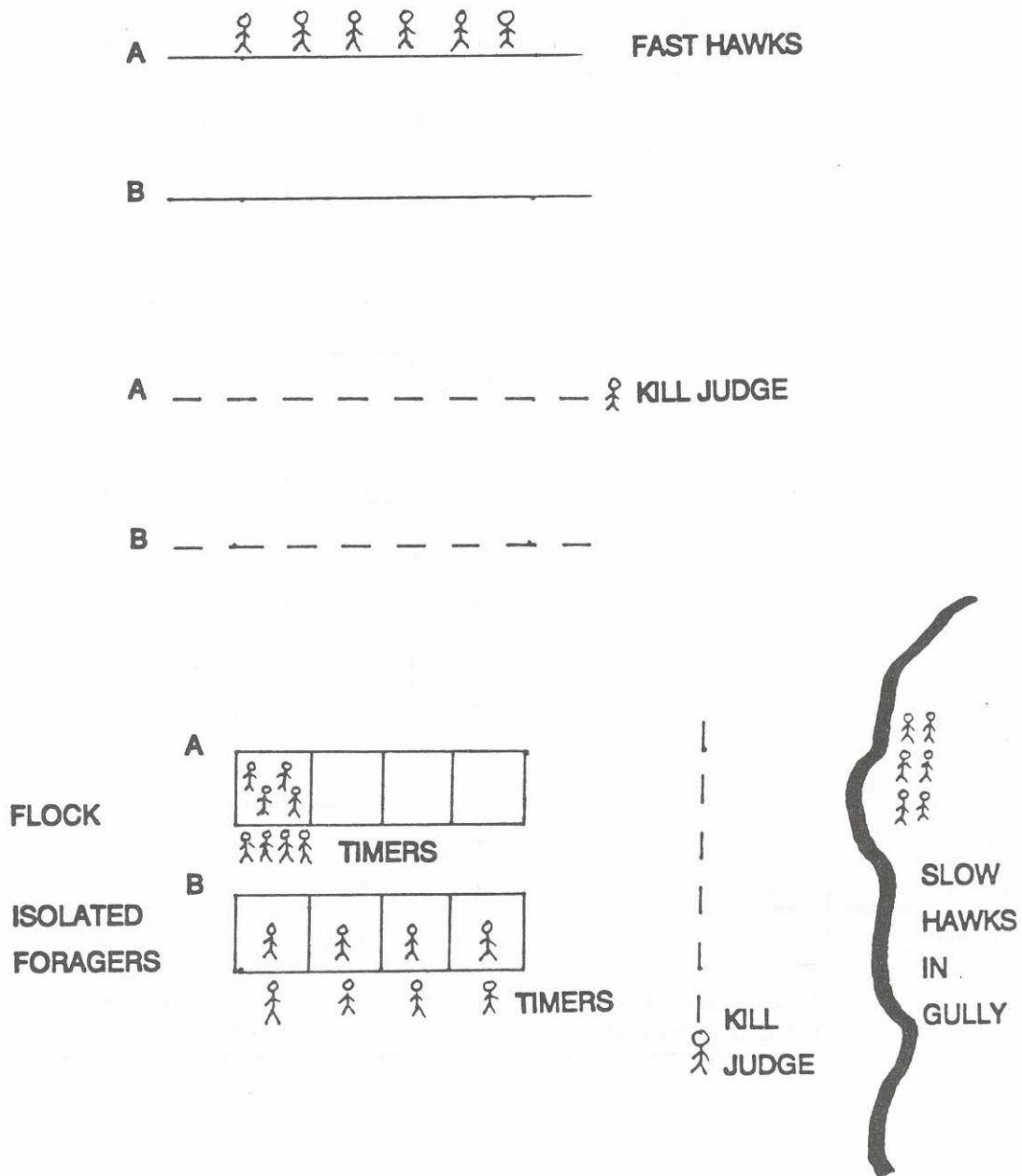
Figure 1.7. A map of the placement of foragers, timers, hawks, and kill judges during a test of the advantage of mixed-species foraging flocks over isolated foraging by individuals. The solid line A is the starting line for fast hawks and dashed line A is the kill line for fast

hawks when attacking foragers in the row of foraging plots marked A. The lines and foraging plots marked B are used in the second half of the experiment.

Table 1.4. Foraging times (in seconds) and predator success (a kill) for four students foraging together in a mixed-species foraging flock and four students foraging in isolation in the same area and food density. Asterisk denotes starvation. See the text and Table 1.3 for further details.

Day	Foragers in mixed flocks				Individual foragers			
	Food (and student)				Food (and student)			
	Pinto	Navy	Macaroni	Kidney	Kidney	Pinto	Macaroni	Navy
	Shane	Shanon	Dave	Kevin	Allen	Laura	Rene	Phil
1	60*	57	40	30	47	kill	30	kill
2	47	20	45	35	40	kill	kill	23
3	11	20	20	15	30	kill	30	26
4	43	22	12	10	15	41	15	17
5	50	40	kill	30	15	46	20	15
6	38	45	43	22	15	22	58	19
7	38	12	10	15	60*	19	kill	kill
8	24	15	35	9	55	41	60*	kill
9	kill	kill	18	36	45	15	30	28
10	33	35	58	25	15	11	30	kill
11	7	25	10	40	45	25	35	26
12	17	15	18	9	40	60*	kill	24
13	kill	30	30	kill	15	11	25	45
14	32	32	13	28	10	kill	35	14
15	14	20	7	40	60*	kill	40	kill
$\bar{x}$	31.8	27.7	25.6	24.6	33.8	29.1	34.0	23.7
	1 death by starvation				4 deaths by starvation			
	5 deaths by predation				13 deaths by predation			

Caraco (1979), Caraco et al. (1980), and Pulliam and Caraco (1984) consider the advantages gained from flocking in reducing the time spent in vigilant searching for predators. Sullivan (1988, 1989) and Weathers and Sullivan (1989) give evidence that vigilance against predator attack is critical in juvenile success in the same species of birds, yellow-eyed juncos, that Caraco studied. Gaddis (1980), Morse (1977), Moynihan (1962), and Sullivan (1984) analyze the evolution of behavior in mixed-species foraging flocks. The evolution of the sound structure of alarm calls is discussed by Marler (1955, 1957) and hypotheses for the social context in which alarm calls are given is reviewed by Sherman (1977) as a basis for analyzing the evolution of alarm calls in Belding's ground squirrels.

Discussion

I run these eight experiments in two 3-hour laboratories in March on grazed Kansas prairie vegetation. Experiments for the first six issues are performed in the first laboratory and the last two in the second laboratory. The weather can often be cold and windy and the laboratories run from 2:30 to 5:30 p.m. so that students are eager to get home for supper. One year a light snow started midway through the laboratory, but the students kept working so that we could measure a very distinct effect of snow cover. All these factors are important in affecting the results of the experiments and are incorporated into discussions of how well the results simulate natural populations. To get a better feel for the difficulties natural populations experience, I give each student a vial at the end of the first laboratory and tell half the students that they are sparrows and must put as many seed kernels in the vial as possible in 10 minutes. The other half are wrens and put live animal matter in their vials. The students with the most seed kernels and animal material are rewarded a bag of M & M candies. Most students who look for seeds do not expose the kernels and are disqualified in spite of earlier warning.

While I have described the conditions for the laboratories as I run them, the basic design is very flexible and can be adjusted to the class level of the students and local vegetation conditions. The laboratory has worked with brown-dyed macaroni on the leaf litter of a forest floor or with yellow macaroni on the short green grass of a campus lawn. Last year the prairie vegetation was so dense that I had to reduce the daily food requirement to three pieces of macaroni. It has been used by high schools and college freshman biology classes as well as my upper-division ecology classes. More advanced questions about optimal foraging (Kamil and Sargent, 1981; MacArthur and Pianka, 1966; Pyke et al., 1977) can be approached by using macaroni of different sizes and assigning them different food values or by renewing the food supply with macaroni marked with ink spots to determine the relative success of new and old prey. The possibilities are limited by the imaginations of the instructor and students. Because this is a very flexible exercise, a specific laboratory exercise that is handed out to students is not provided in this chapter. Teachers should build their own laboratories to fit the time they have available, the background of their students, and the local habitat. Also, building your own laboratory will force you to think through the issues you wish to teach and be better able to respond to student questions. My worst problem in teaching these laboratories has been in devising too much for the students to do during the laboratory and not spending enough time in discussing the issues or involving the students in devising their own experiments.

Materials

1. Surveyor flags (3-foot stiff wire with 3×3-inch brightly-colored plastic flag on one end) (200)
2. 100-foot cloth or steel measuring tapes (3)
3. 250-ml plastic graduate cylinder (1) or top-loading balance (1)
4. 120-foot rope marked at 30 and 70 feet to make right angles (1) or sextant or sighting compass to sight right angles (1)
5. Watches with second hands (usually half the students in a class will be wearing a watch) (1 per 2 students)
6. Small paper bags or plastic sandwich bags
7. Elbow macaroni, navy beans, pinto beans, kidney beans, or any other inexpensive grocery store products that are of the same general size and can be bought in bulk

Literature Cited

Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago, Illinois, 782 pages.

Brower, L. P. 1969. Ecological chemistry. Scientific American, 220(2):22–29.

Brower, L. P. (Editor.) 1988. Mimicry and the evolutionary process. University of Chicago Press, Chicago, Illinois, 127 pages.

Caraco, T. 1979. Time budgeting and group size: A test of theory. Ecology, 60:618–627.

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

Carpenter, F. L. 1987. Introduction to the symposium. Territoriality: Conceptual advances in field and theoretical studies. American Zoologist, 27:223–228.

Cott, H. B. 1940. Adaptive coloration in animals. Oxford University Press, New York, 508 pages.

Davies, N. B. 1978. Ecological questions about territorial behaviour. Pages 317–350, *in* Behavioural ecology: An evolutionary approach (J. R. Krebs and N. B. Davies, Editors). Sinauer, Sunderland, Massachusetts, 494 pages.

Dawkins, R. 1989. The selfish gene. Second edition. Oxford University Press, New York, 372 pages.

Edmunds, M. 1974. Defense in animals: A survey of anti-predator defenses. Longman, New York, 357 pages.

Fisher, R. A. 1958. The genetical theory of natural selection. Second revised edition. Dover, New York, 291 pages.

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

Gaddis, P. 1980. Mixed flocks, accipiters, and antipredator behavior. Condor, 82:348–349.

Geist, V. 1971. Mountain sheep: A study in behavior and evolution. University of Chicago Press, Chicago, Illinois, 383 pages.

Gendron, R. P., and J. E. R. Staddon. 1983. Searching for cryptic prey: The effect of search rate. American Naturalist, 121:172–186.

Kamil, A. C., and T. D. Sargent. (Editors.) 1981. Foraging behavior: Ecological, ethological, and psychological approaches. Garland, New York, 534 pages.

Kettlewell, H. B. D. 1956. Further selection experiments on industrial melanism in the Lepidoptera. Heredity, 10:287–301.

MacArthur, R. H., and E. R. Pianka. 1966. The optimal use of a patchy environment. American Naturalist, 100:603–609.

Marler, P. 1955. Characteristics of some animal calls. Nature, 176:6–8.

———. 1957. Specific distinctiveness in the communication signals of birds. Behaviour, 11:13–39.

Morse, D. H. 1977. Feeding behavior and predator avoidance in heterospecific groups. Bioscience, 27:332–339.

Moynihan, M. H. 1962. The organization and probable evolution of some mixed-species flocks of neotropical birds. Smithsonian Miscellaneous Collections, 143:1–140.

Orians, G. H., and N. E. Pearson. 1979. On the theory of central place foraging. Pages 154–177, *in* Analysis of ecological systems (D. J. Horn, R. D. Mitchell, and G. R. Stairs, Editors). Ohio State University Press, Columbus, Ohio, 312 pages.

Pietrewicz, A. T., and A. C. Kamil. 1981. Search images and the detection of cryptic prey: An operant approach. Pages 311–331, *in* Foraging behavior: Ecological, ethological, and psychological approaches (A. C. Kamil and T. D. Sargent, Editors). Garland, New York, 534 pages.

Pulliam, H. R., and T. Caraco. 1984. Living in groups: Is there an optimal group size? Pages 122–147, *in* Behavioural ecology: An evolutionary approach (Second edition; J. R. Krebs and N. B. Davies, Editors). Sinauer, Sunderland, Massachusetts, 493 pages.

Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. Optimal foraging: A selective review of theory and tests. Quarterly Review of Biology, 52:137–154.

Seastedt, T. R., and S. F. MacLean. 1979. Avian territoriality: Sufficient resources or interference competition. American Naturalist, 114:308–312.

Sherman, P. W. 1977. Nepotism and the evolution of alarm calls. Science, 197:1246–1253.

Smith, C. C. 1968. The adaptive nature of social organization in the genus of tree squirrels *Tamiasciurus*. Ecological Monographs, 38:31–63.

Sullivan, K. A. 1984. Information exploitation by Downy Woodpeckers in mixed-species flocks. Behaviour, 91:294–311.

Sullivan, K. A. 1988. Ontogeny of time budgets in yellow-eye juncos: Adaptation to ecological constraints. Ecology, 69:118–124.

Sullivan, K. A. 1989. Predation and starvation: Age-specific mortality in juvenile juncos (*Junco phaenotus*). Journal of Animal Ecology, 58:275–286.

Sumner, F. B. 1935. Evidence for the protective value of changeable coloration in fishes. American Naturalist, 69:245–266.

Weathers, W. W., and K. A. Sullivan. 1989. Juvenile foraging proficiency, parental effort, and avian reproductive success. Ecological Monographs, 59:223–246.

Weins, J. A. 1977. On competition and variable environments. American Scientist, 65:590–597.

Wickler, W. 1968. Mimicry in plants and animals (R. D. Martin, translator). McGraw-Hill, New York, 255 pages.