## CHAPTER 1

## First steps. . .

We introduce the basic idea for analysis of data from encounters of marked individuals by means of a simple example. Suppose you are interested in exploring the potential costs of reproduction on survival of some species of your favorite taxa (say, a species of bird). The basic idea is pretty simple: an individual that spends a greater proportion of available energy on breeding may have less available for other activities which may be important for survival. In this case, individuals putting more effort into breeding (i.e., producing more offspring) may have lower survival than individuals putting less effort into breeding. On the other hand, it might be that individuals that are of better 'quality' are able to produce more offspring, such that there is no relationship between 'effort' and survival. You decide to reduce the confounding effects of the 'quality' hypothesis by doing an experiment. You take a sample of individuals who all produce the same number of offspring (the idea being, perhaps, that if they had the same number of offspring in a particular breeding attempt, that they are likely to be of similar quality). For some of these individuals, you increase their 'effort' by adding some offspring to the nest (i.e., more mouths to feed, more effort expended feeding them). For others, you reduce effort by removing some offspring from the nest (i.e., fewer mouths to feed, less effort spent feeding them). Finally, for some individuals, you do not change the number of offspring, thus creating a control group.

As described, you've set up an 'experiment', consisting of a control group (unmanipulated nests), and 2 treatment groups: one where the number of offspring has been reduced, and one where the number of offspring has been increased. For convenience, call the group where the number of offspring was increased the 'addition' group, and call the group where the number of offspring was reduced the 'subtraction' group. Your hypothesis might be that the survival probability of the females in the 'addition' group should be lower than the control (since the females with enlarged broods might have to work harder, potentially at the expense of survival), whereas the survival probability of the females in the 'subtraction' group should be higher than the control group (since the females with reduced broods might not have to work as hard as the control group, potentially increasing their survival). To test this hypothesis, you want to estimate the survival of the females in each of the 3 groups. To do this, you capture and individually mark the adult females at each nest included in each of the treatment groups (control, additions, subtractions). You release them, and come back at some time in future to see how many of these marked individuals are 'alive' (the word 'alive' is written parenthetically for a reason which will be obvious in a moment).

Suppose at the start of your study (time $t$ ) you capture and mark 50 individuals in each of the 3 groups. Then, at some later time (time $t+1$ ), you go back out in the field and encounter alive 30 of the marked individuals from the 'additions' treatment, 35 of the marked individuals from the control group, and 30 individuals from the 'subtractions' treatment. The 'encounter data' from our study are tabulated at the top of the next page.

| group | $t$ | $t+1$ |
| :---: | :---: | :---: |
| additions | 50 | 30 |
| control | 50 | 38 |
| subtractions | 50 | 30 |

Hmm. This seems strange. While you predicted that the 2 treatment groups would differ from the controls, you did not predict that the results from the two treatments would be the same. What do these results indicate? Well, of course, you could resort to the time-honored tradition of trying to concoct a parsimonious 'post-hoc adaptationist' story to try to demonstrate that (in fact) these results 'made perfect sense', according to some 'new twist to underlying theory'. However, there is another possibility - namely, that the analysis has not been thoroughly understood, and as such, interpretation of the results collected so far needs to be approached very cautiously.

### 1.1. Return 'rates'

Let's step back for a moment and think carefully about our experiment - particularly, the analysis of 'survival'. In our study, we marked a sample of individual females, and simply counted the numbers of those females that were subsequently seen again on the next sampling occasion. The implicit assumption is that by comparing relative proportions of 'survivors' in our samples (perhaps using a simple $\chi^{2}$ test), we will be testing for differences in 'survival probability'. However (and this is the key step), is this a valid assumption? Our data consist of the number of marked and released individuals that were encountered again at the second sampling occasion. While it is obvious that in order to be seen on the second occasion, the marked individual must have survived, is there anything else that must happen?

The answer (perhaps obviously, but in case it isn't) is 'yes' - the number of individuals encountered on the second sampling occasion is a function of 2 probabilities: the probability of survival, and the probability that conditional on surviving, that the surviving individual is encountered. While the first of these 2 probabilities is obvious (and is in fact what we're interested in), the second may not be. This second probability (which we refer to generically as the 'encounter probability') is the probability that given that the individual is alive and in the sample, that it is in fact encountered (e.g., seen, or 'visually encountered'). In other words, simply because an individual is alive and in the sampling area may not guarantee that it is encountered. So, the proportion of individuals that were encountered alive on the second sampling occasion (which is often referred to in the literature as 'return rate'*) is the product of 2 different probability processes: the probability of surviving and returning to the sampling area (which we'll call 'apparent' or 'local' survival), and the probability of being encountered, conditional on being alive an in the sample (which we'll call 'encounter probability'). So, 'return rate' = 'survival probability' $\times$ 'encounter probability'. Let's let $\varphi$ (pronounced 'fee' or 'fie', depending on where you come from) represent the 'local survival probability', and $p$ represent the 'encounter probability'. Thus, we would write 'return rate' $=\varphi p$.

So, why do we care? We care because this complicates the interpretation of 'return rates' - in our example, differences in 'return rates' could reflect differences in the probability of survival, or they could reflect differences in encounter probability, or both! Similarly, lack of differences in 'return rates' (as we see when comparing the 'additions' and 'subtractions' treatment groups in our example) may not indicate 'no differences in survival' (as one interpretation) - there may in fact be differences in survival, but corresponding differences in encounter probability, such that their products ('return rate') are equal.

[^0]For example, in our example study, the 'return rate' for both the 'additions' and 'subtractions' treatment groups is the same: $(30 / 50)=0.6$. Our initial 'reaction' might have been that these data did not support our hypothesis predicting difference in survival between the 2 groups. However, suppose that in fact the 'treatment' (i.e., manipulating the number of offspring in the nest) not only influenced survival probability (as was our original hypothesis), but also potentially influenced encounter probabilities? For example, suppose the true survival probability of the 'additions' group was $\varphi_{\text {add }}=0.65$ (i.e., a $65 \%$ chance of surviving from $t$ to $t+1$ ), while for the 'subtractions' group, the survival probability is $\varphi_{\text {sub }}=$ 0.80 (i.e., an $80 \%$ chance of surviving). However, in addition, suppose that the encounter probability for the 'additions' group was $p_{\text {add }}=0.923$ (i.e., a $92.3 \%$ chance that a marked individual will be encountered, conditional on it being alive and in the sampling area), while for the 'subtractions' group, the encounter probability was $p_{\text {sub }}=0.75$ (we'll leave it to proponents of the adaptationist paradigm to come up with a 'plausible' explanation for such differences). While there are clear differences between the 2 groups, the products of the 2 probabilities are the same: $(0.65 \times 0.923)=0.6$, and $(0.8 \times 0.75)=0.6$. In other words, it is difficult to compare 'return rates', since differences (or lack thereof) could reflect differences or similarities in the 2 underlying probabilities (survival probability, and encounter probability).

### 1.2. A more robust approach

How do we solve this dilemma? Well, the solution we're going to focus on here (and essentially for the next 900 pages or so) is to collect more data, and using these data, separately estimate all of the probabilities (at least, when possible) underlying the encounters of marked individuals. Suppose for example, we collected more data for our experiment, on a third sampling occasion (at time $t+2$ ). On the third occasion, we encounter individuals marked on the first occasion. But, perhaps some of those individuals encountered on the third occasion were not encountered on the second occasion. How would we be able to use these data? First, we introduce a simple bookkeeping device, to help us keep track of our 'encounter' data (in fact, we will use this bookkeeping system throughout the rest of the book - discussed in much more detail in Chapter 2). We will 'keep track' of our data using what we call 'encounter histories'. Let a ' 1 ' represent an encounter with a marked individual (in this example, we're focusing only on 'live encounters'), and let a ' 0 ' indicate that a particular marked individual was not seen on a particular occasion. Now, recall from our previous discussion that a ' 0 ' could indicate that the individual had in fact died, but it could also indicate that the individual was in fact still alive, but simply not encountered (the problem we face, as discussed, is how to differentiate between the two possibilities). For our 3 occasion study, where individuals were uniquely marked on the first occasion only, there are 4 possible encounter histories:

| encounter history | interpretation <br> 111captured and marked on the first occasion, alive and encountered on <br> the second occasion, alive and encountered on the third occasion |
| :---: | :--- |
| 110 | captured and marked on the first occasion, alive and encountered on <br> the second occasion, and either (i) dead by the third occasion, or (ii) <br> alive on the third occasion, but not encountered |
| captured and marked on the first occasion, alive and not encountered <br> on the second occasion, and alive and encountered on the third <br> occasion |  |

Chapter 1. First steps. . .
captured and marked on the first occasion, and either (i) dead by the second occasion, (ii) alive on the second occasion, and not encountered, and alive on the third occasion and not encountered, (iii) alive on the second occasion, and not encountered, and dead by the third occasion

You might be puzzled by the verbal explanation of the third encounter history: 101. How do we know that the individual is alive at the second occasion, if we didn't see it? Easy - we come to this conclusion logically, since we saw it alive at the third occasion. And, if it was alive at occasion 3, then it must also have been alive at occasion 2. But, we didn't see it on occasion 2, even though we know (logically) that it was alive. This, in fact, is one of the key pieces of logic - the individual was alive at the second occasion but not seen. If $p$ is the probability of detecting (encountering) an individual given that it is alive and in the sample, then $(1-p)$ is the probability of missing it (i.e., not detecting it). And clearly, for encounter history ' 101 ', we 'missed' the individual at the second occasion.

All we need to do next is take this basic idea, and formalize it. As written (above), you might see that each of these encounter histories could occur due to a specific sequence of events, each of which has a corresponding probability. Let $\varphi_{i}$ be the probability of surviving from time $(i)$ to $(i+1)$, and let $p_{i}$ be the probability of encounter at time ( $i$ ). Again, if $p_{i}$ is the probability of encounter at time $(i)$, then $\left(1-p_{i}\right)$ is the probability of not encountering the individual at time ( $i$ ).

Thus, we can re-write the preceding table as:

| encounter history | probability of encounter history |
| :---: | :--- |
| 111 | $\varphi_{1} p_{2} \varphi_{2} p_{3}$ |
| 110 | $\varphi_{1} p_{2}\left[\varphi_{2}\left(1-p_{3}\right)+\left(1-\varphi_{2}\right)\right]$ |
|  | $=\varphi_{1} p_{2}\left(1-\varphi_{2} p_{3}\right)$ |
| 101 | $\varphi_{1}\left(1-p_{2}\right)$ $\varphi_{2} p_{3}$ <br> 100 $\left(1-\varphi_{1}\right)$ $+\varphi_{1}\left(1-p_{2}\right)\left(1-\varphi_{2}\right)+\varphi_{1}\left(1-p_{2}\right) \varphi_{2}\left(1-p_{3}\right)$ <br>  $=1-\varphi_{1} p_{2}-\varphi_{1}\left(1-p_{2}\right) \varphi_{2} p_{3}$ <br>   |

(If you don't immediately see how to derive the probability expressions corresponding to each encounter history, not to worry: we will cover the derivations in much more detail in later chapters).

So, for each of our 3 treatment groups, we simply count the number of individuals with a given encounter history. Then what? Once we have the number of individuals with a given encounter history, we use these frequencies to estimate the probabilities which give rise to the observed frequency. For example, suppose for the 'additions' group we had $N^{111}=7$ (where $N^{111}$ is the number of individuals in our sample with an encounter history of ' $111^{\prime}$ '), $N^{110}=2, N^{101}=5$, and $N^{100}=36$. So, of the 50 individuals marked at occasion 1 , only $(7+2+5)=14$ individuals were subsequently encountered alive (at either sampling occasion 2 , sampling occasion 3, or both), while 36 were never seen again. Suppose for the 'subtractions' group we had $N^{111}=5, N^{110}=7, N^{101}=2$, and $N^{100}=36$. Again, 14 total individuals encountered alive over the course of the study.

However, even though both treatment groups (additions and subtractions) have the same overall 3 -year return rate $(14 / 50=0.28)$, we see clearly that the frequencies of the various encounter histories differ between the groups. This indicates that there are differences among encounter occasions in
survival probability, or encounter probability (or both) between the 2 groups, despite no difference in overall return rate. The challenge, then, is how to estimate the various probabilities (parameters) in the probability expressions, and how to determine if these parameter estimates are different between the 2 treatment groups.

An ad hoc way of getting at this question involves comparing ratios of frequencies of different encounter ratios. For example,

$$
\frac{N^{111}}{N^{101}}=\frac{\varphi 1 p_{2} \varphi 2 D_{3}}{\varphi_{1}\left(1-p_{2}\right) \varphi / D_{3}}=\frac{p_{2}}{1-p_{2}}
$$

So, for the 'additions' group, $\left(N^{111} / N^{101}\right)=(7 / 5)=1.4$. Thus, $\hat{p}_{(2, a d d)}=0.583$. In contrast, for the 'subtractions' group, $\left(N^{111} / N^{101}\right)=(5 / 2)=2.5$. Thus, $\hat{p}_{(2, s u b)}=0.714$. Once we have estimates of $p_{2}$, we can see how we could substitute these values into the various probability expressions to solve for some of the other parameter (probability) values. However, while this is reasonably straightforward (at least for this very simple example), what about the question of 'is this difference between the two different $\hat{p}_{2}$ values meaningful/significant?'. To get at this question, we clearly need something more - in particular we need to be able to come up with estimates of the uncertainty (variance) in our parameter estimates. To do this, we need a robust statistical tool.

### 1.3. Maximum likelihood theory - the basics

Fortunately, we have such a tool at our disposal. Analysis of data from marked individuals involves making inference concerning the probability structure underlying the sequence of events that we observe. Maximum likelihood (ML) estimation (courtesy of Sir Ronald Fisher) is the workhorse of analysis of such data. While it is possible to become fairly proficient at analysis of data from marked individuals without any real formal background in ML theory, in our experience at least a passing familiarity with the concepts is helpful. The remainder of this (short) introductory chapter is intended to provide a simple (very) overview of this topic. The standard 'formal' reference is the 1992 book by AWF Edwards ('Likelihood', Johns Hopkins University Press). Readers with significant backgrounds in the theory will want to skip this chapter, and are encouraged to refrain from comment as to the necessary simplifications we make.

So here we go. . .the basics of maximum likelihood theory without (much) pain. . .

### 1.3.1. Why maximum likelihood?

The method of maximum likelihood provides estimators that are both reasonably intuitive (in most cases) and several have some 'nice properties' (at least statistically):

1. The method is very broadly applicable and is simple to apply.
2. Once a maximum-likelihood estimator is derived, the general theory of maximum-likelihood estimation provides standard errors, statistical tests, and other results useful for statistical inference. More technically:
(a) maximum-likelihood estimators (MLE) are consistent.
(b) they are asymptotically unbiased (although they may be biased in finite samples).
(c) they are asymptotically efficient - no asymptotically unbiased estimator has a smaller asymptotic variance.
(d) they are asymptotically normally distributed - this is particularly useful since it provides the basis for a number of statistic 'tests' based on the normal distribution (discussed in more detail in Chapter 4).
(e) if there is a sufficient statistic for a parameter, then the MLE of the parameter is a function of a sufficient statistic.*
3. A disadvantage of the maximum likelihood method is that it frequently requires strong assumptions about the structure of the data.

### 1.3.2. Simple estimation example - the binomial coefficient

We will introduce the basic idea behind maximum likelihood (ML) estimation using a simple, and (hopefully) familiar example: a binomial model with data from a flip of a coin. Much of the analysis of data from marked individuals involves ML estimation of the probabilities defining the occurrence of one or more events. Probability events encountered in such analyses often involve binomial or multinomial distributions. As you might appreciate, there is a simple, logical connection between binomial probabilities, and analysis of data from marked individuals, since many of the fundamental parameters we are interested in are 'binary' (having 2 possible states). For example, survival probability (live or die), detection probability (seen or not seen), and so on. Like a coin toss (head or tail), the estimation methods used in the analysis of data from marked individuals are deeply rooted in basic binomial theory. Thus, a brief review of this subject is in order.

To understand binomial probabilities, you need to first understand binomial coefficients. Binomial coefficients are commonly used to calculate the number of ways (combinations) a sample size of $n$ can be taken without replacement from a population of $N$ individuals.

$$
\begin{equation*}
\binom{N}{n}=\frac{N!}{n!(N-n)!} \tag{1.1}
\end{equation*}
$$

This is read as 'the number of ways (combination) a sample size of $n$ can be taken (without replacement) from a population of size $N^{\prime}$. Think of $N$ as the number of organisms in a defined population, and let $n$ be the sample size, for example. Recall that the '!' symbol means factorial (e.g., $5!=5 \times 4 \times 3 \times 2 \times 1=$ 120).

A quick example - how many ways can a sample of size 2 (i.e., $n=2$ ) be taken from a population of size 4 (i.e., $N=4$ )? Just to confirm we're getting the right answer, let's first derive the answer by 'brute force'. Let the individuals in the sample all have unique marks: call them individuals $\mathbf{A}, \mathbf{B}, \mathbf{C}$ and $\mathbf{D}$, respectively. So, given that we sample 2 at a time, without replacement, the possible combinations we could draw from the 'population' are:

| AB | AC | AD | BC | BD | CD |
| :--- | :--- | :--- | :--- | :--- | :--- |
| BA | CA | DA | CB | DB | DC |

So, 6 total different combinations are possibly selected ( 6 , not 12 - the pair in each column are equivalent; e.g., ' $\mathrm{AB}^{\prime}$ ' and ' BA ' are treated as equivalent).

[^1]So, does this match with $\binom{4}{2}$ ?

$$
\binom{4}{2}=\frac{4!}{2!(4-2)!}=\frac{24}{2(2)}=\frac{24}{4}=6
$$

Nice when things work out, eh? OK, to continue - we use the binomial coefficient to calculate the binomial probability. For example, what is the probability of 5 heads in 20 tosses of a fair coin. Each individual coin flip is called a Bernoulli trial, and if the coin is fair, then the probability of getting a head is $p=0.5$, while the probability of getting a tail is $(1-p)=0.5$ (commonly denoted as $q$ ). So, given a fair coin, and $p=q=0.5$, then the probability of $y$ heads in $N$ flips of the coin is:

$$
\begin{equation*}
f(y \mid N, p)=\binom{N}{y} p^{y}(1-p)^{(N-y)} \tag{1.2}
\end{equation*}
$$

The left-hand side of the equation is read as 'the probability of observing $y$ events given that we do the experiment - toss the coin $N$ times, and given that the probability of a head in any given experiment (i.e., toss of the coin) is $p^{\prime}$. Given that $N=20$, and $p=0.5$, then the probability of getting exactly 5 heads in 20 tosses of the coin is:

$$
f(5 \mid 20, p)=\binom{20}{5} p^{5}(1-p)^{(20-5)}
$$

First, we calculate $\binom{20}{5}=15,504$ (note: 20 ! is a huge number). If $p=0.5$, then $f(5 \mid 20,0.5)=(15,504 \times$ $0.03125 \times 0.000030517578125)=0.0148$. So, there is a $1.48 \%$ chance of having 5 heads out of 20 coin flips, if $p=0.5$.

Now, in this example, we are assuming that we know both the number of times that we toss the coin, and (critically) the probability of a head in a single toss of the coin. However, if we are studying the survival of some organism, for example, what information on the left side of the probability equation (above) would we know? Well, hopefully we know the number of individuals marked ( $N$ ). Would we know the survival probability (in the above, the survival probability would correspond to $p$-later, we'll call it $S$ )? No! Clearly, this is what we're trying to estimate.

So, given the number of marked individuals ( $N$ ) at the start of the study and the number of individuals that survive ( $y$ ), how can we estimate the survival probability p? Easy enough, actually - we simply work 'backwards' (more or less). We find the value of $p$ that maximizes the likelihood ( $\mathcal{L}$ ) that we would observe the data we did.* So, for example, what would the value of $p$ have to be to give us the observed data?

Formally, we write this as:

$$
\begin{equation*}
\mathcal{L}(p \mid N, y)=\binom{N}{y} p^{y}(1-p)^{(N-y)} \tag{1.3}
\end{equation*}
$$

We notice that the right-hand side of eqn. (1.3) is identical to what it was before in eqn. (1.2) - but the left hand side is different in a subtle, but critical way. We read the left-hand side now as 'the likelihood $\mathcal{L}$ of survival probability $p$ given that $N$ individuals were released and that $y$ survived'. Now, suppose $N=20$, and that we see 5 individuals survive (i.e., $y=5$ ). What would $p$ have to be to maximize the chances of this occurring?

[^2]We'll try a 'brute force' approach first, simply seeing what happens if we set $p=0,0.1,0.2, \ldots$, and so on. Look at the following plot of the binomial probability calculated for different values of $p$ :


As you see, the probability of 'observing 5 survivals out of 20 individuals' rises to a maximum when $p$ is 0.25 . In other words, if $p$, which is unknown, were 0.25 , then this would correspond to the maximal probability of observing the data of 5 survivors out of 20 released individuals. This graph shows that some values of the unknown parameter $p$ are 'relatively unlikely' (i.e., those with low likelihoods), given the data observed. The value of the parameter $p$ at which this graph is at a maximum is the most likely value of $p$ (the probability of a head), given the data. In other words, the chances of actually observing 11 heads and 5 tails are maximal when $p$ is at the maximum point of the curve, and the chances are less when you move away from this point.

While graphs are useful for getting a 'look' at the likelihood, we prefer a more elegant way to estimate the parameter. If you remember any of your basic calculus at all, you might recall that what we want to do is find the maximum point of the likelihood function. Recall that for any function $y=f(x)$, we can find the maximum inflection point over a given domain by setting the first derivative $d y / d x$ to zero and solving. This is exactly what we want to do here, except that we have one preliminary step - we 'could' take the derivative of the likelihood function as written, but it is simpler to convert everything to logarithms first. The main reason to do this is because it simplifies the analytical side of things considerably. The log-transformed likelihood, now referred to as a 'log-likelihood', is denoted as $\ln \mathcal{L}$ ( $q \mid$ data).

Recall that our expression is

$$
f(p \mid N, y)=\binom{N}{y} p^{y}(1-p)^{(N-y)}
$$

The binomial coefficient in this equation is a constant (i.e., it does not depend on the unknown parameter $p$ ), and so we can ignore it, and express this equation in log terms as:

$$
\mathcal{L}(p \mid \text { data })=p^{y}(1-p)^{(N-y)} \rightarrow \ln \mathcal{L}(p \mid \text { data })=y \ln (p)+(N-y) \ln (1-p)
$$

Note that we've written the left-hand side in a sort of short-hand notation - 'the likelihood $\mathcal{L}$ of the parameter $p$, given the data' (which in this case consist of 5 survivors out of 20 individuals). So, now the equation we're interested in is:

$$
\ln \mathcal{L}(p \mid \text { data })=y \ln (p)+(N-y) \ln (1-p)
$$

So, all you need to do is differentiate this equation with respect to the unknown parameter $p$, set equal to zero, and solve.

$$
\frac{\partial[\ln \mathcal{L}(p \mid \text { data })]}{\partial p}=\frac{y}{p}-\frac{(N-y)}{(1-p)}=0
$$

So, solving for $p$, we get:

$$
\hat{p}=\frac{y}{N}
$$

Thus, the value of parameter $p$ which maximizes the likelihood of observing $y=5$ given $N=20$ (i.e., $\hat{p}$, the maximum likelihood estimate for $p$ ) is the same as our intuitive estimate: simply, $y / \mathrm{N}$. Now, your intuition probably told you that the 'only' way you could estimate $p$ from these data was to simply divide the number of survivors by the total number of animals. But we're sure you're relieved to learn that $5 / 20=0.25$ is also the MLE for the parameter $p$.

## closed and non-closed MLE

In the preceding example, we considered the MLE for the binomial likelihood. In that case, we could 'use algebra' to 'solve' for the parameter of interest ( $\hat{p}$ ). When it is possible to derive an 'analytical solution' for a parameter (or set of parameters for likelihoods where there are more than one parameter), then we refer to the solution as a solution in 'closed form'. Put another way, there is a closed form solution for the MLE for the binomial likelihood.
However, not all likelihoods have closed form solutions. Meaning, the MLE cannot be derived 'analytically' (generally, by taking the derivative of the likelihood and solving at the maximum, as we did in the binomial example). MLE's that cannot be expressed in closed form need to be solved numerically. Here is a simple example of a likelihood that cannot be put in closed form. Suppose we are interested in estimating the abundance of some population. We might intuitively understand that unless we are sure that we are encountering the entire population in our sample, then the number we encounter (the 'count' statistic; i.e., the number of individuals in our sample) is a fraction of the total population. If $p$ is the probability of encountering any one individual in a population, and if $n$ is the number we encounter (i.e., the number of individuals in our sample from the larger population), then we might intuitively understand that our canonical estimator for the size of the larger population is simply $(n / p)$. For example, if there is a $50 \%$ chance of encountering an individual in a sample, and we encounter 25 individuals, then our estimate of the population size is $\hat{N}=(25 / 0.5)=50$. (Note: we cover abundance estimation in detail in Chapter 14.)
Now, suppose you are faced with the following situation. You are sampling from a population for which you'd like to derive an estimate of abundance. We assume the population is 'closed' (no entries or exits while the population is being sampled). You go out on a number of sampling 'occasions', and capture a sample of individuals in the population. You uniquely mark each individual, and release it back into the population. At the end of the sampling, you record the total number of individuals encountered at least once - call this $M_{t+1}$. Now, if the canonical estimator for abundance is $\hat{N}=(n / p)$, then $\hat{p}=(n / N)$. In other words, if we knew the size of the population $N$ then we could derive a simple estimate of the encounter probability $p$ by dividing the number encountered in the sample $n$ into the size of the population. Remember, $p$ is the probability of encountering an individual. Thus, the probability of 'missing' an individual (i.e., not encountering it) is simple ( $1-p$ ) $=1-(n / N)$.

So, over $t$ samples, we can write

$$
\left(1-\frac{n_{1}}{N}\right)\left(1-\frac{n_{2}}{N}\right) \ldots\left(1-\frac{n_{t}}{N}\right)=\left(1-p_{1}\right)\left(1-p_{2}\right) \ldots\left(1-p_{t}\right)
$$

where $p_{i}$ is the encounter probability at time $i$, and $n_{i}$ is the number of individuals caught at time $i$.
If you think about it for a moment, you'll see that the product on right-hand side is the overall probability that an individual is not caught - not even once - over the course of the study (i.e., over $t$ total samples). Remember from above that we defined $M_{t+1}$ as the number of individuals caught at least once. So, we can write

$$
\left(1-\frac{M_{t+1}}{N}\right)=\left(1-\frac{n_{1}}{N}\right)\left(1-\frac{n_{2}}{N}\right)\left(1-\frac{n_{3}}{N}\right) \cdots\left(1-\frac{n_{t}}{N}\right)
$$

In other words, the LHS and RHS both equal the probability of never being caught - not even once. Now, if you had estimates of $p_{i}$ for each sampling occasion $i$, then you could write

$$
\begin{aligned}
\left(1-\frac{M_{t+1}}{N}\right) & =\left(1-p_{1}\right)\left(1-p_{2}\right) \ldots\left(1-p_{t}\right) \\
\frac{M_{t+1}}{N} & =1-\left(1-p_{1}\right)\left(1-p_{2}\right) \ldots\left(1-p_{t}\right) \\
\hat{N} & =\frac{M_{t+1}}{1-\left(1-p_{1}\right)\left(1-p_{2}\right) \ldots\left(1-p_{t}\right)}
\end{aligned}
$$

So, the expression is rewritten in terms of $N$ - analytical solution - closed form, right? Not quite. Note that we said if you had estimates of $p_{i}$. In fact, you don't. All you have is the count statistic (i.e., the number of individuals captured on each sampling occasion, $n_{i}$ ). So, in fact, 'all we have' are the count data (i.e., $M_{t+1}, n_{1}, n_{2} \ldots n_{t}$ ), which (from above) we relate algebraically in the following:

$$
\left(1-\frac{M_{t+1}}{N}\right)=\left(1-\frac{n_{1}}{N}\right)\left(1-\frac{n_{2}}{N}\right)\left(1-\frac{n_{3}}{N}\right) \cdots\left(1-\frac{n_{t}}{N}\right)
$$

It is not possible to 'solve' this equation so that only the parameter $N$ appears on the LHS, while all the other terms (representing data - i.e., $M_{t+1}, n_{1}, n_{2} \ldots n_{t}$ ) appear on the RHS. Thus, the estimator for $N$ cannot be expressed in closed form.

However, the expression does have a solution - but it is a solution we must derive numerically, rather than analytically. In other words, we must use numerical, iterative methods to find the value of $N$ that 'solves' this equation. That value of $N$ is the MLE, and would be denoted as $\hat{N}$.
Consider the following data:

$$
n_{1}=30, n_{2}=15, n_{3}=22, n_{4}=n_{t}=45, \text { and } M_{t+1}=79
$$

Thus, one wants the value of $N$ that 'solves' the equation

$$
\left(1-\frac{79}{N}\right)=\left(1-\frac{30}{N}\right)\left(1-\frac{15}{N}\right)\left(1-\frac{22}{N}\right)\left(1-\frac{45}{N}\right)
$$

One could try to solve this equation by 'trial and error'. That is, one could plug in a guess for population size and see if the LHS = RHS (not very likely unless you can guess very well). Thinking about the problem a bit, one realizes that, logically, $N \geq M_{t+1}$ (i.e., the size of the population $N$ must be at least as large as the number of unique individuals caught at least once, $M+t+1$ ). So, at least, one has a lower bound (in this case, 79 if we restrict the parameter space to integers). If the first guess for $N$ does not satisfy the equation, one could try another guess and see if that either (1) satisfies the equation or (2) is closer than the first guess. The log-likelihood functions for many (but not all) problems are unimodal (for the exponential family); thus, you can usually make a new guess in the right direction.


#### Abstract

One could keep making guesses until a value of $N$ (an integer) allows the LHS = RHS, and take this value as the MLE, $\hat{N}$. Clearly, the 'trial-and-error' method will unravel if there is more than 1 or 2 parameters. Likewise, plotting the log-likelihood function is useful only when 1 or 2 parameters are involved. We will quickly be dealing with cases where there are 30-40 parameters, thus we must rely on efficient computer routines for finding the maximum point in the multidimensional cases. Clever search algorithms have been devised for the 1-dimensional case. Computers are great at such routine computations and the MLE in this case can be found very quickly. Many (if not most) of the estimators we will work with cannot be put in closed form, and we will rely on computer software - namely, program MARK - to compute MLEs numerically.


Why go to all this trouble to derive an estimate for $p$ ? Well the maximum likelihood approach also has other uses - specifically, the ability to estimate the sampling variance. For example, suppose you have some data from which you have estimated that $\hat{p}=0.6875$. Is this 'significantly different' (by some criterion) from, say, 0.5 ? Of course, to address this question, you need to consider the sampling variance of the estimate, since this is a measure of the uncertainty we have about our estimate. How would you do this? Of course, you might try the 'brute force' approach and simply repeat your 'experiment' a large number of times. Each time, derive the estimate of $p$, and then calculate a mean and variance of the parameter. While this works, there is a more elegant approach - again using ML theory and a bit more calculus (fairly straightforward stuff).

Conceptually, the sampling variance is related to the curvature of the likelihood at its maximum. Why? Consider the following: let's say we release 16 animals, and observe 11 survivors. What would the MLE estimate of $p$ be? Well, we now know it is $(y / N)=(11 / 16)=0.6875$. What if we had released 80 animals, instead of 16 ? Suppose we did this experiment, and observed 55 survivors (i.e., the expected values assuming $p=0.6875)$. What would the likelihood look like in this case? Well, clearly, the maximum of the likelihood in both 'experiments' should occur at precisely the same point: 0.6875 .

But what about the 'shape' of the curve. In the following, we plot the likelihoods for both experiments ( $N=16$ and $N=80$ respectively).


Clearly, the larger sample size $(N=80)$ results in a 'narrower' function around the ML parameter
estimate, $\hat{p}=0.6875$. If the sampling variance is related to the degree of curvature of the likelihood at its maximum, then we would anticipate the sampling variance of the parameter in these 2 experiments to be quite different, given the apparent differences in the likelihood functions.

What is the basis for stating that 'variance is related to curvature'? Think of it this way - values of the likelihood at increasing distances from the MLE are increasingly 'unlikely', relative to the MLE. The degree to which they are less likely is a function of how rapidly the curve drops away from the maximum as you move away from the MLE (i.e., the 'steepness' of the curve on either side of the MLE).

How do we address this question of 'curvature' analytically? Well, again we can use calculus. We use the first derivative of the likelihood function to find the point on the curve where the rate of change was 0 (i.e., the maximum point on the function). This first derivative of the likelihood is known as Fisher's score function.

We can then use the derivative of the score function with respect to the parameter(s) (i.e., the second derivative of the likelihood function, which is known as the Hessian), evaluated at the estimated value of the parameter ( $p$, in this case), to 'tell us something about the curvature' at this point. In fact, more than just the curvature, Fisher showed that the negative inverse of the second partial derivative of the $\log$-likelihood function (i.e., the negative inverse of the Hessian), evaluated at the MLE, is the MLE of the variance of the parameter. This negative inverse of the Hessian, evaluated at the MLE, is known as the information function, or matrix.

For our example, our estimate of the variance of $p$ is

$$
\widehat{\operatorname{var}}(\hat{p})=\left[-\left(\frac{\partial^{2} \ln \mathcal{L}(p \mid \text { data })}{\partial p^{2}}\right)\right]_{p=\hat{p}}^{-1}
$$

So, we first find the second derivative of the log-likelihood (i.e., the Hessian):

$$
\frac{\partial^{2} \mathcal{L}}{\partial p^{2}}=-\frac{y}{p^{2}}-\frac{N-y}{(1-p)^{2}}
$$

We evaluate this second derivative at the MLE, by substituting $y=p N($ since $\hat{p}=y / N)$. This gives

$$
\begin{aligned}
\left.\frac{\partial^{2} \mathcal{L}}{\partial p^{2}}\right|_{y=p N} & =-\frac{N p}{p^{2}}-\frac{N(1-p)}{(1-p)^{2}} \\
& =-\frac{N}{p(1-p)}
\end{aligned}
$$

The variance of $p$ is then estimated as the negative inverse of this expression (i.e., the information function, or matrix), such that:

$$
\widehat{\operatorname{var}}(\hat{p})=\frac{p(1-p)}{N}
$$

Some of you may recognize this as the often-used estimator of the variance of a binomial proportion - it is in all the 'stats books'. But now you can sleep more easily knowing how it was derived!

So, how do the sampling variances of our 2 experiments compare? Clearly, since $p$ and (1-p) are the same in both cases (i.e., same ML estimate for $\hat{p}$ ), the only difference is in the denominator, $N$. Since $N=80$ is obviously larger than $N=16$, we know immediately that the sampling variance of the larger sample will be smaller (0.0027) than the sampling variance of the smaller sample (0.0134).

### 1.3.3. Multinomials: a simple extension

A binomial probability involves 2 possible states (e.g., live or dead). What if there are more than 2 states? In this case, we use multinomial probabilities. As with our discussion of the binomial probability (above), we start by looking at the multinomial coefficient - the multinomial equivalent of the binomial coefficient. The multinomial is extremely useful in understanding the models we'll discuss in this book. The multinomial coefficient is nearly always introduced by way of a die tossing example. So, we'll stick with tradition and discuss this classic example here. You'll recall that a die has 6 sides - therefore 6 possible outcomes if your roll a die once. The multinomial coefficient corresponding to the 'die' example is

$$
\binom{N}{n_{1} n_{2} n_{3} n_{4} n_{5} n_{6}}=\frac{N!}{n_{1}!n_{2}!n_{3}!n_{4}!n_{5}!n_{6}!}=\frac{N!}{\prod_{i=1}^{k} n_{i}!}
$$

Note the use of the product operator ' $\Pi$ ' in the denominator. In a multinomial context, we assume that individual trials are independent, and that outcomes are mutually exclusive and all inclusive. Consider the 'classic' die example. Assume we throw the die 60 times $(N=60)$, and a record is kept of the number of times a $1,2,3,4,5$ or 6 is observed. The outcomes of these 60 independent trials are shown below.

| face | frequency | notation |
| :---: | :---: | :---: |
| 1 | 13 | $y_{1}$ |
| 2 | 10 | $y_{2}$ |
| 3 | 8 | $y_{3}$ |
| 4 | 10 | $y_{4}$ |
| 5 | 12 | $y_{5}$ |
| 6 | 7 | $y_{6}$ |

Each trial has a mutually exclusive outcome ( 1 or 2 or 3 or 4 or 5 or 6 ). Note that there is a type of dependency in the cell counts in that once $n$ and $y_{1}, y_{2}, y_{3}, y_{4}$ and $y_{5}$ are known, then $y_{6}$ can be obtained by subtraction, because the total $(N)$ is known. Of course, the dependency applies to any count, not just $y_{6}$. This same dependency is also seen in the binomial case - if you know the total number of coin tosses, and the total number of heads observed, then you know the number of tails, by subtraction.

The multinomial distribution is useful in a large number of applications in ecology. The probability function for $k=6$ is

$$
P\left(y_{i} \mid n, p_{i}\right)=\binom{n}{y_{i}} p_{1}^{y_{1}} p_{2}^{y_{2}} p_{3}^{y_{3}} p_{4}^{y_{4}} p_{5}^{y_{5}} p_{6}^{y_{6}}
$$

Again, as was the case with the binomial probability, the multinomial coefficient does not involve any of the unknown parameters, and is conveniently ignored for many estimation issues.

This is a good thing, since in the simple die tossing example the multinomial coefficient is

$$
\binom{n}{y_{i}}=\frac{60!}{13!10!8!10!12!7!}
$$

which is an absurdly big number - beyond the capacity of your simple hand calculator to calculate. So, it is helpful that we can ignore it for all intents and purposes.

Some simple examples - suppose you role a 'fair' die 6 times (i.e., 6 trials), First, assume ( $y_{1}, y_{2}, y_{3}$, $y_{4}, y_{5}, y_{6}$ ) is a multinomial random variable with parameters $p_{1}=p_{2}=\ldots p_{6}=0.1667$ and $N=6$. What
is the probability that each face is seen exactly once? This is written simply as:

$$
\begin{aligned}
P(1,1,1,1,1,1 \mid 6,1 / 6,1 / 6,1 / 6,1 / 6,1 / 6,1 / 6) & =\frac{6!}{1!1!1!1!1!1!}\left(\frac{1}{6}\right)^{6} \\
& =\left(\frac{5}{324}\right)=0.0154
\end{aligned}
$$

What is the probability that exactly four 1's occur, and two 2's occur in 6 tosses? In this case,

$$
\begin{aligned}
\mathcal{L}(4,2,0,0,0,0 \mid 6,1 / 6,1 / 6,1 / 6,1 / 6,1 / 6,1 / 6) & =\frac{6!}{4!2!0!0!0!0!}\left(\frac{1}{6}\right)^{4}\left(\frac{1}{6}\right)^{2} \\
& =\left(\frac{5}{15,552}\right) \ll 0.0154
\end{aligned}
$$

As noted in our discussion of the binomial probability theorem, we are generally faced with the reverse problem - we do not know the parameters, but rather we want to estimate the parameters from the data. As we saw, these issues are the domain of the likelihood and log-likelihood functions. The key to this estimation issue is the multinomial distribution, and, particularly, the likelihood and log-likelihood functions

$$
\mathcal{L}(q \mid \text { data }) \text { or } \mathcal{L}\left(p_{i} \mid n_{i}, y_{i}\right)
$$

which we read as 'the likelihood of the parameters, given the data' - the left-hand expression is the more general one, where the symbol $q$ indicates one or more parameters. The right-hand expression specifies the parameters of interest.

At first, the likelihood function looks pretty messy, but it is only a slightly different view of the probability function. Just as we saw from the binomial probability function, the multinomial function assumes $N$ is given. The probability function further assumes that the parameters are given, while the likelihood function assumes the data are given. The likelihood function for the multinomial distribution is

$$
\mathcal{L}\left(p_{i} \mid n_{i}, y_{i}\right)=\binom{N}{y_{i}} p_{1}^{y_{1}} p_{2}^{y_{2}} p_{3}^{y_{3}} p_{4}^{y_{4}} p_{5}^{y_{5}} p_{6}^{y_{6}}
$$

Since the first term - the multinomial coefficient - is a constant, and since it doesn't involve any parameters, we ignore it. Next, because probabilities must sum to 1 (i.e., $\left\{\right.$ sum of $p_{i}$ over all $\left.i\right\}=1$ ), there are only 5 'free' parameters, since the 6th one is defined by the other 5 (the 'dependency' issue we mentioned earlier), and the total, $N$. We will use the symbol $K$ to denote the total number of estimable parameters in a model. Here, $K=5$.

The likelihood function for $K=5$, for example, is

$$
\mathcal{L}\left(p_{i} \mid N, y_{i}\right)=\binom{N}{y_{i}} p_{1}^{y_{1}} p_{2}^{y_{2}} p_{3}^{y_{3}} p_{4}^{y_{4}} p_{5}^{y_{5}}\left(1-\sum_{i=1}^{5} p_{i}\right)^{\left(N-\sum_{i=1}^{5} p_{i}\right)}
$$

So, just as we saw for the binomial example, we use a maximization routine (either analytical or numerical, depending on whether or not the likelihood can be expressed in closed form) to find the values of $p_{1}, p_{2}, p_{3}, p_{4}$ and $p_{5}$ that maximize the likelihood of the data that we observe. Remember - all we are doing is finding the values of the parameters which maximize the likelihood of observing the data that we see. Nothing more than that - at least conceptually.

### 1.4. Application to mark-recapture

Let's look at an example relevant to the task at hand (no more dice, or flipping coins.). Let's pretend we do a three year mark-recapture study, with 55 total marked individuals from a single cohort.* Once each year, we go out and look to see if we can 'see' (encounter) any of the 55 individuals we marked alive and in our sample. For now, we'll assume that we only encounter 'live' individuals.

The following represents the basic 'structure' of our sampling protocol:


In this diagram, each of the sampling events (referred to as 'sampling occasions') is indicated by a shaded grey circle. Our 'experiment' has three sampling occasions, numbered $1 \rightarrow 3$, respectively. In this diagram, time is moving forward going from left to right (i.e., sampling occasion 2 occurs one time step after sampling occasion 1 , and so forth). Connecting the sampling occasions we have an arrow the direction of the arrow indicates the direction of time - again, moving left to right, forward in time. We've also added two variables (symbols) to the diagram: $\varphi$ and $p$. What do these represent?

For this example, these represent the two primary parameters which we believe (assume) govern the encounter process: $\varphi_{i}$ (the probability of surviving from occasion $i$ to $i+1$ ), and $p_{i}$ (the probability that if alive and in the sample at time $i$, that the individual will be encountered). So, as shown on the diagram, $\varphi_{1}$ is the probability that an animal encountered and released alive at sampling occasion 1 will survive the interval from occasion $1 \rightarrow$ occasion 2 , and so on. Similarly, $p_{2}$ is the probability that conditional on the individual being alive and in the sample, that it will be encountered at occasion 2 , and so on. Why no $p_{1}$ ? Simple $-p_{1}$ is the probability of encountering a marked individual in the population, and none are marked prior to occasion 1 (which is when we start our study). In addition, the probability of encountering any individual (marked or otherwise) could only be calculated if we knew the size of the population, which we don't (this becomes an important consideration we will address in later chapters where we make use of estimated abundance). The important thing to remember here is the probability of being encountered at a particular sampling occasion is governed by two parameters: $\varphi$ and $p$.

Now, as discussed earlier, if we encounter the animal, we record it in our data as ' 1 '. If we don't encounter the animal, it's a ' 0 '. So, based on a 3 year study, an animal with an encounter history of ' 111 ' was 'seen in the first year (the marking year), seen again in the second year, and also seen in the third year'. Compare this with an animal with an encounter history of '101'. This animal was 'seen in the first year, when it was marked, not seen in the second year, but seen again in the third year'. For a 3 occasion study, where the occasion refers to the sampling occasion, with a single release cohort, there are 4 possible encounter histories:

| encounter history |
| :---: |
| 111 |
| 101 |
| 110 |
| 100 |

[^3]Now, the key question we have to address, and (in simplest terms) the basis for analysis of data from marked individuals, is 'what is the probability of observing a particular encounter history?'. The probability of a particular encounter history is determined by a set of parameters - for this study, we know (or assume) that the parameters governing the probability of a given encounter history are $\varphi$ and $p$. Based on the diagram on the previous page, we can write a probability expression corresponding to each of these possible encounter histories:

| encounter history | probability |
| :---: | :--- |
| 111 | $\varphi_{1} p_{2} \varphi_{2} p_{3}$ |
| 110 | $\varphi_{1} p_{2}\left(1-\varphi_{2} p_{3}\right)$ |
| 101 | $\varphi_{1}\left(1-p_{2}\right) \varphi_{2} p_{3}$ |
| 100 | $1-\varphi_{1} p_{2}-\varphi_{1}\left(1-p_{2}\right) \varphi_{2} p_{3}$ |

For example, take encounter history ' 101 '. The individual is marked and released on occasion 1 (the first 1 in the history), is not encountered on the second occasion, but is encountered on the third occasion. Now, because of this encounter on the third occasion, we know that the individual was in fact alive on the second occasion, but simply not encountered. So, we know the individual survived from occasion $1 \rightarrow 2$ (with probability $\varphi_{1}$ ), was not encountered at occasion 2 (with probability $1-p_{2}$ ), and survived to occasion 3 (with probability $\varphi_{2}$ ) where it was encountered (with probability $p_{3}$ ). So, the probability of observing encounter history ' 101 ' would be $\varphi_{1}\left(1-p_{2}\right) \varphi_{2} p_{3}$.

Here are our 'data' - which consist of the observed frequencies of the 55 marked individuals with each of the 4 possible encounter histories:

| encounter history | frequency |
| :---: | :---: |
| 111 | 7 |
| 110 | 13 |
| 101 | 6 |
| 100 | 29 |

So, of the 55 individual marked and released alive in the release cohort, 7 were encountered on both sampling occasion 2 and sampling occasion 3, 13 were encountered on sampling occasion 2 , but were not seen on sampling occasion 3 , and so on.

The estimation problem, then, is to derive estimates of the parameters $p_{i}$ and $\varphi_{i}$ which maximizes the likelihood of observing the frequency of individuals with each of these 4 different encounter histories. Remember, the encounter histories are the data - we want to use the data to estimate the parameter values. What parameters? Again, recall also that the probability of a given encounter history is governed (in this case) by two parameters: $\varphi$, and $p$.

OK, so we've been playing with multinomials (above), and you might have suspected that these encounter data must be related to multinomial probabilities, and likelihoods. Good guess! The basic idea is to realize that the statistical likelihood of an actual encounter data set (as is tabulated above) is merely the product of the probabilities of the possible capture histories over those actually observed. As noted by Lebreton et al. (1992), because animals with the same encounter history have the same probability expression, then the number of individuals observed with each encounter history appears as an exponent of the corresponding probability in the likelihood.

Thus, we write

$$
\begin{aligned}
\mathcal{L}= & \left(\varphi_{1} p_{2} \varphi_{2} p_{3}\right)^{N_{(111)}} \times\left[\varphi_{1} p_{2}\left(1-\varphi_{2} p_{3}\right)\right]^{N_{(110)}} \times\left[\varphi_{1}\left(1-p_{2}\right) \varphi_{2} p_{3}\right]^{N_{(101)}} \\
& \times\left[1-\varphi_{1} p_{2}-\varphi_{1}\left(1-p_{2}\right) \varphi_{2} p_{3}\right]^{N_{(100)}}
\end{aligned}
$$

where $N_{(i j k)}$ is the observed frequency of individuals with encounter history $i j k$.
As with the binomial, we take the log transform of the likelihood expression, and after substituting the frequencies of each history, we get:

$$
\begin{aligned}
\ln \mathcal{L}\left(\varphi_{1}, p_{2}, \varphi_{2}, p_{3}\right) & =7 \ln \left(\varphi_{1} p_{2} \varphi_{2} p_{3}\right)+13 \ln \left[\varphi_{1} p_{2}\left(1-\varphi_{2} p_{3}\right)\right]+6 \ln \left[\varphi_{1}\left(1-p_{2}\right) \varphi_{2} p_{3}\right] \\
& +29 \ln \left[1-\varphi_{1} p_{2}-\varphi_{1}\left(1-p_{2}\right) \varphi_{2} p_{3}\right]
\end{aligned}
$$

All that remains is to derive the estimates of the parameters $\varphi_{i}$ and $p_{i}$ that maximize this likelihood.
Let's go through a worked example, using the encounter history data tabulated on the preceding page. To this point, we have assumed that these encounter histories are governed by 'time-specific' variation in $\varphi$ and $p$. In other words, we would write the probability statement for encounter history ${ }^{\prime} 111$ ' as $\varphi_{1} p_{2} \varphi_{2} p_{3}$.

These time-specific parameters are indicated in the following diagram:


Again, the subscripting indicates a different survival and recapture probability for each interval or sampling occasion.

However, what if instead we assume that the survival and recapture probabilities do not vary over time? In other words, $\varphi_{1}=\varphi_{2}=\varphi$, and $p_{2}=p_{3}=p$. In this case, our diagram would now look like


What would the probability statements be for the respective encounter histories? In fact, in this case deriving them is very straightforward - we simply drop the subscripts from the parameters in the probability expressions:

| encounter history | probability |
| :---: | :--- |
| 111 | $\varphi p \varphi p$ |
| 110 | $\varphi p(1-\varphi p)$ |
| 101 | $\varphi(1-p) \varphi p$ |
| 100 | $1-\varphi p-\varphi(1-p) \varphi p$ |

Chapter 1. First steps. . .

So, what would the likelihood look like? Well, given the frequencies, the likelihood would be:

$$
\mathcal{L}=(\varphi p \varphi p)^{N^{111}}[\varphi p(1-\varphi p)]^{N^{110}}[\varphi(1-p) \varphi p]^{N^{101}}[1-\varphi p-\varphi(1-p) \varphi]^{N^{100}}
$$

Thus,

$$
\ln \mathcal{L}(\varphi, p)=7 \ln (\varphi p \varphi p)+13 \ln [\varphi p(1-\varphi p)]+6 \ln [\varphi(1-p) \varphi p]+29 \ln [1-\varphi p-\varphi(1-p) \varphi p]
$$

Again, we can use numerical methods to solve for the values of $\varphi$ and $p$ which maximize the likelihood of the observed frequencies of each encounter history. The likelihood profile for these data is plotted as a 2-dimensional contour plot, shown below:


We see that the maximum of the likelihood occurs at $p=0.542$ and $\varphi=0.665$ (where the 2 dark black lines cross in the figure).

For this example, we used a numerical approach to find the MLE. In fact, for this example where $\varphi$ and $p$ are constant over time, the probability expressions are defined entirely by these two parameters, and we could (if we really had to) write the likelihood as two closed-form equations in $\varphi$ and $p$, and derive estimates for $\varphi$ and $p$ analytically. All we need to do is (1) take the partial derivatives of the likelihood with respect to each of the parameters ( $\varphi, p$ ) in turn ( $\partial \mathcal{L} / \partial \varphi, \partial \mathcal{L} / \partial p$ ), (2) set each partial derivative to 0 , and ( 3 ) solve the resulting set of simultaneous equations.

Solving simultaneous equations is something that most symbolic math software programs (e.g., MAPLE, Mathematica, GAUSS, Maxima) does extremely well. For this problem, the ML estimates are derived analytically as $\hat{\varphi}=0.665$ and $\hat{p}=0.542$ (just as we saw earlier using the numerical approach). However, recall that many of the likelihoods we'll be working with cannot be evaluated analytically
in closed form, so we will rely in numerical methods. Program MARK evaluates all likelihoods (and functions of likelihoods) numerically.

What is the actual value of the likelihood at this point? On the $\log$ scale, $\ln (\mathcal{L})$ is maximized at -65.041. For comparison, the maximized $\ln (\mathcal{L})$ for the model where both $\varphi$ and $p$ were allowed to vary with time is -65.035. Now, these likelihoods aren't very far apart - only in the second and third decimal places. Further, the two models (with constant $\varphi$ and $p$, and with time varying $\varphi$ and $p$ ) differ by only 1 estimable parameter (we'll talk a lot more about estimable parameters in coming lectures). So, a $\chi^{2}$ test would have only 1 df . The difference in the $\ln (\mathcal{L})$ is 0.006 (actually, the test is based on $2 \ln (\mathcal{L})$, so the difference is actually 0.012 ). This difference is not significant (in the familiar sense of 'statistical significance') at $P \gg 0.5$. So, the question we now face is, which of the two models do we use for inference? This takes us to one of the main themes of this book - model selection - which we'll cover in some detail in Chapter 4. But, for the moment, a glimpse of where we're headed.

### 1.5. Variance estimation for $>1$ parameter

Earlier, we considered the derivation of the MLE, and the variance, for a simple situation involving only a single parameter. If in fact we have more than one parameter, the same idea we've just described for one parameter still works, but there is one important difference: a multi-parameter likelihood surface will have more than one second partial derivative. In fact, what we end up with a matrix of second partial derivatives, called the Hessian.
Consider for example, the log-likelihood of the simple mark-recapture data set we just analyzed in the preceding section:

$$
\ln \mathcal{L}(\varphi, p)=7 \ln (\varphi p \varphi p)+13 \ln [\varphi p(1-\varphi p)]+6 \ln [\varphi(1-p) \varphi p]+29 \ln [1-\varphi p-\varphi(1-p) \varphi p]
$$

Thus, the Hessian $\mathbf{H}$ (i.e., the matrix of second partial derivatives of the likelihood $\mathcal{L}$ with respect to $\varphi$ and $p$ ) would be

$$
\mathbf{H}=\left[\begin{array}{cc}
\frac{\partial^{2} \mathcal{L}}{\partial \varphi^{2}} & \frac{\partial^{2} \mathcal{L}}{\partial \varphi \partial \varphi} \\
\frac{\partial^{2} \mathcal{L}}{\partial p \partial \varphi} & \frac{\partial^{2} \mathcal{L}}{\partial p^{2}}
\end{array}\right]
$$

We'll leave it as an exercise for you to derive the second partial derivatives corresponding to each of the elements of the Hessian. It isn't difficult, just somewhat cumbersome.

For example,

$$
\begin{aligned}
\frac{\partial^{2} \mathcal{L}}{\partial \varphi^{2}}= & -\frac{26}{\varphi^{2}}-\frac{26 p}{\varphi(1-\varphi p)}-\frac{13\left[p(1-\varphi p)-\varphi p^{2}\right]}{\varphi^{2} p(1-\varphi p)}+ \\
& \frac{13\left[p(1-\varphi p)-\varphi p^{2}\right]}{\varphi(1-\varphi p)^{2}}-\frac{58(1-p) p}{1-\varphi p-\varphi^{2}(1-p) p}-\frac{29[-p-2 \varphi(1-p) p]^{2}}{\left[1-\varphi p-\varphi^{2}(1-p) p\right]^{2}}
\end{aligned}
$$

Pretty ugly (and this for a simple model with only 2 parameters - $\varphi$ and $p$ - both of which are held constant over time in this example). Good thing MARK handles all this messy stuff for you.

Next, we evaluate the Hessian at the MLE for $\varphi$ and $p$ (i.e., we substitute the MLE values for our parameters $-\hat{\varphi}=0.6648$ and $\hat{p}=0.5415$ - into the Hessian), which yields the information matrix, $\mathbf{I}$ :

$$
\mathbf{I}=\left[\begin{array}{ll}
-203.06775 & -136.83886 \\
-136.83886 & -147.43934
\end{array}\right]
$$

The negative inverse of the information matrix $\left(-\mathbf{I}^{-1}\right)$ is the variance-covariance matrix for parameters $\varphi$ and $p$

$$
-\mathbf{I}^{-1}=-\left[\begin{array}{ll}
-203.06775 & -136.83886 \\
-136.83886 & -147.43934
\end{array}\right]^{-1}=\left[\begin{array}{rr}
0.0131 & -0.0122 \\
-0.0122 & 0.0181
\end{array}\right]
$$

Note that the variances are found along the diagonal of the matrix, while the off-diagonal elements are the covariances.

In general, for an arbitrary parameter $\theta$, the variance of $\theta_{i}$ is given as the elements of the negative inverse of the information matrix corresponding to

$$
\frac{\partial^{2} \ln \mathcal{L}}{\partial \theta_{i} \partial \theta_{i}}
$$

while the covariance of $\theta_{i}$ with $\theta_{j}$ is given as the elements of the negative inverse of the information matrix corresponding to

$$
\frac{\partial^{2} \ln \mathcal{L}}{\partial \theta_{i} \partial \theta_{j}}
$$

Obviously, the variance-covariance matrix is the basis for deriving measures of the precision of our estimates. But, as we'll see in later chapters, the variance-covariance matrix is used for much more including estimating the number of estimable parameters in the model. While MARK handles all this for you, it's important to have a least a feel for what MARK is doing 'behind the scenes', and why.

### 1.6. More than 'estimation' - ML and statistical testing

In the preceding, we focussed on the maximization of the likelihood as a means of deriving estimates of parameters and the sampling variance of those parameters. However, the other primary use of likelihood methods is for comparing the fits of different models.

We know that $\mathcal{L}(\hat{\theta})$ is the value of the likelihood function evaluated at the MLE $\hat{\theta}$, whereas $\mathcal{L}(\theta)$ is the likelihood for the true (but unknown) parameter $\theta$. Since the MLE maximizes the likelihood for a given sample, then the value of the likelihood at the true parameter value $\theta$ is generally smaller than the MLE $\hat{\theta}$ (unless by chance $\hat{\theta}$ and $\theta$ happen to coincide).

This, combined with other properties of ML estimators noted earlier lead directly to several classic and general procedures for testing the statistical hypothesis that $H_{0}: \theta=\theta_{0}$. Here we briefly describe three of the more commonly used tests.

## Fisher's Score Test

The 'score' is the slope of the log-likelihood at a particular value of $\theta$. In other words, $S(\theta)=$ $\partial \ln \mathcal{L}(\theta) / \partial \theta$. At the MLE, the score (slope) is 0 (by definition of a maximum).

Recall from earlier in this chapter that

$$
\widehat{\operatorname{var}}(\hat{\theta})=\left[-\left(\frac{\partial^{2} \ln \mathcal{L}(\theta \mid \text { data })}{\partial \theta^{2}}\right)\right]_{\theta=\hat{\theta}}^{-1}
$$

The term inside the inner parentheses is known as Fisher information

$$
I(\theta)=-\frac{\partial^{2} \ln \mathcal{L}(\theta)}{\partial \theta^{2}}
$$

It can be shown that the score statistic

$$
S_{0}=\frac{S\left(\theta_{0}\right)}{\sqrt{I\left(\theta_{0}\right)}}
$$

is asymptotically distributed as $\mathcal{N}(0,1)$ under $H_{0}$.

## Wald test

The Wald test relies on the asymptotic normality of the MLE $\hat{\theta}$. Given the normality of the MLE, we can calculate the test statistic

$$
Z_{0}=\frac{\hat{\theta}-\theta_{0}}{\sqrt{\widehat{\operatorname{var}}(\hat{\theta})}}
$$

which is asymptotically distributed as $\mathcal{N}(0,1)$ under the null $H_{0}$.

## Likelihood ratio test

It is known that

$$
2\left[\ln \mathcal{L}(\hat{\theta})-\ln \mathcal{L}\left(\theta_{0}\right)\right]
$$

follows an asymptotic $\chi^{2}$ distribution with one degree of freedom.
The basic relationship among these tests is shown in the following diagram:


In general, these three tests are asymptotically equivalent, although in some applications, the score test has the practical advantage of not requiring the computation of the MLE at $\hat{\theta}$ (since $S_{0}$ depends only on the null value $\theta_{0}$, which is specified in $H_{0}$ ). We consider one of these tests (the likelihood ratio test) in much more detail in Chapter 4.

### 1.7. Technical aside: a bit more on variances

As we discussed earlier, the classic MLE approach to variance calculation (for purposes of creating a SE and so forth) is to use the negative inverse of the $2^{\text {nd }}$ derivative of the MLE evaluated at the MLE. However, the problem with this approach is that, in general, it leads to derivation of symmetrical $95 \%$ CI, and in many cases - especially for parameters that are bounded on the interval [ 0,1$]$ - this makes no sense. A simple example will show what we mean. Suppose we release 30 animals, and find 1 survivor. We know from last time that the MLE for the survival probability is $(1 / 30)=0.03333$. We also know from earlier in this chapter that the classical estimator for the variance, based on the $2^{\text {nd }}$ derivative, is

$$
\begin{aligned}
\widehat{\operatorname{var}}(\hat{p}) & =\frac{\hat{p}(1-\hat{p})}{N} \\
& =\frac{0.0333(1-0.0333)}{30}=0.0010741
\end{aligned}
$$

So, based on this, the $95 \%$ CI using classical approaches would be $\pm 1.96$ (SE), where the SE (standard error) is estimated as the square-root of the variance. Thus, given $\widehat{\operatorname{var}}=0.001074$, the $95 \% \mathrm{CI}$ would be $\pm 1.96$ (0.03277), or [0.098, -0.031]. OK, so what's wrong with this? Well, clearly, we don't expect a $95 \%$ CI to ever allow values $<0$ (or > 1) for a parameter that is logically bounded to fall between 0 and 1 (like $\varphi$ or $p$ ). So, there must be a problem, right? Well, somewhat. Fortunately, however, there is a better way, using something called the profile likelihood approach, which makes more explicit use of the shape of the likelihood. We'll go into the profile likelihood in further detail in later chapters, but to briefly introduce the concepts - consider the following diagram, which shows the maximum part of the log likelihood for $\varphi$, given $N=30, y=23$ (i.e., 23/30 survive).


Profile likelihood confidence intervals are based on the log-likelihood function. For a single parameter, likelihood theory shows that the 2 points 1.92 units down from the maximum of the $\log$ likelihood
function provide a $95 \%$ confidence interval when there is no extra-binomial variation (i.e., $c=1$; see Chapter 5). The value 1.92 is half of the $\chi_{1}^{2}=3.84$. Thus, the same confidence interval can be computed with the deviance by adding 3.84 to the minimum of the deviance function, where the deviance is the log-likelihood multiplied by -2 minus the $-2 \log$ likelihood value of the saturated model (more on these concepts in later chapters).

Put another way, we use the critical value of 1.92 to derive the profile - you take the value of the log likelihood at the maximum (for this example, the maximum occurs at -16.30 ), add 1.92 to it (yielding -18.22; note we keep the negative sign here), and look to see where the -18.22 line intersects with the profile of the log likelihood function. In this case, we see that the intersection occurs at approximately 0.6 and 0.9 . The MLE is $(23 / 30)=0.767$, so clearly, the profile $95 \%$ CI is not symmetrical around this MLE value. But, it is bounded on the interval [ 0,1 ]. The profile likelihood is the preferred approach to deriving $95 \%$ CI. The biggest limit to using it is computational - it simply takes more work to derive a profile likelihood (and corresponding CI). Fortunately, MARK does all the work for us.

### 1.8. Summary

That's it for Chapter 1! Nothing about MARK, but some important background. Beginning with Chapter 2, we'll consider formatting of our data (the 'encounter histories' we introduced briefly in this chapter). After that, the real details of using program MARK. Our suggestion at this stage is to (i) leave your own data alone - you need to master the basics first. This means working through at least chapters $3 \rightarrow 8$, in sequence, using the example data sets. Chapter 9 and higher refer to specific data types - one or more may be of particular interest to you. Then, when you're ready (i.e., have a good understanding of the basic concepts), (ii) get your data in shape - this is covered in Chapter 2.

## CHAPTER 2

## Data formatting: the input file ...

Clearly, the first step in any analysis is gathering and collating your data. We'll assume that at the minimum, you have records for the individually marked individuals in your study, and from these records, can determine whether or not an individual was 'encountered' (in one fashion or another) on a particular sampling occasion. Typically, your data will be stored in what we refer to as a 'vertical file' - where each line in the file is a record of when a particular individual was seen. For example, consider the following table, consisting of some individually identifying mark (ring or tag number), and the year. Each line in the file (or, row in the matrix) corresponds to the animal being seen in a particular year.

| tag number | year |
| :---: | :---: |
| $1147-38951$ | 73 |
| $1147-38951$ | 75 |
| $1147-38951$ | 76 |
| $1147-38951$ | 82 |
| $1147-45453$ | 74 |
| $1147-45453$ | 78 |

However, while it is easy and efficient to record the observation histories of individually marked animals this way, the 'vertical format' is not at all useful for capture-mark-recapture analysis. The preferred format is the encounter history. The encounter history is a contiguous series of specific dummy variables, each of which indicates something concerning the encounter of that individual - for example, whether or not it was encountered on a particular sampling occasion, how it was encountered, where it was encountered, and so forth. The particular encounter history will reflect the underlying model type you are working with (e.g., recaptures of live individuals, recoveries of dead individuals). Consider for example, the encounter history for a typical mark-recapture analysis (the encounter history for a mark-recapture analysis is often referred to as a capture history, since it implies physical capture of the individual). In most cases, the encounter history consists of a contiguous series of ' 1 's and ' 0 's, where ' 1 ' indicates that an animal was recaptured (or otherwise known to be alive and in the sampling area), and ' 0 ' indicates the animal was not recaptured (or otherwise seen). Consider the individual in the preceding table with tag number '1147-38951'. Suppose that 1973 is the first year of the study, and that 1985 is the last year of the study. Examining the table, we see that this individual was captured and marked during the first year of the study, was seen periodically until 1982, when it was seen for the last time. The corresponding encounter-history for this individual would be: '1011000001000'.

In other words, the individual was seen in 1973 (the starting ' 1 '), not seen in 1974 (' 0 '), seen in 1975 and 1976 (' $11^{\prime}$ ), not seen for the next 5 years (' $00000^{\prime}$ ), seen again in 1982 (' $1^{\prime}$ ), and then not seen again
('000').
While this is easy enough in principal, you surely don't want to have to construct capture-histories manually. Of course, this is precisely the sort of thing that computers are good for - large-scale data manipulation and formatting. MARK does not do the data formatting itself - no doubt you have your own preferred 'data manipulation' environment (dBASE, Excel, Paradox, SAS). Thus, in general, you'll have to write your own program to convert the typical 'vertical' file (where each line represents the encounter information for a given individual on a given sampling occasion; see the example on the preceding page) into encounter histories (where the encounter history is a horizontal string). In fact, if you think about it a bit, you realize that in effect what you need to do is to take a vertical file, and 'transpose' (or, 'pivot') it into a horizontal file - where fields to the right of the individual tag number represent when an individual was recaptured or resighted. However, while the idea of a 'transpose' or 'pivot' seems simple enough, there is one rather important thing that needs to be done - your program must insert the ' 0 ' value whenever an individual was not seen. We'll assume for the purposes of this book that you will have some facility to put your data into the proper encounter-history format. For those of you who have no idea whatsoever on how to approach this problem, we provide some practical guidance in the Addendum at the end of this chapter. Of course, you could always do it by hand, if absolutely necessary!
begin sidebar

## editing the .INP file

Many of the problems people have getting started with MARK can ultimately be traced back to problems with the . INP file. One common issue relates to choice of editor used to make changes/additions to the .INP file. You are strongly urged to avoid - as in 'like the plague' - using Windows Notepad (or, even worse, Word) to do much of anything related to building/editing .INP files. Do yourself a favor and get yourself a real ASCII editor. There are a number of very good 'free' applications you can (and should) use instead of Notepad (e.g., Notepad++, EditPad Lite, jEdit, and so on...)

### 2.1. Encounter histories formats

Now we'll look at the formatting of the encounter histories file in detail. It is probably easiest to show you a 'typical' encounter history file, and then explain it 'piece by piece'. The encounter-history reflects a mark-recapture experiment.


Superficially, the encounter histories file is structurally quite simple. It consists of an ASCII (text) file, consisting of the encounter history itself (the contiguous string of dummy variables), followed by one or more additional columns of information pertaining to that history. Each record (i.e., each line)
in the encounter histories file ends with a semi-colon. Each history (i.e., each line, or record) must be the same length (i.e., have the same number of elements - the encounter history itself must be the same length over all records, and the number of elements 'to the right' of the encounter history must also be the same) - this is true regardless of the data type. The encounter histories file should have a .INP suffix (for example, EXAMPLE1.INP). Generally, there are no other 'control statements' or 'PROC statements' required in a MARK input file. However, you can optionally add comments to the INP file using the 'slash-asterisk asterisk/slash' convention common to many programming environments - we have included a comment at the top of the example input file (shown at the bottom of the preceding page). The only thing to remember about comments is that they do not end with a semi-colon.

Let's look at each record (i.e., each line) a bit more closely. In this example, each encounter history is followed by a number. This number is the frequency of all individuals having a particular encounter history. This is not required (and in fact isn't what you want to do if you're going to consider individual covariates - more on that later), but is often more convenient for large data sets. For example, the summary encounter history

```
110000101 4;
```

could also be entered in the INP files as

110000101 1;
110000101 1;
110000101 1;
110000101 1;

Note again that each line - each 'encounter history record' - ends in a semi-colon. How would you handle multiple groups? For example, suppose you had encounter data from males and females? In fact, it is relatively straightforward to format the INP file for multiple groups - very easy for summary encounter histories, a bit less so for individual encounter histories. In the case of summary encounter histories, you simply add a second column of frequencies to the encounter histories to correspond to the other sex. For example,

```
110100111 23 17;
110000101 4 2;
101100011 1 3;
```

In other words, 23 of one sex and 17 of the other have history ' 110100111 ' (the ordering of the sexes which column of frequencies corresponds to which sex - is entirely up to you). If you are using individual records, rather than summary frequencies, you need to indicate group association in a slightly lessobvious way - you will have to use a ' 0 ' or ' 1 ' within a group column to indicate the frequency - but obviously for one group only. We'll demonstrate the idea here. Suppose we had the following summary history, with frequencies for males and females (respectively):

```
110000101 4 2;
```

In other words, 4 males, and 2 females with this encounter history (note: the fact that males come before females in this example is completely arbitrary. You can put whichever sex - or 'group' - you want in any column you want - all you'll need to do is remember which columns in the INP file correspond to which groups).

To 'code' individual encounter histories, the INP file would be modified to look like:

| 110000101 | 1 | $0 ;$ |
| :--- | :--- | :--- |
| 110000101 | 1 | $0 ;$ |
| 110000101 | 1 | $0 ;$ |
| 110000101 | 1 | $0 ;$ |
| 110000101 | 0 | $1 ;$ |
| 110000101 | 0 | $1 ;$ |

In this example, the coding ' 10 ' indicates that the individual is a male (frequency of 1 in the male column, frequency of 0 in the female column), and ' $01^{\prime}$ indicates the individual is a female (frequency of 0 in the male column, and frequency of 1 in the male column). The use of one-record per individual is only necessary if you're planning on using individual covariates in your analysis.

### 2.1.1. Groups within groups...

In the preceding example, we had 2 groups: males and females. The frequency of encounters for each sex is coded by adding the frequency for each sex to the right of the encounter history.

But, what if you had something like males, and females (i.e., data from both sexes) and good colony and poor colony (i.e., data were sampled for both sexes from each of 2 different colonies - one classified as good, and the other as poor). How do you handle this in the INP file? Well, all you need to do is have a frequency column for each (sex.colony) combination: one frequency column for females from the good colony, one frequency column for females from the poor colony, one frequency column for males from the good colony, and finally, one frequency column for males from the poor colony. An example of such an INP file is shown below:

| - multi_group.inp - Notepad |  |  |  |  |  | $\square$ | $x$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| File Edit Format View Help |  |  |  |  |  |  |  |
| /* females: | good | fema | es: | - - |  |  | $\wedge$ |
| 00010 | 150 | 145 | 171 | 167; |  |  |  |
| 00011 | 200 | 205 | 179 | 183; |  |  |  |
| 00100 | 213 | 198 | 131 | 77; |  |  |  |
| 00101 | 14 | 26 | 32 | 50; |  |  |  |
| 00110 | 54 | 59 | 95 | 101; |  |  |  |
| 00111 | 69 | 67 | 92 | 122; |  |  |  |
| 01000 | 93 | 64 | 74 | 51; |  |  | $\checkmark$ |
| < |  |  |  |  |  |  | $\cdots$ |

As we will see in subsequent chapters, building models to test for differences between and among groups, and for interactions among groups (e.g., an interaction of sex and colony in this example) is relatively straightforward in MARK - all you'll really need to do is remember which frequency column codes for which grouping (hence the utility of adding comments to your INP file, as we've done in this example)

### 2.2. Removing individuals from the sample

Occasionally, you may choose to remove individuals from the data set at a particular sampling occasion. For example, because your experiment requires you to remove the individual after its first recapture, or because it is injured, or for some other reason. The standard encounter history we have looked at so far records presence or absence only. How do we accommodate 'removals' in the INP file? Actually,
it's very easy - all you do is change the 'sign' on the frequencies from positive to negative. Negative frequencies indicates that that many individuals with a given encounter history were removed from the study. For example,

| 100100 | 1500 | $1678 ;$ |
| ---: | ---: | ---: | ---: |
| 100100 | -23 | $-25 ;$ |

In this example, we have 2 groups, and 6 sampling occasions. In the first record, we see that there were 1,500 individuals and 1,678 individuals in each group marked on the first occasion, not encountered on the next 2 occasions, seen on the fourth occasion, and not seen again. In the second line, we see the same encounter history, but with the frequencies ' $-23^{\prime}$ and ' $-25^{\prime}$ '. The negative values indicate to MARK that 23 and 25 individuals in both groups were marked on the first occasion, not seen on the next 2 occasions, were encountered on the fourth occasion, at which time they were removed from the study. Clearly, if they were removed, they cannot have been seen again.
begin sidebar
uneven time-intervals between sampling occasions?
In the preceding, we have implicitly assumed that the sampling interval between sampling occasions is identical throughout the course of the study (e.g., sampling every 12 months, or every month, or every week). But, in practice, it is not uncommon for the time interval between occasions to vary either by design, or because of 'logistical constraints'. This has clear implications for how you analyze your data.
For example, suppose you sample a population each October, and again each May (i.e., two samples within a year, with different time intervals between samples; October $\rightarrow$ May ( 7 months), and May $\rightarrow$ October ( 5 months)). Suppose the true monthly survival rate is constant over all months, and is equal to 0.9 . As such, the estimated survival for October $\rightarrow$ May will be $0.9^{7}=0.4783$, while the estimated survival rate for May $\rightarrow$ October will be $0.9^{5}=0.5905$. Thus, if you fit a model without accounting for these differences in time intervals, it is clear that there would 'appear' to be differences in survival between successive samples, when in fact the monthly survival does not change over time.

So, how do you 'tell MARK' that the interval between samples may vary over time? You might think that you need to 'code' this interval information in the .INP file in some fashion. In fact, you don't you specify the time intervals when you are specifying the data type in MARK, and not in the .INP file. In the .INP file, you simply enter the encounter histories as contiguous strings, regardless of the true interval between sampling occasions. We will discuss handling uneven time-intervals in more detail in a later chapter.

### 2.3. Different encounter history formats

Up until now, we've more or less used typical mark-recapture encounter histories (i.e., capture histories) to illustrate the basic principles of constructing an . INP file. However, MARK can be applied to far more than mark-recapture analyses, and as such, there are a number of slight permutations on the encounter history that you need to be aware of in order to use MARK to analyze your particular data type. First, we summarize in table form (on the next page) the different data types MARK can handle, and the corresponding encounter history format.

| recaptures only | LLLL |
| :---: | :--- |
| recoveries only |  |
| both | LDLDLDLD |
| known fate | LDLDLDLD |
| closed captures | LDLDLDLD |
| BTO ring recoveries | LLLL |
| robust design | LDLDLDLD |
| multi-strata | LLLL |

Each data type in MARK requires a primary from of data entry provided by the encounter history. Encounter histories can consist of information on only live encounters (LLLL) or information on both live and dead (LDLDLDLD). In addition, some types allow a summary format (e.g., recovery matrix) which reduces the amount of input. The second column of the table shows the basic structure for a 4 occasion encounter history. There are, in fact, broad types: live encounters only, and mixed live and dead (or known fate) encounters. For example, for a recaptures only study (i.e., live encounters), the structure of the encounter history would be 'LLLL' - where 'L' indicates information on encountered /not encountered status. As such, each 'L' in the history would be replaced by the corresponding 'coding variable' to indicate encountered or not encountered status (usually ' 1 ' or ' 0 ' for the recaptures only history). So, for example, the encounter ' 1011 ' indicates seen and marked alive at occasion 1, not seen on occasion 2, and seen again at both occasion 3 and occasion 4 . For data types including both live and dead individuals, the encounter history for the 4 occasion study is effectively 'doubled' - taking the format 'LDLDLDLD', where the ' L ' refers to the live encountered or not encountered status, and the ' D ' refers to the dead encountered or not encountered status. At each sampling occasion, either 'event' is possible - an individual could be both seen alive at occasion $(i)$ and then found dead at occasion ( $i$ ), or during the interval between $(i)$ and ( $i+1$ ). Since both 'potential events' need to be coded at each occasion, this effectively doubles the length of the encounter history from a 4 character string to an 8 character string.

For example, suppose you record the following encounter history for an individual over 4 occasions - where the encounters consist of both live encounters and dead recoveries. Thus, the history ' 10001100 ' reflects an individual seen and marked alive on the first occasion, not recovered during the first interval,
not seen alive at the second occasion and not recovered during the second interval, seen alive on the third occasion and then recovered dead during the third interval, and not seen or recovered thereafter (obviously, since the individual was found dead during the preceding interval).

### 2.4. Some more examples

The MARK help files contain a number of different examples of encounter formats. We list only a few of them here. For example, suppose you are working with dead recoveries only. If you look at the table on the preceding page, you see that it has a format of 'LDLDLDLD'. Why not just 'LLLL', and using ' 1 ' for live', and ' 0 ' for recovered dead? The answer is because you need to differentiate between known dead (which is a known fate), and simply not seen. ' 0 ' alone could ambiguously mean either dead, or not seen (or both!).

### 2.4.1. Dead recoveries only

The following is an example of dead recoveries only, because a live animal is never captured alive after its initial capture. That is, none of the encounter histories have more than one ' 1 ' in an $L$ column. This example has 15 encounter occasions and 1 group. If you study this example, you will see that 500 animals were banded each banding occasion.

| 000000000000000000000000000010 | $465 ;$ |
| ---: | ---: | ---: |
| 000000000000000000000000000011 | $35 ;$ |
| 0000000000000000000000001000 | $418 ;$ |
| 000000000000000000000000001001 | $15 ;$ |
| 00000000000000000000000001100 | $67 ;$ |
| 000000000000000000000000100000 | $395 ;$ |
| 000000000000000000000000100001 | $3 ;$ |
| 000000000000000000000000100100 | $25 ;$ |
| 000000000000000000000000110000 | $77 ;$ |

Traditionally, recoveries only data sets were summarized into what are known as recovery tables. MARK accommodates recovery tables, which have a 'triangular matrix form', where time goes from left to right (shown below). This format is similar to that used by Brownie et al. (1985).

| 7 | 4 | 1 | 0 | $1 ;$ |
| ---: | ---: | ---: | ---: | ---: |
|  | 8 | 5 | 1 | $0 ;$ |
|  |  | 10 | 4 | $2 ;$ |
|  |  |  | 16 | $3 ;$ |
|  |  |  |  | $12 ;$ |
| 99 | 88 | 153 | 114 | $123 ;$ |

Following each matrix is the number of individuals marked each year. So, 99 individuals marked on the first occasion, of which 7 were recovered dead during the first interval, 4 during the second, 1 during the third, and so on.

### 2.4.2. Individual covariates

Finally, an example of known fate data, where individual covariates are included. Comments are given at the start of each line to identify the individual (this is optional, but often very helpful in keeping track of things). Then comes the capture history for this individual, in a 'LDLDLD. . .' sequence. Thus the first capture history is for an animal that was released on occasion 1, and died during the interval. The second animal was released on occasion 1, survived the interval, released again on occasion 2, and died during this second interval. Following the capture history is the count of animals with this history (always 1 in this example). Then, 4 covariates are provided. The first is a dummy variable representing age ( $0=$ subadult, $1=$ adult ), then a condition index, wing length, and body weight.

| $/ * 01 * /$ | 1100000000000000 | 1 | 1 | 1.16 | 27.7 | $4.19 ;$ |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| $/ * 04 * /$ | 1011000000000000 | 1 | 0 | 1.16 | 26.4 | $4.39 ;$ |
| $/ * 05 * /$ | 1011000000000000 | 1 | 1 | 1.08 | 26.7 | $4.04 ;$ |
| $/ * 06 * /$ | 1010000000000000 | 1 | 0 | 1.12 | 26.2 | $4.27 ;$ |
| $/ * 07 * /$ | 1010000000000000 | 1 | 1 | 1.14 | 27.7 | $4.11 ;$ |
| $/ * 08 * /$ | 1010110000000000 | 1 | 1 | 1.20 | 28.3 | $4.24 ;$ |
| $/ * 09 * /$ | 1010000000000000 | 1 | 1 | 1.10 | 26.4 | $4.17 ;$ |

What if you have multiple groups, such that individuals are assigned (or part of) a given group, and where you also have individual covariates? There are a couple of ways you could handle this sort of situation. You can either code for the groups explicitly in the .inp file, or use an individual covariate for the groups. There are pros and cons to either approach (this issue is discussed in Chapter 11).

Here is an snippet from a data set with 2 groups coded explicitly, and an individual covariate. In this data fragment, the first 8 contiguous values represent the encounter history, followed by 2 columns representing the frequencies depending on group: ' 10 ' indicating group 1 , and ' 01 ' indicating group 2 , followed by the value of the covariate:

```
11111111 1 0 123.211;
11111111 0 1 92.856;
11111110 1 0 122.115;
11111110 1 0 136.460;
```

So, the first record with an encounter history of '11111111' is in group 1, and has a covariate value of 123.211. The second individual, also with an encounter history of ' $11111111^{\prime}$, is in group 2 , and has a covariate value of 92.856 . The third individual has an encounter history of ' $11111110^{\prime}$, and is in group 1 , with a covariate value of 122.115 . And so on.

If you wanted to code the group as an individual covariate, this same input file snippet would look like:

```
11111111 1 1 123.211;
111111111 1 0 92.856;
11111110 1 1 122.115;
11111110 1 1 136.460;
```

In this case, following the encounter history, is a column of 1's, indicating the frequency for each individual, followed by a column containing a $0 / 1$ dummy code to indicate group (in this example, we've used a 1 to indicate group 1,0 to indicate group 2 ), followed by the value of the covariate.

A final example - for three groups where we code for each group explicitly (such that each group has it's own 'dummy column' in the input file), an encounter history with individual covariates might look like:

```
11111 1 0 0 123.5;
11110 0 1 0 99.8;
11111 0 0 1 115.2;
```

where the first individual with encounter history ' $11111^{\prime}$ is in group 1 (dummy value of 1 in the first column after the encounter history, and 0 's in the next two columns) and has a covariate value of 123.5 , second individual with encounter history ' $11110^{\prime}$ ' is in group 2 (dummy code of 0 in the first column, 1 in the second, and 0 in the third) and a covariate value of 99.8 , and a third individual with encounter history ' 11111 ' in group 3 ( 0 in the first two columns, and a 1 in the third column), with a covariate value of 115.2.

As is noted in the help file (and discussed at length in Chapter 11), it is helpful to scale the values of covariates to have a mean on the interval $[0,1]$ to ensure that the numerical optimization algorithm finds the correct parameter estimates. For example, suppose the individual covariate 'weight' is used, with a range from $1,000 \mathrm{~g}$ to $5,000 \mathrm{~g}$. In this case, you should scale the values of weight to be from 0.1 to 0.5 by multiplying each 'weight' value by 0.0001 . In fact, MARK defaults to doing this sort of scaling for you automatically (without you even being aware of it). This 'automatic scaling' is done by determining the maximum absolute value of the covariates, and then dividing each covariate by this value. This results in each column scaled to between -1 and 1 . This internal scaling is purely for purposes of ensuring the success of the numerical optimization - the parameter values reported by MARK (i.e., in the output that you see) are 'back-trasformed' to the original scale. Alternatively, if you prefer that the 'scaled' covariates have a mean of 0 , and unit variance (this has some advantages in some cases), you can use the 'Standardize Individual Covariates' option of the 'Run Window' to perform the default standardization method (more on these in subsequent chapters).

More details on how to handle individual covariates in the input file are given in Chapter 11.

## Summary

That's it! You're now ready to learn how to use MARK. Before you leap into the first major chapter (Chapter 3), take some time to consider that MARK will always do its 'best' to analyze the data you feed into it. However, it assumes that you will have taken the time to make sure your data are correct. If not, you'll be the unwitting victim to perhaps the most telling comment in data analysis: 'garbage in...garbage out'. Take some time at this stage to make sure you are confident in how to properly create and format your files.

## Addendum: generating .inp files

Andrew Sterner, Marine Turtle Research Group, University of Central Florida

As noted at the outset in this chapter, MARK has no capability of generating input (.INP) files. This is something you will need to do for yourself. In this short addendum, we introduce one approach to generating . INP files, based on 'Excel pivot tables'. Since there are any number of different software applications for managing and manipulating data, we state for the record that we are going to demonstrate creating. INP files using Excel, not as a point of advocacy for using Excel, but owing more to its near ubiquity (note: most of what follows applies generally to Access databases as well).

We will demonstrate the basic idea using an example where we will reformat an Excel spreadsheet containing some live encounter data. We wish to format these data into an . INP file. The data are contained in the Excel spreadsheet csj-pivot.xlsx (note, we're clearly using Excel 2007 or later). Here are what the data look like before we transform them into an input file.

| E1 |  |  | ( |
| :---: | :---: | :---: | :---: |
| 4 | A | B |  |
| 1 | Tag | Year |  |
| 2 | ATS150 | 2000 |  |
| 3 | ATS150 | 2002 |  |
| 4 | ATS150 | 2003 |  |
| 5 | ATS151 | 2006 |  |
| 6 | ATS153 | 2004 |  |
| 7 | ATS155 | 2001 |  |
| 8 | ATS155 | 2005 |  |
| 9 | ATS155 | 2009 |  |
| 10 | ATS155 | 2010 |  |
| 11 | ATS156 | 2006 |  |
| 12 | ATS157 | 2000 |  |
| 13 | ATS158 | 2000 |  |
| 14 | ATS158 | 2006 |  |
| 15 | ATS159 | 2003 |  |
| 16 | ATS159 | 2006 |  |
| 17 | ATS160 | 2006 |  |
| 18 | ATS161 | 2006 |  |
| 19 | ATS164 | 2003 |  |
| 20 | ATS164 | 2006 |  |
| 21 | ATS165 | 2000 |  |
| 22 | ATS165 | 2006 |  |
| 23 | ATS166 | 2004 |  |
| 24 | ATS167 | 2001 |  |
| 25 | ATS167 | 2002 |  |

The file consists of two data columns: TAG (indicating the individual), and YEAR (the year that the individual was encountered). This data file contains encounter data for 14 marked individuals, with encounter data collected from 2000 to 2010 (thus, the encounter history will be 11 characters in length).

Our challenge, then is to take this 'vertical' file (one record per individual each year encountered), and 'pivot' it horizontally. For example, take the first individual in the file, ATS150. It was first encountered in 2000, again in 2002, and again (for the final time) in 2003. The second individual, ATS151, was seen for the first time in 2006, and then not seen again. The third individual, ATS153, was seen in 2004, and not seen again after that. And so on. If we had to generate the . INP file by hand for these individuals, their encounter histories would look like:

```
/* ATS150 */ 101100000 1;
/* ATS151 */ 000000100 1;
/* ATS153 */ 000010000 1;
```

As it turns out, we can make use of the 'pivot table' in Excel (and some simple steps involving 'search and replace' and the CONCATENATE function), to generate exactly what we need. The process can be more involved for more complicated data types (e.g., robust design), but the basic principle of 'pivoting' applies.

Here are the basic steps. First, we select the rows and columns containing the data. Then, select 'Insert | PivotTable | PivotTable', as shown to the right (make sure you select PivotTable and not PivotChart). This will bring up a dialog window (shown at the top of the next page) asking you to choose the data you want to 'pivot', and where you want the pivot table to be placed.



The 'Table/Range' field will already be filled with the rows and columns of the data you selected. We strongly recommend you put the pivot table into a 'New Worksheet' (this is selected by default). Once you click ' OK ', you will be presented with the template from which you will generate the pivot table:


All you really need to do at this point is specify the 'row labels', the 'column labels', and the 'values' (on the right hand side of the template). So, to specify the row labels, we simply select 'tag'

and then drag the 'tag' field down to the 'row labels' box at the bottom-right:


Then, do the same thing for the 'Year' field: select 'Year', and drag it down to the 'column labels' box.


Once you have done this, you will quickly observe that a table (the 'pivot table') has been inserted into the main body of the template (see top of the next page). The table has row labels (individual tag numbers) and column labels (the years in your data file), plus some additional rows and columns for 'Grand total' (reflecting the fact that pivot tables were designed primarily for business applications).


However, at present, there is nothing in the table (all of the cells are blank). Now, drag the 'year' field label down to the 'values' box in the lower right-hand corner.


What we see is that the year during which an encounter has occurred for a given individual has been entered explicitly into the table, in the column corresponding to that year. But, for an encounter history, we want a ' 1 ' to indicate the encounter year, not the year itself, and a ' 0 ' to indicate a year when an encounter did not occur. Achieving the first objective is easy. Simply pull down the 'Sum of Year' menu, and select 'Value Field Settings...':


Then, switch the 'Summarize value field by' selection from 'Sum' to 'Count':


As soon as you do this, then all of the years in the pivot table will be changed to 1 . Why? Simple - all you've told the pivot table to do is count the number of times a year occurs in a given cell. Since the data file contains only a single record for each individual for each year it was encountered, then it makes sense that the tabulated 'Count' should be a 1. Moreover, now the 'Grand Total' rows and columns have some relevance - they indicate the number of individuals encountered in a given year (column totals), or the number of times a given individual was caught over the interval from 2000 to 2010 (row totals).

OK, on to the next step - putting a ' 0 ' in the blank cells for those years when an individual wasn't caught. This sounds easy enough in principle - a reasonable approach would be to select the rows and columns, and execute a 'search and replace', replacing blank cells with ' 0 '. In fact, this is exactly what we want to do. However, for various reasons, you can't actually edit a pivot table. What you need to do first is select and copy the rows and columns (including the row labels, but excluding row and column totals), and paste them into a new worksheet. Then, simply do a 'Find \& Select'), replacing blanks
(simply leave the 'Find what' field empty) with a ' 0 '. The result is shown below:

(Alternatively, if you navigate to 'PivotTable | PivotTable Name | Options', you will see an option to specify what an empty cell should show. Simply change it to a ' 0 ').

We're clearly getting closer. All that remains is to do the following. First, we remember that each line of the encounter history file must end with a frequency - where each line in the file corresponds to a single individual, then this frequency is simply ' 1 ;'. So, we simply enter ' 1 ;' into column K , and copy it down for as many rows as there are in the data (there are a number of ways to copy a value down a set of rows - we'll assume here you know of at least one way to do this).

Now, for a final step - we ultimately want an encounter history (. INP file) where the encounters form a contiguous string (i.e., no spaces). We can achieve this relatively easily by using the CONCATENATE function in Excel. Simply click the top-most cell in the next empty column (column $L$ in our example), and then go up into the function box, and enter
=CONCATENATE("/* ",A1," */ ",B1,C1,D1,E1,F1,G1,H1,I1,J1," ",K1)

In other words, we want to 'concatenate' (merge together without spaces), various elements - some from within the spreadsheet, others explicitly entered (e.g., the delimiters for comments, so we can include the tag information, and some spacer elements).

Once you execute this cell macro, you can copy it down in column $L$ over all rows in the file. If you manage to do this correctly, you will end up with a spreadsheet looking like the one shown at the top of the next page. All that remains is to select column L (which contains the formatted, concatenated encounter histories), and paste them into an ASCII text file. (A reminder here that you should avoid - as in 'like the plague' - using Word or Notepad as your ASCII editor. Do yourself a favor and get yourself a real ASCII editor. As mentioned earlier, there are a number of very good 'free' applications you can - and should - use instead of Notepad (e.g., Notepad++, EditPad Lite, jEdit, and so on...).


## Other data types

Here we will consider 2 other data types, the robust design, and multi-state. Clearly, there are more data types in MARK, but these two represent very common data types, and if you understand steps in formatting. INP files for these two data types, you'll more than likely be able to figure out other data types on your own.

## multi-state

Here we will demonstrate formatting an .INP file for a multi-state data set (see Chapter 10). The encounter data we will use are contained in the Excel spreadsheet MS-pivot.xlsx. The file consists of 3 columns: TAG (indicating the individual), YEAR (the year the individual was encountered), and the STATE (for this example, there are 3 possible states: $\mathrm{F}, \mathrm{U}, \mathrm{N}$ ).

We start by noting that STATE is a character (i.e., a letter). This might seem perfectly reasonable, since the most appropriate state name (indicator) might be a character. Unfortunately, Excel can't handle characters in the table cells when you pivot the table. As such, you first need to (i) select the column containing the state variable, (ii) copy this into the first empty column, and (iii) execute a 'Find and Replace' in this column, such that you change $\mathrm{F} \rightarrow 1, \mathrm{U} \rightarrow 2$, and $\mathrm{N} \rightarrow 3$. Once finished, your Excel spreadsheet shoot look something like what is shown to the right.

| - | A | B | C | D |
| :---: | :---: | :---: | :---: | :---: |
| 1 | Tag | Year | State | State (numeric |
| 2 | ATS150 | 2000 | F | 1 |
| 3 | ATS150 | 2001 | U | 2 |
| 4 | ATS150 | 2002 | N | 3 |
| 5 | ATS150 | 2003 | N | 3 |
| 6 | ATS150 | 2009 | F | 1 |
| 7 | ATS150 | 2010 | N | 3 |
| 8 | ATS151 | 2000 | N | 3 |
| 9 | ATS151 | 2001 | U | 2 |
| 10 | ATS151 | 2002 | F | 1 |
| 11 | ATS151 | 2003 | U | 2 |
| 12 | ATS151 | 2004 | N | 3 |
| 13 | ATS151 | 2005 | N | 3 |
| 14 | ATS151 | 2006 | F | 1 |
| 15 | ATS151 | 2007 | N | 3 |

Next, select the data, and inset a Pivot Table into a new sheet in the spreadsheet. Drag TAG to the 'Row Labels' box, YEAR to the 'Column Labels' box, and State (numeric) to the 'Values' box, as shown below.


Next, copy the TAGS, YEARS and table values to a new worksheet. Then 'Find and Replace' all the blank cells with zeros. At this point, you have a decision to make: you can either (i) 'Find and Replace' the states from numeric back to their original character values (i.e., $1 \rightarrow F, 2 \rightarrow U$ and $3 \rightarrow N$ ), or (ii) leave the states numeric, and simply inform MARK what the states mean. For this example, we'll 'Find and Replace' the states from numeric back to their original character values. Finally, add a column of '1;' to the new worksheet.

Then click the top-most cell in the next empty column (column $L$ in our example), and then go up into the function box, and enter
=CONCATENATE("/* ",A1," */ ",B1,C1,D1,E1,F1,G1,H1,I1,J1,K1,L1," ",M1)

In other words, we want to 'concatenate' (merge together without spaces), various elements - some from within the spreadsheet, others explicitly entered (e.g., the delimiters for comments, so we can include the tag information, and some spacer elements). Once you execute this cell macro, you can copy it down in column L over all rows in the file. The final worksheet should look something like the one shown at the top of the next page. At this point, you simply copy your concatenated encounter histories from column $\mathbf{N}$ into an editor, and save into an . INP file.


## robust design

For our final example, we consider formatting an . INP file for a robust design analysis (the robust design is covered in Chapter 15). In brief, the robust design combines closed population samples embedded (nested) within open population samples. Consider the figure at the top of the next page. As shown, there are 3 'open population' samples (known as primary period samples). Between open samples, population abundance can change due to emigration, death, immigration or birth. Within each open sample period are embedded $k$ 'closed population' (or secondary) samples. The trick here is to encode the encounter history taking into account the presence of both primary and secondary samples (where the number of secondary samples may vary among primary samples). As you might expect, the greater complexity of the RD encounter file might require a somewhat higher level of Excel proficiency than the first two examples we discussed earlier.


In this example (data contained in RD-pivot. xlsx), we assume primary samples from 2000-2010. Within each primary period, we have 4 secondary samples, which occur from May 1 to May 15
(secondary sample 1), May 16 to May 30 (secondary sample 2), June 1 to June 15 (secondary sample 3), and June 16 to June 30 (secondary sample 4). For each secondary sample, and encountered individual is recorded only once. We imagine that your data are stored in the following way. For each individual (TAG), for each primary sample (YEAR), you have a series of columns, one for each secondary sampling period.

| 4 | A | B | C | D | E | F | G |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1 | Tag | Date | Year |  |  |  |  |
| 2 |  |  |  |  |  |  |  |
| 3 | ATS150 |  | 2000 |  | 5/30/12 |  | 6/17/12 |
| 4 | ATS150 |  | 2001 | 5/2/12 |  |  | 6/24/12 |
| 5 | ATS150 |  | 2002 |  |  | 6/4/12 |  |
| 6 | ATS150 |  | 2003 |  | 5/23/12 | 6/2/12 | 6/25/12 |
| 7 | ATS150 |  | 2009 |  |  |  |  |
| 8 | ATS150 |  | 2010 | 5/6/12 | 5/17/12 | 6/10/12 | 6/17/12 |
| 9 | ATS151 |  | 2000 | 5/13/12 | 5/18/12 |  |  |
| 10 | ATS151 |  | 2001 | 5/7/12 |  |  |  |
| 11 | ATS151 |  | 2002 |  |  | 6/10/12 | 6/18/12 |
| 12 | ATS151 |  | 2003 |  |  | 6/1/12 | 6/16/12 |
| 13 | ATS151 |  | 2004 | 5/6/12 | 5/25/12 | 6/10/12 | 6/19/12 |
| 14 | ATS151 |  | 2005 | 5/11/12 | 5/18/12 |  |  |
| 15 | ATS151 |  | 2006 | 5/11/12 | 5/28/12 |  |  |
| 16 | ATS151 |  | 2007 | 5/9/12 |  |  |  |
| 17 | ATS151 |  | 2008 | 5/2/12 |  |  |  |
| 18 | ATS151 |  | 2009 |  |  |  | 6/23/12 |
| 19 | ATS151 |  | 2010 |  |  | 6/12/12 | 6/25/12 |
| 3 | -TS15] |  | วกก2 | 5/12/12 | 5/25/12 | 6/2/12 | 6/ว9/17 |

For example, in the preceding figure, we see that individual with tag 'ATS150' was observed during primary sample, 2000, 2001, 2002, 2003, 2009, and 2010. In 2000, the individual was not observed during the first secondary sample (May 1 to May 15), was observed during the second secondary sample (May 16 to May 30), was not observed during the third secondary sample (June 1 to June 15), and was observed during the fourth and final secondary sample (June 16 to June 30). In contrast, in 2010, the individual with tag 'ATS 1150 ' was observed in all 4 secondary samples.

Now, you may be wondering why we've entered dates in terms of 2012, even for primary encounter years <2012. For example, for 'ATS150', we enter '5/30/12' as the date for the encounter during the second secondary sample period. We need to do this in order to make use of some very handy Excel functions. For example, consider the 'year' function. This function extracts the year associated with a given date (such that if you type in '=year(B2)' and B2 is a date, it will return the year associated with that date. So, for robust design data, you may have intervals (for a secondary sample period) spanning from 5/1/12 to $5 / 15 / 12$, and you want to know if the encounter date falls between them.

All you need to do is

- use the AND function to determine if a date falls within a given range. For example, in cell H3 in the spreadsheet, we enter
| =AND (D3>=H1,D\#<=H2)
- What you are asking Excel is: "Is D3 (my date of capture) greater than or equal to my first date, $5 / 1 / 12$, and less than or equal to $5 / 15 / 12^{\prime \prime}$. We do the same thing for each of the other 3 secondary sample periods.
- This may seem a bit odd at first but keep in mind that Excel treats all dates as a number of days since January 1, 1900 or 1904 (depending on which version of Excel you are using)
- The AND function will return a TRUE value is the criteria in the parenthesis are met or a FALSE value if they are not
- Once you have got all of your TRUE and FALSE values copy them into a separate set of columns. Note that instead of just 'paste'or 'ctrl+v', you want to right click and 'paste special' and select the 'Values' box. This tells Excel to just give you the displayed number text or whatever appears in the box without any of the underlying formulas.
- Now you can 'Find and Replace' TRUE with 1 and FALSE with 0

These steps (and cell macros) are shown in worksheet ' RD within season period trick'. At this point, you will se something that look like

| 110 |  |  | - | f. $=$ AND (E10>=\$ $1 \$ 1, \mathrm{E} 10<=\$ 1 \$ 2)$ |  |  |  |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 4 | A | B | C | D | E | F | G | H | 1 | J | K | L | M | N | 0 | P |
| 1 | Tag | Date | Year |  |  |  |  | 5/1/2012 | 5/16/2012 | 6/1/2012 | 6/16/2012 |  | Interval 1 | Interval 2 | Interval 3 | Interval 4 |
| 2 |  |  |  |  |  |  |  | 5/15/2012 | 5/30/2012 | 6/15/2012 | 6/30/2012 |  |  |  |  |  |
| 3 | ATS150 |  | 2000 |  | 5/30/12 |  | 6/17/12 | FALSE | TRUE | FALSE | TRUE |  | 0 | 1 | 0 | 1 |
| 4 | ATS150 |  | 2001 | 5/2/12 |  |  | 6/24/12 | TRUE | FALSE | FALSE | true |  | 1 | 0 | 0 | 1 |
| 5 | ATS150 |  | 2002 |  |  | 6/4/12 |  | FALSE | FALSE | TRUE | FALSE |  | 0 | 0 | 1 | 0 |
| 6 | ATS150 |  | 2003 |  | 5/23/12 | 6/2/12 | 6/25/12 | FALSE | TRUE | TRUE | TRUE |  | 0 | 1 | - 1 | 1 |
| 7 | ATS150 |  | 2009 |  |  |  |  | FALSE | FALSE | FALSE | FALSE |  | 0 | 0 | 0 | 0 |
| 8 | ATS150 |  | 2010 | 5/6/12 | 5/17/12 | 6/10/12 | 6/17/12 | true | true | True | TRUE |  | 1 | 1 | 1 | 1 |
| 9 | ATS151 |  | 2000 | 5/13/12 | 5/18/12 |  |  | TRUE | TRUE | FALSE | FALSE |  | 1 | 1 | 0 | 0 |
| 10 | ATS151 |  | 2001 | 5/7/12 |  |  |  | TRUE | FALSE | FALSE | FALSE |  | 1 | 0 | 0 | 0 |
| 11 | ATS151 |  | 2002 |  |  | 6/10/12 | 6/18/12 | FALSE | FALSE | TRUE | TRUE |  | 0 | 0 | 1 | 1 |
| 12 | ATS151 |  | 2003 |  |  | 6/1/12 | 6/16/12 | FALSE | FALSE | true | TRUE |  | 0 | 0 | 1 | 1 |
| 13 | ATS151 |  | 2004 | 5/6/12 | 5/25/12 | 6/10/12 | 6/19/12 | TRUE | TRUE | TRUE | TRUE |  | 1 | 1 | 1 | 1 |
| 14 | ATS151 |  | 2005 | 5/11/12 | 5/18/12 |  |  | TRUE | TRUE | FALSE | FALSE |  | 1 | 1 | 0 | 0 |
| 15 | ATS151 |  | 2006 | 5/11/12 | 5/28/12 |  |  | TRUE | True | FALSE | FALSE |  | 1 | 1 | 0 | 0 |
| 16 | ATS151 |  | 2007 | 5/9/12 |  |  |  | TRUE | FALSE | FALSE | FALSE |  | 1 | 0 | 0 | 0 |
| 17 | ATS151 |  | 2008 | 5/2/12 |  |  |  | TRUE | FALSE | FALSE | FALSE |  | 1 | 0 | 0 | 0 |
| 18 | ATS151 |  | 2009 |  |  |  | 6/23/12 | FALSE | FALSE | FALSE | TRUE |  | 0 | 0 | 0 | 1 |
| 19 | ATS151 |  | 2010 |  |  | 6/12/12 | 6/25/12 | FALSE | FALSE | TRUE | TRUE |  | 0 | 0 | 1 | 1 |
| n | .rn |  | nann | rlanlan | rinrian | - Man | rianian | +mir | -mir | rnur | mor |  | - | - | - | - |

At this point, the remaining steps are similar to the same steps we used for CJS and MS data types (as described earlier). You simply

1. copy the the data to a new worksheet (shown in 'capture data-robust design')
2. Select the data, then 'Insert | Pivot Table | Pivot Table'
3. Drag Tag to 'Row Label', Year to 'Column Label'
4. Now here is another difference for the RD: there are multiple occasions per year. So just drag each one to the values box in the order that they occur!
5. concatenate into a contiguous encounter history, and you're done. Have a look at the worksheet ' RD Input Construction' for what it should look like.

[^0]:    * The term 'return rate' is something of a misnomer, since it is not a rate, but rather a proportion. However, because the term 'return rate' is in wide use in the literature, we will continue to use it here.

[^1]:    * Sufficiency is the property possessed by a statistic, with respect to a parameter, when no other statistic which can be calculated from the same sample provides any additional information as to the value of the parameter. For example, the arithmetic mean is sufficient for the mean ( $\mu$ ) of a normal distribution with known variance. Once the sample mean is known, no further information about $\mu$ can be obtained from the sample itself.

[^2]:    * The word 'likelihood' is often used synonymously for 'probability' but in statistical usage, they are not equivalent. One may ask 'If I were to flip a fair coin 10 times, what is the probability of it landing heads-up every time?' or 'Given that I have flipped a coin 10 times and it has landed heads-up 10 times, what is the likelihood that the coin is fair?' but it would be improper to switch 'likelihood' and 'probability' in the two sentences.

[^3]:    * In statistics and demography, a cohort is a group of 'subjects' defined by experiencing a common event (typically birth) over a particular time span. In the present context, a cohort represents a group of individuals captured, marked, and released alive at the same point in time. These individuals would be part of the same release cohort.

