25 HABITAT SELECTION

In collaboration with David N. Bonter

Objectives

- Develop a spreadsheet model of ideal-free habitat selection.
- Compare the ideal-free and ideal-despotic habitat selection models.

INTRODUCTION

Imagine it is time for dinner, and you are deciding where to eat this evening. Your options are either ordering pizza or going to the dining hall. You'd prefer pizza, but you know that as soon as the pizza delivery person appears, everyone in the dorm will be interested in getting a piece of your pizza. Although your first choice is pizza, competition for each slice may leave you hungry. On the other hand, you know that there will be plenty to eat at the dining hall. It may not be pizza, but at least you won't be hungry while studying tonight. Which do you choose? Does it depend on how many friends are in the dorm tonight?

Similarly, organisms must routinely choose between habitat patches that present different opportunities for meeting foraging and other resource needs. The choice between the dining hall (suboptimal forage) and pizza delivery (optimal forage) is analogous to the choice between habitat patches, where the number of people in the dorm is the density of organisms within the habitat. Competitors may decrease an organism's intake through interference or by reducing the resources available in a patch through exploitation competition. Facing these circumstances, an organism may do better by moving to a patch with fewer competitors, even if the overall resources are inferior. In other words, if your dorm is crowded tonight with many hungry competitors for pizza, you may reach your daily foraging requirements better by eating in the dining hall!

Ideal-Free Habitat Selection

The **intrinsic** or **basic suitability** of a habitat may depend on factors such as food and predators; some patches are higher in quality than others. Individuals that compete for similar resources can reduce this basic suitability, so that "crowded" habitats may be much lower in actual suitability, even if the basic suitability is high. Thus, even though one habitat may be intrinsically "better" than the other, an organism can do equally well in either habitat, depending on the density of individuals within the habitats. This model of habitat selection is known as **ideal-free**, because individuals are assumed to have full or "ideal" knowledge of what the intrinsic suitabilities of each habitat are, as well as the densities in each habitat, and individuals are "free" to select and enter habitats that will optimize their fitness. Hence, individuals make behavioral decisions based on the behavior of other individuals in the population (Fretwell and Lucas 1970).

Numerous assumptions are usually associated with the ideal-free distribution model.

- Individuals are of identical competitive ability.
- Habitat patches vary in quality.
- Competitors are free to move without costs or constraints.
- Each competitor will move to where its expected gains are highest.
- The value of a patch declines as more individuals exploit that patch.
- Maximum patch suitability occurs when the population density approaches zero.

The model predicts that all competitors will experience equal gains and that the average rate of gain in all habitats is equal. In other words, at equilibrium, no individual should be able to improve its situation by moving to another patch.

Obviously, many of these assumptions are violated in the real world, and we will address some of these assumptions later. But the ideal-free distribution provides a sound place to start our model. Mathematically, we can express the **suitability** of the *i*th habitat as a function of its basic (or intrinsic) suitability, modified by the density of organisms in the habitat:

$$S_i = B_i - f_i(d_i) \qquad \text{Equation 1}$$

where S_i is the realized suitability of habitat i, B_i is the basic (intrinsic) suitability of habitat i, and d_i is the density of organisms in habitat i. The term $f_i(d_i)$ expresses the lowering effect on suitability as a result of an increase in density. When f_i is large, each individual occupying the habitat reduces the basic suitability of the habitat by a large amount.

A hypothetical comparison between the suitability of two habitats is shown in Figure 1.

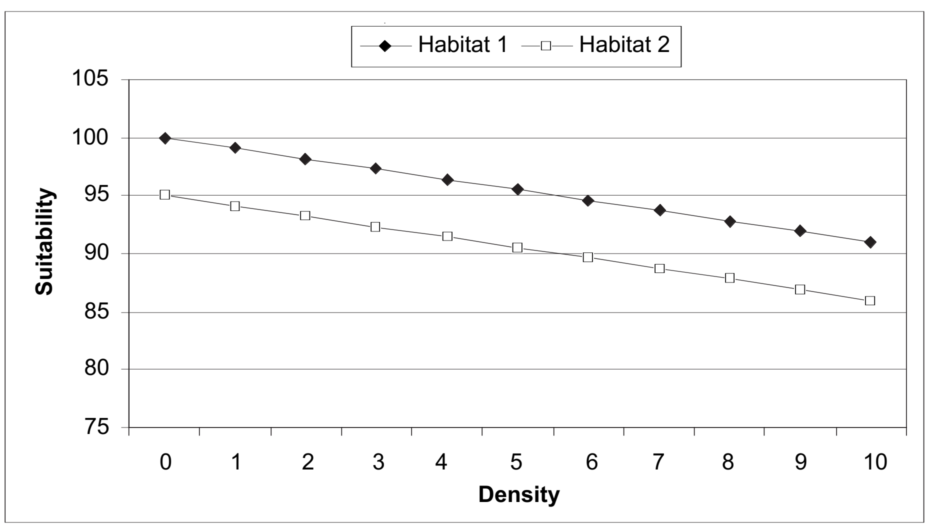

Figure 1 In this example, the basic suitability of habitat 1 is 100 units and that of habitat 2 is 95 units. The amount that each resident lowers suitability, $f_i(d_i)$, is the same for both habitat patches. As individuals begin to colonize the two empty habitats, selecting habitat 1 will maximize their fitness. However, after the first five individuals have established residence in habitat 1, the suitability of this habitat has decreased to be identical to that of habitat 2 (still with 0 occupants). The sixth colonist would do best to colonize habitat 2. This colonist will then reduce the quality of habitat 2 such that habitat 1 will be selected by the seventh colonist, and so on.

Ideal-Despotic Habitat Selection

If individuals are not free to occupy the patch of their choice, we can modify our model of habitat selection and develop the **ideal-despotic** model. In this model, some individuals cannot freely occupy a habitat because other individuals (the "despots," or "dictators") already present in the patch prevent them from colonizing. Thus, for example, decisions of unsettled birds are influenced by the behavior of resident birds—the nonresidents are not always free to select the habitat they want. Mathematically, the lowered suitability of a habitat patch for future colonists due to resident behavior can be expressed by

$$T_i = S_i\,[1 - t(d_i)] \qquad \text{Equation 2}$$

where T_i is the *apparent suitability* of the habitat for the unsettled bird, or how the colonizing individual perceives the quality of habitat *i*. Equation 2 says that the apparent suitability is equal to the realized, or actual, habitat suitability, S_i (calculated in Equation 1), discounted by a factor that takes into account the density of occupants already present in the habitat (d_i) and the resistance of those occupants to new colonists (t). When $t = 0$, the occupants do not resist new colonists at all, and $T_i = S_i$ (there is no despotism). When $t = 1$, the occupants strongly resist new colonists. As long as $t > 0$, $1 - t(d_i)$ is less than 1, and higher densities mean lowered apparent suitability. The relationship between a site's basic or intrinsic suitability, its suitability when population density is factored in (from the ideal-free model), and its apparent suitability (from the ideal-despotic model) is represented in Figure 2.

Various factors can act to decrease the apparent suitability of a habitat patch. Often an organism will have to choose between habitat patches that differ in predation risk in addition to resource availability. We may think that by adding predation risk to habitat selection considerations, the ideal site will have plentiful resources, few competitors,

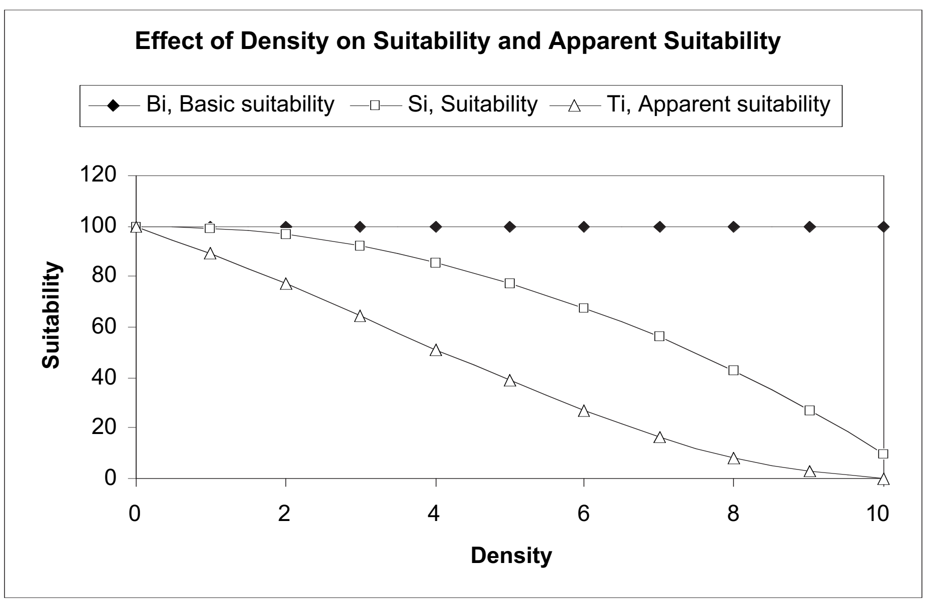

Figure 2 The basic (intrinsic) suitability of a habitat patch is fixed and remains constant regardless of population density. However, this relationship is unlikely to represent conditions in the real world. Basic suitability is often diminished as a function of population density, $f_i(d_i)$, because individuals compete for resources. Here we see that 10 individuals reduce the suitability of the habitat by 90%. If patch residents act to exclude future colonists, the apparent suitability is reduced even further, by $t(d_i)$. In this example, the patch is no longer hospitable to future colonists after 10 individuals have established residence.

and a low predation risk. However, the interrelationships between habitat characteristics may be more complicated. For instance, choosing a patch with numerous conspecifics may reduce predation risk. In this situation, allies in predation avoidance become competitors in resource acquisition. The nature of the relationship between gain and risk with group size will influence which habitat patches are exploited (Moody et al. 1996). Abiotic factors may also impact habitat suitability. Differences in temperature or exposure to wind may produce differential energetic costs in different habitat patches.

PROCEDURES

This exercise presents a simple model that focuses only on a density-dependent decrease in habitat suitability. In this model, competition for resources in "good" patches may result in lower energetic gains due to loss of resources to rivals. In "poor" patches, it may be harder to locate available resources, but less competition may make this choice worthwhile. The ideal-free distribution model often successfully predicts the distribution of organisms in the real world, and has become the basis for more complex models.

In this exercise, you will develop a spreadsheet model of the ideal-free distribution and explore its consequences on habitat selection. You'll also compare the ideal-free model to the ideal-despotic model. As always, save your work frequently to your disk.

INSTRUCTIONS

ANNOTATION

A. Set up an ideal-free model for two-habitats.

1. Open a new spreadsheet and set up column headings as shown in Figure 3.

	A	B	C	D	E	F	G	H	I	J	K	L
1	***Habitat Selection***											
2												
3						**Habitat 1**	**Habitat 2**					
4	***B i* = Basic suitability**				**===>**							
5	***f i* = Lowering effect**				**===>**							
6	***t* = Resistance to settling**				**===>**							
7												
8				**HABITAT 1**						**HABITAT 2**		
9	**Density**	***Bi***	***f * d***	***Si***	***t * d***	***Ti***	**Density**	***B i***	***f * d***	***Si***	***t * d***	***Ti***

Figure 3

2. Enter 100 in cell F4 and 95 in cell G4.

We will consider two habitats, habitat 1 and habitat 2.
Habitat 1 has a higher basic suitability than habitat 2. The values entered reflect the basic or intrinsic suitabilities of each habitat. Remember, these basic suitability scores are based on factors such as food abundance, predators, and so on, when the patches are not yet occupied by colonists.

3. Enter 0.9 in cells F5 and G5.

These values represent *f(i)* for the two habitats, or the "lowering effect" of habitat quality of each new individual occupying the habitat. Each individual occupying a habitat will reduce the habitats' quality by this amount.

4. Enter densities from 0–10 for habitat 1 in cells A10–A20

First we'll focus on habitat 1, then we'll repeat the steps for habitat 2 to examine how basic suitability is lowered as more individuals colonize the different habitats.
Enter 0 in cell A10. Enter **=1+A10** in cell A11, and copy this formula down to cell A20.

5. In cells B10–B20, enter a value for the habitat's basic suitability.

The basic suitability (B_i) for habitat 1 is given in cell F4, so enter the value **=$F$4** in cells B10–B20.
This is the suitability of the habitat based on intrinsic qualities such as the amount of food, number of predators, and so on.

6. In cell C10, enter a formula for the lowering effect of density on the suitability of habitat 1.

This is the value in cell $F$5 times the density (given in cell A10) in habitat 1. So, enter the formula **=A10*$F$5** in cell C10 and copy this formula down to cell C20.
The lowering effect, *f*, is a fixed value currently set at 0.9. For any given density, however, the total reduction in suitability is the product of *f* times the density in the habitat.

7. In cell D10, enter a formula to calculate the realized suitability of habitat 1. Copy this formula down to cell D20.

In cell D10, enter the formula **=B10-C10**. Copy this formula down to cell D20.
The suitability of habitat 1, according to the Fretwell-Lucas model (1970), is $S_i = B_i - f_i (d_i)$. Take a good look at this equation. It says that the suitability of a habitat is its intrinsic suitability (cell B10) minus the density of individuals in the patch times the amount that each individual lowers the basic suitability ($f_i \times d_i$) in cell C10.

8. Repeat steps 4–7 to fill out cells G10–J20.

Now we are ready to concentrate on habitat 2. Make sure to reference parameters associated with habitat 2 in cells G4–G5 in your formulae.

9. For habitat 1, make a graph that compares the basic suitability with the actual suitability.

You will be graphing the values in cells A9–B20 and those in cells D9–D20. Use the XY scatter graph option and label your axes fully. Your graph should resemble Figure 4.

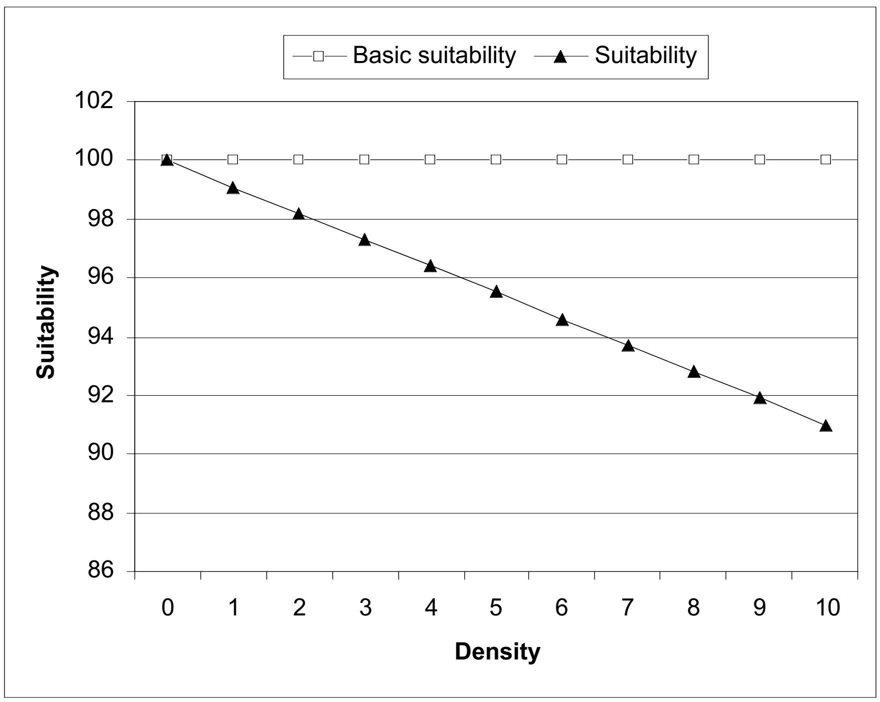

Figure 4

10. Graph the suitabilities of both habitat types as a function of density.

You will be graphing the values in cells A9–A20, D9–D20, and cells J9–J20. Remember to hold down the <Control> key to select cells that are not contiguous. Use the XY scatter graph option and label your axes fully. Your graph should resemble Figure 5.

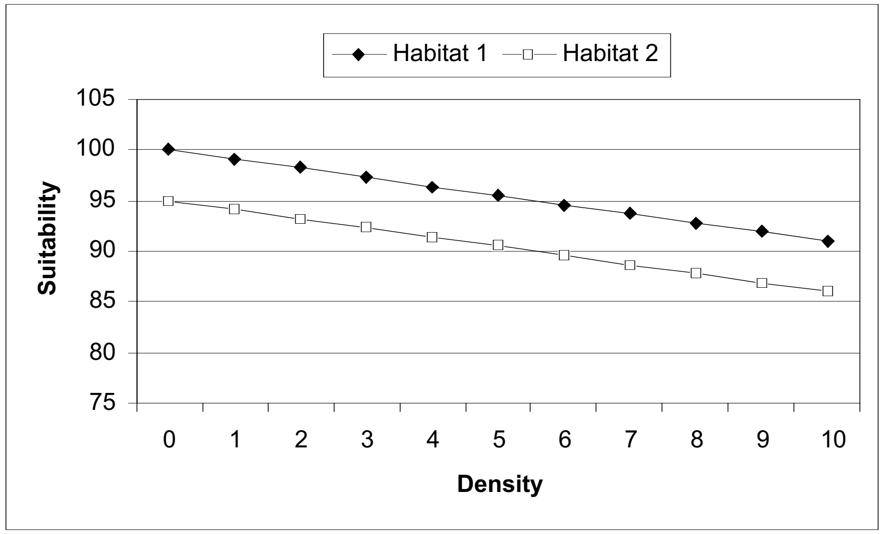

Figure 5

11. Save your work.

B. Simulate settlement patterns of individuals.

1. Set up new column headings as shown in Figure 6.

	M	N	O	P	Q	R
6	**HABITAT SELECTION SIMULATION - 10 INDIVIDUALS**					
7						
8		**Habitat**	**Habitat 1**		**Habitat 2**	
9	**Individual**	**choice**	**Running total**	**Suitability**	**Running total**	**Suitability**

Figure 6

2. Enter the numbers 1–10 in cells M10–M19.

Let's imagine that both habitats are completely empty; then 10 individuals arrive (not all at once) and have options of settling into habitat 1 or habitat 2. Remember, the goal for individuals is to maximize their success, so they will choose whatever habitat has the highest suitability. In this step you will simulate the decisions of the 10 individuals on your spreadsheet.

3. In cell N10, enter the formula **=IF(F4>G4,1,2)**. In cell O10, enter the formula **=IF(N10=1,1,0)**. In cell Q10, enter the formula **=IF(N10=1,0,1)**.

For the first individual, the decision is easy. It will select the habitat with the greatest basic suitability. We can use an **IF** function in the spreadsheet to return the choice made. An **IF** function returns one value if a condition you specify is true and another value if it is false. It has the syntax **IF(logical_test,value_if_true,value_if_false)**.
The formula in cell N10 tells the spreadsheet to examine the contents of cells F4 and G4, the basic suitabilities of the two habitats. If F4 > G4, the spreadsheet will return the number 1 (which indicates habitat 1 was selected); otherwise, it will return the number 2 (which indicates habitat 2 was selected). Use IF functions in cell O10 and Q10 to keep a running total of individuals in habitats 1 and 2.

4. In cell P10, enter the formula **=VLOOKUP (O10,$A$10:$D$20,4)**. Copy this formula down to cell P19.

We need to record the suitabilities of each habitat, depending on what their current densities are. We'll use **VLOOKUP** to do this. The **VLOOKUP** function searches for a value in the leftmost column of a table, and then returns a value in the same row from a column you specify in the table. It has the syntax **VLOOKUP(lookup_value, table_array,col_index_num,range_lookup)**, where **lookup_value** is the value to be found in the first column of the table, **table_array** is the table of information in which the data are looked up, and **col_index_num** is the column in the table that contains the value you want the spreadsheet to return. **Range_lookup** is either true or false (use false for your formula). For example, the formula in cell P10 tells the spreadsheet to look up the value in O10 (which is the running tally of individuals in habitat 1) in the table in cells A10–D20, and return the value associated with the fourth column of the table that is associated with the value listed in O10.

5. Use the **VLOOKUP** formula in cell R10 to return the current suitability of habitat 2 (based on its current occupancy). Copy the formula down to cell R19.

In cell R10 enter the formula **=VLOOKUP(Q10,$G$10:$J$20,4)**.

6. In cell N11, enter the formula **=IF(P10>=R10,1,2)**. Copy this formula down to cell N19.

Now we need to focus on the second individual. The **IF** formula tells the spreadsheet to determine if the value in cell P10 is greater than or equal to (**>=**) the value in cell R10. If so, the spreadsheet returns a 1 (indicating a selection of habitat 1); otherwise the spreadsheet returns a 2 (indicating a selection of habitat 2).

7. Enter the formula **=COUNTIF($N$10:N11,1)** in cell O11 and the formula **=COUNTIF($N$10:N11,2)** in cell Q11. Copy these formulae down to cells O19 and Q19, respectively.

To keep a running tally of how many individuals are in habitats 1 and 2, we can use the **COUNTIF** function. The **COUNTIF** function counts the number of cells within a range that meet the given criteria. It has the syntax **COUNTIF**(**range**,**criteria**), where **range** is the range of cells from which you want to count cells, and **criteria** is what you want to count. For example, the formula in cell O11 tells the spreadsheet to count how many 1s there are in cells N10–N11.

8. Graph the running population totals of habitat 1 and habitat 2.

You will be graphing the values in cells O9–O19 and cells Q9–Q19. Use a line graph and use the values in cells M10–M19 as your *x*-axis (under the Series tab). Your graph should resemble Figure 7.

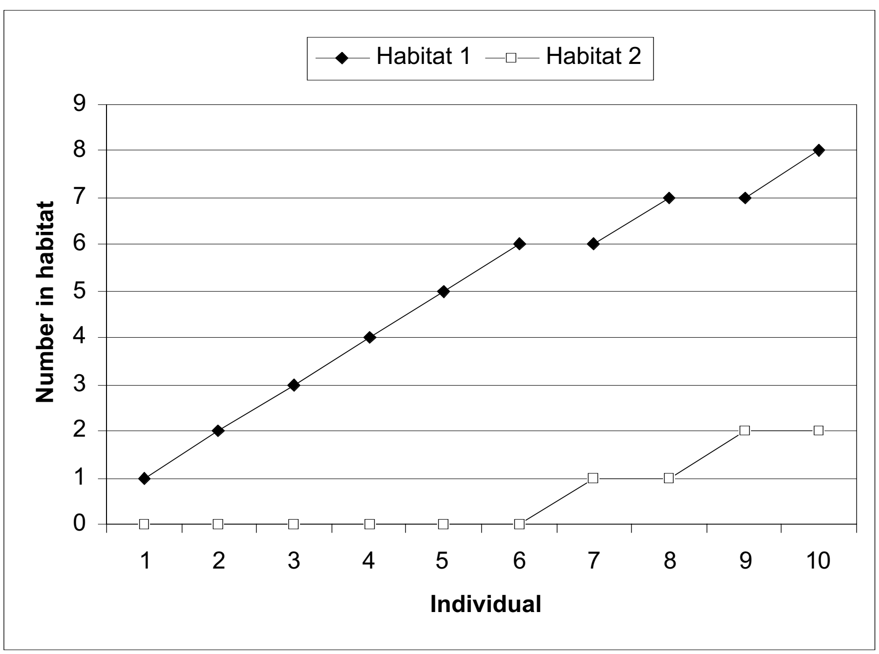

Figure 7

9. Save your work, and answer Questions 1–4 at the end of the exercise before proceeding.

C. Enter parameters for the ideal-despotic model.

Now we will consider the ideal-despotic model of habitat selection, where unsettled individuals are restricted by the "despotic" behavior of already settled individuals. Thus, even though they may "choose" to settle in a particular habitat based on its suitability, the colonists may not successfully settle and hence their success will be lower than expected for that habitat.

1. Enter 0.1 in cells F6 and G6.

The parameter t represents how "resistant" a resident individual is to new colonizers. Its value ranges from 0 to 1, where 0 means no resistance to new settlers and 1 indicates full resistance to new settlers. For now, $t = 0.01$, indicating little resistance. You will be able to change this value later in the exercise.

2. In cell E10, enter the formula **=$F$6*A10**. Copy this formula down to cell E20.

The total resistance of the habitat to new colonizers is a function of how many residents there are in the habitat. Thus, the term $t \times d$ is an indication of the overall resistance to new colonists.

3. In cell F10, calculate the apparent suitability, T, as $S_i[1 - (td_i)]$. Copy your formula down to cell F20.

T is the apparent suitability of a habitat, from the perspective of an individual looking to settle into a habitat. We used the formula **=D10*(1-E10)** in cell F10 to calculate the apparent suitability of habitat 1 when habitat 1 is vacant.

4. Enter formulae in cells K10–L20 for habitat 2.

Now consider the influence of despotic behavior on the apparent suitability of habitat 2. We used the formula **=$G$6*G10** in cell K10 and **=J10*(1–K10)** in cell L10.

5. Graph the suitabilities and apparent suitabilities for habitat 1.

Highlight cells A9–A20, D9–D20, and F9–F20. Use the XY scatter graph option and label your axes fully. Your graph should resemble Figure 8.

6. Save your work, and answer questions 5–7.

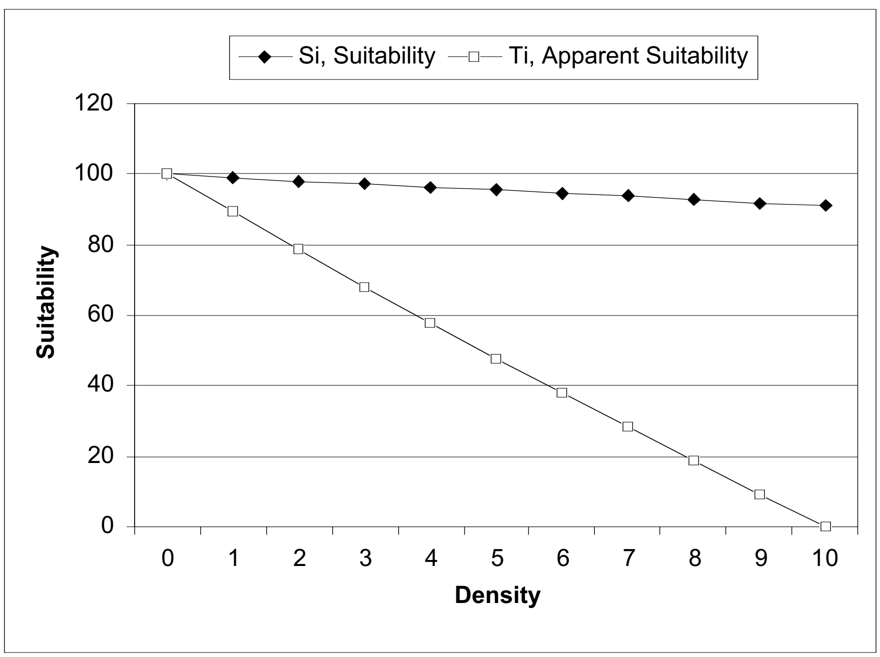

Figure 8

QUESTIONS

1. Based on your graph and the parameters used in the model in Section A of the exercise, if the density of habitat 1 is 3, and the fourth individual is looking for a place to settle, which habitat should it select? What if the density in habitat 1 is 8 and the density in habitat 2 is 0, which habitat should an individual select? When all 10 individuals have settled into their respective habitats, how do the two habitats compare in terms of per capita fitness?
2. In the ideal-free model, how does f affect suitability? Enter various values into the spreadsheet and examine graphical results from Section A of the exercise for habitat 1.
3. Your ideal-free model suggests a linear decline in suitability as density increases. Is this assumption justified? Modify your model so that each additional individual adds more and more of a "penalty" to suitability. For example, each new individual decreases suitability by a squared function of the density [$S_i = B_i - f_i(d_i^2)$]. How does your modification change your basic results?
4. One assumption of the ideal-free model is that all individuals are free to move into any habitat patch. In reality, individuals currently occupying a habitat patch may attempt to prevent others from entering. What influence would these "despots" have on the apparent suitability of a habitat patch? Consider how *you* would modify your model to be an ideal-despotic model. (We will do this in Part C, but your ideas may be better than ours.)
5. In the ideal-despotic model, what effect does t have on habitat suitability? Enter various values in your model and interpret your results.
6. Does the ideal-despotic distribution lead to a condition similar to what we found in the ideal-free model, where T_i is relatively equal in all habitats?
7. Both the ideal-free and the ideal-despotic models assume that individuals have "ideal" knowledge of relative habitat quality. Hypothesize about the effects on habitat selection if this assumption were violated.

LITERATURE CITED

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

Moody, A.L., A. I. Houston and J. M. McNamara. 1996. Ideal free distributions under predation risk. *Behavioural Ecology and Sociobiology* 38: 131–143.