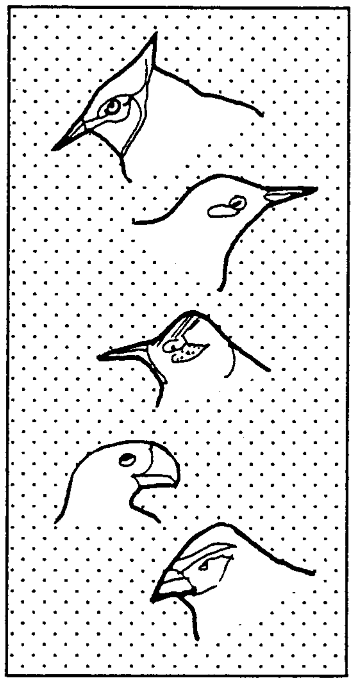
FORAGING AND FLOCKING BEHAVIOR

ESA lab

Written, tested and presented in Ecological Society of America session by Christopher Smith, Division of Biology, Kansas State University, Manhattan, KA 66506

A version of this exercise also appears in the Proceedings of the 13th (1991) Workshop/Conference of the Association for Biology Laboratory Education (ABLE) and is used here with permission.

INTRODUCTION



The problems animals face when looking for food while trying to avoid predation in natural environments are often difficult to understand. The following field activities are designed to enhance your understanding of several of these problems. Specifically, you will take on the role of foragers and predators to examine the following issues: 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 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 for one out of several types of prey, and 8. the advantages of foraging in mixed species flocks for avoiding predation.

Testing the above issues of foraging and flocking behavior will enable you to understand how environmental variables affect the short term behavioral decisions that animals make during their daily search for food. These activities will also illustrate how the same variables affect the evolution of social behavior.

environmental variables

Environmental variables that are important to short term choice are the structure of the habitat as it affects the ease of finding food and the ability of the foragers to look out for predators. Ease of finding food is affected by the density of the vegetation in which the food is hiding, the spacing and density of the food items, the color of the food relative to its background, whether the forager is looking for one specific kind of food rather than many, and how much the forager can learn from experience. These variables interact in affecting the ease of finding food and you should think about how they interact.

behavioral variables

One behavioral pattern that evolves to affect the ease of finding food is territoriality. This gives an individual or family exclusive use of a resource instead of having to worry about other individuals taking it. A second contrasting behavioral pattern is the flocking of individuals from the same or different species. Flocking increases the potential for competition, but allows a better chance of escaping predation while foraging because many individuals are available to look for predators and to give warnings when they appear.

make predictions

You will gain more from these exercises if you think about what variables affect foraging behavior and social behavior before you carry out the activities. **Read the specific exercises and predict their outcomes before actually performing them.**

OBJECTIVES

conceptual

1. Understand how the environmental variables of habitat structure, vegetation density and food color interact to affect short term behavioral decisions that animals make during their daily search for food.
2. Understand how habitat structure affects the ease of finding food and the avoidance of predators.
3. Understand how predator attributes such as food preference, experience, territoriality, and flocking influence food-seeking behavior.

procedural

4. Learn to graph and interpret experimental data.

MATERIALS

equipment

200 surveyor flags (3 foot stiff wire with 3" x 3" brightly colored plastic flag on one end)
100-foot cloth or steel measuring tapes (3)
250' rope marked at 30 and 70 feet to make right angles or 1 sextant or sighting compass to sight right angles
watch with second hand (1 for each 2 students)

small paper bags or plastic sandwich baggies
elbow macaroni, navy beans, pinto beans, kidney beans, etc.

supplies

BASIC PROCEDURE

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

ISSUE #1

set-up

1. Assemble at the field site. In teams of two, you will be assigned to grid units. One of each pair is a timer, the other is a forager. (See Figure 1.)

2. Timer - Pick up a bag of 100 food items (the prey) and scatter it throughout your assigned 100 square feet in the 10 X 10 foot square that is marked out in the field.

foraging

3. Forager - On cue from the timer, begin at the starting place (nest) at the edge of your square and search until you have picked up 5 food items. Return to your nest. We assume that animals place nests in safe, sheltered locations and return there whenever possible.

4. Timer - Record (in the DATA SHEET on page 4) the time the forager needed to find his/her daily requirement (the 5 items). This simulates the first foraging day of a "winter" period of no food renewal which arbitrarily will be set to last 12 days.

5. Repeat steps 2-4 until the forager cannot find 5 pieces of food in 60 seconds (even if this exceeds the 12 day "winter" period) at which time she/he has starved to death.

6. Following "starvation" in one grid unit, switch roles and repeat the entire procedure in a new grid unit.

DATA ANALYSIS

graphing the data

1 Using only the times for days foragers find their 5 food items, calculate and plot mean foraging time for all living class members for each day in the space provided.

2. Using the times for the days foragers find their 5 food items <u>plus</u> 60 seconds for all days after an individual dies, calculate and plot on the

site set-up

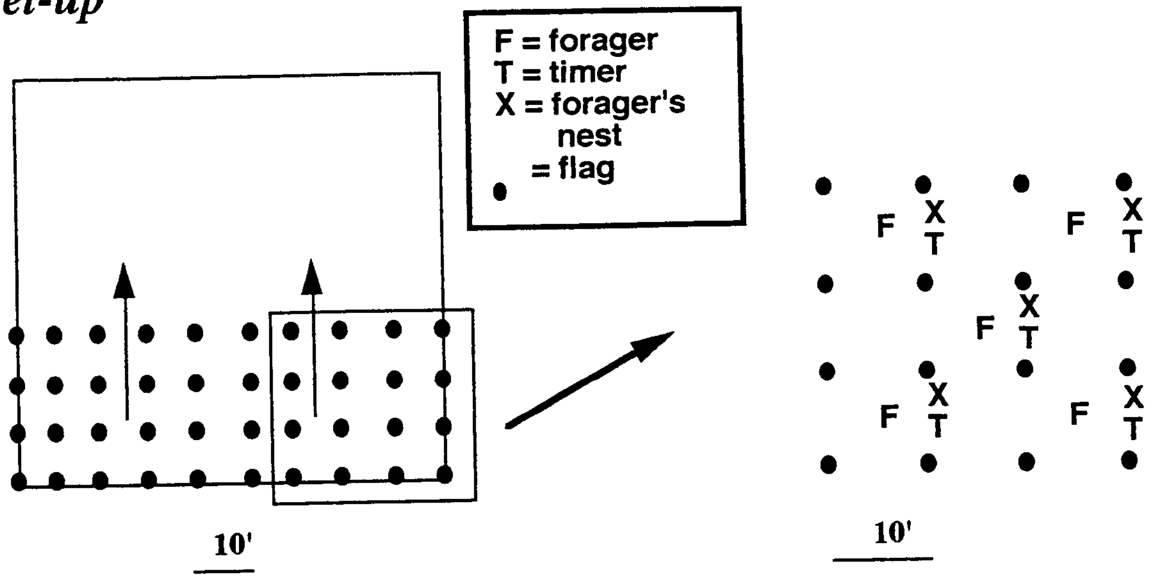
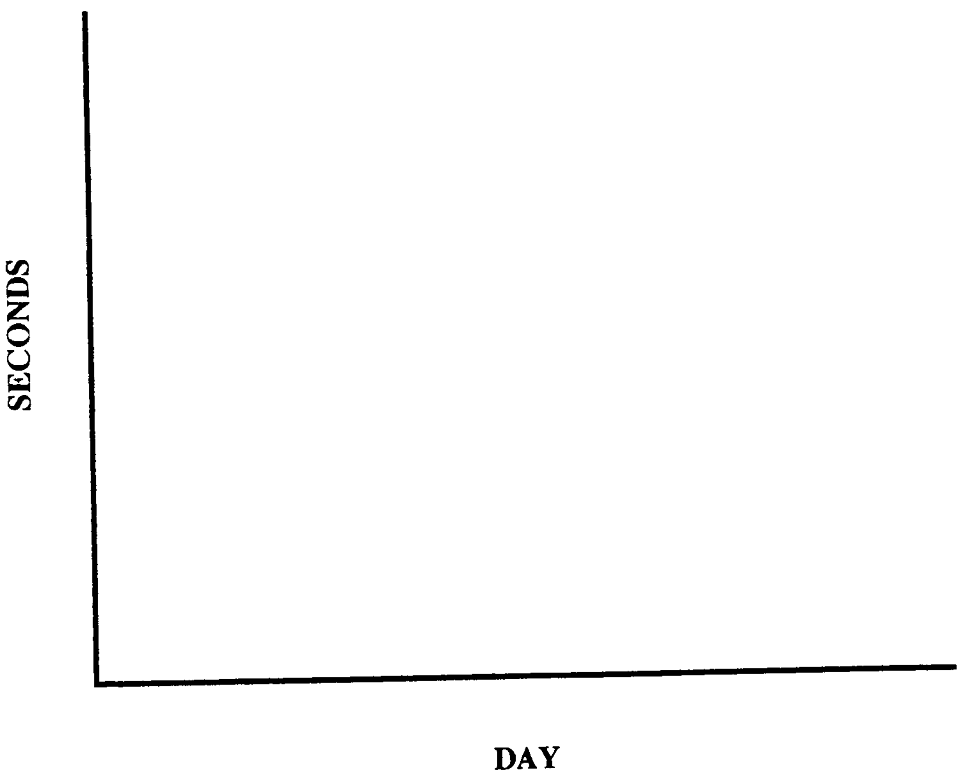


Figure 1. Outline of grid for foraging activities. Surveyor flags are placed at 10-foot intervals within a grid that can be made using three 100-foot tapes to mark three sides of a square. The grid can be completed by moving the middle tape up between the other two. Foragers use alternate squares within the grid, thus food is not placed in any adjacent squares.

CLASS DATA
issue # 1



DATA SHEET for Testing Issues in Foraging and Flocking: Issue # ________

student	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	$\bar{X}$[1]	$\bar{X}$[2]	$\bar{X}$[3]
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1 = Mean using time only for day the students survived.
2 = Mean using 60 for the day a student dies and every day after that.
3 = Mean using 60 only for the day a student dies.

Comments concerning field site:

same graph mean foraging time for all living and dead class members for each day until all individuals are dead.

questions

1. How do the foraging times of more skilled foragers (emphasized by analysis method 1) contrast with the times of the less skilled foragers (emphasized by analysis method 2)?

2. In what situations would you expect the population of foragers to go extinct? In what situations might the prey populations go extinct?

PROCEDURAL VARIATIONS

ISSUE # 2

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

change the habitat

1. Four to six of you will repeat the basic procedure in a different habitat, one with taller vegetation or greater vegetational density.

2. Graph these data in the manner similar to that described for the basic procedure. To compromise between the two methods, plot the mean number of seconds foragers used to find 5 pieces of macaroni plus 60 seconds for the one day an individual dies. Recalculate the data from issue #1 using this method and plot it on this same graph. Use only the times from issue 1 for students participating in issue 2.

questions

1. What do the two sets of data show about the ease of foraging in the two habitats?

2 Explain how population density (of foragers, of prey) and habitat quality might interact to facilitate or hinder foraging activity.

DATA SHEET for Testing Issues in Foraging and Flocking: Issue # ________

student	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	$\bar{X}$
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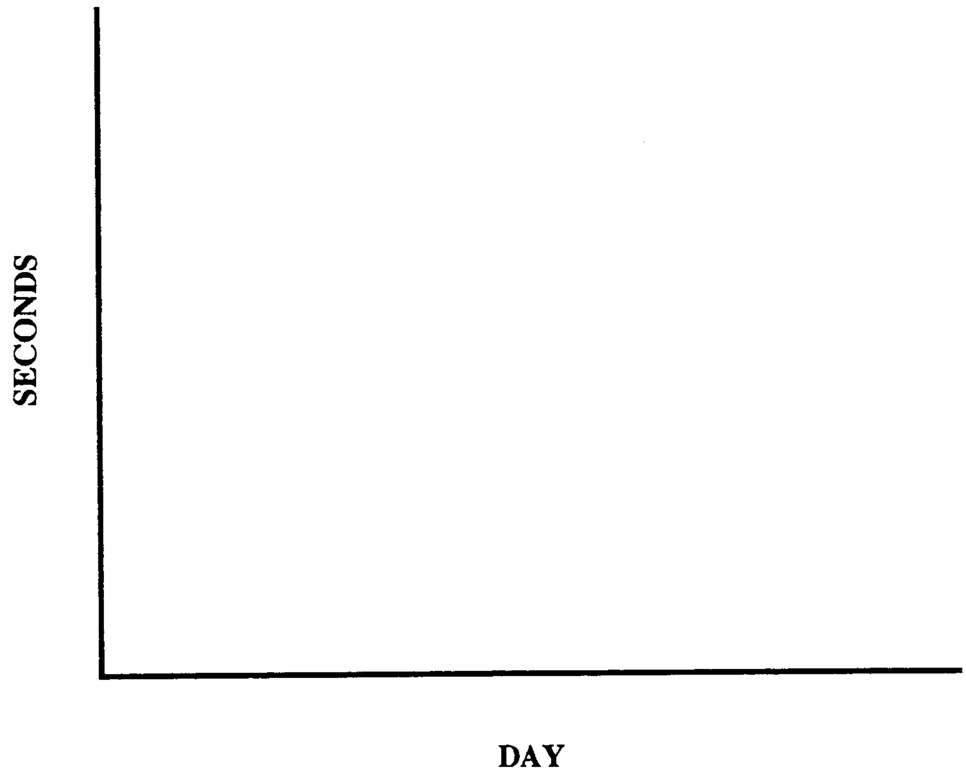
Comments concerning field site:

CLASS DATA
issues # 1 & 2



ISSUE # 3

experienced foragers

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

1. Four to six of you will repeat the basic procedure in the habitat used for issue # 1.

2. Plot the mean number of seconds foragers used to find 5 pieces of macaroni plus 60 seconds for the one day an individual dies. Recalculate the data from issue #1 using this method and plot it on this same graph. Use only the times from issue 1 for the student participating in issue 3.

questions

1. Were the foragers more efficient after having previous experience? If so, how much longer did they live? Did they take less time each day to find their food?

2. Speculate on the relative success with this exercise with humans aged 2, 4, 10, 20, 50 and 80. What is the difference in ability based on age and ability based on experience?

DATA SHEET for Testing Issues in Foraging and Flocking: Issue # ________

student	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	$\bar{X}$
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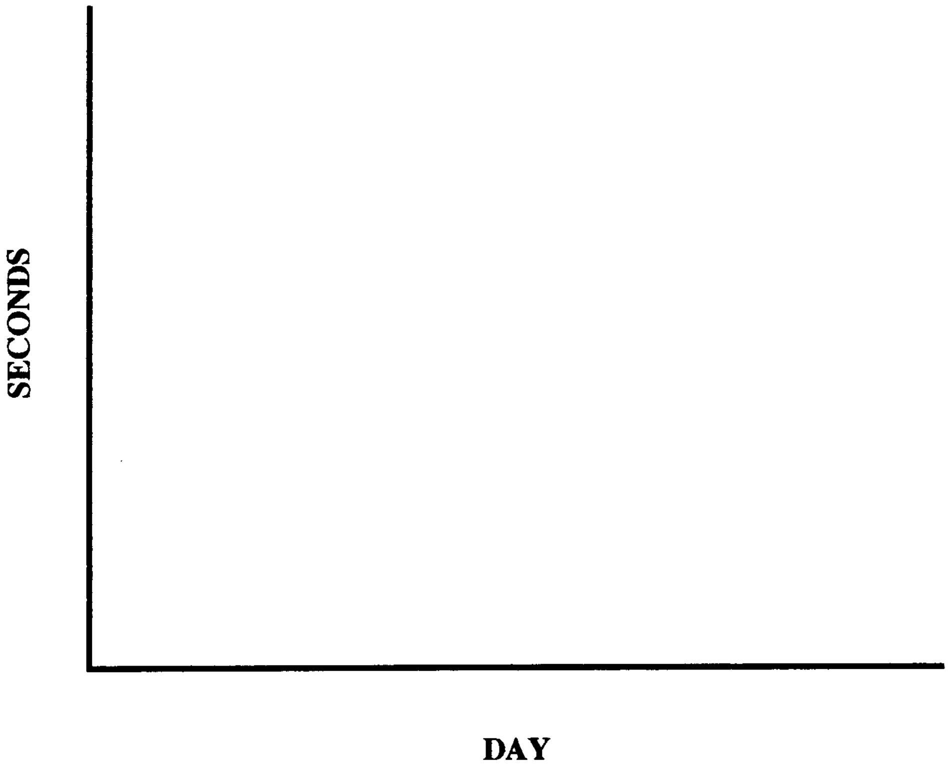
Comments concerning field site:

CLASS DATA
issues # 1 & 3



ISSUE # 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?

exclusive ranges

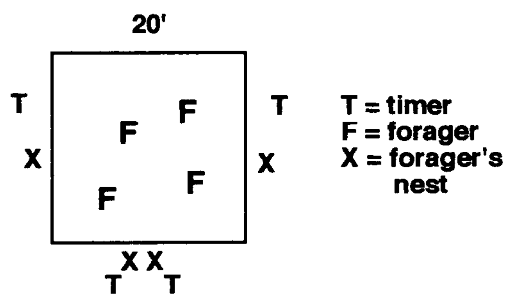


FIGURE 2. Positions of timers, foragers, and nests for testing issue #4.

1. In two or three teams of eight (4 foragers, 4 timers) you will forage together in a separated area following the design shown in Figure 2. All 4 will begin together in a square 20 feet on a side (400 ft^2) in which one timer has scattered 400 pieces of macaroni.

2. Timers - One of you will start all 4 foragers together for each day. Then, each timer will keep track of the time it takes his/her forager to find 5 pieces of macaroni.

3. Foragers - After finding 5 pieces of macaroni and leaving them at your nest you may return to the foraging area to mildly harass the

DATA SHEET for Testing Issues in Foraging and Flocking: Issue # ________

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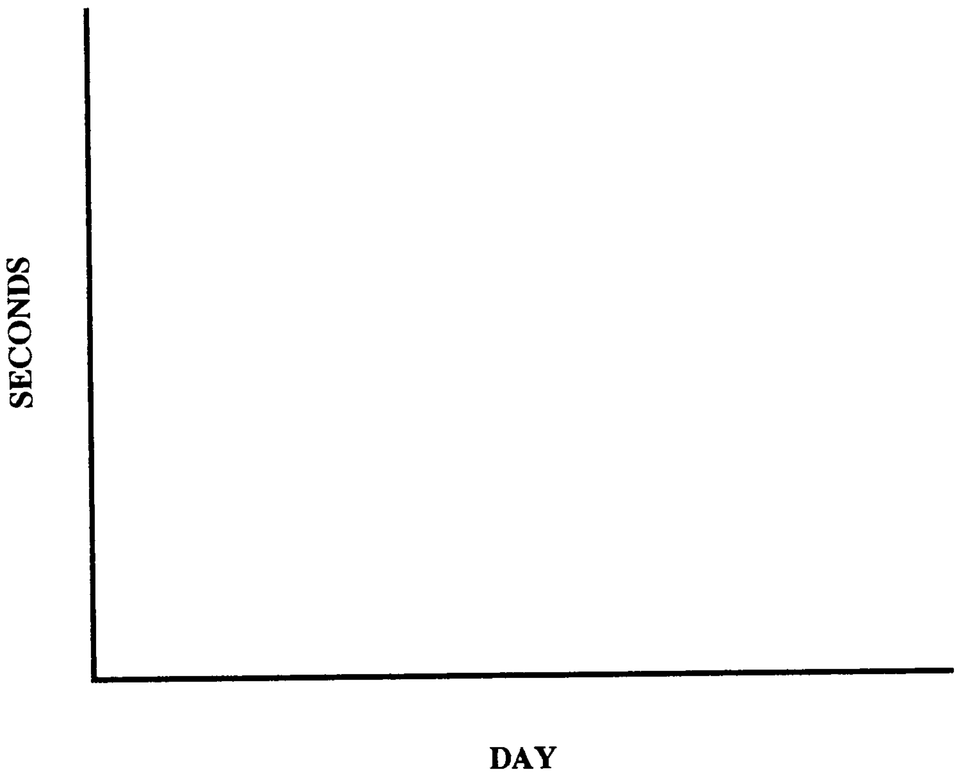
Comments concerning field site:

remaining foragers until they have found their food.

2. Plot the mean number of seconds foragers used to find 5 pieces of macaroni plus 60 seconds for the one day an individual dies. Recalculate the data from issue #1 using this method and plot it on this same graph. Use only the times from issue 1 for the foragers that are involved in issue 4.

CLASS DATA
issues 1 & 4



questions

1. Is the mean day of death sooner or later in this system of interference competition than in the first foraging activity? Explain.

2. How did the harassment from other foragers influence foraging success?

ISSUE # 5

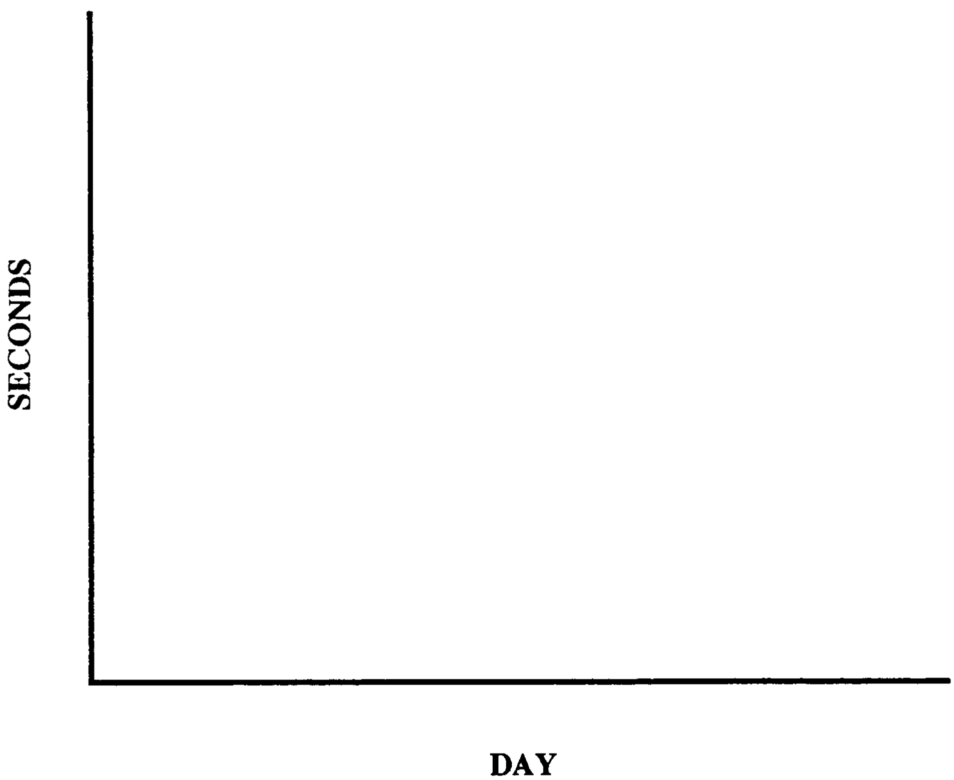
food density

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

1. Three to six of you will forage individually in squares of different sizes: 14' 2" on a side (200 ft^2), 17' 4" on a side (300 ft^2) and 20' on a side (400 ft^2). The habitat and foraging rules are the same as in the basic procedure.

2. Plot the mean number of seconds foragers used to find 5 pieces of macaroni plus 60 seconds for the one day an individual dies. Recalculate the data from issue #1 using this method and plot it on this same graph to show the results from the 100 ft^2 square area.

CLASS DATA
issues 1 & 5



questions

1. How does the density of food affect the foraging rate?

2. At which food density would you expect a predator to survive the longest?

3. Would you expect animals to defend territories with more food in them when the food is less densely spaced and harder to find?

DATA SHEET for Testing Issues in Foraging and Flocking: Issue # ________

food density	1/2 per ft^2								1/3 per ft^2								1/4 per ft^2							
student	1	2	3	4	5	6	7	$\bar{X}$	1	2	3	4	5	6	7	$\bar{X}$	1	2	3	4	5	6	7	$\bar{X}$
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Comments concerning field site:

ISSUE # 6

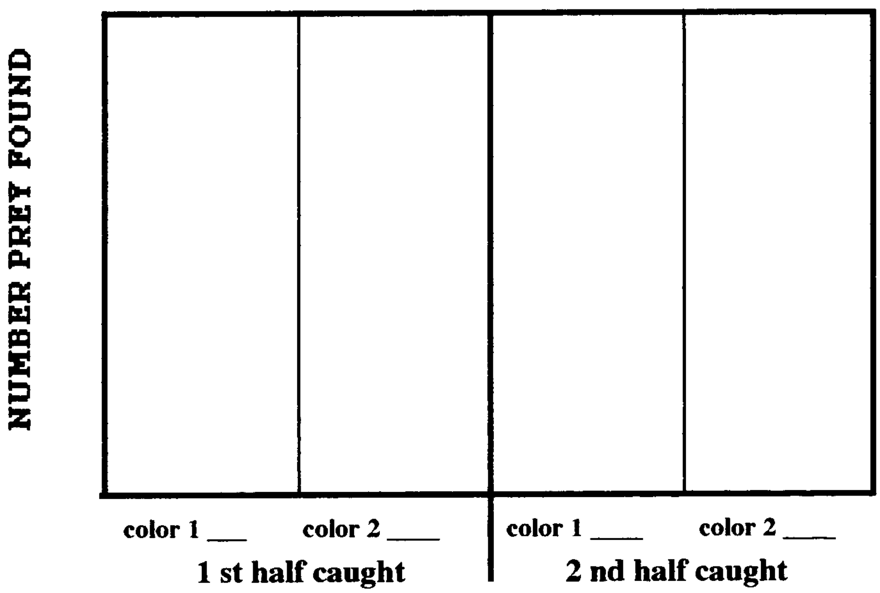
camoflage (cryptic coloration)

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

1. Four to six of you will forage on 50 pieces of macaroni matching the vegetation in color and 50 pieces contrasting in color to the vegetation (in 100 ft^2 squares). Record the number of each type of food found each day as well as the number of seconds it takes to find 5 pieces of any kind.

2. For each forager divide the number of days survived in half. Add up all the food of each color for the first half and then do the same for the second half. If the forager survived an odd number of days, do not count the food on the day that would be split into the two halves. Then add all the food from all the foragers for each color for the first half and then the same for the second half of their survival time and plot the totals in the graph below.

CLASS DATA
issue # 6



questions

1. What is the advantage of cryptic coloration? Is it as significant in the second half of the foraging period as it is earlier in the foraging period?

2. In what circumstance might a contrasting (brighter) color be a protective color?

DATA SHEET for Testing Issues in Foraging and Flocking: Issue # ________

student day	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
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A	
B	C

A = seconds used to find 5 food items of any color
B = number of food items of color 1 found that day by that student
C = number of food items of color 2 found that day by that student

Comments concerning field site:

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?

ISSUE # 7

specialization

1. To test this issue, you will become specialists for one of the 4 types of prey (food items). Divide the class into four equal groups. Each group of individuals will specialize on foraging on a different type of food.

2. Foragers - First, each of you will forage separately in different 100 ft^2 areas on 100 pieces of your special food. You represent 4 different species, each specialized to eat a different type of food. Timers record number of seconds to find 5 pieces of food each day. Duplicate the DATA SHEET as needed for class size.

3. Every member of the class will then forage separately in a 100 ft^2 area where there are 25 pieces of each of the four types of food. Foragers take the first five pieces of any kind of food they see each day. Timers record the number of each type of food found each day and the number of seconds it takes to find the 5 pieces of any kind of food. Duplicate the DATA SHEET as needed for class size.

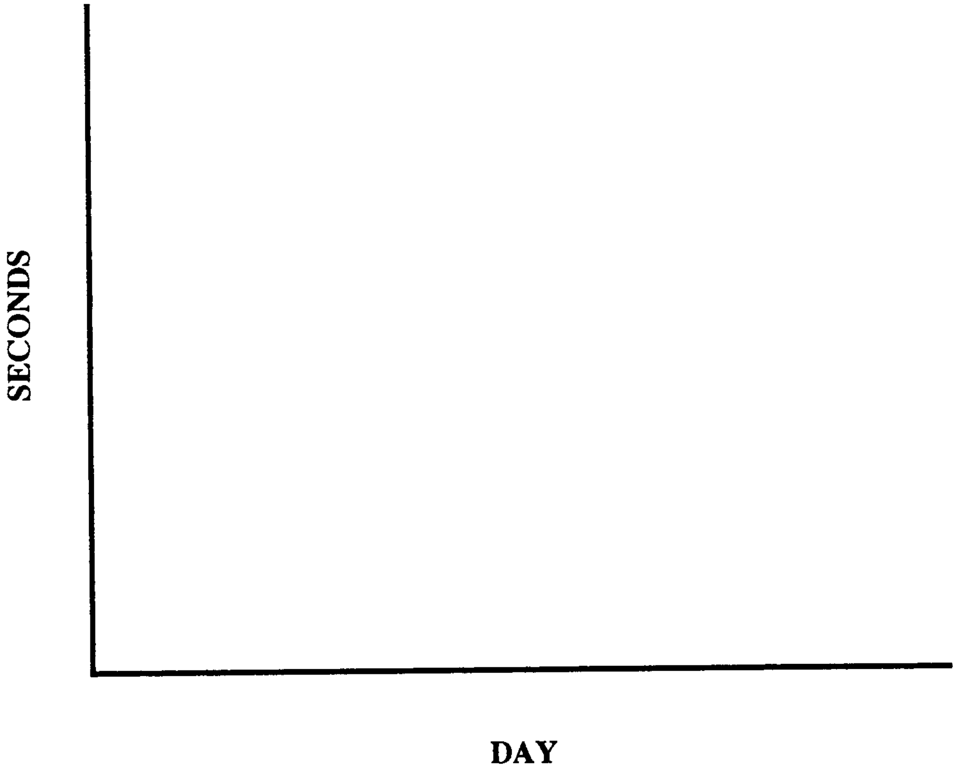
food type

4. Some types of food are found and picked up more easily than other types. To demonstrate the differences among food types, plot the mean number of seconds foragers used to find 5 pieces of their food speciality on each successive day when they forage on only their specialty. Use only the times for days in which foragers found the 5 units of food.

experience

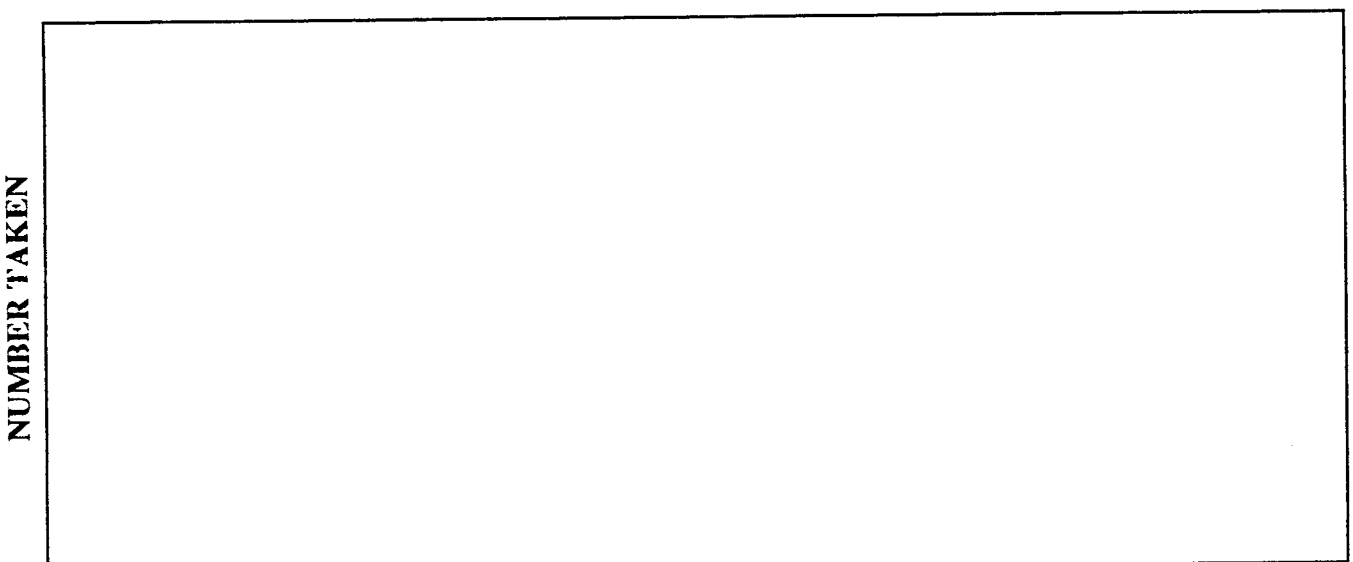
5. Experience is finding one type of food may make a forager more likely to find that food among other types of food than would a forager without experience in finding the first food type. To test for this possibility, consider only the first half of the number of days each forager lives when foraging on a mixture of 25 pieces of each type of food. Make a separate bar graph for each type of food specialist. Plot four bars on each graph. The first bar is the number of items of the specialty food type found by all the specialists for that type of food (i.e., all the navy beans found by navy bean specialists). The second bar is the sum of all the other food items found by this specialist (i.e., non-navy bean food items found by navy bean specialists). The third bar is all the specialty food items found by non-specialists (i.e., navy beans found by non-navy bean specialists). The fourth bar is all the non-specialty food items found by non-specialists (i.e., non-navy beans found by non-navy bean specialists.).

CLASS DATA
issue 7:
food type



CLASS DATA issue 7: experience

For each forager circle the # indicating his/her specialty.



food	other	food	other	food	other	food	other	food	other	food	other	food	other	food	other
1	food	1	food	2	food	2	food	3	food	3	food	4	food	4	food
specialist		non spec.		specialist		non spec.		specialist		non spec.		specialist		non spec.	
FOOD 1				FOOD 2				FOOD 3				FOOD 4			

FOOD AND FORAGING SPECIALTIES

DATA SHEET for Testing Issues in Foraging and Flocking: Issue #7, Food Type ________

student	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
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Comments concerning field site:

DATA SHEET for Testing Issues in Foraging and Flocking: Issue #7, mixed diet

student	1				2				3				4				5				6			
food type	M	K	P	N	M	K	P	N	M	K	P	N	M	K	P	N	M	K	P	N	M	K	P	N
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M = macaroni
K = kidney bean
P = pinto bean
N = navy bean

Comments concerning field site:

questions

1. Which types of prey are found most easily? Does the ease of finding prey relate to their size, their color, or both?

2. For a given food, do specialists on that food find a higher proportion of it in mixed food communities than nonspecialists find? In other words, is bar 1 divided by bar 2 a larger value than bar 3 divided by bar 4 for each food type?

3. Considering the results from testing issue # 7, would you argue that prey type or foraging experience is more important in determining which prey a forager will select more often? Explain your reasoning.

ISSUE # 8

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

adding hawks

1. Mark out two rows of four 400 ft^2 foraging areas parallel to each other. Place rows of flags at about 40 and 80 feet from each of these rows of foraging areas (Figure 3). One end of the rows of foraging areas should be about 40 ft from a gully or a row of trees or shrubs and a row of flags should be placed about 20 ft from the gully (Figure 3).

2. Timers - Scatter 400 pieces of each of the 4 types of food from the previous experiment in each square in one of the rows (Row A). Each "day" one of you will start all 4 foragers then individual timers will record the time it takes your forager to find 5 pieces of food that day.

foraging in a flock

3. Foragers - Each of you are specialists and you can only use your own food type. You will forage together in one square. On successive days you will rotate to the next square until all 4 squares have been used then return to the original square to repeat the pattern.

slow and fast hawks

4. Hawks - A group of you will hide in the gully and act as 'slow hawks". Another group acting as "fast hawks" will wait in the open behind the line 80 ft 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.

5. An attack is initiated when a slow hawk leaves the gully or a fast hawk crosses the 80-foot line. An attack is successful if a slow hawk crosses the 20-foot line of flags or the fast hawk crosses the 40-foot line of flags before any of the foragers give an alarm call. A judge will stand at each line and yell "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. The hawk will designate the forager that has been killed and the timers will keep track of whether their forager has been killed. If any one of the foragers gives an alarm call by yelling "hawk", he/she and all other foragers are assumed to be saved by the warning. If a forager is killed or starves, he/she is allowed to be revived for the next day. This activity will continue for a preset number of days, then you will change to the second row of squares (Row B).

6. After you have found 5 food items, keep foraging and looking for the hawks at the same rate so that you will not be able to serve as a sentinel for other hawks.

foraging separately

7. Foragers - When using the second row (B) of squares, each of you will search in a different square. You will rotate to another square each day so that the same amount of food depletion and movement will occur in these squares as in Row A.

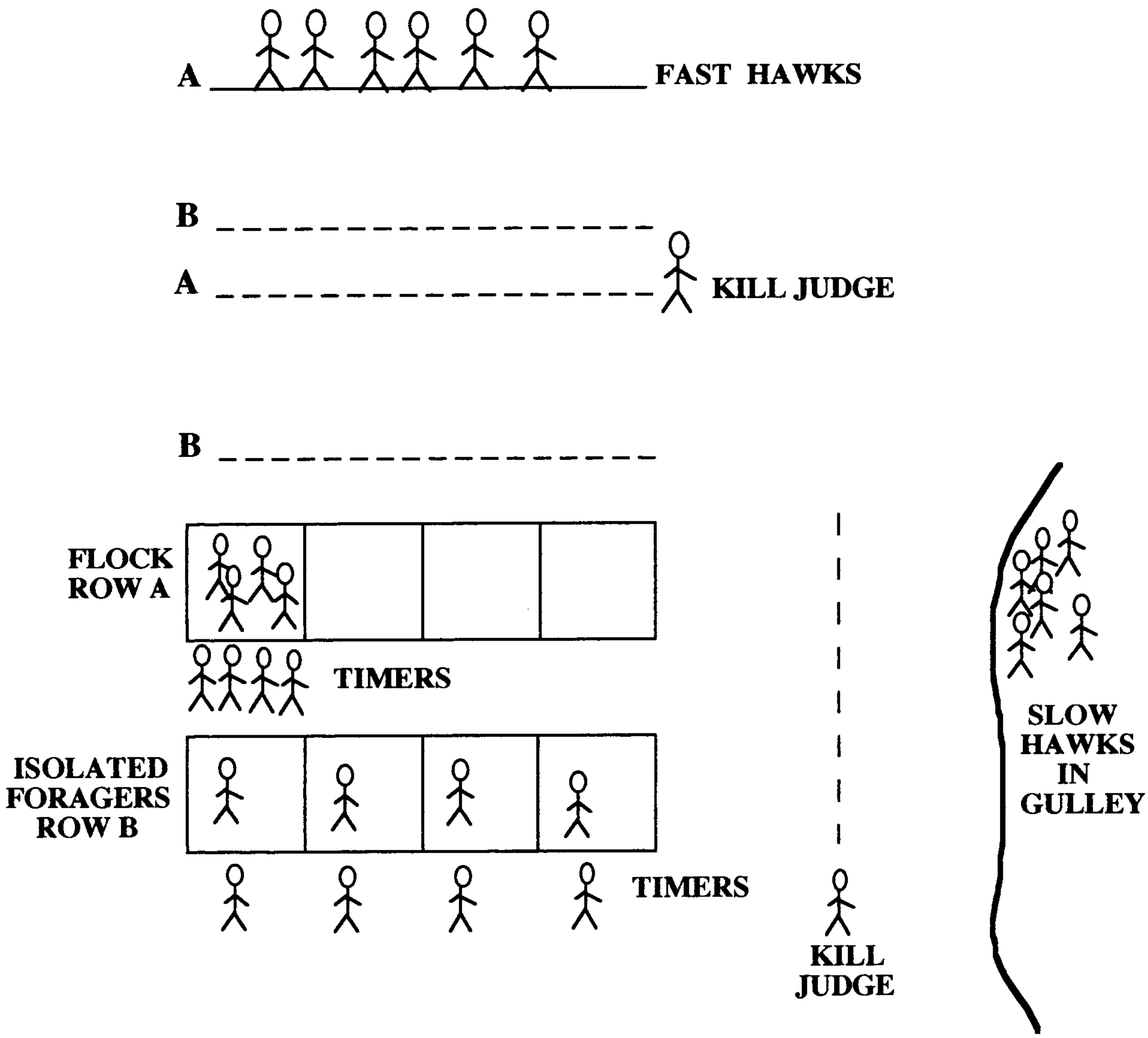

FIGURE 3. Map of placement of foragers, timers, hawks and kill judges during the test of the advantage of mixed species foraging flocks over isolated foraging by individuals. The solid line A is the starting line for fast hawks and the dashed line A is the kill line for fast hawks when attacking foragers in the row of foraging plots marked A. The lines and foraging plots marked B are used in the second half of the experiment.

DATA SHEET for Testing Issues in Foraging and Flocking: Issue #8

	FLOCK												ALONE											
student	1	2	3	4	5	6	7	8	9	10	11	12	1	2	3	4	5	6	7	8	9	10	11	12
food	M	K	P	N	M	K	P	N	M	K	P	N	M	K	P	N	M	K	P	N	M	K	P	N
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M = macaroni
K = kidney bean
P = pinto bean
N = navy bean

Comments concerning field site:

8. As isolated foragers you will not give alarm calls, instead you will give a hand signal to your timer that you have seen the hawk. The hawk should have only one forager in mind and only register a kill if that forager has not signaled.

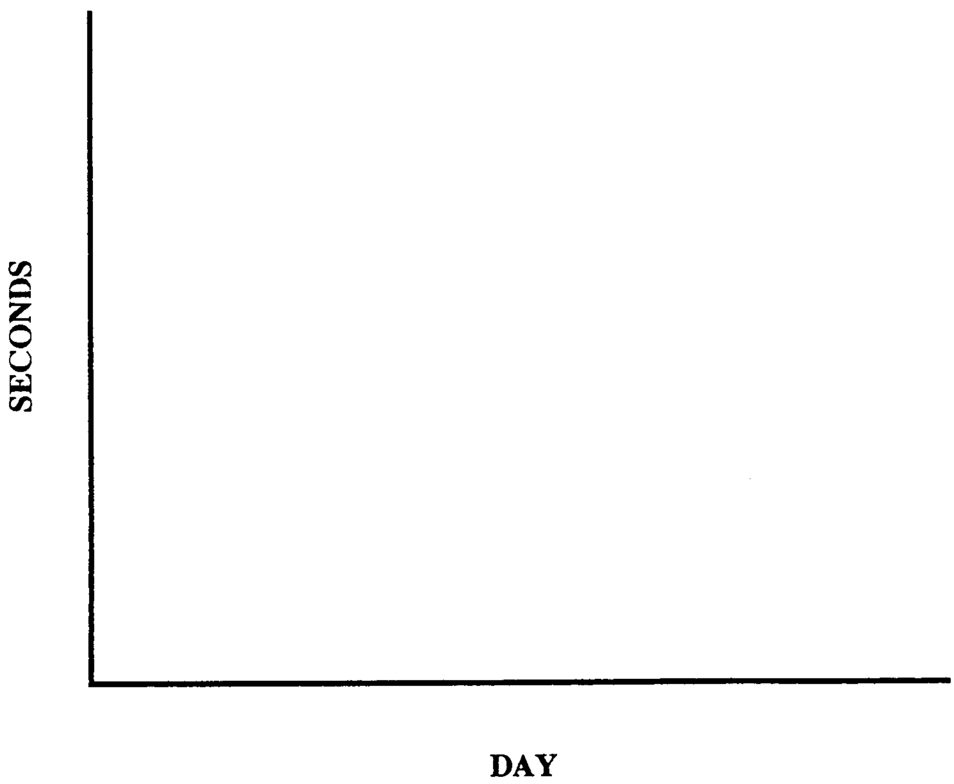
9. After finding 5 pieces of food, individual foragers should return to the safety of their nests.

10. For each foraging procedure (as a flock, individually) plot the mean number of seconds foragers used to find 5 pieces of food and use 60 seconds for any day an individual starves. Do not use times for days when a forager is killed by a hawk.

1. Which foraging strategy was more effective? Explain.

question

CLASS DATA
issue # 8



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NOTES TO INSTRUCTORS

GENERAL COMMENTS

using the prairie

These field exercises were developed so that the students could have first-hand experience in simulating the problems animals face when foraging and at the same time avoiding their own predators. Time, space, and food requirements are condensed to allow the simulations to occur in two 3-hour lab periods, but the results are usually consistent with theories supported by empirical evidence from field studies of other animals. All of the exercises are modifications of one basic foraging design. The selective factors influencing each of the issues are simulated by varying the appropriate conditions.

In March on grazed Kansas prairie vegetation, the first six issues are performed in the first lab and the last two in the second. The weather can often be cold and windy and the labs run from 2:30-5:30 P.M. The students are eager to get home for supper. One year a light snow started midway through the lab, but the students kept working so that we could measure a very distinct effect of snow cover. Many factors are important in affecting the results of the experiments and these are incorporated into discussions of how well the results simulate natural populations.

sparrows and wrens

For the students to get a better feel for the difficulties natural populations experience, they are given a vial at the end of the first lab, half are told 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 and M/s. Most students who look for seeds do not expose the kernels and are disqualified in spite of an earlier warning.

flexible design

The basic design is very flexible and can be adjusted to the class level of the students and to the local vegetation. The lab has worked with brown dyed macaroni on the leaf litter of a forest or with yellow macaroni on the short green grass of a campus lawn. One year the prairie vegetation was so dense the daily food requirements needed to be reduced to 3 pieces of macaroni.

potential additions

The lab has been used by high schools and college freshmen as well as for 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 only by the imaginations of the instructor and students.

It is **important** that before doing these exercises in class, the instructor thinks through them carefully to decide how they can best be done in the local situation. My (the author's) worst problem in teaching these labs has been in devising too much for the students to do during the lab and not spending enough time in discussing the issues or involving the students in developing their own experiments.

SETTING UP THE LAB

the prey

1. Before the laboratory period the instructors need to do two things, 1. measure out macaroni or other foraging items into groups of 100 pieces 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 of each different food type must be counted separately.

making the grid or "checkerboard"

2. Making the grids of surveyor flags requires some method of ensuring that the grids are square. The right angles can be made by a 3-4-5 right triangle. Another method is to make one side of a 100 ft square, placing flags at 10 foot intervals and then to use a sextant or sighting compass set at 90^0 to sight the other sides of the square. Once three sides of a square are marked 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 (see Fig. 1 in the lab exercise pages). 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 checkerboard with students only using alternate (i.e. the black) squares to forage. A 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 and by making squares in grids, large numbers can be made quickly.

summary of basic procedure

3. During the actual laboratory period students are taken to the field side, asked to work in groups of two, and assigned to squares of the grid. 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 he/she scatters it throughout the 100 square feet of the 10 x 10 food square. The forager then starts at the edge of the square and on cue from the timer enters the square

and searches until 5 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 5 pieces of food in 60 seconds at which time she/he has starved to death. The students are told that 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 each day. Once the first forager has died, the pair can be assigned a new square and their roles reversed.

4. During the first 3-hour lab have each student in the class forage for the first issue so that there will be a background time to compare against for other issues. For issues 2, 3, an 6 and each density in issue 5 only one fifth of the students need to be involved if the class has 20 or more students. Issue 4 need be done by only 2 or 3 groups of 4 foragers. The times for issues 2 - 6 should be compared against the times for the same specific students in issue 1 to reduce the effect of differences in student ability. By reducing the number of students in issues 2 - 6 the actual field time can be reduced to less than 2 hours. During the second 3-hour lab each student forages once on his/her specialty food and once on a mixture of the 4 types of food used for issue 7. For issue 8 the flock and individual foragers are each allowed to forage 16 or 20 days to make 4 or 5 cycles of the 4 foraging squares. Small 3 by 5 inch spiral notebooks are handy for recording the data in the field as long as students are careful to write their name and the issue by each series of days and times. The data can be transferred to the summary data sheets back at school.

SPECIFIC ISSUES

ISSUE #1

the length of winter

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 (see example data) 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 sparce, there will be an appreciable amount of prey undiscovered when all the students have starved (approximately 1/3 of the food in the example data). Figure 4 shows some example data plotted for issue # 1.

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. 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 hawks are added 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 Wiens (1977) have generated controversies 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 may lead to erroneous conclusions about natural populations.

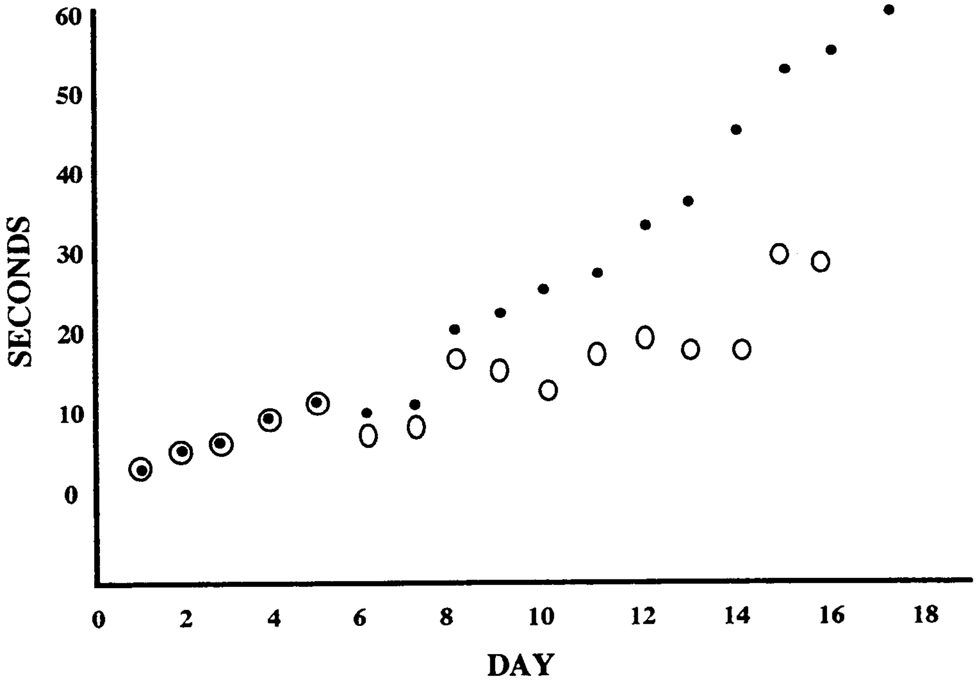
DATA SHEET for Testing Issues in Foraging and Flocking: Issue # 1 - example data

student	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	AVE
day																							
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				50	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	60.0
18																							

Comments concerning field site: grazed Kansas tallgrass prairie - starting food supply 100 pieces of macaroni.

Forage times (seconds) for 22 students to find 5 pieces of macaroni in 100 square foot area. Students foraged on successive days until the day they could not find 5 pieces of macaroni within 60 seconds and were assumed to have starved to death. The winter period of no food renewal was assumed to be 12 days long.

FIGURE 4.
example data
issue # 1



Plot of mean number of seconds students used to find 5 pieces of macaroni on successive days. Circles are means for days in which students survived by finding 5 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.

ISSUE # 2

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

vegetation density and prey density

Choosing markedly denser vegetation will help counteract the improvement in foraging that students gain from experience. When the difference in foraging is less marked than in Figure 5, 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.

ISSUE # 3

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

extended survival

In the past two 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

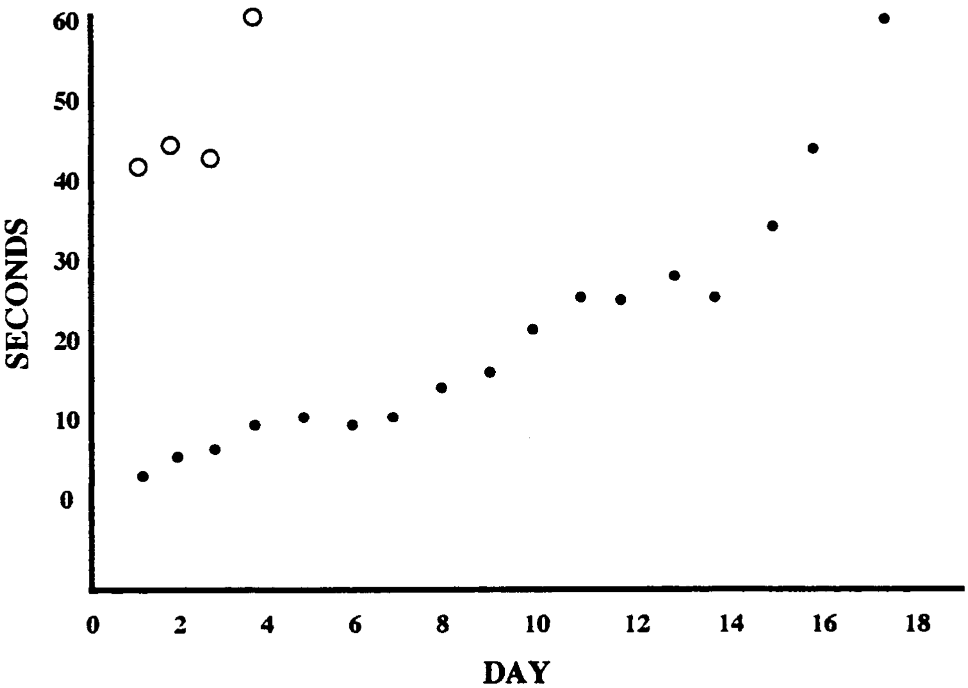


FIGURE 5.
example data
issue # 2

Plot of mean number of seconds students used to find 5 pieces of macaroni on successive days in short, grazed and in tall, ungrazed prairie vegetation. Sixty seconds was used as the time on the day a student died, but not on following days.

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 the natural population, but it is good for encouraging students to be critical.

ISSUE # 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?

competition

The mean day of death has been 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 1 of 3 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.

position effects

In the design for this experiment, two of the four nests for student foragers are beside each other and two are more isolated (Fig. 2). This is intended to get the students to think about position effects on competition, but the distances are too small to have a significant effect.

references

Theoretical considerations of central place foraging (Smith, 1968; Orians and Pearson, 1979) and the costs and benefits of territorial defense (Davies, 1978, Seastedt and MacLean, 1979, Carpenter, 1987 [and following papers]) 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.

ISSUE # 5

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

food density

There is always a tendency for foraging time to increase and survival time to decrease with decreasing food density (Fig. 6). The change in foraging time is not, however, proportional to the area in which the macaroni is dispersed. Considerations of how traveling 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).

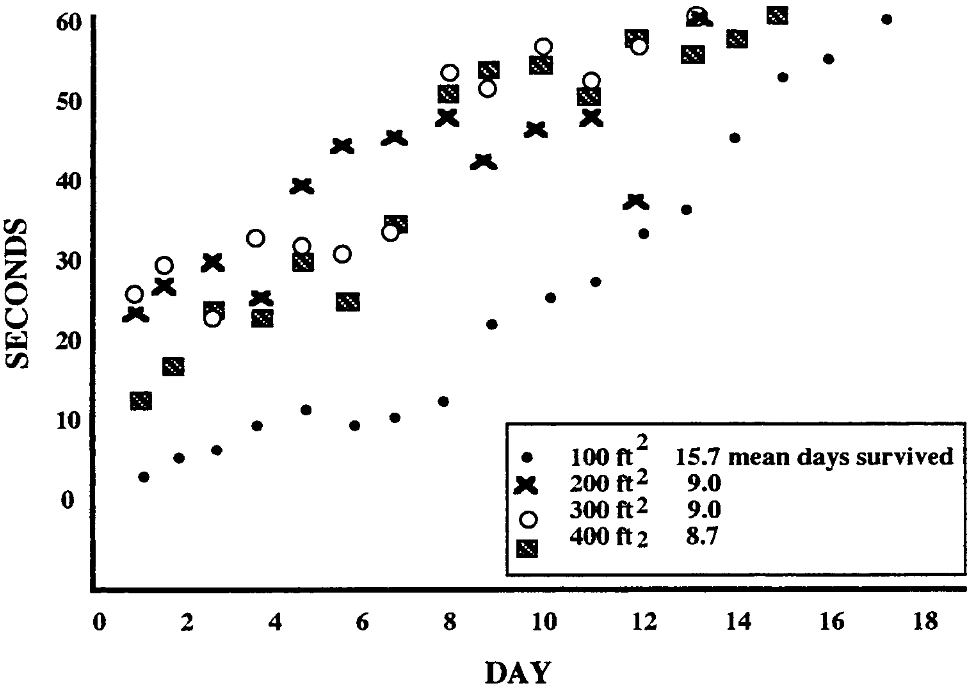
ISSUE # 6

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

prey color

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

FIGURE 6.
example data
issue # 5



Plot of mean number of seconds students used to find 5 pieces of macaroni on successive days in areas with different food density. Sixty seconds uas used on the day a student died, but not on following days.

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 bar graph can be drawn as suggested in the students' directions or a contingency 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 (Fig. 7). There is almost always a tendency for the cryptic color to be found less frequently than the non matching color in the first half of the food items found, but the difference is statistically significant less than half 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 vege-

data analysis

using insects

tation. 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). Keep track for 100 insects 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 students found by searching the vegetation. Alfalfa fields with aposematic ladybird beetles and cryptic aphids give excellent results, but the comparison works just about anywhere.

references

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). None the less, the comparison of cryptic and aposematic species does give a quick demonstration that color influences the ease with which visual predators find prey. 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).

FIGURE 7. contingency test for issue # 6

	RED	YELLOW
FIRST 10 DAYS	163 (149.5)	137 (150.5)
AFTER DAY 10	125 (138.5)	153 (139.5)
	$X^2 = 5.05$	$X^2 < 0.05$

A 2 by 2 contingency test to test whether conspicuous red macaroni was found more often during the first half of students' 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 parantheses are the expected numbers, compared with the observed numbers above them.

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?

ISSUE # 7

special problems

As with the previous exercise, there is the problem with nonrenewed food supplies; as the more easily found food is taken it becomes a smaller fraction of the remaining food. To help with this problem, only the first half of the food found by each student is considered as the advantage of experience is more likely to show up when most of the food is available. There is a second problem; because of size and color differences, some types of food are easier to find than others (Fig. 8). To factor these differences out from consideration of the influence of experience, 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

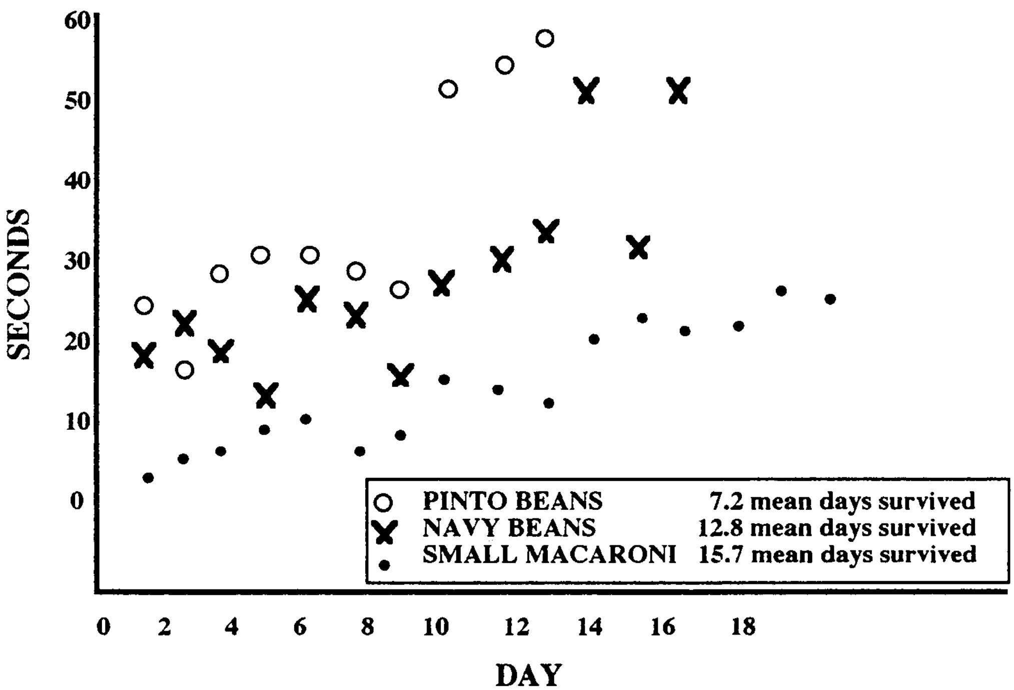


FIGURE 8. example data issue # 7

Plot of mean number of seconds students used to find 5 pieces of their food specialty on successive days in a 100 ft^2 area. The plot for kidney beans is nc shown because it was so close to small macaroni used in all other experiment except protective coloration. Only the times for days in which foragers found 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.

data analysis

the food or by someone with no such experience. A bar graph can be used as suggested for the students or a contingency test may be used (Fig. 9). The results tend 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. However, this experiment gets students to think about the issue and it also sets up the next experiment which usually gives good results. Some of the considerations for learned search images are

references

found in Pietrewicz and Kamil (1981) and Gendron and Staddon (1983).

FIGURE 9.
contingency test
for issue # 7

	EXPERIENCED FORAGER	OTHER FORAGERS
EXPERIENCED FOOD	313 (296.3)	872 (888.7)
OTHER FOODS	872 (888.7)	2683 (2666.3)
	$X^2 = 1.67$	P = .20

A 2 by 2 contingency test to test whether food, for which foragers have more experience, is taken more often than foo for which foragers have less experience. Values in parentheses are the expected numbers, compared with the observed numbers above them.

ISSUE # 8

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

adding hawks

In this exercise a hawk should have only one forager in mind when attacking and only register a kill if that forager has not signalled. To make the simulation realistic, ask the students in the flock to keep foraging and looking up for predators at the same rate after they have found 5 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 2), but that is not realistic because the hawk would only have a chance to kill one isolated prey. Table 2 does represent an advantage for giving an alarm call within the hearing of close kin.

references

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 groundsquirrels.

TABLE 2. Foraging times (seconds) and predator success (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. See the text and Figure 3 for details.

	Foragers in Mixed Flocks				**Individual Foragers**			
food	pinto	navy	macaroni	kidney	kidney	pinto	macaroni	navy
student	Shane	Shanon	Dave	Kevin	Allen	Laura	Rene	Phil
day								
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
ave	31.8	27.7	25.6	24.6	33.8	29.1	34.0	23.7
	1 death by starvation 5 deaths by predation				4 deaths by starvation 13 deaths by predation			

EXPERIMENTS TO TEACH ECOLOGY FEEDBACK FORM

FORAGING AND FLOCKING BEHAVIOR

Please complete this form after you have used this experiment and mail it to the address given on the reverse side of this page.

1. Was the introduction clear and informative? What changes would you suggest?

2. Was the list of materials complete? Would you suggest any additions or modifications?

3. Were the initial set-up directions clear? Are there changes you would suggest?

4. Were the procedures easy to follow? What changes would you suggest?

5. Were the illustrations and data charts adequate? What others would you include?

6. Were the instructor's notes complete? If you noted any omissions, what were they?

7. What level of students used the experiment? Was it suitable for this level? If not, what changes would you suggest?

8. Did your students learn from these experiments? Would you suggest any modifications or additions?

9. On a scale of 1-10, with 10 as outstanding and 1 as terrible, how would you rate this experiment? Would you recommend this experiment to others?

10. Was it helpful for this exercise to have been written for the student rather than as an instructor's guide?

Please mail the completed form to: Dr. Jane M. Beiswenger
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