COMAP
R4R

# Refresh for Relevance

WWW.COMAP.ORG/R4R

The Consortium for Mathematics and Its Applications (COMAP)
175 Middlesex Turnpike, Suite 3B
Bedford, MA 01730

Published and distributed by

COMAP, Inc.
www.comap.org

UMAP

# Module 688

## Time Resources in Animals

Kevin Mitchell
Steven Kolmes

Published in
cooperation with
the Society for
Industrial and
Applied
Mathematics, the
Mathematical
Association of
America, the
National Council of
Teachers of
Mathematics, the
American
Mathematical
Association of Two-
Year Colleges, The
Institute of
Management
Sciences, and the
American Statistical
Association.

COMAP

INTERMODULAR DESCRIPTION SHEET: UMAP UNIT 688

TITLE: Time Resources in Animals

AUTHOR:

Kevin Mitchell
Department of Mathematics and Computer Science
Steven Kolmes
Department of Biology
Hobart and William Smith Colleges
Geneva, NY 14456

ABSTRACT:

This unit presents an alternative to the classical optimal foraging models in behavioral ecology. In contrast to optimizing the net energy intake in a forager's diet, the model presented in this reading is concerned with a time-budgeting process dependent only upon whether an animal is hungry or satiated at a given moment. The analysis of the model is carried out using simple Markov chains. Computer programs included in the unit are used to generate "field data," which are then used to determine the proportion of time various animals will spend foraging and resting. This process exposes beginning students to elementary analysis of rather complex data sets.

PREREQUISITES: We use this unit in a course that has no mathematical or biology prerequisites. Only high-school algebra is required. If students are to generate data or their own, then access to a computer is necessary. We have found that supplying compiled versions of the programs to the class makes the data collection exercises easy, even for students with no previous computer experience.

RELATED UNITS: The Pace of Life: An Introduction to Empirical Model Fitting (Unit 551), by Bruce King; reprinted in *The UMAP Journal* 3(2) (1982): 221–248, and in *UMAP Modules: Tools for Teaching 1982*, 133–160.

# Time Resources in Animals

Kevin Mitchell
Department of Mathematics and Computer Science
Steven Kolmes
Department of Biology
Hobart and William Smith Colleges
Geneva, NY 14456

## Contents

## MODULES AND MONOGRAPHS IN UNDERGRADUATE MATHEMATICS AND ITS APPLICATIONS (UMAP) PROJECT

The goal of UMAP is to develop, through a community of users and developers, a system of instructional modules in undergraduate mathematics and its applications to be used to supplement existing courses and from which complete courses may eventually be built.

The Project was guided by a National Advisory Board of mathematicians, scientists, and educators. UMAP was funded by a grant from the National Science Foundation and is now supported by the Consortium for Mathematics and Its Applications (COMAP), Inc., a non-profit corporation engaged in research and development in mathematics education.

### COMAP STAFF

| | |
|---|---|
| Paul J. Campbell | Editor |
| Solomon A. Garfunkel | Executive Director, COMAP |
| Laurie W. Aragon | Business Development Manager |
| Philip A. McGaw | Production Manager |
| Evelyn Moore | Copy Editor |
| Roland Cheyney | Project Manager |
| Dale Jolliffe | Production Assistant |
| Annemarie S. Morgan | Administrative Assistant |
| John Gately | Distribution |

# 1. Time Resources

## 1.1 The Daily Pie

*This module is an adaptation of an article by Joan M. Herbers, which gave one explanation of why some animals apparently idle away such a large portion of their "active" time* [Herbers 1981].

An animal surviving in the wild has a wide array of tasks to perform. For example, it must seek and consume food, find or construct shelter, and mate. Because each day consists of only 24 hours, we can think of it as a "pie" that can be sliced various ways as portions of time are allocated to different tasks. This pie can be cut variously but can never be made more generous in total. Despite this limitation, many animals appear to act as though they have "all the time in the world." Rather than rushing from task to task, many organisms have daily time budgets that seem to reflect a considerable amount of spare time. In this Module, we will examine why that might be so. We shall focus specifically on eating, and examine various models that show how an animal that is either hungry or not hungry at a given moment will behave in the immediate future. We shall begin with general time budgeting and proceed through a series of increasingly-detailed models until we begin to approach situations that may elucidate how animals behave in the real world.

***"... many animals appear to act as though they have 'all the time in the world.'"***

Let's first turn our attention to some of the data compiled from the research in this area. Each of the studies represented in **Table 1** was done by a different researcher using slightly different procedures on wildly different animals. In general you can think of a "resting"

**Table 1.**
The allocation of time resources by several animals [Herbers 1981].

| | Proportion of Time Spent | | | | |
|---|---|---|---|---|---|
| Animal | Foraging | Resting | Social | Moving | Other |
| short-tailed shrew | 0.3 | 68.3 | | 31.5 | |
| olympic marmot | < 50 | > 50 | | | |
| *Eulampis* hummingbird | 11.9 | 84.0 | 3.0 | 0.6 | 4.8 |
| *Colibri* hummingbird | 31.8 | 65.9 | 0.4 | 1.1 | |
| seaside sparrow | 61.1 | 4.9 | 3.7 | | 20.9 |
| walrus | 17.6 | 66.9 | 12.6 | 0.3 | 2.6 |
| howling monkey | 30.0 | 70.0 | | | |
| orangutan | 45.9 | 39.4 | 3.7 | 11.1 | |
| chimpanzee | 55.0 | 23.0 | 5.9 | 14.2 | |
| gorilla | 25.0 | 51.0 | 5.9 | 11.0 | |

animal as being motionless during a period of time when activity might normally be expected.

***"... a tremendous range in the proportion of time that an animal spends foraging...."***

This table makes one thing clear immediately. There is a tremendous range in the proportion of time that an animal spends foraging, ranging from 0.3% (short-tailed shrew) to 61.1% (seaside sparrows) of available time. Any model that attempts to explain all of these values will have to be broadly designed indeed! And resting is often a very important category; for example, it is 70% of available time for howling monkeys and 84% of available time for *Eulampis* hummingbirds. Any model that does not predict both foraging and resting won't explain these data in a useful fashion.

Some "resting" behavior in animals is certainly biologically important. We know as humans that the extra flow of blood to our digestive organs and the rise in blood-sugar levels after a large meal makes us feel disinclined to activity and may even lead to a nap. Remaining huddled in a motionless condition can decrease the exposed surface area of an animal and hence help prevent chilling in cold situations; a cat sitting on a cold stairway with its legs and tail drawn protectively under its body is an example of this behavior. If predators are present, temporarily motionless animals may avoid observation and so "live to move another day." But the very high values for "resting" presented in the accompanying data, especially for very large vegetarian animals in warm climates (which eat continual small meals, have few if any predators, and do not generally need to conserve bodily warmth), as is apparent for gorillas, makes us suspect that not all "resting" is serving a biologically crucial function. We can refer to such resting in excess of apparent need as "laziness."

***"We can refer to such resting in excess of apparent need as 'laziness.'"***

One additional point must be made before we continue. The term "laziness" has the potential of slipping into anthropomorphic errors if it is used loosely. In this module, we are not attempting to infer anything whatsoever about an animal's "personality" by the use of the term "lazy." In Section 4 a mathematical definition of "laziness" will be presented that will let us use the term unambiguously. Until that point, we can do no better than to repeat Herbers's [1981] cautionary statement about the word "laziness":

> This term is unfortunately loaded with anthropomorphic connotations; the usage of "laziness" is restricted here to denote those periods of inactivity for which observers cannot demonstrate a physiological or ecological function, and for which such functions indeed may not exist. Laziness is but a subset of the summed observations of resting and inactivity, since some quiescence does serve a purpose.

## 1.2 Key Concepts

To understand the following *thermostat models* of feeding behavior, designed to help explain laziness, we need to understand certain key concepts. The biological concepts necessary to thinking about the models will be covered first, to be followed by mathematical constructions built from these biological ideas.

Some animals forage on a short-term basis, others on a long-term basis. Squirrels store nuts for the winter, acorn woodpeckers make holes in hollow trees to store acorns, honeybees collect nectar from flowers and concentrate it by evaporation to produce honey stores. All three of these are examples of long-term foraging, in which foraging behavior is based upon "expectations of future need" (food reserves to survive the winter, acorns collected to feed nestling woodpeckers at a later time) rather than upon whether the animal is hungry at the moment it begins to forage. The following models of feeding *exclude* consideration of long-term foraging because of the complications it introduces. All of the models we will consider will be of short-term foraging, which acts to respond to immediate hunger by collecting whatever amount of food is required. Short-term foragers often collect perishable food items that could not be stored. Raw fish becomes unattractive in a warm climate in only a short period of time, so ospreys (fish hawks) cannot store fish the way acorn woodpeckers store acorns.

***"The following models of feeding exclude consideration of long-term foraging. . . ."***

The following models also assume that an animal can only do one thing (forage or rest) at a time. There are situations when an organism can be both foraging and doing something else simultaneously, as the behavior of humans in sport fishing so eloquently attests. Unlike human sports fishers, most animals cannot drink beverages or sleep while foraging; and it is on the situation of mutually exclusive activities that we will focus.

We can think of hunger as the result of a stomach becoming empty. In a simple way, we can think of a stomach as continually being emptied at a slow rate as digestive processes proceed, and occasionally being filled at a rapid rate when we eat. (In actuality an animal can temporarily divert most of the blood flow from its digestive system to its skeletal muscles, and hence temporarily stop digesting food, to have additional blood flow to muscles in order to escape from a predator. We will ignore this real-world complication and assume digestion to be a continuous process.) If a stomach is being emptied from its full capacity, at some point we will say that it reaches a "critical emptiness," at which time nervous impulses proceed from nerves around the stomach to the brain and signal that the organism is now "hungry."

In three of the following four models, the possibility of starvation is not considered to be important. The fourth model is of an animal in an environment that presents a foraging situation harsh enough that starvation is a possibility.

# 2. The Thermostat Model of Feeding

## 2.1 The Activity and Appetite Functions

As mentioned earlier, we presume that the animals we are describing have a distinct foraging mode and that an observer can tell when these animals are foraging. We are interested only in whether the animal is foraging or not. So we can describe such an animal's activity at any time $t$ by an *activity* function, $a(t)$, which has just two values:

$$a(t) = \begin{cases} 1, & \text{if the animal is foraging at time } t; \\ 0, & \text{if the animal is not foraging at time } t. \end{cases}$$

We presume an animal forages when it "feels hungry" and does not forage when it "feels full." It is here that the "thermostat" enters the picture. At any time $t$, we imagine that the animal has an appetite or *hunger* level, $h(t)$, which corresponds directly to how full the gut is. Thus, the values of $h(t)$ fall in a range from $h(t) = 0$, when the gut is completely empty, to $h(t) = h_{\max}$, when the gut is completely full, where $h_{\max}$ represents the capacity of the animal's gut.

There are some natural expectations here. When $h(t)$ is close to $h_{\max}$ and the animal's gut is sufficiently full, the animal does not forage, so $a(t) = 0$. However, when $h(t)$ is nearly 0 and the gut is rather empty, then the animal feels hungry and forages, so $a(t) = 1$. *A basic assumption of the thermostat model is that a non-foraging animal always experiences hunger at the same appetite level or set point*, to use the thermostat analogy. This set point will be denoted by $u$; obviously $0 \le u \le h_{\max}$. *As soon as the animal feels hunger, we assume that it switches to the foraging mode with no delay.* In other words, at the time $t$ when $h(t)$ falls to $u$, activity "clicks on." Only the gut is controlling foraging; no memory of when the last meal was eaten is taken into account. The animal will stay in the foraging mode until it has eaten enough to fill its gut sufficiently to feel hungry no longer. That is, *it will forage until it raises $h(t)$ to a higher set point, $s$, at which the animal is satiated* (the thermostat "clicks off"). Thus we must have $0 \le u < s \le h_{\max}$.

## 2.2 Changing Activities

From what has been said so far, it is clear that if $h(t) \leq u$ then $a(t) = 1$ (the animal is hungry so it forages). Similarly if $h(t) \geq s$ then $a(t) = 0$ (the animal is satiated so it does not forage). But what happens in between these set points when $u < h(t) < s$? It all depends on what the animal was doing previously. This becomes a bit clearer if we imagine time as being "discrete" rather than continuous. In particular, think of $\Delta t$ as equal to one unit of time. (We might take $\Delta t$ to be the minimum amount of time for a predator to find and swallow a mouthful of prey.) With this convention for $\Delta t$, time $t$ represents the present moment, time $t - 1$ represents the moment $\Delta t$ in the past, and time $t + 1$ represents the moment $\Delta t$ into the future.

Now let's return to the question of evaluating $a(t)$ when $u < h(t) < s$. The answer depends on whether the gut is in the process of filling (animal has been foraging) or whether the gut is emptying (the animal has not been foraging). If the animal has just been foraging and $a(t-1) = 1$, then, since $h(t) < s$, it will continue to forage. The animal is not yet satiated. By contrast, if the animal has not been foraging and $a(t-1) = 0$, then, since $h(t) > u$, it is not yet hungry enough to forage. That is, the animal continues not to forage and $a(t) = 0$. In either case, we see that when $u < h(t) < s$, the animal continues to do what it has just been doing. *When the animal is between set points, it must exceed one of them in order to change its behavior.*

We see then that *the animal's activity is governed by only two factors: its current gut level, $h(t)$, and its previous activity, $a(t-1)$.* If the gut level is at or above satiation, then the animal does not forage. If the gut is at or below the hunger set point, the animal forages. When the gut level is between the two set points the animal continues to do what it has just been doing.[1] We can summarize mathematically the succession of activities as follows:

if $a(t-1) = 0$ and $h(t) > u$, then $a(t) = 0$ ("stays off");
if $a(t-1) = 0$ and $h(t) \leq u$, then $a(t) = 1$ ("clicks on");
if $a(t-1) = 1$ and $h(t) < s$, then $a(t) = 1$ ("stays on");
if $a(t-1) = 1$ and $h(t) \geq s$, then $a(t) = 0$ ("clicks off").

---

[1] The process of states $\{h(t), a(t)\}$ is an example of a Markov chain. The current state at time $t$ is independent of all previous states up to but not including the state at time $t - 1$.

The activity function is quite simple, having only two possible values, corresponding to foraging and not foraging. It would be an oversimplification to use the same representation for the appetite function, $h(t)$. Such a two-state function would mean that the gut registered either empty or full. We know that in digestion the gut empties in a continuous way. On the other hand, food items generally come in "units," and an animal can only ingest as much as its mouth will hold. So there is some reason to think of $h(t)$ as a discrete variable, and we will do so. That is, we will view $h(t)$ as changing only by a discrete amount $\Delta h$, where we assume that $\Delta h$ can take on only a finite number of values (typically only a few). The magnitude of the change in appetite level, $\Delta h$, when feeding will depend on the profitability of the particular food item (prey). The advantage in making $\Delta h$ discrete is that now $h(t)$ can assume only finitely many values between 0 and $h_{\max}$. This means that the possible number of states for the pairs $\{h(t), a(t)\}$ is also finite. At any moment $t$, we can place the animal in a particular state, and we can ask what are the chances of it staying in its present state, or changing to some other state, at the next moment in time, $t + 1$.

# 3. Model I: An Oversimplified Example

## 3.1 Putting the Model Together: Caterpillars

To illustrate the model, we now consider the following oversimplified situation. In later examples we will add more complex and realistic assumptions to the model.

All of the general assumptions made in Section 2 and their consequences continue to hold, including that fact that the animal's activity is governed by only two factors, its current gut level and its previous activity level. There are several specific assumptions we now make for this model.

1) *There are enough resources available so that when the animal forages, it never gets hungrier.* This means that $\Delta h$ is never negative while the animal is actively foraging.

2) *Food items ingested by the animal are all assumed to have the same value, 1.* This means that when the animal is foraging, $\Delta h$ is either 0 (if no food is currently being consumed) or $\Delta h$ is 1 (if some item is actually being eaten).

3) *We assume a specific probability $b$ of the animal actually eating something at any moment while it is in the foraging mode.* To make things

particularly simple, we will assume that there is a fifty-fifty chance of the animal being successful at foraging, that is, *we will set* $b = 0.5$. Consequently,[2] the probability of the animal being unsuccessful while foraging at any moment is $1 - b = 0.5$.

4) *When the animal is not foraging,* $\Delta h$ *cannot be positive.* In this example *we assume that* $\Delta h$ *is either* $-1$ *or* $0$ *when the animal is not foraging*, depending perhaps on the "activity" of the animal in its non-foraging mode. In particular, *we assume that* $\Delta h = -1$ *(that is, the gut is emptying) with probability* $d$. Of course, this means that $\Delta h = 0$ (the gut level is not changing) with probability $1 - d$.

As a biological realization of this simple example, consider a caterpillar on an edible leaf. To such an animal, standing on a relatively enormous expanse of food, its world is literally a buffet. Once the animal begins to forage, there is no possibility of it becoming hungrier. A hungry caterpillar merely reaches down to the surface it is standing on, opens its mandibles, and begins to chew. There is no possibility of a vexing delay before its stomach begins to fill with food. Further, we can image that such a caterpillar always chews at a specific rate. Since a leaf is a fairly uniform surface, there are neither especially unrewarding areas to feed in, nor especially wonderful ones. Intervals of $\Delta t$ when a caterpillar is in the feeding mode which do not produce any additional gut contents ($\Delta h = 0$) might correspond to the caterpillar taking a few steps, once it has consumed all of the leaf within reach of its mandibles. Next, we can imagine that periods of gut emptying ($\Delta h = -1$) correspond to periods during which it is strolling around on the leaf. Whenever the caterpillar stands still, it expends less energy; and its gut temporarily ceases to empty ($\Delta h = 0$). Standing and strolling are non-feeding activities, so $a(t) = 0$ for both of these situations. (You may prefer to imagine this as a stationary animal whose gut empties at a variable rate, which leads to the same mathematical description.)

To summarize the assumptions we have made so far:

$$\text{if } a(t-1) = 1, \text{ then } \Delta h = \begin{cases} 1 & \text{with probability } 0.5, \\ 0 & \text{with probability } 0.5; \end{cases}$$

$$\text{if } a(t-1) = 0, \text{ then } \Delta h = \begin{cases} -1 & \text{with probability } d, \\ 0 & \text{with probability } 1 - d. \end{cases}$$

---

[2] As in any probabilistic situation, the probabilities must sum to 1 (here $(1 - b) + b = 1$), *and every probability* $p$ *involved must satisfy* $0 \leq p < 1$. In the case under consideration, this simply means that $0 \leq b \leq 1$, which forces $1 - b$ to satisfy the same inequality.

We have stated things in terms of what is happening at time $t-1$ simply because we will be concentrating on how the animal's state changes from one moment, $t-1$, to the next moment, $t$. In other words, if we know the animal's last state, what is the probability it will be in some designated state at the current time?

Before we can answer such questions, we need to know the set points for hunger and satiation. *We set the hunger point* $u$ *to* 0 *and the satiation point* $s$ *to* $h_{\max}$ *which we presume to be* 2. That is, the animal starts to forage only when the gut is completely empty ($h(t) = u = 0$). Its state, $\{h(t), a(t)\}$, at this moment is $\{0,1\}$. The animal stops feeding only when the gut is completely full ($h(t) = s = h_{\max} = 2$). Its state at this moment is $\{2,0\}$.

The activity function $a(t)$ has only its two possible values, while $h(t)$ can assume any of three values: 0, 1, and 2. There are a total of $2 \times 3 = 6$ potential states, but not all of them are realizable. When the gut is empty the animal must be foraging, so the state $\{0,1\}$ is possible but $\{0,0\}$ is not. Similarly, when $h(t) = 2$, $a(t) = 0$ so the state $\{2,0\}$ is possible while $\{2,1\}$ is not. The two remaining states $\{1,0\}$ and $\{1,1\}$ are both possible. The former occurs while the gut is emptying but has not yet reached the hunger set point. The latter occurs when the animal is foraging but has not yet reached satiation.

## 3.2 Keeping Track of Changing States

We are ready to examine how an animal changes from one state to another over time. Given that the animal was in a designated state at time $t-1$, can we determine the probability that it will be in a certain state at time $t$? For example, let us assume that the state of the animal at time $t-1$ was given by $\{h(t-1), a(t-1)\} = \{1,0\}$. As discussed above,

$$\text{when } a(t-1) = 0, \text{ then } \Delta h = \begin{cases} -1 & \text{with probability } d, \\ 0 & \text{with probability } 1-d. \end{cases}$$

This allows us to calculate the possible values of $h$ at time $t$. In particular,

$$h(t) = h(t-1) + \Delta h = \begin{cases} 1-1=0 & \text{with probability } d, \\ 1+0=1 & \text{with probability } 1-d. \end{cases}$$

Next, the corresponding values for $a(t)$ can be computed, since they depend only on $a(t-1)$ and the current value of $h(t)$. We find that when $a(t-1) = 0$,

$$a(t) = \begin{cases} 1 & \text{with probability } d, \\ 0 & \text{with probability } 1 - d. \end{cases}$$

Thus, if the previous state were $\{h(t-1), a(t-1)\} = \{1,0\}$, then only two of the four states are possible at the next moment: $\{h(t), a(t)\} = \{0,1\}$ or $\{1,0\}$. Consequently, we conclude that

$$\text{if } \{h(t-1), a(t-1)\} = \{1,0\},$$

$$\text{then } \{h(t), a(t)\} = \begin{cases} \{0,1\} & \text{with probability } d, \\ \{1,0\} & \text{with probability } 1 - d, \\ \{1,1\} & \text{with probability } 0, \\ \{2,0\} & \text{with probability } 0. \end{cases}$$

The transition probabilities for moving from state to state are given schematically in **Figure 1**.

The transition diagram shows the four realizable states of the animal. The arrows, between the states or from a state back to itself, indicate permissible changes of state which have nonzero probability in the direction of the arrow. The number by each arrow indicates the probability of moving in that direction from one state to the other.

***"A transition diagram gives a rough indication of the time an animal spends foraging or resting."***

A transition diagram gives a rough indication of the time an animal spends foraging or resting. Whether the animal stays in its present state or moves to another depends on the probabilities assigned to the arrows leading out of and back to the current state. In the particular example under discussion, we see that four of these probabilities are already determined, while four others depend on the value assigned to $d$. Our expectations about whether the animal will rest more or forage more depend on the value of $d$. We might reason this way: Assume first that $d$ is large, say $d > 0.5$. Then the

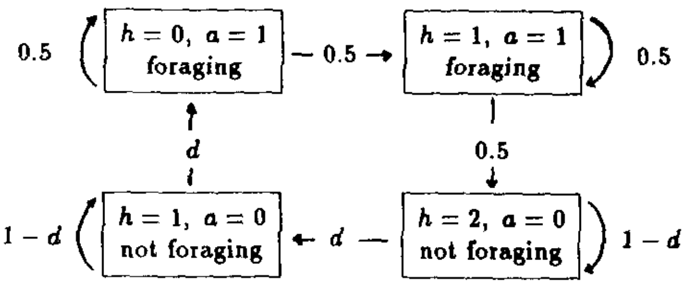


**Figure 1.** The transition diagram for a caterpillar ($u = 0$, $s = 2$).

animal is more likely than not to become hungry while resting and thus should move quickly out of the resting states $\{2,0\}$ and $\{1,0\}$ to the active state $\{0,1\}$, as the transition diagram indicates. Thus, we expect the animal to forage more than rest (all other things being equal). Of course, if $d < 0.5$, then the opposite conclusion holds. Now $1 - d > 0.5$, so the animal is more likely than not to stay full in a resting state. This means it will take a longer time to become active again. We expect the animal to rest more than forage.

## 3.3 Western Tent Caterpillars

Is it reasonable to talk about analyzing the feeding behavior of real animals in terms of measuring changes in state in their behavior? Is there any simple way to see whether something as small as a caterpillar is feeding or not? Both answers turn out to be "yes," so long as we select animals to watch on the basis of knowledge about their natural history.

Consider the Western tent caterpillar, *Malacosoma pluviale*. These animals live in groups of approximately 100 to 300. They use silk glands to produce a communal refuge that looks like a dirty silken tent suspended in the branches of a tree. They leave their tent to feed on nearby leaves and return to it to rest between feeding periods. The tent provides them with shelter from predators, and protects them from the drying influence of the sun [Wellington 1957]. Here are animals whose changes of behavioral state can be monitored simply by observing the intervals during which they leave their tent to feed.

Experiments on these caterpillars have shown them to be social groups with varying behavioral characteristics. Because all of the animals in one tent are siblings produced from the egg mass of one female moth, inherited behavioral differences bequeathed to each group of larvae by their mother can be observed. Some groups of larvae spend more time resting in their tents, while others spend more time outside of their tents feeding. Laboratory simulations of this natural variability in resting time have demonstrated that groups of larvae that feed more and rest less (spending less than an hour in their tent per hour of feeding activity) grow and develop more rapidly than groups of larvae that rest more and feed less (spending more than an hour and a half in their tent per hour of feeding activity) [Wellington 1957]. Not only are naturally-occurring differences experimentally observable in the tendencies of caterpillars to rest, they are measurably important to the biology of the animals.

**Exercises**

1. Suppose now that we fix the probability $d$ of the gut emptying while at rest at 0.6 and let the probability $b$ of the animal finding food while foraging vary. That is,

$$\text{if } a(t-1)=1, \text{ let } \Delta h = \begin{cases} 1 & \text{with probability } b, \\ 0 & \text{with probability } 1-b; \end{cases}$$

$$\text{if } a(t-1)=0, \text{ let } \Delta h = \begin{cases} -1 & \text{with probability } 0.6, \\ 0 & \text{with probability } 0.4. \end{cases}$$

Draw a transition diagram (similar to **Figure 1**) that illustrates this same information.

2. We have been examining the simplest of situations: an animal whose gut is either full, empty, or at a single state in between. We now enlarge the gut capacity and adjust the satiation point of the caterpillar accordingly.
   - Assume that the gut capacity $h_{\max}$ is now 3 (instead of 2).
   - Assume that the hunger point $u$ is still 0 (empty gut) and that the satiation point $s$ is now 3 (full gut).
   - Maintain the general assumptions about the transitions between states for the caterpillar, namely:

$$\text{if } a(t-1)=1, \text{ then } \Delta h = \begin{cases} 0 & \text{with probability } 1-b, \\ 1 & \text{with probability } b, \end{cases}$$

$$\text{and if } a(t-1)=0, \text{ then } \Delta h = \begin{cases} -1 & \text{with probability } d, \\ 0 & \text{with probability } 1-d. \end{cases}$$

   a. There are still two activity levels: $a(t) = 0$ or 1, but there are now four gut levels: $h(t) = 0$, 1, 2, or 3. So there are eight potential states for $\{h(t), a(t)\}$. Which of these can the caterpillar actually realize?

   b. Draw the transition diagram for this model.

## 3.4 Generating Data by Computer Simulation

There is a simple way to test our tentative expectations concerning the animal's time budget. (We will now assume that the probability of finding food while foraging is fixed at $b = 0.5$; the probability $d$ of getting hungrier while at rest will vary.) We (and you) will

**Table 2.**
The amount of time spent in various states changes with $d$.

| | Times in State ($b = 0.5$) | |
|---|---|---|
| State | $d = 1/3$ | $d = 2/3$ |
| $\{1,0\}$ | 3026 | 2160 |
| $\{2,0\}$ | 2903 | 2137 |
| $\{0,1\}$ | 2020 | 2857 |
| $\{1,1\}$ | 2051 | 2846 |
| Total | 10000 | 10000 |

use a computer program called *caterpillar* to simulate what happens over time to such an animal.[3] The following method is used. For convenience, the process starts with the animal in state $\{2,0\}$ (full and not foraging). The computer generates a random number $p$ such that $0 \leq p < 1$. If $0 \leq p < d$, then our interpretation is that $\Delta h = -1$, so that the animal becomes hungrier and moves to state $\{1,0\}$. If instead $d \leq p < 1$ then $\Delta h = 0$; the animal stays full and in state $\{2,0\}$. Another random number $p'$ is generated; and the animal moves or stays in its current state, according to the value of $p'$. Similar remarks apply to the animal when it is foraging, except that the random numbers generated are compared to $b = 0.5$ to decide whether the foraging bout has been successful ($\Delta h = 1$) or not ($\Delta h = 0$). We iterate this process a large number of times and simply count the number of times we find the animal in each of the four states. **Table 2** gives these data for 10,000 iterates of the process, for two different values of $d$: $d = 2/3$ and $d = 1/3$.

We determine the proportion of time the caterpillar spends at rest by summing together all of the times the animal was at rest. That is, we take the number of times the caterpillar was in state $\{2,0\}$ and add this to the number of times the caterpillar was in state $\{1,0\}$ and then divide by the total number of iterates. When $d = 1/3$ we find that proportion of time at rest is $\frac{5929}{10000} \approx 0.59$. Of course, the proportion of time spent foraging must then be about $0.41 = 1.0 - 0.59$. When $d = 2/3$ we find that the proportion of time at rest drops to 0.43 and the proportion of time foraging is about 0.57. Our expectations are confirmed. As $d$ increases, the amount of time at rest decreases and foraging increases. Is it possible

---

[3] Any device that generates "random" numbers and records the results could be used. For example, a fair die and a diligent student to record the "data" might just as easily have been used, though more time would be needed to complete a large number of trials.

to describe this variation more precisely? Is it possible to find a relationship between $d$ and time spent resting?

## 3.5 The Relationship Between *d* and Resting Time

Our goal is to obtain a clearer understanding of the connection between the proportion of resting time and $d$, the probability of getting hungrier while at rest. For the moment we operate under the assumption that the probability $b$, of success in finding food while foraging, continues to be 0.5. We can generate "field data" for our model using the *caterpillar* computer simulation by systematically varying $d$ and keeping track of the results. We let $d$ vary from 0.1 to 1.0 using increments of 0.1. **Table 3** summarizes the results for 10,000 iterates of the process for each value of $d$. Again, we see that as $d$ increases, the amount of rest time decreases. However, the precise relationship between rest time and $d$ is not obvious from the data.

To begin our analysis on the data from **Table 3**, we first determine the proportion of time spent at rest for each of the values of $d$ by adding together the number of times the caterpillar was in states $\{1,0\}$ and $\{2,0\}$ and dividing by 10,000. These data and their graph, shown in **Figure 2**, confirm our earlier expectations. As $d$ increases, the proportion of resting time decreases. To repeat, this makes sense because when $d$ is large the animal gets hungry more quickly, and therefore must cycle through the foraging state more often, than when $d$ is small. Yet we still do not know the precise relationship between $d$ and the proportion of time at rest.

Let $R$ denote the *proportion of the total time spent at rest*. One approach to analyzing the graph in **Figure 2** is to transform the data so that the slope of the graph is *increasing*. There are two simple ways to do this: either graph $R$ vs. $1/d$; or graph $1/R$, the inverse of

**Table 3.**
The amount of time spent in the four states as $d$ varies and $b = 0.5$.

| | Times in State for Various $d$ | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **State** | 0.1 | 0.2 | 0.3 | 0.4 | 0.5 | 0.6 | 0.7 | 0.8 | 0.9 | 1.0 |
| $\{1,0\}$ | 4146 | 3625 | 2988 | 2839 | 2484 | 2312 | 2097 | 1903 | 1792 | 1661 |
| $\{2,0\}$ | 4244 | 3582 | 3268 | 2758 | 2496 | 2272 | 2127 | 1907 | 1795 | 1660 |
| $\{0,1\}$ | 801 | 1427 | 1844 | 2204 | 2491 | 2687 | 2849 | 2986 | 3126 | 3337 |
| $\{1,1\}$ | 809 | 1366 | 1900 | 2199 | 2519 | 2729 | 2927 | 3204 | 3287 | 3342 |

| $d$ | Time Resting |
|---|---|
| 0.1 | 0.84 |
| 0.2 | 0.72 |
| 0.3 | 0.63 |
| 0.4 | 0.56 |
| 0.5 | 0.50 |
| 0.6 | 0.46 |
| 0.7 | 0.42 |
| 0.8 | 0.38 |
| 0.9 | 0.36 |
| 1.0 | 0.33 |

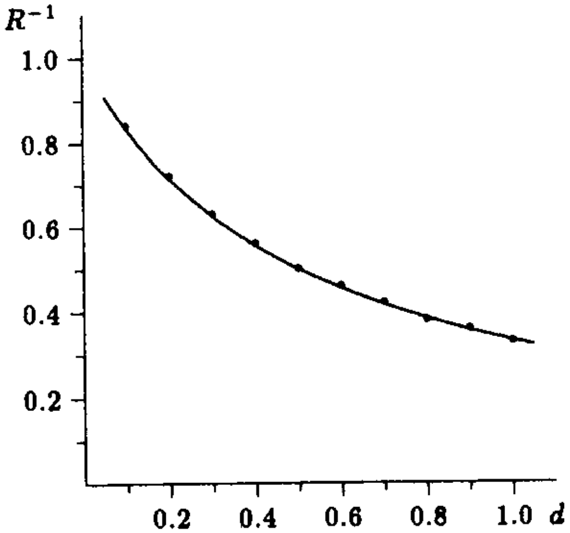


**Figure 2.** The proportion of time at rest as $d$ varies ($b$ = 0.5).

| $d$ | $R$ | $R^{-1}$ |
|---|---|---|
| 0.1 | 0.84 | 1.19 |
| 0.2 | 0.72 | 1.39 |
| 0.3 | 0.63 | 1.59 |
| 0.4 | 0.56 | 1.79 |
| 0.5 | 0.50 | 2.00 |
| 0.6 | 0.46 | 2.17 |
| 0.7 | 0.42 | 2.38 |
| 0.8 | 0.38 | 2.63 |
| 0.9 | 0.36 | 2.78 |
| 1.0 | 0.33 | 3.03 |

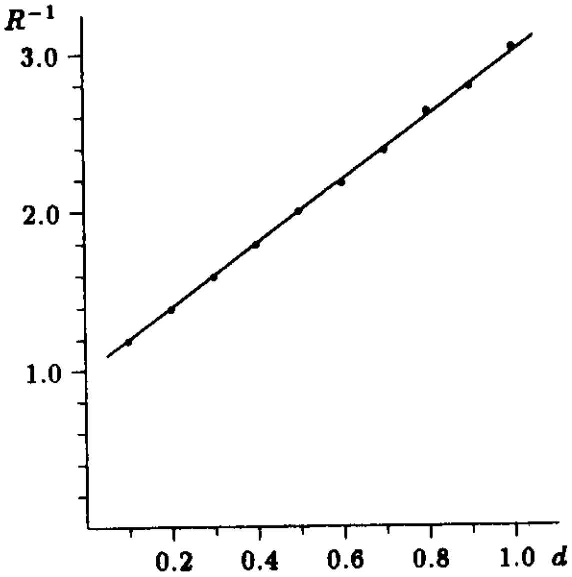


**Figure 3.** The reciprocal of the proportion of time at rest as $d$ varies ($b$ = .5).

**Table 4.**
Predicted and observed values of $R$ compared for various $d$ ($b = 0.5$).

| $d$ | Predicted Value of $R$: $(2d + 1)^{-1}$ | Observed Value of $R$ |
|---|---|---|
| 0.09 | .85 | .85 |
| 0.17 | .75 | .74 |
| 0.25 | .67 | .66 |
| 0.33 | .60 | .59 |
| 0.67 | .43 | .43 |
| 0.75 | .40 | .39 |
| 0.95 | .34 | .35 |

resting time, vs. $d$. The latter approach works quite well here.[4] (Also notice that the graph looks like a hyperbola.) First we calculate $1/R = R^{-1}$ for each of the rest times in the chart in **Figure 2**. These data are given in the table accompanying **Figure 3**, where we have actually plotted $R^{-1}$ vs. $d$.

The points in **Figure 3** fall very nearly along a line. The equation of this line can be obtained by inspecting the graph to determine the intercept and the slope. The vertical intercept appears to be 1. When $d$ is 1, then $R^{-1}$ is roughly 3. Consequently, the slope of the line in **Figure 3** is given by

$$m \approx \frac{3 - 1}{1 - 0} = 2.$$

So the approximating line has equation $R^{-1} = 2d + 1$. By taking inverses we find that when $b = 0.5$ then

$$R = \frac{1}{2d + 1}.$$

At last we have an equation relating the proportion of resting time to $d$. Just how good is this equation for $R$? We can test the model equation $R = (2d + 1)^{-1}$ by first choosing values of $d$, then calculating a predicted value for $R$, and finally using the computer simulation *caterpillar* to evaluate $R$ directly. **Table 4** gives this

---

[4] See [King 1982] for a good discussion of simple techniques that can be used to analyze data.

information for various values of $d$. As you can see (and test for *yourself*), *the equation gives a remarkably good fit!*

**Exercises**

**3.** Notice that when $d = 1.0$ and $b = 0.5$ in **Table 3**, the animal spends a third of its time at rest. How can you explain this? Shouldn't the animal spend nearly all of its time foraging if it is always getting hungry ($d = 1$)?

**4.** In general, as $b$ gets larger do you expect the animal to rest more or less? Why?

**5.** In this exercise we will try to find a relationship between $d$ and the proportion of time spent at rest, $R$, for values of $b$ other than 0.5.

- **a.** Use the *caterpillar* computer program to fill in the table below *for your own value* of $b$. Remember that the program runs 10,000 iterates for each $b$ and $d$ value.

| | Times and Proportion of Time at Rest | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| $d$ | 0.1 | 0.2 | 0.3 | 0.4 | 0.5 | 0.6 | 0.7 | 0.8 | 0.9 | 1.0 |
| $\{1,0\}$ | | | | | | | | | | |
| $\{2,0\}$ | | | | | | | | | | |
| $R$ | | | | | | | | | | |
| $R^{-1}$ | | | | | | | | | | |

- **b.** Use the information in your table to make a graph of $R^{-1}$ vs. $d$ for your particular value of $b$.

- **c.** Can you spot a (linear) relationship between $R^{-1}$ and $d$? How would you express it? Now solve for $R$ in terms of $d$, for your value of $b$.

- **d.** Use your equation to predict new values of $R$ for the values of $d$ in the table below. Run the computer simulation to check on the accuracy of your predictions. Are you satisfied with the results? Why or why not?

| $d$ | Predicted value of $R$ | Observed Value of $R$ |
|---|---|---|
| 0.25 | | |
| 0.33 | | |
| 0.67 | | |
| 0.75 | | |
| 0.95 | | |

**e.** What happens in your model if $d = 0$? Does your predicted value of $R$ match the computer-simulated value of $R$? Is this a "realistic" possibility? Why or why not?

## 3.6 The Relationship Between $b, d$, and Resting Time

So far we have worked only with fixed values of the success rate for foraging, $b$. We expect that as $b$ increases the rest time should also increase, since the animal should need less time to reach the satiation point when $b$ is large. For the specific value $b = 0.5$, we systematically varied $d$ and found that $R = (2d + 1)^{-1}$ gave an extremely good approximation for the proportion of time at rest. In the preceding exercises you have found other expressions for $R$ in terms of $d$, for different but fixed values of $b$. The results for an entire class taken as a whole allow one to see how the equation for $R$ in terms of $d$ systematically varies with $b$. **Table 5** gives this same type of information as $b$ varies in increments of one-sixth of a unit.

There is clearly a pattern to the values of $R$ in **Table 5**. In fact, if we rewrite each of the equations for $R$ after having divided both the numerator and denominator by the coefficient of $d$, then we obtain the equations in **Table 6**, which are now in an especially convenient form.

The relationship between $b, d$, and $R$ appears to be $R = b/(b + d)$. The first way to check this formula is to see whether it "predicts"

**Table 5.**
Equations for $R$ in terms of $d$ as $b$ varies.

| $b$ | $1/6$ | $1/3$ | $1/2$ | $2/3$ | $5/6$ | $1$ |
|---|---|---|---|---|---|---|
| Predicted $R$ | $\frac{1}{6d+1}$ | $\frac{1}{3d+1}$ | $\frac{1}{2d+1}$ | $\frac{2}{3d+2}$ | $\frac{5}{6d+5}$ | $\frac{1}{d+1}$ |

**Table 6.**
Rewritten equations for $R$ in terms of $d$ as $b$ varies.

| $b$ | 1/6 | 1/3 | 1/2 | 2/3 | 5/6 | 1 |
|---|---|---|---|---|---|---|
| Predicted $R$ | $\frac{1/6}{d + 1/6}$ | $\frac{1/3}{d + 1/3}$ | $\frac{1/2}{d + 1/2}$ | $\frac{2/3}{d + 2/3}$ | $\frac{5/6}{d + 5/6}$ | $\frac{1}{d + 1}$ |

**Table 7.**
Predicted and observed values of $R$ for arbitrary values of $b$ and $d$.

| $b$ | $d$ | Predicted $R$ | Observed $R$ |
|---|---|---|---|
| .37 | .63 | .37 | .37 |
| .18 | .44 | .29 | .29 |
| .92 | .81 | .53 | .53 |
| .26 | .17 | .60 | .62 |
| .77 | .21 | .79 | .78 |

the formula that you derived in **Exercise** 5 for your specific value of $b$. Next we can use the equation for $R$ to predict the results of computer simulations for arbitrary values of $b$ and $d$. Such a test was carried out and the results are given in **Table** 7. Again, the fit is remarkably good.

## 3.7 Eastern Tent Caterpillars

Is there any real-world evidence that rest time and feeding success are related to one another in the way our model has suggested? Consider the Eastern tent caterpillar (*Malacosoma americanum*). Like its relative the Western tent caterpillar (*Malacosoma pluviale*), these caterpillars feed on leaves and retreat during rest periods to the refuge of a nearby tent that they have constructed. The behavior of Eastern tent caterpillars feeding on leaves of different quality has been studied [Fitzgerald and Peterson 1983].

Young leaves represent an ideal food source for tent caterpillars. Leaves begin their lives as entities that are soft and readily chewable. As leaves age, they become tougher and more challenging to the rather small jaws of a caterpillar and are of less nutritional value. In our model this aging of leaves can be interpreted as a decrease in $b$, because in any given instant a caterpillar is less likely to be able to bite off a hunk of older, harder leaf.

Among the variety of things [Fitzgerald and Peterson 1983] measured about caterpillar feeding was the amount of time spent between leaving their tent to commence feeding and returning to their tent to rest. The data from six replicate experiments showed that the amount of active caterpillar foraging time was significantly greater for larvae feeding on tough old leaves (an average of 47.7 minutes per foraging period) than for larvae feeding on fresh young leaves (an average of 25.5 minutes per foraging period). As $b$ increased, time away from their resting area decreased; and hence $b$, $d$, and $R$ interacted in these experiments generally as our model predicted they should.

## Exercises

We have found in the simplest case that the rest time, $R$, for the caterpillar is quite accurately predicted by the formula $R = b/(b + d)$. Does the equation for $R$ depend on the number of transition states? To find out, you will re-examine in detail the situation of **Exercise 2**. Begin by reviewing the assumptions that were made there concerning the caterpillar with a gut capacity of three units, then complete the following steps.

6. From **Exercise 2**, there are three possible rest states: $\{3,0\}$, $\{2,0\}$, and $\{1,0\}$. To test whether the rest-time equation still holds under these circumstances, you will run a computer simulation called *caterpillar2* of 10,000 trials for various values of $b$ and $d$. First choose 10 pairs of values between 0 and 1 for $b$ and $d$ and fill these in the table below.

7. Next use the equation $R = b/(b + d)$ to predict the rest time for each pair of $b$ and $d$ values. Fill these predictions in the table.

| $b$ | $d$ | Predicted $R$ | $\{3,0\}$ | $\{2,0\}$ | $\{1,0\}$ | Observed $R$ |
|---|---|---|---|---|---|---|
| | | | | | | |
| | | | | | | |
| | | | | | | |
| | | | | | | |
| | | | | | | |
| | | | | | | |
| | | | | | | |
| | | | | | | |
| | | | | | | |
| | | | | | | |

**8.** Now run *caterpillar2* for each $b$ and $d$ pair. Fill in the number of times the caterpillar is in each of the rest states (out of a possible 10,000).

**9.** Compute the observed $R$ value for each $b$ and $d$ pair. Decide whether the rest time formula is still valid.

**10.** Find an equation for the proportion of time spent foraging in terms of $b$ and $d$.

# 4. Laziness

Now we can ask under what circumstances will the caterpillar we have been studying appear to be "lazy." We will say that if an animal appears to do nothing in particular for more than half the time, then that animal is *lazy.* For us, this criterion translates into determining when rest time $R$ occupies more than half the time budget. We see that

$$R > \frac{1}{2} \Leftrightarrow \frac{b}{b+d} > \frac{1}{2} \Leftrightarrow 2b > b + d \Leftrightarrow b > d.$$

In this simplest of examples, the caterpillar is lazy whenever $b > d$.

***"... even low rates of success when foraging can result in a lazy animal."***

It may seem counterintuitive that even low rates of success when foraging can result in a lazy animal. For example, in **Table 7** when $b = 0.26$, the animal rested 60% of the time, because $d = 0.17$. Let us consider this situation more closely. How likely an animal is to get hungrier in any moment ($\Delta h = -1$, the gut is emptying) depends on how rapidly its moment-by-moment activities drain its nutrient reserves. An animal that is very active (e.g., a human being walking outside on a cold day, needing to both move and produce body heat) uses up energy rapidly. Such an organism has a high $d$ value; it will become hungry quickly. By contrast, a spider sitting motionless in a web uses very little energy. It is not likely to get appreciably more hungry in any short time interval ($\Delta h = 0$ is normal), because it is draining its nutrient reserve neither for movement nor to produce a body temperature higher than the ambient air temperature.[5] For a

---

[5] We refer to animals that use internally-generated heat to maintain a high body temperature as *endotherms*. *Ectotherms* allow their body temperatures to fluctuate with environmental temperatures, although they may use their behavior to help them remain in warm environments (e.g., snakes basking on warm rocks).

spider that is motionless in a web, its energetically-undemanding existence ($d$ is low) allows even an occasional fly ($b$ is low) to satisfy its nutritional needs. Mostly, spiders in webs just sit there!

# 5. Model II: Varying Prey Values

## 5.1 The Heron as Forager

For a slightly more complicated example, consider a heron wading in a pond or marsh that contains many fish. If the density of fish is high enough, the bird will never become hungrier once it is motivated to feed, because it will simply reach over and nab a fish. This type of foraging behavior is simply not active enough to contribute to any depletion of the bird's energetic reserves.

If there are small and large fish present in a pond, a heron that simply nabs the closest fish when it becomes hungry will feed at one of two rates. It will either consume a small fish and add some small amount to its gut contents, or eat a large fish and add a large amount to its gut contents. The probabilities of each of these feeding events will be directly proportional to the encounter rates for the two sizes of fish and hence to fish densities.

## 5.2 The Assumptions about Herons

When a heron is in the active mode, $\Delta h$ can assume one of three values depending on the outcome of the foraging bout: 0 if the heron captures no fish, 1 if it captures a small fish, or 2 if the heron nabs a large fish. The likelihood of any one of these outcomes varies with the density of the prey. We describe the general situation by saying:

$$\text{if } a(t-1)=1, \text{ then } \Delta h = \begin{cases} 0 & \text{with probability } 1-b-c, \\ 1 & \text{with probability } b, \\ 2 & \text{with probability } c. \end{cases}$$

As with caterpillars, when the heron is not foraging, $\Delta h$ is either 0 or $-1$, depending on the level of non-foraging activity. Again we have

$$\text{if } a(t-1)=0, \text{ then } \Delta h = \begin{cases} -1 & \text{with probability } d, \\ 0 & \text{with probability } 1-d. \end{cases}$$

The final assumptions concern the thermostat set points. In this model we will presume that $h_{\max}$, the maximum value of $h(t)$, is 4.

In other words, it takes four small fish or two large fish to completely fill the heron's gut. As before, we will assume that the hunger set point is $u = 0$. Only when $h(t)$ falls to 0 and the gut is empty will the heron begin to forage. We set the satiation point to be $s = 3$. That is, when $h(t) \geq 3$, the heron will stop foraging. Notice this means that the heron need not be completely full ($h(t) = 4$) to stop foraging.

To illustrate how the transitions occur this time, consider the following situation. Assume that $a(t-1) = 1$ and that $h(t-1) = 2$. (The heron is foraging, but not yet satiated.) Then the assumptions on $\Delta h$ outlined above imply that

$$\begin{aligned} h(t) &= h(t-1) + \Delta h = 2 + \Delta h \\ &= \begin{cases} 2 + 0 = 2 & \text{with probability } 1 - b - c, \\ 2 + 1 = 3 & \text{with probability } b, \\ 2 + 2 = 4 & \text{with probability } c. \end{cases} \end{aligned}$$

The value of $a(t)$ is now determined; in the later two situations the animal is satiated so $a(t) = 0$, while in the first situation the heron will continue to forage so $a(t) = 1$. Thus, the possible new states are

$$\{h(t), a(t)\} = \begin{cases} \{2,1\} & \text{with probability } 1 - b - c, \\ \{3,0\} & \text{with probability } b, \\ \{4,0\} & \text{with probability } c. \end{cases}$$

Notice that it is possible to be satiated with or without being completely full. A similar analysis for all possible states leads to the transition diagram in **Figure 4**.

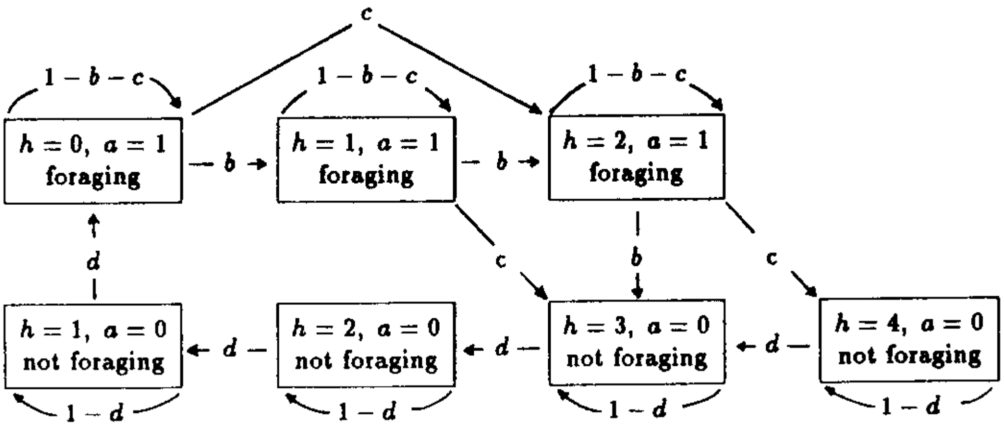


**Figure 4.** The general transition diagram for herons.

**Exercises**

11. Why was the satiation point of $s$ for the heron not set at $h_{\max} = 4$ here? (Hint: What could happen if the heron were still foraging when $h(t-1) = 3$?)

12. Draw a transition diagram for a heron that has a gut capacity of 5 units, a satiation point $s = 4$, and a hunger set point of $u = 0$, where the probabilities for changing states, $b$, $c$, and $d$, have the same meaning as in **Figure 4**.

## 5.3 Two Special Cases

As in the caterpillar example, we will do a computer simulation of the heron model which we have outlined. The goal is to determine the relationship between $R$ and the probabilities $b$, $c$, and $d$. We start by considering two extreme but informative cases: 1) $c = 0$ and $0 < b \leq 1$, and 2) $b = 0$ and $0 < c \leq 1$.

### The Case $c = 0$

When $c = 0$, if we assume that the heron starts out with an empty gut and is foraging (that is, in state $\{0, 1\}$, then the general transition diagram for herons in **Figure 4** simplifies to **Figure 5**. This is the same transition diagram you worked out for caterpillars with gut capacity 3 in **Exercise** 2. (Why is the state $\{4, 0\}$ not feasible here?) **Exercises 6–9** showed that rest time in this case is still described by the formula $R = b/(b + d)$; no new work needs to be done.

### The Case $b = 0$

Now consider the other extreme: Assume that $0 < c \leq 1$ and that $b = 0$. Starting in state $\{1, 0\}$, the general transition diagram in **Figure 4** reduces to the six states shown in **Figure 6**.

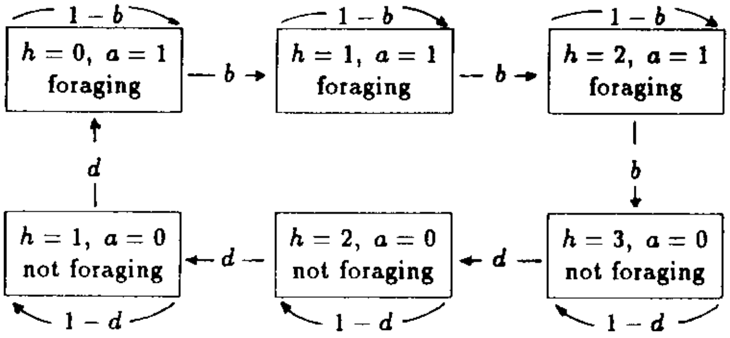


**Figure 5.** The transition diagram for herons when $c = 0$.

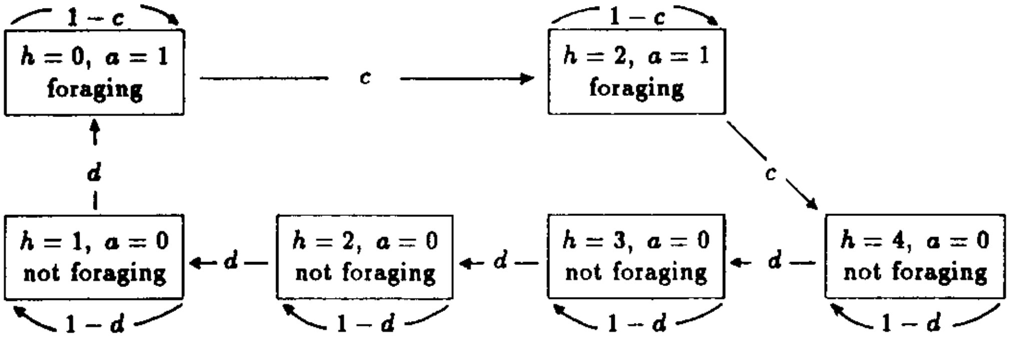


**Figure 6.** The transition diagram for a heron when $c$ and $d$ vary and $b = 0$.

Notice that there are only two foraging states, while there are four resting states. How does this asymmetry affect the rest-time equation? Using the computer program *heron*, we can gather some simulated field data on this situation. The *heron* simulation works much the same way as the *caterpillar* simulation, except that the number of states has been expanded and the foraging transitions have been appropriately modified. As with the caterpillar model, we start our analysis by allowing only one of the variables to change and hold the other constant. When the probability $c$ of catching prey items of value two was kept fixed at 0.5, and the probability $d$ of the gut emptying one unit while at rest was allowed to vary, the data in **Table 8** were obtained.

The data in **Table 8** were then used to compute the proportion of time at rest for each value of $d$, by adding together the times in states $\{1,0\}$, $\{2,0\}$, $\{3,0\}$, and $\{4,0\}$ and then dividing by 10,000 (see **Table 9**). As in the caterpillar model, as $d$ increases, the rest

**Table 8.**
Time spent in states as $d$ varies ($c = 0.5$, $b = 0$).

| | Times in State for Various $d$ | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **State** | 0.1 | 0.2 | 0.3 | 0.4 | 0.5 | 0.6 | 0.7 | 0.8 | 0.9 | 1.0 |
| $\{1,0\}$ | 2115 | 2072 | 2009 | 1804 | 1627 | 1551 | 1481 | 1386 | 1318 | 1242 |
| $\{2,0\}$ | 2403 | 2104 | 1944 | 1759 | 1701 | 1542 | 1464 | 1390 | 1305 | 1242 |
| $\{3,0\}$ | 2128 | 2079 | 2016 | 1730 | 1649 | 1577 | 1449 | 1384 | 1325 | 1242 |
| $\{4,0\}$ | 2428 | 2133 | 1797 | 1800 | 1661 | 1597 | 1522 | 1405 | 1302 | 1242 |
| $\{0,1\}$ | 443 | 784 | 1129 | 1452 | 1673 | 1868 | 2016 | 2209 | 2375 | 2495 |
| $\{2,1\}$ | 443 | 828 | 1105 | 1455 | 1689 | 1865 | 2068 | 2166 | 2375 | 2537 |

**Table 9.**
The proportion of time at rest as $d$ varies ($c = 0.5$, $b = 0$).

| $d$ | 0.1 | 0.2 | 0.3 | 0.4 | 0.5 | 0.6 | 0.7 | 0.8 | 0.9 | 1.0 |
|---|---|---|---|---|---|---|---|---|---|---|
| Time Resting | .91 | .84 | .78 | .71 | .66 | .63 | .59 | .56 | .53 | .50 |

time decreases. But, **Table 9** is quite different from the corresponding table in **Figure 2** for caterpillars. The rest times for herons are larger for the same values of $d$ when $c = 0.5$ and $b = 0$ than they are for the caterpillar when $b = 0.5$ (and implicitly $c = 0$). Is there a simple rest-time formula for the heron, as there was for the caterpillar?

We start our data analysis by using the same trick as in the caterpillar model; we compare $R^{-1}$ to $d$ while $c$ is held fixed at 0.5 and $b$ is held fixed at 0. This yields the data and graph in **Figure 7**.

The data points in **Figure 7** appear to fall along a straight line, which indicates that there is a linear relationship between $R^{-1}$ and $d$. The vertical intercept of the approximating line appears to be 1, and the line also passes through the point $(1, 2)$. Consequently, the slope of the line is about 1 and its equation is: $R^{-1} = d + 1$. From this we conclude that when $c = 0.5$ and $b = 0$, then $R = 1/(1 + d)$.

| $d$ | $R^{-1}$ |
|---|---|
| 0.1 | 1.10 |
| 0.2 | 1.19 |
| 0.3 | 1.28 |
| 0.4 | 1.41 |
| 0.5 | 1.52 |
| 0.6 | 1.58 |
| 0.7 | 1.69 |
| 0.8 | 1.79 |
| 0.9 | 1.89 |
| 1.0 | 2.00 |

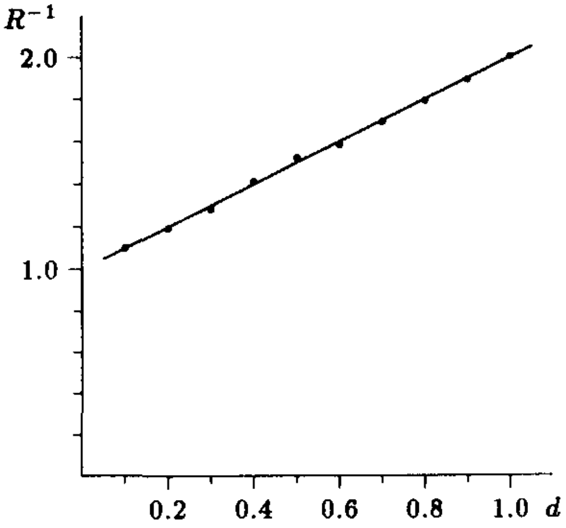


**Figure 7.** The graph of $R^{-1}$ as a function of $d$ when $c = 0.5$ and $b = 0$.

**Exercises**

**13.** What would the transition diagram for the case $c = 0$ look like if the heron started in the state $\{4,0\}$?

**14.** For your own value of $c$, produce a linear equation using the same procedure as in the text. Use this to express $R$ as a function of $d$. You will need to use the *heron* computer simulation program. Please report all the data you collect as well as appropriate graphs.

## 5.4 The Relationship Between *c*, *d* and Rest Time ($b = 0$)

So far we have worked with a single value of $c$ and we have let $d$ vary. However, the exercise above and our work with the caterpillar model indicate that a relationship between $c$, $d$, and $R$ might be found. Analogous to the analysis of the caterpillar model in Section 3.5, we now let both $c$ and $d$ vary. For any arbitrary but fixed value of $c$, we can allow $d$ to change in a systematic way, much as we did in the previous section when $c = 0.5$. The *heron* simulation can then be used to gather rest-time data for each value of $c$ as $d$ varies. A relationship between $R$ and $d$ can then be found for each particular value of $c$. The hope is that all of these relationships fall into a recognizable pattern. The results of such a series of calculations are given in **Table 10**.

**Table 10.**
Equations derived for $R$ as $c$ and $d$ vary ($b = 0$).

| $c$ | 1/6 | 1/3 | 1/2 | 2/3 | 5/6 | 1 |
|---|---|---|---|---|---|---|
| $R$ | $\frac{1/3}{1/3 + d}$ | $\frac{2/3}{2/3 + d}$ | $\frac{1}{1 + d}$ | $\frac{4/3}{4/3 + d}$ | $\frac{5/3}{5/3 + d}$ | $\frac{2}{2 + d}$ |

**Table 11.**
Predicted and observed values of $R$ for arbitrary $c$ and $d$ ($b = 0$).

| $c$ | $d$ | Predicted $R$ | Observed $R$ |
|---|---|---|---|
| .41 | .73 | .53 | .53 |
| .29 | .44 | .57 | .57 |
| .81 | .34 | .83 | .83 |
| .59 | .55 | .68 | .69 |
| .18 | .56 | .39 | .39 |
| .27 | .11 | .83 | .83 |

The relationship between $c$, $d$, and $R$ in **Table 10** seems to be $R = 2c/(2c + d)$. In light of the caterpillar model, this makes sense. The prey values are doubled in the current situation. We can check the model by seeing how accurately it predicts $R$ for a variety of values of $c$ and $d$. A series of simulations was carried out using the *heron* program, and the results are reported in **Table 11**.

**Exercises**

**15.** Does the formula $R = 2c/(2c + d)$ predict the relationship you found between $c$ and $d$ in Exercise 14?

**16.** When $b = 0$ what must the relationship be between $c$ and $d$ to ensure that $R > 0.5$, that is, that the animal is "lazy?"

## 5.5 Combining the Results

So far we have examined two special cases of the heron model, which reduced a three-variable problem to a manageable two-variable situation. We saw that

1. if $c = 0$, then $R = \dfrac{b}{b + d}$;
2. if $b = 0$, then $R = \dfrac{2c}{2c + d}$.

As a first guess as to what happens when neither $b$ nor $c$ is 0, we might hypothesize that the relation between $R$, $b$, $c$ and $d$ is given by the simplest sort of combination of these two equations:

$$R = \frac{b + 2c}{b + 2c + d}.$$

Notice that if $c = 0$ this general formula specializes to the first equation above, and if $b = 0$ the general formula specializes to the second equation. We tested this general formula by using it to predict values of $R$ for various choices of $b$, $c$, and $d$. We then used the *heron* simulation to check the accuracy of the predictions. The result are given in **Table 12**. Again the fit is quite good!

Our equation for $R$ tells us when a heron will be lazy. That is,

$$R > \frac{1}{2} \Leftrightarrow \frac{b + 2c}{b + 2c + d} > \frac{1}{2} \Leftrightarrow 2b + 4c > b + 2c + d$$
$$\Leftrightarrow b + 2c > d.$$

**Table 12.**
Predicted and observed values of $R$ for arbitrary values of $b$, $c$, and $d$.

| $b$ | $c$ | $d$ | Predicted $R$ | Observed $R$ |
|---|---|---|---|---|
| .20 | .10 | .40 | .50 | .50 |
| .31 | .21 | .61 | .54 | .55 |
| .42 | .14 | .27 | .71 | .72 |
| .62 | .05 | .44 | .62 | .62 |
| .12 | .18 | .63 | .43 | .42 |

For the heron, which expends little energy in its foraging behavior, laziness is the rule (unless the probability of becoming hungrier in any time interval becomes *very* large compared to the probability of finding food). If either large or small fish become rare, a heron will still be in a favorable foraging situation as long as the fish of other sizes remain available in reasonable numbers. This points out the advantage of diet breadth in terms of a stable foraging strategy. If $b$ and $c$ referred to two different species of fish, herons would be able to forage effectively regardless of population density fluctuations in any one prey species.

**Exercises**

**17.** If $b = 0.3$ and $d = 0.4$, what value for $c$ leads to a heron that rests two-thirds of the time?

**18.** If $c = 0.2$, what are possible values for $b$ and $d$ if the heron is to rest 60% of the time?

**19.** If $d = 0.3$, what is the maximum possible value for rest time for the heron?

# 6. A Different Analysis: Rates of Change

In several situations now, we have been quite successful in empirically deriving formulas that predict rest time. Further, these formulas have been quite similar. Now that we know *what* these formulas are, we ask *why* these equations take the forms that they do. One way of answering this question lies in reinterpreting the foraging and rest transition cycle as a problem of rates and distances.

***"... we ask why these equations take the forms that they do."***

Consider the following analogy. Suppose that you go to visit Grandma who lives $n$ miles away. On the way there, you drive at a rather rapid rate of $b$ miles per hour in anticipation of seeing her. After eating a large and wonderful meal that she prepared, you drive home at a more modest rate of $d$ miles per hour. Since *rate* × *time* = *distance*, travel time is obtained by dividing the distance by the rate. Therefore, the drive to Grandma's takes $n/b$ hours, while the drive home takes $n/d$ hours. Thus the fraction or ratio of time spent driving home to total driving time is

$$\frac{n/d}{(n/b) + (n/d)} = \frac{1/d}{(1/b) + (1/d)} = \frac{b}{b + d},$$

which was also the caterpillar rest-time formula.[6] What is the connection? Recall that for the caterpillar:

$$\text{if } a(t-1) = 1, \text{ then } \Delta h = \begin{cases} 1 & \text{with probability } b, \\ 0 & \text{with probability } 1 - b. \end{cases}$$

Here $b$ represents the *rate* of successful foraging per unit time $\Delta t$. The *value* or reward of a successful foraging bout in this case is $\Delta h = 1$, while an unsuccessful trial is worth nothing. Thus the *average rate of change in* $h(t)$ *with respect to time* is just the rate of successful foraging times its value, plus the rate of unsuccessful foraging times its value. Algebraically this is simply:

$$\frac{\Delta h}{\Delta t} = b \cdot 1 + (1 - b) \cdot 0 = b.$$

An entirely similar analysis applies when the animal is at rest:

$$\text{if } a(t-1) = 0, \text{ then } \Delta h = \begin{cases} -1 & \text{with probability } d, \\ 0 & \text{with probability } 1 - d. \end{cases}$$

This time the average rate of change in $h(t)$ with respect to time is given by:

$$\frac{\Delta h}{\Delta t} = d \cdot (-1) + (1 - d) \cdot 0 = -d.$$

The negative sign indicates that $h$ is *decreasing* or *returning* to 0 at $d$ units per unit time. That is, $d$ is the speed; the negative sign indicates the direction.

---

[6] Notice that $n$, the number of miles travelled each way, does not appear in the final expression.

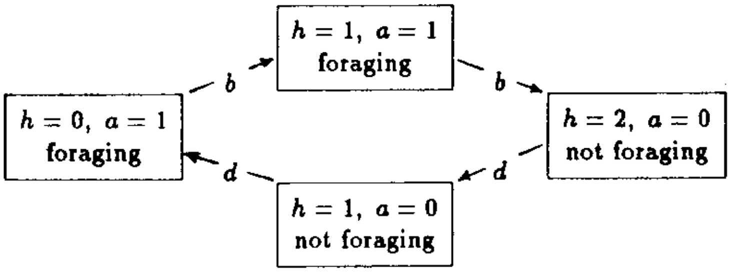


**Figure 8.** The transition cycle as a "round trip."

Now think of the transition cycle as a round trip from an empty gut, $\{0,1\}$, to satiation, $\{2,0\}$, back to an empty gut, $\{0,1\}$. (The comparison with the trip to Grandma's is now obvious.) During the trip to satiation, the caterpillar "travels" at an average rate of $\Delta h(t)/\Delta t = b$; the caterpillar "travels" *back* to the hunger point at an average rate of $\Delta h/\Delta t = d$. (See **Figure 8.**)

The return trip, or drop from satiation to hunger, is rest time. Using the round-trip analysis, the ratio of return time to total travel time, or in this context the ratio of rest time to total time is $b/(b + d)$. The fact that the "distance" travelled does not appear in this equation explains why the formula predicts rest time for the caterpillar regardless of the number of states involved, as you saw in **Exercises 6–9**.

How does this analysis apply to herons? Recall that for herons,

$$\text{if } a(t-1) = 1, \text{ then } \Delta h = \begin{cases} 2 & \text{with probability } c, \\ 1 & \text{with probability } b, \\ 0 & \text{with probability } 1 - b - c. \end{cases}$$

The average rate of change in $h(t)$ is calculated exactly as before. Take the various success rates for foraging, multiply by the respective prey values, and sum these results together. In this situation we have

$$\frac{\Delta h}{\Delta t} = b \cdot 1 + c \cdot 2 + (1 - b - c) \cdot 0 = b + 2c.$$

The rate of change in $h(t)$ while at rest has not changed and remains $-d$. Using the trip analogy again, the ratio of rest time to total time should be

$$\frac{b + 2c}{b + 2c + d}.$$

Indeed, this was our earlier result.

A final remark concerning this analysis is in order. The *rate* × *time* = *distance* equation that is essential to this interpretation presupposes that the rates for each half of the trip are *constant*. That is, we can only use this quick method of producing a rest-time formula when $\Delta h/\Delta t$ is constant for all foraging states and perhaps different but still constant for all rest states.

**Exercises**

Suppose we alter the heron model and now assume that its gut empties at three different rates depending on the level of activity while not foraging. Assume that when the heron is not foraging, $\Delta h$ can be 0, $-1$, or $-2$. That is,

$$\text{if } a(t-1)=0, \text{ then } \Delta h = \begin{cases} -2 & \text{with probability } e, \\ -1 & \text{with probability } d, \\ 0 & \text{with probability } 1-d-e. \end{cases}$$

When the heron is active, assume that there are only two possibilities:

$$\text{if } a(t-1)=1, \text{ then } \Delta h = \begin{cases} 0 & \text{with probability } 1-b, \\ 1 & \text{with probability } b. \end{cases}$$

Next assume that gut capacity, $h_{\max}$ is 4. Set the satiation point $s$ to be $h_{\max} = 4$. Finally assume that the hunger set point is $u = 1$.

**20.** Why was the hunger set point not 0 (empty gut) in this model? What could happen to the heron's gut if it were at rest when $h(t-1) = 1$?

**21.** Draw the transition diagram for this model.

**22.** What is the average rate of change in $\Delta h/\Delta t$ when the animal is foraging?

**23.** What is the average rate of change in $\Delta h/\Delta t$ when the animal is not foraging?

**24.** You now have all the pieces required to use the "rate analysis" or "round-trip analogy" to produce a formula that will predict rest time for this animal (in terms of the variables $b$, $d$, and $e$). What will that formula be?

# 7. Model III: Energy Loss During Foraging

## 7.1 The Cat as Forager

***"...a cat can get hungrier once it begins to forage."***

A cat has a far more expensive means of foraging than a heron or a caterpillar. While a caterpillar bends down to eat, and a heron stands and waits for the approach of a fish, a cat must stalk its prey. The slow progress through the hedge or around the rosebush, followed by a sudden leap, means that a hungry cat expends energy in the course of its foraging behavior. Because of this, a cat can get hungrier once it begins to forage.

Imagine a cat in a yard with both sparrows and robins present. The end result of any one stalking sequence could be one of three things. The cat might not catch anything; this corresponds to its stomach becoming emptier once it has begun to forage. The cat might catch only a scrawny sparrow barely worth the expense of stalking it; this corresponds to "breaking even" on stomach contents during the foraging bout. Or a cat might catch a nice fat robin; this corresponds to the cat gaining more energy than it expended while foraging.

## 7.2 The Mathematical Assumptions

Unlike earlier models, this one incorporates negative values of $\Delta h$ while foraging. At the same time, we also assume that the possibility of starvation is so small that it can be ignored. Let us see how these assumptions are reflected in the way the cat moves between states.

First assume that the animal is actively foraging: $a(t-1) = 1$. Then

if $h(t-1) \geq 1$, we assume

$$\Delta h = \begin{cases} -1 & \text{with probability } a, \\ 0 & \text{with probability } 1 - b - a, \\ 1 & \text{with probability } b, \end{cases}$$

and if $h(t-1) = 0$, we assume

$$\Delta h = \begin{cases} 1 & \text{with probability } r, \\ 0 & \text{with probability } 1 - r. \end{cases}$$

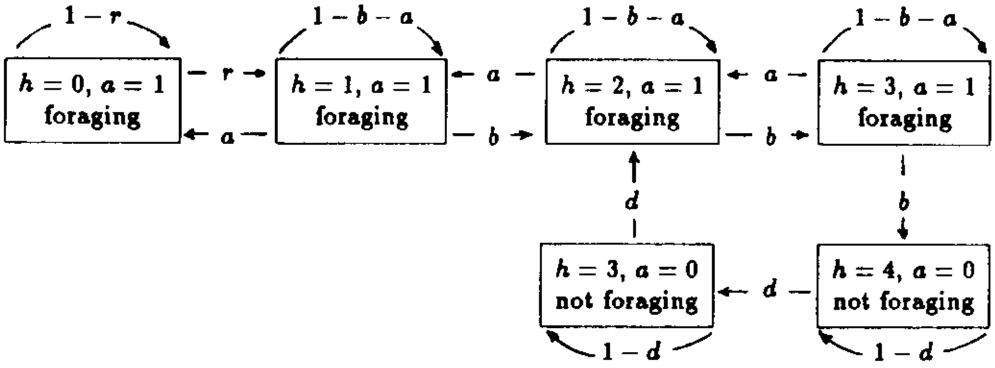


**Figure 9.** The transition diagram for a cat.

Notice that we have distinguished two types of foraging states: $h(t-1) \geq 1$ and $h(t-1) = 0$. This is necessary, because if we allowed $\Delta h = -1$ when $h(t-1) = 0$, then this would permit $h(t) = h(t-1) + \Delta h = 0 - 1 = -1$. That is, the amount in the cat's gut would be negative! This makes no sense in this context, but in the final model of this paper we will interpret this to mean that death by starvation has occurred. Notice that in the other foraging states, $\Delta h = -1$ is allowed. In these cases, $h(t) = h(t-1) + \Delta h \geq 1 + (-1) = 0$, which is meaningful. In the non-active state we assume as before that:

$$\text{if } a(t-1) = 0, \text{ then } \Delta h = \begin{cases} -1 & \text{with probability } d, \\ 0 & \text{with probability } 1 - d. \end{cases}$$

Next we set the thermostat points. We assume that the cat has a gut capacity of 4. We set the satiation point at $s = h_{\max} = 4$ and the hunger point at $u = 2$. (Setting $u = 2$ leaves room for some decrease in gut levels while foraging.) The transition diagram with six states is now easily constructed; see **Figure** 9.

## 7.3 A Single Simplification

The description of the cat as forager that we have given in the preceding section is quite general. It involves four different variables and seven different ways to change states. In Herbers's article there is a complete derivation of the rest time formula for the general situation [Herbers 1981]. The analysis is substantially more complicated here than for the equations for $R$ that we have worked out earlier. A consequence of her work is that the proportion of time at rest in this model is described by the formula:

$$R = \frac{2b^4r}{2b^4r + d\big(a^3(b+a) + r(2b^3 + 2b^2a + 2ba^2 + a^3)\big)}.$$

However, we will see that there is a single simplification that we can make to the model which will allow us to analyze the situation using our earlier techniques.

We start by analyzing the average rate of change in $h(t)$ with respect to time. When the animal is inactive ($a(t-1) = 0$), as we have seen twice before:

$$\frac{\Delta h}{\Delta t} = d \cdot (-1) + (1-d) \cdot 0 = -d.$$

When the cat is active ($a(t-1) = 1$), there are two cases. If $h(t-1) = 0$, then

$$\frac{\Delta h}{\Delta t} = r \cdot (1) + (1-r) \cdot 0 = r.$$

On the other hand, if $h(t) \geq 1$ there is the potential for becoming hungrier while foraging, since $\Delta h = -1$ with probability $a$, as well as the potential for successful foraging or breaking even. The average rate of change in $h(t)$ here is:

$$\frac{\Delta h}{\Delta t} = b \cdot (1) + (1-b-a) \cdot 0 + a \cdot (-1) = b - a.$$

To apply the rate analysis technique of Section 6, the rates of change in $h(t)$ while foraging must be constant. Therefore, we now *make the additional assumption that* $r = b - a$. This simplification, though primarily motivated by mathematics, has a biological meaning, as will be discussed in Section 7.4. With this assumption, the average rate of change in $h(t)$ in every foraging state is the constant $b - a$. The rate of change is also constant while at rest, so the rate analysis technique applies. We expect the ratio of rest to total time to be:

$$R = \frac{b-a}{b-a+d}.$$

This formula for $R$ was tested using the simulation *kitty* (similar to the *caterpillar* and *heron* programs) for various values of $a$, $b$, and $d$ and gave very accurate predictions (**Table 13**). Note that although setting $r = b - a$ allows us to use previous analytical techniques, it also means that $b - a$ must be nonnegative, since it represents the probability of a certain event occurring. Herbers's more general model does not have this restriction.

Consider the energetically-expensive darting and hovering foraging technique of a hummingbird. Unsuccessful foraging bouts lead to

**Table 13.**
Predicted and observed values of $R$ for the cat.

| $b$ | $a$ | $d$ | Predicted $R$ | Observed $R$ |
|---|---|---|---|---|
| .50 | .20 | .30 | .50 | .50 |
| .35 | .10 | .75 | .25 | .25 |
| .73 | .23 | .60 | .45 | .46 |
| .47 | .21 | .31 | .46 | .45 |
| .67 | .23 | .29 | .60 | .61 |

negative values of $\Delta h$ ($a$ is not 0). Data collected on male Anna hummingbirds (*Calypte anna*) show that even these birds spend a great deal of time resting, because the nutritional reward they receive from nectar-secreting flowers is reliable and generous [Stiles 1971]. (That is, $b$ is significantly larger than $a$.) Even male hummingbirds that engaged in vigorous territorial defense ($d$ is large) were able to perch approximately 60% of the time. Costly foraging techniques do not preclude significant resting time as long as foraging is quite successful ($b$ is relatively large).

## 7.4 A Comment on Desperation

Should foraging probabilities change depending on how full an animal's gut is? Shouldn't it forage in the same (optimal) fashion regardless of gut contents? Why should an animal be susceptible to getting hungrier while foraging only when its gut is not empty? Why doesn't it forage as if its gut were empty all of the time, and therefore avoid becoming hungrier? Isn't changing the probabilities when the gut is empty equivalent to "getting something for nothing?" Isn't the $r = b - a$ simplification of Section 7.3 "cheating" somehow?

***"... our model deals only with gut contents...."***

Remember that our model deals only with gut contents, not with other costs associated with foraging. A very hungry animal might be desperate enough to alter its foraging strategy in ways that improved its chances of finding food but caused other problems not expressed in this model. A cat that got hungry enough might stalk birds in a yard guarded by a dog. This entry into a previously unhunted area might increase the cat's odds of finding prey. However, a new probability (call it $x$) may enter the picture—that of the cat getting killed by the dog! The variable $x$ doesn't fit into our model, so it looks as if the cat is foraging better (i.e., $\Delta h \neq -1$ when $h(t-1) = 0$) as it gets hungrier. Actually it may just be a riskier strategy that looks like a very good idea only from the viewpoint of a very hungry cat (or a very bored dog). The simplification $r = b - a$ that we used in Section 7.3 will have associated costs that do not appear in terms of those three variables, but which are nonetheless real.

In modeling group hunting behavior of lions, Clark found that these predators should be hunting in smaller groups as the availability of Thomson's gazelles decreases and the lions' bodily reserves decline. This switch involves a trade-off, with a more risk-prone strategy (smaller groups of lions are less likely to catch prey) being accepted in order to achieve a greater possible reward (a Thomson's gazelle just doesn't provide enough wild venison to feed fully very many lions) [Clark 1987]. Here, hunger and prey density are jointly expected to modify the level of acceptable risk in foraging behavior, which is reminiscent of our house cat unhappily creeping about a dog's backyard.

**Exercises**

**25.** Show that when $r = b - a$, Herbers's complicated formula for rest time at the beginning of Section 7.3 simplifies to our formula.

**Exercises 26–29** combine the ideas of the heron and the cat examples. Assume that the cat will on occasion catch a pigeon ($\Delta h = 2$) as well as sparrows and robins. Specifically, when the cat is actively foraging and $a(t-1) = 1$, then

if $h(t-1) \geq 1$, we assume

$$\Delta h = \begin{cases} -1 & \text{with probability } a, \\ 0 & \text{with probability } 1 - b - c - a, \\ 1 & \text{with probability } b, \\ 2 & \text{with probability } c. \end{cases}$$

When the cat's gut is empty, we prevent the cat from starving ($\Delta h \neq -1$) but we also do not let it catch pigeons ($\Delta h \neq 2$), to simplify the model. So

if $h(t-1) = 0$, we assume

$$\Delta h = \begin{cases} 1 & \text{with probability } r, \\ 0 & \text{with probability } 1 - r. \end{cases}$$

Finally, when resting,

if $a(t-1) = 0$, we assume

$$\Delta h = \begin{cases} -1 & \text{with probability } d, \\ 0 & \text{with probability } 1 - d. \end{cases}$$

**26.** If the hunger set point is $u = 2$ and the satiation set point is $s = 4$, why must the gut capacity, $h_{\max}$, of the cat be at least 5?

**27.** Draw the transition diagram for this cat with $h_{\max} = 5$.

**28.** What value of $r$ allows you to use the "rate of change" technique to produce a formula for rest time, $R$? (Hint: What is the average rate of change in $h$ when the cat is active and $h(t-1) \geq 1$?)

**29.** Using your assumption about $r$ from **Exercise 28**, what do you expect the rest time formula to be?

# 8. Model IV: The Possibility of Starvation

We now consider a case in which a predator may starve to death. If a cat is stalking prey during the winter, it faces both increased energetic expenses (staying warm in the cold air) and a decreased probability of rewards (there are far fewer birds around to eat, and perhaps the birds themselves are getting thinner). The cat's gut will empty more rapidly and its gut will fill more slowly.

A decrease in temperature (say from freezing to 10°F below freezing) can be thought of as an example of a process increasing the rate at which food reserves will be used up in a warm-blooded animal. Similarly, the fewer (or scrawnier) the birds in the yard are, the lower the rate of gut filling will be. Changes in either or both of the aspects of the cat's environment will alter its prospects for survival.

## 8.1 The Changes of State for the Stressed Cat

Our assumptions for the cat under stress are very similar to those in Section 7.2. In particular, energy loss during foraging is possible. However, when the cat is actively foraging, we will not distinguish the case when the gut is empty ($h(t-1) = 0$) from the case when it is not empty ($h(t-1) \geq 1$). First let us focus on the situation when the gut is empty and the cat is, of course, active. If the cat is unable to forage successfully or at least hold its own when $h(t-1) = 0$, then $\Delta h$ will be $-1$. Thus the new gut level will be

$$h(t) = h(t-1) + \Delta h = 0 + (-1) = -1.$$

We interpret this to mean that the animal has starved to death, and the activity function becomes 0. The cat cannot leave the state $\{-1, 0\}$ of the transition process (none of our cats have nine lives). With this modification in mind, the changes of state can be described in the usual fashion:

if $a(t-1) = 1$, we assume

$$\Delta h = \begin{cases} -1 & \text{with probability } a, \\ 0 & \text{with probability } 1 - b - a, \\ 1 & \text{with probability } b. \end{cases}$$

Next,

if $a(t-1) = 0$ and $h(t-1) \geq 0$,

$$\text{then } \Delta h = \begin{cases} -1 & \text{with probability } d, \\ 0 & \text{with probability } 1 - d. \end{cases}$$

Finally, the starvation condition is described by saying:

if $a(t-1) = 0$ and $h(t-1) = -1$,
then $\Delta h = 0$ with probability 1.

As usual, satiation will occur at $s = h_{\text{max}} = 4$. However, it will prove convenient to allow the hunger set point to vary for different cases. So for now we will insist only on the necessary restriction that $0 \leq u \leq 3$.

**Exercises**

**30.** Draw the transition diagram for the cat under stress with hunger set point $u = 2$.

**31.** Draw the transition diagram for the cat under stress with hunger set point $u = 0$.

**32.** What are the differences between the two diagrams? Does one seem more advantageous for the cat than the other? Why?

## 8.2 New Questions: Surviving the Winter

More important than describing rest time in this situation is determining whether or not a cat can survive the stressful conditions we have outlined. Let us assume that starvation becomes a possibility for the cat *only* during the winter season. Our goal is to determine (in a general way) how the various probabilities $a$, $b$, and $d$, as well as the hunger point $u$, affect the cat's survival.

We begin by defining *winter* as a time interval 500 units of $\Delta t$ in duration (any sufficiently long period of time will do). Next we say that the cat *survives* the winter if its gut level $h(t)$ never falls to $-1$ during 500 iterates of the change of state process (i.e., the passage of 500 units of $\Delta t$). We will be kind and start the transition process with the cat in the full, resting state $\{4, 0\}$. To mitigate the effects of having a particularly lucky or unlucky cat, we put 1000 cats at a time through our winter stress test and count the number that survive. We used the computer simulation *koolcat* to keep track of all of this. It is similar to the other simulations we have used, except of course, that the transition process is terminated for any cat whose gut level drops to $-1$.

Consider a simple case: assume that the probability $b$ of increasing the gut level while foraging ($\Delta h = 1$) is one-third. Similarly, assume that the probability $a$ of the gut emptying during foraging ($\Delta h = -1$) is also one-third. This means that for the final one-third of the time the cat forages, it breaks even ($\Delta h = 0$). In other words, all three outcomes are equiprobable. Finally, assume that the probability $d$ of the gut emptying during rest is one-half, meaning the gut is just as likely to empty as not while at rest. Just as we did in the unstressed cat model, we let the hunger set point be $u = 2$. We carried out the *koolcat* stress test under these conditions and *none of the cats survived the winter*! The equally grisly details are reported in **Table 14** for other values of $u$, and we also list the average winter lifetime of the cats in units of $\Delta t$.

***"... none of the cats survived the winter!"***

What happened? Are the winter conditions too severe? How can we help the cats survive? In the next few sections, we will briefly investigate the effects of varying $b$, $a$, $d$, and $u$ to determine which changes, if any, have a significant effect on the cat's chance for survival.

***"... the sooner the cat gets hungry, the better its chances are of survival... ."***

One point is already obvious from **Table 14**: the higher the hunger set point, the longer the average lifespan. While this is of little consolation here since all of the cats died anyway, it is something to keep in mind. We can interpret these data as saying *the sooner the cat gets hungry, the better its chances are of survival or prolonging its lifespan*. While it may seem cruel for the cat to be constantly hungry,

**Table 14.**
The average lifespan and the number of cats surviving winter out of 1000, as $u$ varies.

| $b$ | $a$ | $d$ | $u$ | Survivors | Average Lifetime |
|---|---|---|---|---|---|
| .33 | .33 | .50 | 0 | 0 | 17 |
| .33 | .33 | .50 | 1 | 0 | 25 |
| .33 | .33 | .50 | 2 | 0 | 33 |
| .33 | .33 | .50 | 3 | 0 | 40 |

this turns out to be crucial for its survival. In general, the sooner the cat looks for food (i.e., the higher the hunger set point), the less likely the gut level will drop to the starvation level of $-1$. We will keep track of this effect at each stage as we vary $b$, $a$, and $d$. The data in **Table 14** will serve as a baseline from which to judge the effects of all such variations.

## 8.3 Improving the Rate of Successful Foraging

Suppose that the cat is able to increase its rate of successful foraging, $b$. As $b$ increases, the cat is able to find prey more often, thereby staving off starvation. In particular, if we allowed the rate $b$ to rise from one-third to two-thirds, we would expect the cat's chances for survival to improve markedly, presuming the other factors were kept constant. *Table 15* shows the results of such a simulation.

*Table 15.*
The average lifespan and the number of cats surviving winter out of 1000, as $b$ varies.

| $b$ | $a$ | $d$ | $u$ | Survivors | Average Lifetime |
|---|---|---|---|---|---|
| .333 | .333 | .500 | 0 | 0 | 17 |
| | | | 1 | 0 | 25 |
| | | | 2 | 0 | 33 |
| | | | 3 | 0 | 40 |
| .417 | .333 | .500 | 0 | 0 | 20 |
| | | | 1 | 0 | 31 |
| | | | 2 | 0 | 43 |
| | | | 3 | 0 | 55 |
| .500 | .333 | .500 | 0 | 0 | 21 |
| | | | 1 | 0 | 36 |
| | | | 2 | 0 | 55 |
| | | | 3 | 0 | 73 |
| .583 | .333 | .500 | 0 | 0 | 24 |
| | | | 1 | 0 | 42 |
| | | | 2 | 0 | 64 |
| | | | 3 | 5 | 106 |
| .667 | .333 | .500 | 0 | 0 | 27 |
| | | | 1 | 0 | 48 |
| | | | 2 | 2 | 84 |
| | | | 3 | 26 | 132 |

The data in **Table 15** do show that as $b$ is increased, lifespans do lengthen marginally. By the time $b$ reaches two-thirds, there are some survivors (when $u = 3$) but fewer than 3%! Indeed, notice that for $u = 0$, allowing $b$ to rise from one-third to two-thirds has about the same affect on average lifespan as keeping $b$ fixed at one-third and letting $u$ rise to 1 or 2. In general, we see that increasing $u$ has more effect than increasing $b$, and that the effect of increasing $u$ is greater as $b$ gets larger.

## 8.4 The Effect of Lowered Energy Loss at Rest

Suppose the cat manages to rest more quietly and in a warmer place. This will decrease the energy costs associated with resting, with the result that the gut should take longer to empty. This will mean that the cat will stay satiated longer and will face the problems of foraging less frequently. We would predict that this will increase the lifespan of the cats and increase the number of cats surviving winter. **Table 16** shows the effect of decreasing $d$ from 0.500 to 0.050 while keeping $b$ and $d$ fixed at their baseline values of one-third.

**Table 16.**
The average lifespan and the number of cats surviving winter out of 1000, as $d$ varies.

| $b$ | $a$ | $d$ | $u$ | Survivors | Average Lifetime |
|---|---|---|---|---|---|
| .333 | .333 | .500 | 0 | 0 | 17 |
| | | | 1 | 0 | 25 |
| | | | 2 | 0 | 33 |
| | | | 3 | 0 | 40 |
| .333 | .333 | .350 | 0 | 0 | 22 |
| | | | 1 | 0 | 28 |
| | | | 2 | 0 | 37 |
| | | | 3 | 0 | 42 |
| .333 | .333 | .200 | 0 | 0 | 33 |
| | | | 1 | 0 | 42 |
| | | | 2 | 0 | 46 |
| | | | 3 | 5 | 56 |
| .333 | .333 | .050 | 0 | 1 | 106 |
| | | | 1 | 3 | 113 |
| | | | 2 | 7 | 120 |
| | | | 3 | 19 | 124 |

The effects are not much different from increasing *b*. There are only a few survivors at the lowest *d* value. Again the changes attributable to *u* are seen to be more significant than those caused by varying *d*.

## 8.5 Moderating Winter

What happens if the winter season is milder, so that the energy costs of foraging are reduced? This means the probability *a* of losing energy while foraging will be decreased. With lower values of *a* we expect increased lifespans for the cats. Will the effects be only marginal, as they have been for increased values of *b* and decreased values of *d*? Intuition should tell us that the effects of reducing *a* to nearly 0 should be quite dramatic. After all, when $a = 0$, starvation is not possible and all cats survive. *Just how low will a need to be before we see significant changes in survival rates?* **Table 17** reports

**Table 17.**
The average lifespan and the number of cats surviving winter out of 1000, as *a* varies.

| *b* | *a* | *d* | *u* | Survivors | Average Lifetime |
|---|---|---|---|---|---|
| .333 | .333 | .500 | 0 | 0 | 17 |
| | | | 1 | 0 | 25 |
| | | | 2 | 0 | 33 |
| | | | 3 | 0 | 40 |
| .333 | .250 | .500 | 0 | 0 | 23 |
| | | | 1 | 0 | 37 |
| | | | 2 | 0 | 55 |
| | | | 3 | 0 | 80 |
| .333 | .150 | .500 | 0 | 0 | 40 |
| | | | 1 | 5 | 92 |
| | | | 2 | 51 | 166 |
| | | | 3 | 165 | 235 |
| .333 | .100 | .500 | 0 | 1 | 61 |
| | | | 1 | 59 | 175 |
| | | | 2 | 337 | 312 |
| | | | 3 | 637 | 406 |
| .333 | .050 | .500 | 0 | 23 | 130 |
| | | | 1 | 495 | 363 |
| | | | 2 | 868 | 464 |
| | | | 3 | 959 | 489 |

the simulation data for a decrease in *a* from the baseline value of one-third to a value of one-twentieth.

**Table 17** shows that it takes rather low values of *a* (0.1 or less) before there are significant numbers of cats surviving the winter. Just as important, the data indicate that if the cats wait until the last second to forage ($u = 0$), they still will not survive even when the costs of foraging are very small. That the hunger set point is not 0 is crucial to the cats' survival.

## 8.6 Tentative Conclusions

Of the three probability variables, only one of them by itself has a major impact on survival rates of the cats over winter. Lowering *a* by itself can significantly alter lifespans and increase the number of cats surviving winter. Raising *b* alone or simply lowering *d* will change the results only marginally. In the exercises that follow we ask you to explore the consequences of changing two or more of the variables at a time, as well as to investigate some special adaptations that animals have to the winter season.

The inability of changes in successful foraging (*b*) or energy loss at rest (*d*) to improve winter survival significantly is intuitively satisfying to anyone familiar with a northern winter. When the temperature is well below freezing, where are the birds? Do they manage to survive by improving the way they search for seeds (increase *b*) in the snow? Do they build enormous fluffy nests (decrease *d*) and sit tight up in the trees? Neither of these possibilities occurs. Actually, they fly south in the autumn! By moving themselves to a warmer region, they "moderate the winter" (decrease *a*) and live to return the following spring. This is clearly a viable strategy for an organism as mobile as a bird, and it matches our simulation results closely. But what about animals that lack wings? Finally, review Section 1.2 in this module and consider possible strategies for winter survival that fall outside this model's scope.

**Exercises**

**33.** List at least three strategies that animals in the wild exhibit which allow them to survive the winter. How does each of these strategies affect (if at all) the probability variables *b*, *a*, and *d* as well as the hunger set point *u*?

**34.** Can the combination of raising the rate *b* of success at foraging *and* lowering the energetic costs *d* of resting have an impact on the survival rates for cats? Choose appropriate values of *b*, *a*, and *d* to test this hypothesis using the *koolcat* simulation. Report the results and interpret their meaning.

**35.** When $a$ is low (say 0.1), does changing $b$ or $d$ or both have an impact on survival rates, or is survival primarily a function of $a$ alone? Choose an appropriate set of values of $b$ and $d$ which will test this hypothesis. Use the *koolcat* simulation to gather data. Report and interpret the results.

**36.** The Effects of Hibernation: Instead of a cat, suppose we were studying the black bear, *Ursus americanus*, whose habitat includes much of the eastern United States. (They are pests in some parts of Pennsylvania and New Jersey and are more than occasionally seen in the confines of that famous wilderness preserve, the Garden State Parkway.) The black bear survives the winter season by hibernating. In terms of the model we have outlined, the black bear reduces the energy costs of resting to almost 0. Since food resources for the bear are scarce during winter, the baseline values for $b$ and $a$ of one-third each are not entirely inappropriate. Assume that hibernation reduces $d$ to .001.

**a.** What will be the outcome of putting 1,000 such black bears through the *koolcat* stress test? In particular, for the given values of $b$, $a$ and $d$, which value of $u$ do you predict will yield the highest survival rate? Why? (Please take time now to think this through *before* you actually run the computer simulation!)

**b.** Fill in the table below with the results of the *koolcat* simulation for the black bear's probability values.

| $b$ | $a$ | $d$ | $u$ | Survivors | Average Lifetime |
|---|---|---|---|---|---|
| .333 | .333 | .001 | 0 | | |
| | | | 1 | | |
| | | | 2 | | |
| | | | 3 | | |

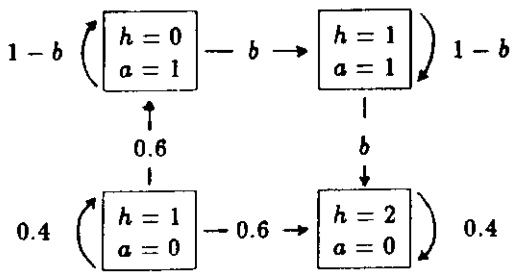
**c.** Do your data support or refute your prediction? If your prediction was not valid, do you now have an explanation for the results? What is it?

# 9. Conclusion

When we consider the tremendous variety of feeding methods employed by animals, we also realize that considerable elaboration of the thermostat models presented in this unit are possible. Baleen whales consume enormous numbers of tiny marine arthropods called *krill.* At certain times of year, the whales feed in Antarctic waters, where the energy demand for maintaining a high body temperature is extreme. Leeches gorge on blood meals, often consuming many times their body weight. A leech may have to eat only two or three blood meals a year, and it also expends no metabolic energy to raise its body temperature above that of the ambient environment. Gorillas live in social groups that move slowly through the forest, feeding on plant materials (wild celery forms an important component of a gorilla's diet, and the noise of a troop of them eating must be amazing). Social interactions among gorillas certainly affect which individuals have the first access to which food items. When you think of all of these sets of circumstances, and consider how any of them might affect $\Delta h$, $\Delta t$, $b$, $c$, $d$, or any of the other variables we have been discussing, you cannot help but see vistas of unmodeled regions awaiting the future students of biology and mathematics!

# 10. Answers to Selected Exercises

1.



2. **a.** Only states $\{0,0\}$ and $\{3,1\}$ are impossible.
   **b.** The required diagram is the same as **Figure 5** in Section 5.3.1.

3. Though the caterpillar gets hungrier during each unit of $\Delta t$ while at rest, the fact remains that each time the caterpillar is satiated, it rests for the next two units of $\Delta t$.

4. As $b$ gets larger, the caterpillar becomes a more successful forager and becomes satiated more quickly. Thus, it will spend less time foraging and have more time for rest.

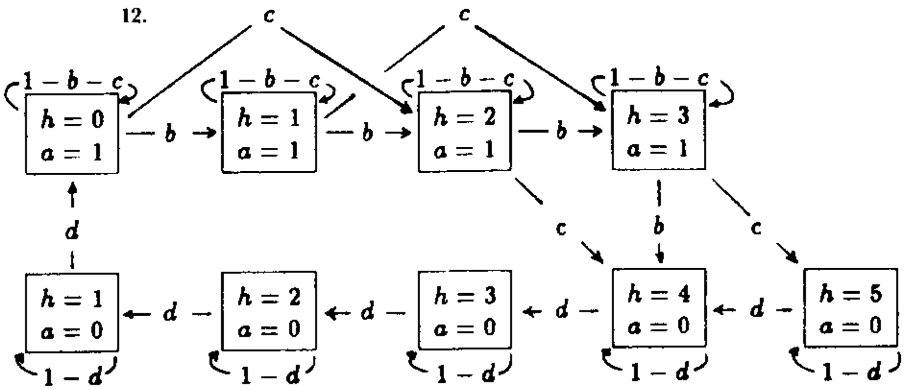
5. **e.** When $d = 0$, the animal never becomes hungry (unrealistic) and $R = 1$.

10. The proportions of time spent foraging and the proportion of time spent resting sum to 1. Thus the proportion of time spent foraging is

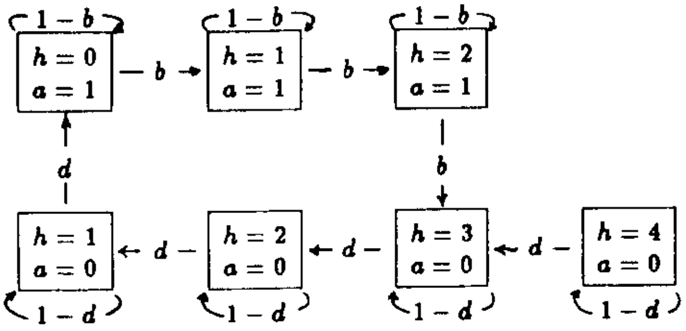
$$1 - R = 1 - \frac{b}{b+d} = \frac{d}{b+d}.$$

**11.** If a value 2 food item were eaten, the heron's gut capacity would be exceeded.

**12.**



**13.**



The heron can never get back to state $\{4,0\}$.

**16.** $R = \dfrac{2c}{2c + d} > 0.5 \Leftrightarrow 2c > c + 0.5d \Leftrightarrow c > 0.5d$. We must also have $b + c = 0 + c \leq 1$. Thus $0.5d < c \leq 1$.

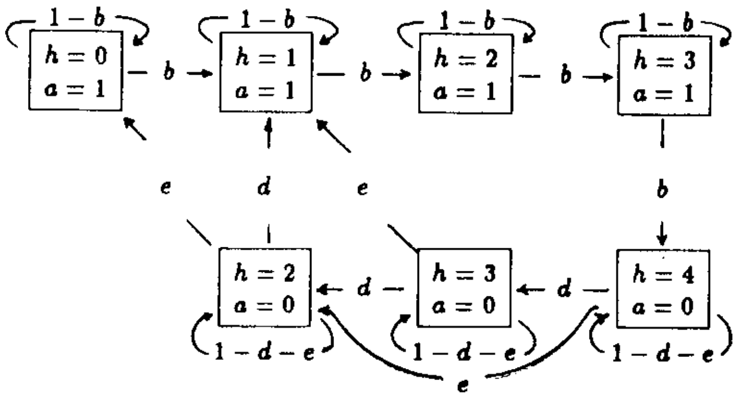
**17.** $R = \dfrac{b + 2c}{b + 2c + d} = \dfrac{0.3 + 2c}{0.3 + 2c + 0.4} \geq 2/3 \Leftrightarrow c \geq 0.25$. We also need $b + c = 0.3 + c \leq 1$, so $c \leq 0.7$. Thus $0.25 \leq c \leq 0.7$.

**18.** $R = \dfrac{b + 2c}{b + 2c + d} = \dfrac{b + 0.4}{b + 0.4 + d} \geq 0.6 \Leftrightarrow 0.4b + 0.16 \geq d$. We also need $b + c = b + 0.2 \leq 1$, so $b \leq 0.8$. Thus $0 \leq b \leq 0.8$. This range of $b$ values forces $d$ to satisfy the inequalities: $0.16 \leq d \leq 0.96$ which is acceptable.

**19.** $R$ is maximized when $c = 1$ and $b = 0$, that is, when the heron always captures prey with value 2. If $c = 1$, $b = 0$, and $d = 0.3$, then $R \approx 0.87$.

**20.** If the heron were in state $\{1,0\}$ at $t - 1$ and if $\Delta h = -2$, then the new gut level at time $t$ would be $1 - 2 = -1$, which is impossible.

21.



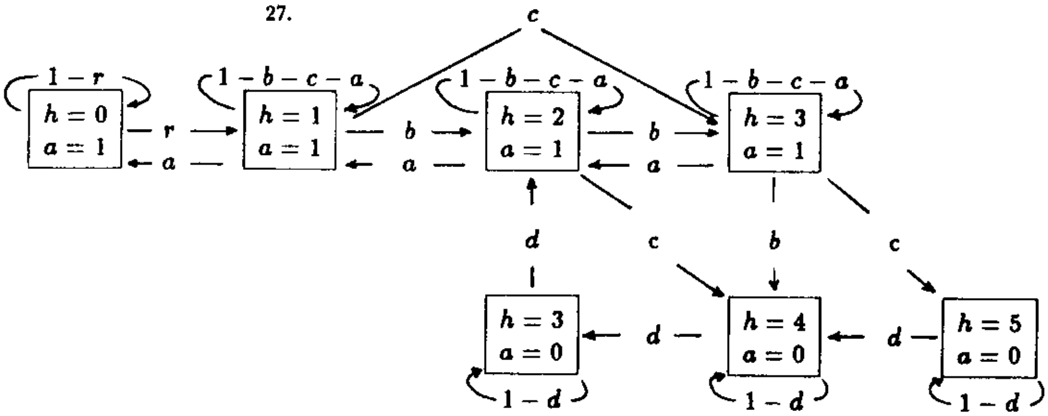
22. $b$.

23. $\frac{\Delta h}{\Delta t} = -2 \times e + (-1) \times d + 0 \times (1 - d - e) = -(2e + d)$.

24. $R = \frac{b}{b + 2e + d}$.

26. Since satiation occurs at gut level 4, the cat can still be foraging at gut level 3. If it captured a prey item of value 2 at this stage, its new gut level would be 5 (which must not be more than the maximum gut level).

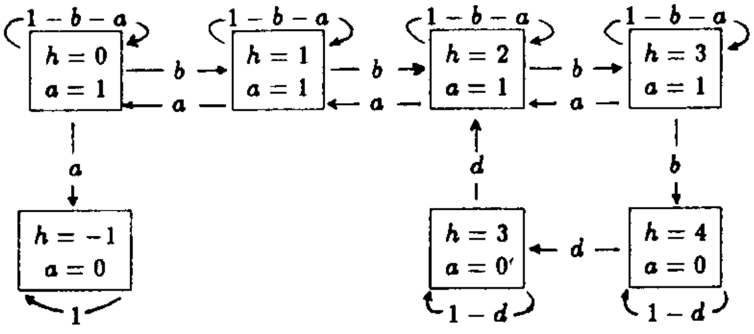
27.



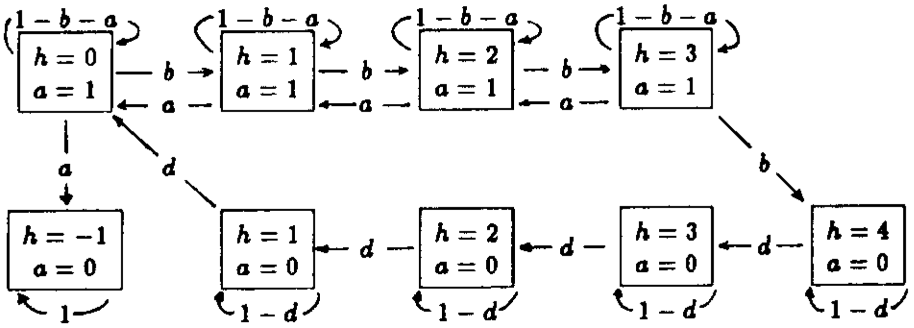
28. Let $r$ be the average change in gut level when the gut is not empty, that is, $r = -1 \times a + 0 \times (1 - b - c - a) + 1 \times b + 2 \times c = b + 2c - a$.

29. $R = \frac{b + 2c - a}{b + 2c - a + d}$.

30.



31.



32. In the second case, the animal comes to the brink of starvation before it begins to forage. The probability of starvation should be greater in this case.

33. Hibernating (lowers $d$), storing food (raises $b$ and consequently lowers $a$), flying south (lowers $a$, raises $b$, and lowers $d$).

# References

Clark, Colin W. 1987. The lazy, adaptable lions: A Markovian model of group foraging. *Animal Behaviour* 35: 361–368.

Fitzgerald, T. D., and S. C. Peterson. 1983. Elective recruitment by the Eastern tent caterpillar (*Malacosoma americanum*). *Animal Behaviour* 31: 417–423.

Herbers, Joan M. 1981. Time resources and laziness in animals. *Oecologia* 49: 252–262.

King, Bruce. 1982. The pace of life: An introduction to empirical model fitting. UMAP Modules in Undergraduate Mathematics and Its Applications: Module 551. *The UMAP Journal* 3(2): 221–248. 1983. Reprinted in *UMAP Modules: Tools for Teaching 1982*, 133–160. Lexington, MA: COMAP, Inc.

Stiles, F. Gary. 1971. Time, energy, and territoriality of the Anna hummingbird (*Calypte anna*). *Science* 173: 818–821.

Wellington, W. G. 1957. Individual differences as a factor in population dynamics: The development of a problem. *Canadian Journal of Zoology* 35: 293–323.

# Acknowledgment

The authors express their thanks to David Eck for his considerable technical and TEXnical advice.

# About the Authors

Kevin Mitchell received his B.A. in mathematics and philosophy from Bowdoin College and his Ph.D. in mathematics from Brown University. His main area of interest is algebraic geometry. Hobart and William Smith Colleges' emphasis on multidisciplinary work has permitted him to explore new areas, including team-teaching a course entitled "Mathematical Models and Biological Systems." He is also the proud father of twin daughters.

Steve Kolmes received his B.S. in zoology from Ohio University, and his M.S. and Ph.D. degrees in zoology from the University of Wisconsin at Madison. His main area of interest is the division of labor and ergonomic efficiency in honeybees. He teaches biology at Hobart and William Smith Colleges, and of late has been seen skulking near the Department of Mathematics and Computer science.

# Appendix: Computer Programs

The following Pascal programs can be used to generate data of the type used in the text and exercises. Making a single compiled version of each program available to the class will simplify the data collection process for those with little or no computer experience.

The first program, *caterpillar*, is listed in complete detail. The next four programs are variants on the first, and only the required modifications are listed. The programs may be further modified to permit additional experiments, with parameter changes that might be suggested from class discussion of the unit.

## caterpillar

```
program caterpillar(input, output);
const hmax = 2; u = 0; s = 2;                {gut capacity; hunger & satiation points}
type gut_type = 0..hmax;
     activity_type = (resting, foraging);
     state_type = array[gut_type, activity_type] of integer;
var b, d: real;                                            {probability variables}
    state: state_type;              {entries in state are (gut level, activity) pairs}
function Random(var seed: integer): real;
{Generates a pseudo-random number such that 0 < = Random < 1. See Oh! Pascal!,
by Doug Cooper and Michael Clancy (New York: W. W. Norton, 1985), 144-147.
Caution: This function is designed to be well-behaved on 16-bit machines. Your
system may have a built-in random number generator that you may wish to employ
instead. This function is called by Change_State.}
  const modulus = 65536;                   {constants use to produce random #'s}
        multiplier = 25173;
        increment = 13849;
  begin
    seed := ((multiplier * seed) + increment)mod modulus;
      {makes seed an integer such that 0 < = seed < modulus-1}
    Random := seed/modulus;                              {makes 0 < = Random < 1}
  end;                                                                  {Random}
procedure Initialize(var seed: integer; var state: state_type);
{Initializes seed and the state array.}
  var gut_level: gut_type;
      activity: activity_type;
  begin
    seed := clock;
    {Initialize seed for random number generator. While "clock" is not standard
    Pascal, most Pascal implementations have some sort of function that represents
    the time of day. You may substitute a constant for "clock" but this will produce
    the same set of "random" numbers each time the program is run.}
    for activity := resting to foraging do
      for gut_level := 0 to hmax do state[gut_level, activity] := 0;
  end;                                                              {Initialize}
procedure Start_Animal(var gut_level: gut_type; var activity: activity_type);
  begin
    gut_level := hmax;                        {the animal starts with a full stomach}
    activity := resting;                                           {and at rest}
  end;                                                            {Start_Animal}
procedure Check_Value (var p: real);
{Does the probability lie between 0 and 1? Called from Enter_b and Enter_d.}
  var in_range: boolean;            {flag that a probability variable is in range}
  begin
    in_range := false;                                       {initialize the flag}
    repeat
      readln(p);                                            {read the probability}
      in_range := ((p > = 0) and (p < = 1));
      writeln;
      if not in_range then
        write('Probability value is not between 0 and 1. Re-enter it:');
      until in_range;
```

```
  end;                                                        {Check_Value}
procedure Enter_d(var d: real);
{Input probability of energy loss at rest. This procedure calls Check_Value.}
  begin
    writeln; writeln;
    write('Enter probability d of energy loss at rest:');
    Check_Value(d);
  end;                                                        {Enter_d}
procedure Enter_b(var b: real);
{Input probability of finding value 1 food. This procedure calls Check_Value.}
  begin
    writeln;
    write('Enter probability b of finding value 1 food when foraging:');
    Check_Value(b);
  end;                                                        {Enter_b}
procedure Change_State(b, d: real; var state: state_type);
{Stimulates changes in gut and activity levels over 10000 units of time. Calls the
function Random. It has a subprocedure Foraging_Bout.}
  var time: 0..10000;
      gut_level: gut_type;
      activity: activity_type;
      seed: integer;                          {seed for random number generator}
      rnd: real;                                              {random number}
  procedure Foraging_Bout(var gut_level: gut_type);
  {For the foraging caterpillar, if 0 < = rnd < b, it finds food and the gut level
  increases. If b < = rnd < 1 then it does not find food and the gut level is
  unchanged.}
    begin
      if rnd < b then gut_level := gut_level + 1;
    end;                                                      {Foraging_Bout}
  begin                                                       {Change_State}
    Initialize(seed, state);
    Start_Animal(gut_level, activity);
    for time := 1 to 10000 do begin
              {Pick a random number to determine the new gut_level.}
      rnd := Random(seed);
      if(activity = foraging) then Foraging_Bout(gut_level);
      if((activity = resting) and (rnd > 1 - d))
        then gut_level := gut_level - 1;
        {While resting, if 0 < = rnd < 1 - d, then the gut is unchanged. If 1 - d
        < = rnd < 1, the gut empties a unit.}
      {Have activity switch points have been reached or exceeded?}
      if gut_level < = u then activity := foraging;           {hunger point}
      if gut_level > = s then activity := resting;          {satiation point}
      {Update state tracking the number of times each (gut_level, activity) pair
      occurs.}
      state[gut_level, activity] := state[gut_level, activity] + 1;
    end;                                                      {for time}
  end;                                                        {Change_States}
procedure Print_Results(state: state_type);
{Print the entries of state showing the number of times the animal was in each state.}
  var gut_level: gut_type;
      activity: activity_type;
  begin
```

```
      writeln; writeln;
      writeln('State', 'Number':20);
      writeln;
      for activity := resting to foraging do
        for gut_level := 0 to hmax do                 {consider only feasible states}
          if(((activity = resting) and (gut_level > u)) or
          ((activity = foraging) and (gut_level < s))) then
          writeln('{', gut_level;1, ',', activity:9, '}',state[gut_level, activity]);
    end;                                                             {Print_Results}
  begin                                                                  {MAINLINE}
    Enter_d(d);
    Enter_b(b);
    Change_State(b, d, state);
    Print_Results(state);
  end.
```

## caterpillar2

Change the first two lines of *caterpillar* to:

```
program caterpillar2(input, output);
const hmax = 3; u = 0; s = 3;        {gut capacity; hunger & satiation points}
```

## heron

Change the first two and sixth lines of *caterpillar* to:

```
program heron(input, output);
const hmax = 4; u = 0; s = 3;        {gut capacity; hunger & satiation points}
var b, c, d: real;                                    {probability variables}
```

Add the following procedure to *caterpillar* after the procedure *Enter_b*.

```
procedure Enter_c(var c: real);
{Input probability of finding value 2 food. This procedure calls Check_Value.}
  begin
    writeln;
    write('Enter probability c of finding value 2 food when foraging:');
    Check_Value(c);
  end;                                                              {Enter_c}
```

Change the arguments of the procedure *Change_State* to:

```
procedure Change_State(b, c, d: real; var state: state_type);
```

Change the subprocedure *Foraging_Bout* to the following.

```
  procedure Foraging_Bout(var gut_level: gut_type);
  {For the foraging heron, if 0 < = rnd < b, it finds value 1 food; if b < = rnd <
  1 - c, the animal finds no food; if 1 - c < = rnd < 1, the animal finds value 2
  food.}
    begin
      if rnd < b then gut_level := gut_level + 1
      else if rnd > = (1 - c) then gut_level := gut_level + 2;
    end;                                                      {Foraging_Bout}
```

Change the Mainline of *caterpillar* to:

```
begin                                                              {MAINLINE}
```

```
  Enter_d(d);
  repeat
    Enter_b(b);
    Enter_c(c);
    if b + c > 1 then writeln('b + c > 1; Re-enter data');
    until b + c < = 1;                    {probabilities b and c must sum to <= 1}
    Change_State(b, c, d, state);
    Print_Results(state);
end.
```

## kitty

Change the first two and sixth lines of *caterpillar* to:

```
program kitty(input, output)
const hmax = 4; u = 2; s = 4;              {gut capacity; hunger & satiation points}
var a, b, d: real;                                          {probability variables}
```

Add the following procedure to *caterpillar* after the procedure *Enter_b*.

```
procedure Enter_a(var a: real);
{Input probability of losing energy while foraging. Calls Check_Value.}
  begin
    writeln;
    write('Enter probability a of losing energy while foraging:');
    Check_Value(a);
  end;                                                              {Enter_a}
```

Change the arguments of the procedure *Change_State* to:

```
procedure Change_State(b, a, d: real; var state: state_type);
```

Change the subprocedure *Foraging_Bout* to the following.

```
  procedure Foraging_Bout(var gut_level: gut_type);
  {For the foraging cat, if the gut level > 0 then: if 0 < = rnd < b, it finds value 1
  food; if b < = rnd < 1 - a, the animal finds no food; if 1 - a < = rnd < 1, the
  animal finds value 2 food. If the gut level = 0 then: if 0 < = rnd < (b - a) then it
  finds value 1 food; if (b - a) < = rnd < 1, then it finds no food. (Recall: b - a =
  r.)}
    begin
      if gut_level > 0 then begin
        if rnd < b then gut_level := gut_level + 1
        else if rnd > = (1 - a) then gut_level := gut_level - 1;
        end
      else if rnd < (b - a) then gut_level := gut_level + 1;
    end;                                                       {Foraging_Bout}
```

Change the Mainline of *caterpillar* to:

```
begin                                                               {MAINLINE}
  Enter_d(d);
  repeat
    Enter_b(b);
    Enter_a(a);
    if b - a < = 0 then writeln('b - a < = 0; Re-enter data');
    if b + a > 1 then writeln('b + a > 1; Re-enter data');
  until((b + a < = 1) and (b - a > 0));    {probabilities are restricted by the model}
  Change_State(b, a, d, state);
  Print_Results(state);
end.
```

## koolcat

The *koolcat* program requires several changes in the *kitty* program. The entire program is outlined in detail below.

```
program koolcat(input, output);
const hmax = 4; s = 4;
type activity_type = (resting, foraging);
     gut_type = -1..4;
var a, b, d: real;                                   {probability variables}
```

The next function and five procedures are exactly the same as in *kitty*.

```
function Random(var seed: integer): real;
procedure Start_Animal(var gut_level: gut_type; var activity: activity_type);
procedure Check_Value(var p: real);
procedure Enter_d(var d: real);
procedure Enter_b(var b: real);
procedure Enter_a(var a: real);
```

The procedures *Change_State* and *Print_Results* are to be replaced by the following procedure.

```
procedure Determine_Survivors(b, a, d: real);
{Determine how many of 1000 cats survive 'winter' (the passage of 500 units of time)
and determine the average life span of the cats.}
  var u: 0..3;                                       {the hunger point will vary}
     gut_level: gut_type;
     activity: activity_type;
     cats: 1..1000;                    {number of cat put through the simulation}
     time: 0..500;                       {time period simulated is 500 units long}
     survivors: 0..1000;                   {cats surviving the winter simulation}
     total_lifespans: integer;                       {total of all cats' lifespans}
     seed: integer;
     rnd: real;
  begin
    seed := clock;                                   {see comments in caterpillar}
    for u := 0 to 3 do begin                         {the hunger point will vary}
      survivors := 0; total_lifespans := 0;                          {initialize}
      for cats := 1 to 1000 do begin
        Start_Animal(gut_level, activity);
        time := 0;                                              {initialize time}
        repeat
          rnd := Random(seed);
          if activity = foraging then begin
            {if foraging then: if 0 < = rnd < b, the cat finds value 1 food; if
            b < = rnd < (1 - a), it finds no food; if (1 - a) < = rnd < 1 it loses
            energy.}
              if rnd < b then gut_level := gut_level + 1
              else if rnd > = (1 - a) then gut_level := gut_level - 1;
          end;                                                    {if activity}
          if((activity = resting) and (rnd > 1 - d))
            then gut_level := gut_level - 1;                         {as usual}
          {Have activity switch points been reached or exceeded?}
          if gut_level < = u then activity := foraging;
          if gut_level > = s then activity := resting;
          time := time + 1;
        until((time = 500) or (gut_level = -1));             {survives or starves}
        total_lifespans := total_lifespans + time;       {update total_lifespans}
```

```
        if time = 500 then survivors := survivors + 1;      {update survivors}
      end;                                                          {for cats}
      writeln; writeln;                                       {output results}
      writeln ('For u = ', u:2, survivors:4,' out of 100 survived.');
      writeln ('The average lifespan was', total_lifespans/1000);
    end;                                                               {for u}
  end;                                                  {Determine_Survivors}
```

The new Mainline is:

```
begin                                                             {MAINLINE}
  Enter_d(d);
  repeat
    Enter_b(b);
    Enter_a(a);
    if b + a > 1 then writeln ('b + a > 1; Re-enter data');
  until b + a < = 1;               {foraging probabilities must sum to < = 1}
  Determine_Survivors(b, a, d);
end.
```