Ch. 8

Estimation of population size: closed populations

"My parents removed to Missouri in the early 'thirties; I do not remember just when, for I was not born then and cared nothing for such things…[our] home was made in the wee village of Florida, in Monroe County, and I was born there in 1835. The village contained a hundred people and I increased the population by 1 per cent. It is more than many of the best men in history could have done for a town. It may not be modest in me to refer to this, but it is true. There is no record of a person doing as much-- not even Shakespeare. But I did it for Florida, and it shows that I could have done it for any place--even London, I suppose."
-- Mark Twain

Questions to ponder:
- *Is there a fixed period of time that should be considered 'closed' for all species?*
- *What kind of information is needed for a simple Lincoln-Petersen estimate of N?*
- *How can I assess the potential for bias with a simple Lincoln-Petersen estimate when I have small samples?*

A bit of history (*histoire*)

The Lincoln-Petersen estimator was first used to estimate the population size of a **closed** wildlife population in 1896 when **C. G. Johannes Petersen**, a marine biologist in Denmark, estimated the size of a population of plaice (*Pleuronectes platessa*)—a species of flatfish, similar to flounder (Petersen 1896).

Frederick C. Lincoln, an American ornithologist, described the method in 1930 in USDA Circular 118: "*Calculating Waterfowl Abundance on the Basis of Banding Returns.*" Lincoln, who also developed the 'flyway' concept for migratory birds, devised the method to estimate the continental population size of waterfowl (Lincoln 1930).

Although we give Lincoln and Petersen credit for this method, the general idea of using a 'known ratio' to estimate components of an 'unknown ratio' is much older. Ken Pollock, of North Carolina State University, suggests that the first use of the Lincoln-Petersen-type estimator was by a chap named **Laplace** in

$$\hat{N} = \frac{n_1 n_2}{m_2}$$

1783. Laplace wanted to estimate something useful—the population of France. There were a lot of people in France, and census-type data were not common at this time. But, one thing was known—the number of births in the whole of France. So, Laplace knew how many babies (think of babies as 'marked animals' in time 1).

In a small subset of the parishes (a small, local geographic region similar to 'counties' in the US) in France, Laplace could obtain a relatively accurate count for the total number of people in the parishes (think of this as n_2), and he was also able to obtain the number of babies born in those same parishes (again, babies are 'marked individuals', so think of this as m_2).

So, he was ready to apply the estimator. If he assumed that the birth rate (babies/population) was the same in those parishes as it was in the whole of France, he could estimate the population of France (N) as equal to $n_1 * n_2 / m_2$ (Laplace 1783).

Perhaps it is useful for you to see that this estimator has been used for a very long time?!

Closed population models

In Chapter 7, we compared open and closed population models. Here, we will continue with the topic of closed populations. Thus, we will assume no births and no deaths during the sampling of our population. The simplest form of a closed mark-recapture analysis is called the **Lincoln-Petersen** method. Although it is simple, the Lincoln-Petersen method provides an unbiased maximum likelihood estimate of N for a two-occasion sample. The underlying assumption is that the proportion of marked animals remains the same during the two sample periods.

The L-P method begins with the basic idea that an unknown portion of the population is captured and marked during the first time period. And, although you don't know what that proportion is, we can denote it as the capture probability, p. That is, the unknown proportion of the population that is marked during the first time period is equal to the capture probability (if p = 0.35 during time 1, then you should capture 35 percent of the population).

But, we obviously don't know anything except how many animals we captured. This sounds like the example earlier in this chapter of 100 animals captured in a study area, doesn't it? Well, never fear, Lincoln and Petersen both came up with a brilliant plan to estimate p, and therefore estimate N.

The brilliantly simple idea is that if you have a second capture occasion and you look around at all of your captured animals, the proportion of the animals with marks in your sample SHOULD be the same proportion of the population that you captured (and marked) during time 1. So simple! We can see this graphically in Figure 8.1.

If those proportions are equal, then we can use an equation to state:

$$\frac{m_2}{n_2} = \frac{n_1}{N} \quad\Longrightarrow\quad \hat{N} = \frac{n_1 n_2}{m_2}$$

That is, the portion of animals caught (n_1) from the population (N) during the first time period is equal to the portion of the sample during time 2 (n_2) that have marked on them (m_2). By rearranging with algebra, we can solve for the only unknown in the equation, which is the parameter whose value we want to estimate: N.

Lincoln and Petersen's method is simple, and has a few **assumptions**. First, we assume that capture probability is the same for all animals in the population. Interestingly, p_1 and p_2 do not have to be the same, nor do the capture methods need to be the same. In fact, Lincoln used traps to band and mark ducks and then he used hunter kills as the second capture method.
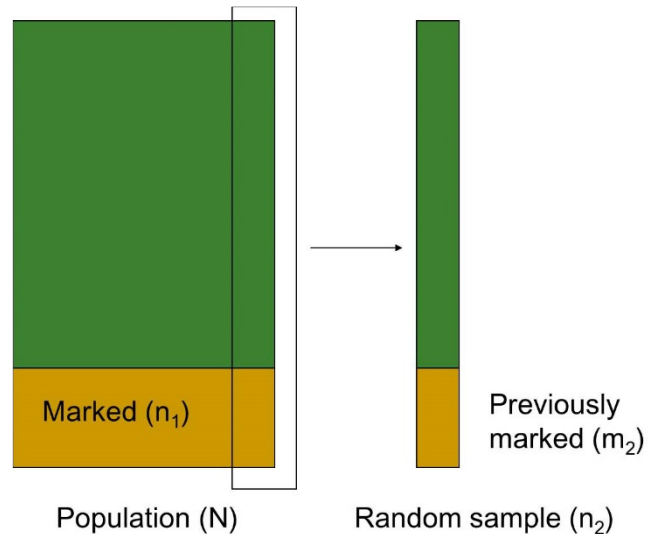
Other assumptions:
- the marking of an animal does not affect p_2.
- marks are not lost between capture occasions.
- all marks at time 2 are reported.
- each sample of the population (during time 1 and 2) is a random sample of the population.

Figure 8.1: *The logic behind the 2-sample Lincoln-Petersen approach to estimation of population size. First (left), a population of unknown size (N) is sampled and n_1 individuals are marked (the unmarked portion of the population is represented by dark color). A second random sample (n_2) of the population is taken (right). The proportion of marked animals can be determined in the second sample, and it should be equal to the proportion of marked animals in the population immediately after the first sampling/marking.*

You try it!

Ready to try your hand at a problem?

Pollock et al. (1990) described a study in Florida in which 148 northern bobwhite (quail [*Colinus virginianus*]) were marked with leg bands after being trapped in cornfields during January of 1982. During a 3-day controlled hunt in February 1982, 39 of 82 shot quail were determined to have leg bands.

What is the estimate of the population size ($\hat{N}$) by the Lincoln-Petersen estimator? To provide the estimate, you need to figure out the values for n_1, n_2, and m_2. You'll find the answer at the end of this chapter.

Generalizing the Lincoln-Petersen

Thus far, we have used summaries of n_1, n_2, and m_2 to estimate population size. But, we need to be working towards an understanding of the generalization of the method—how does it work when you have a set of capture histories that will be the input for a more complicated analysis in a software package such as Program MARK?

Four possible capture histories	Probability of having capture history	Number of animals with this capture history
10	$p_1 q_2$	$n_1 - m_2$
01	$q_1 p_2$	$n_2 - m_2$
11	$p_1 p_2$	m_2
00	$q_1 q_2$	$N\text{-}r$ (NOTE: *can't observe*)

The table above shows the four possible capture histories of animals in a population under the 2-sample Lincoln-Petersen research design. Note that the first three will be the animals in your data set, and the 4th capture history ("00") is not observable—these are the animals that are never captured.

We can also define the capture probability as p and the probability of not being captured as q (which is also, by definition, $1\text{-}p$). You have seen n_1, n_2, and m_2 before. The last definition we need is for r, which is the total number of captured animals. Although r is helpful, we are really interested in N, the population size.

If we allow capture probability to be different in each time interval (thus, the use of p_1 and p_2 to indicate that capture probability may be different in time 1 and time 2), we can see that the probability of having a capture history of 11 is: $p_1 * p_2$. That is, the probability of being captured during time 1 is p_1 and the probability of being captured during time 2 is p_2. To have a capture history of 11, *both* of these events have to occur (i.e., captured in each period), so we multiply the two probabilities together.

Similarly, to have a history of 01, an animal must avoid capture in time 1 and be captured in time 2. Thus, the probability is: $q_1 * p_2$. And, the opposite is true for a history of 10: $p_1 * q_2$.

These are the probability statements that a maximum likelihood estimator will use to find the best estimate for p. And, when we estimate capture probability, we can estimate N. Remember that, in general form, $N = n/p$? That is, if we can estimate the proportion of the population that we didn't capture, we can estimate population size—because we know the number of animals we captured. In the table above, if you add the first three cells together, we can calculate how many

animals we captured as the sum of animals with 11, 10, and 01 capture histories. Or, mathematically, $r = (n_1-m_2)+(n_2-m_2)+m_2$.

Chapman wasn't satisfied

Like all maximum likelihood estimators, the L-P estimator is unbiased for very large samples. But, it is biased for small samples. This bias can be shown by putting 10 white balls in a hat (a very small population, which ensures small samples). If you randomly draw a sample of 4 balls (a small sample) and mark them, we'll now have 6 unmarked and 4 marked balls in our 'population' of balls. We know (because we set up this experiment) that the marked proportion of the population is 0.4. And, $n_1 = 4$.

Now, if we draw a sample of four more balls, we could get a variety of results. Using simple logic, if 40% of our population is marked, we might predict that we'll most likely get two marked balls in our sample of four balls that we randomly draw. You'll notice that it is impossible for us to get exactly 40% of our sample (0.4 * 4 = 1.6, and we are not splitting balls in half…just as you cannot split animals in half during sampling!). And, that is the reason that the L-P is biased for small samples.

To carry the example forward, if $m_2=2$ and $n_2=4$, then our population estimate would be: $\widehat{N}=4*4/2 = 8$.

Now, let's allow a random occurrence to happen…and let's say we got, instead, 1 marked ball in our sample. Such an event might occur with such a small sample. Now, $m_2 = 1$. And, $\widehat{N} = 4*4/1 = 16$. A change in one marked ball in our sample doubles our population estimate.

We can pause and state that most scientists would never attempt to do a mark-recapture exercise if the size of the population was thought to be near 10! We have used such a small population and small samples to illustrate the problem. But, it might be common for your samples to be less than 30 in some situations. For example, what happens to the L-P method if $m_2 = 0$ (no marked animals captured)? $\widehat{N}$ is undefined, as you cannot divide n_1*n_2 by 0.

The Lincoln-Petersen estimator was modified by Chapman, and the resulting estimator is known as the "**Chapman modification**" (yes, we biologists are often very literal in the names we give to methods!). The modification has less bias for small samples than the L-P estimator. Chapman based his modification on the hypergeometric probability distribution, which is used when sampling without replacement. We mention this simply to note that there is statistical rigor and theory behind the modification. However, it is not a maximum likelihood estimator:

$$\hat{N} = \frac{(n_1 + 1) \times (n_2 + 1)}{(m_2 + 1)} - 1$$

The modified method does solve, mathematically, the problem of situations when m_2 is 0. However, we would remind the reader that if a study does not result in capturing a marked animal, it is more likely that the best course of action is to reconsider the study design. How might you mark more animals during time 1? Or, how might one might work with a species that is either so rare or so trap-timid that no marked animals are caught.

You try it!

Estimate $\hat{N}$ using the Pollock et al. (1990) quail data from above. Were the samples small enough to warrant use of the Chapman method? Compare your answers to those found at the end of the chapter.

Schnabel had more data…

The **Schnabel method** expanded the basic philosophy of Lincoln-Petersen to be used when the number of capture occasions is larger than 2. When Zoe Emily Schnabel, a mathematician at the University of Wisconsin, developed this method in the 1930's, only 2-occasion studies could be used. So, her work redefined possibilities for wildlife science. The Schnabel method is a closed form method, which means it can be condensed to an equation. But, it is an approximation to a maximum likelihood estimation method that can be found in modern software tools. White et al. (1982) noted that many biologists have disregarded a note that Schnabel wrote about her method: *"It should be emphasized, however, that none of the solutions can be expected to provide more than a general estimate of the order of magnitude of the total population."*

For this method, C_t is defined as the number of captures during time t. R_t is the number of recaptures (marked animals, captured again) captured during time t. And, M_t is the number of animals marked in the population, at time t.

$$\hat{N} = \frac{\sum_t (C_t \times M_t)}{\sum_t R_t}$$

Note: To properly calculate M_t*, do* NOT *count animals that are marked for the first time during time t. That is,* M_t *is the number of animals marked in the population just as you begin to conduct your observations of the traps or nets. Or, you can also think of* M_t *as the number of marked animals in the population that were at 'risk' of being trapped during time t.*

You try it!

During 2006, students from the University of Nebraska-Lincoln traveled to a 7-ha island off the coast of Puerto Rico. The island was named Isla Magueyes, and it had a population of Cuban rock iguanas (*Cyclura nubila*). These iguanas are a species of conservation concern elsewhere in their range, but their population was causing damage on Isla Magueyes. A small population of iguanas had been left on the island when a zoo was removed. No one knew how many iguanas were on the island.

So, the students marked animals each morning for three days. On the first day, the students found 155 iguanas, and they squirted them with small marks of latex paint to mark them. The marks were not individual ID's, but the marks were easy to see on day 2 and 3.

On day 2, the students saw 109 marked animals and 66 unmarked animals. They marked any animals that were not marked. On day 3, the students observed 116 marked animals, and only 15 unmarked animals. Use the Schnabel method to estimate the population size.

	Animals Observed	**Animals with Marks When Seen**
Day 1:	155	0
Day 2:	175	109
Day 3:	131	116

The first step is to complete a summary table. M_t can be a tricky statistic to calculate, so we have added a 'newly marked column' here. The numbers of newly marked animals have been added to help you stay on track. In addition, we have noted that $M_1 = 0$ (no marked animals in the population before the first period).

Day	C_t (Captures during time t)	R_t (Number of recaptures captured during time t)	**Number newly marked**	M_t (Number of animals marked in the population, just before you conduct trapping during time t)
1			155	0
2			66	
3			15	

Population size estimate: _____

See the end of this chapter for answers after you have given this a try.

Modern closed-population methods

The analytical methods described above can be accomplished by **batch marking** individuals, rather than going to the effort of applying an individual identifying letter and/or number combination to each animal. For example, the Lincoln-Petersen and the Schnabel data can be gathered by applying a basic mark—like the splotch of paint used on the iguanas in our example. In the third time period, there is no need to know whether a marked animal was previously marked in the first or second time period—it is enough to know that it was marked at some point in the past.

The assumption of the Lincoln-Petersen and the Schnabel is that all animals in the population at a given time period have the same probability of capture. What if that is not true? For example,

what if the iguanas that encountered students were less likely to be in the accessible areas of the island on the second day, while their unmarked friends were content to sunbathe on sidewalks that would eventually be used by students who marked them? If we break that assumption, the L-P estimator does not work as it should.

The alternative is to use **individual marks**, which allow the application of more modern closed-population estimation methods (Figure 8.2).

Otis et al. (1978) proposed several models for use in estimation of population size that are still in general use today. The most important contribution was the notion that animals could become "trap happy" (recapture rates are higher than initial capture rates) or "trap shy" (recapture rates are lower than initial capture rates). Today, we define **capture rate**, p, as the

Figure 8.2: *A prairie rattlesnake (Crotalus viridis) is marked with a Passive Integrated Transponder (PIT) tag to provide individual identification upon recapture. Photo provided by Dennis Ferraro and used with permission.*

probability of initial capture and **recapture rate**, c, as the probability of recapture after being captured at least once.

And, although Otis et al. (1978) did not use AIC to compare alternative models that described variation in capture probability, their suggestion to compare multiple models led biologists toward the idea that capture estimates from "poor" models should not be used. Rather, estimates from models judged to be better should be used. The application of AIC for model selection (see Chapter 4) in ecology developed from this work.

By the use of individual marks, we can develop individual capture histories, which are not possible with batch marking (e.g., data often used for Schnabel method). Capture histories are important, because we can tie specific probability statements to each capture history—that is, each capture history has a specific probability of occurrence. For example, the probability of an animal having specific capture histories in a 10-occasion, closed-population, mark-recapture study is:

Capture history	Probability
0100111000	$(1-p_1)p_2(1-c_3)(1-c_4)c_5c_6c_7(1-c_8)(1-c_9)(1-c_{10})$
1000110101	$p_1(1-c_2)(1-c_3)(1-c_4)c_5c_6(1-c_7)c_8(1-c_9)c_{10}$
0000001101	$(1-p_1)(1-p_2)(1-p_3)(1-p_4)(1-p_5)(1-p_6)c_7c_8(1-c_9)c_{10}$

With an adequate sample of marked animals, you may use software that uses maximum likelihood estimators to estimate the capture and recapture rates, as well as population size for the species in your study. In the above example, we show variation caused by behavior (capture and recapture rates not equal), as well as time (different capture and recapture rates for each time period). However, you might explore alternative models. For example, we might hypothesize that behavior has no impact on recapture rates, and hence $c = p$. Therefore, the probability statement for the first capture history above could be represented using only p and no c (the recapture probability):

0100111000 $\qquad$ $(1-p_1)p_2(1-p_3)(1-p_4)p_5p_6p_7(1-p_8)(1-p_9)(1-p_{10})$

A third model that we might explore could state that behavior causes differences in capture and recapture, but time is not important. So, the probability statement for the first capture history in the table above would not have any time-specific references (no subscript numbers):

0100111000 $\qquad$ $(1-p)p(1-c)(1-c)ccc(1-c)(1-c)(1-c)$

And, last (at least for our simple example), we might hypothesize one last model—a null model—that neither behavior nor time cause capture rate to vary. Thus, the likelihood statement can be represented using only p and not c, the recapture probability. It also does not include time-specific p's (no subscripts):

0100111000 $\qquad$ $(1-p)p(1-p)(1-p)ppp(1-p)(1-p)(1-p)$

Which model is best? We could use **AIC** to tell us which model is the most likely to represent reality, given our data (Chapter 4). And, we would report the population size and capture probabilities estimated by the best model.

Lukacs (2014) provides a description of many modifications of the closed-population mark-recapture models. We suggest the beginning user start with **full likelihood** (p and c) or **Huggins'** (p and c) models. Each allows the user to explore the basic models we have outlined above.

Conclusion

Simple models to estimate population size require the assumption of closure during the sampling period: no births, deaths, or movements in or out. The history of estimating the size of a population started with a simple 2-occasion mark-recapture experiment: the Lincoln-Petersen scenario. The Schnabel method allows an estimate based on more than one period, which paved the way for modern methods. All of these methods are based on the same general concept: for a set of captured and marked animals, if you have a second capture occasion and you look at the second set of captured animals, the proportion of the animals with marks in your sample is assumed to be the same proportion of the population that you marked during the first capture period. Most modern methods require individual marks on animals, and the methods allow the exploration of multiple hypotheses regarding the variation of capture probability in the population during the study.

Answers: You try it!

Pollock et al. (1990) quail problem: 148 northern bobwhite (quail) were marked with leg bands; of 82 shot quail in the next month, 39 were marked with leg bands.

$n_1 = 148$
$n_2 = 82$
$m_2 = 39$

$\hat{N} = 311$ *(rounded)*

Chapman modification for the Pollock et al. (1990) quail problem:

$\hat{N} = 308$ *(rounded)*.

Were the samples small enough to warrant use of the Chapman method? The difference between 308 and 311 (a measure of the bias of the Lincoln-Petersen estimator) is pretty small (just a difference of 3 animals).

Schnabel method (iguana problem):

	Animals Observed	Animals with Marks When Seen
Day 1:	155	0
Day 2:	175	109
Day 3:	131	116

Day	C_t	R_t	Number newly marked	M_t
1	155	0	155	0
2	175	109	66	155
3	131	116	15	155+66=221

$$\hat{N} = \frac{(155 \times 0) + (175 \times 155) + (131 \times 221)}{0 + 109 + 116} = \frac{0 + 27125 + 28951}{225} = 249.2$$

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For more information on topics in this chapter

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A maned wolf (Chrysocyon brachyurus) is measured by a research team prior to marking with a radio-telemetry transmitter in Brazil. Photo taken by Adriano Gambarini. Lucia Corral: left, Nucharin Songsasen: right) and used with permission of the photographer.