EXERCISE 7: ROYLE-NICHOLS ABUNDANCE INDUCED HETEROGENEITY

Estimating mean abundance from repeated presence-absence surveys

In collaboration with Kurt Rinehart, University of Vermont, Rubenstein School of Environment and Natural Resources

Please cite this work as: Donovan, T. M. and J. Hines. 2007. Exercises in occupancy modeling and estimation. <http://www.uvm.edu/envnr/vtcfwru/spreadsheets/occupancy.htm

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OBJECTIVES

- To understand the basics of the Poisson and Binomial distributions.
- To learn and understand the basic mixture model for estimating abundance, and how it fits into a multinomial maximum likelihood analysis.
- To use Solver to find the maximum likelihood estimates for the probability of detection and lambda, the average site abundance.
- To assess deviance of the saturated model.
- To introduce concepts of model fit.
- To learn how to simulate basic mixture data.

INTRODUCTION

Suppose that you want to estimate the size of an animal population. For one reason or another, you are not able to employ standard population estimation techniques like capture-recapture or distance sampling, so instead you gather presence-absence data (or more properly, detection-non detection data). Your data could be detections of some insect species found on crop plants, detections of a singing bird species, or secondary sign counts of mammals. Let's suppose you are interested in the abundance of a particular mammalian carnivore. On each visit, you search for fresh sign (tracks, feces, etc.). You see some scat and some fresh tracks at two different spots within a site. Are they from the same or different individuals? You can't tell because the animals are not marked. Another situation might involve remote camera surveys for a species, in which all the individuals look the same: 3 pictures could be from 3, 2, or just 1 individual. In both examples, you can't correlate the number of signs to the number of animals because one animal may have produced many signs; you can only record the detection or non-detection of the species.

Because you can't sample individuals, you will sample the area itself. You check to see if the site is occupied by the species of interest and record any signs at that site as a single detection. This is an occupancy survey. You won't do it just once - you'll go back for repeated visits and record detection or non-detection at each subsequent visit. The detection history at a site will be recorded as a sequence of 1's and 0's (1 = detection, 0 = no detection) across the sample periods. Let's let T equal the total number of visits. An example encounter history for a site sampled 5 times (T = 5) might be 00110. There were no detections in either of the first two visits, detections for visits three and four, and no detection again on the fifth visit.

Now let's suppose you sample a number of different sites in your study area. Let R equal the total number of sites that are surveyed. At each of the R sites, you will determine whether or not you detect your target species at each time interval. Here is a sample data sheet for a survey of 20 sites (R = 20), each sampled on 5 different occasions (T = 5):

	Survey				
Site (i)	1	2	3	4	5
1	0	0	0	0	0
2	0	1	1	1	0
3	1	0	1	1	1
4	0	0	1	0	1
5	0	0	0	0	0
6	1	1	1	1	1
7	1	0	1	1	1
8	0	1	0	1	0
9	0	0	1	0	1
10	1	1	1	1	1
11	1	1	0	1	1
12	0	0	0	1	0
13	1	1	1	1	1
14	1	1	1	1	1
15	1	0	0	1	1
16	1	1	1	1	1
17	1	1	1	1	1
18	1	1	0	1	1
19	0	0	0	0	0
20	1	1	1	0	1

Many surveys produce this kind of data. The question is, how can we analyze these numbers in a meaningful way—a way that will allow us to estimate the abundance of animals?

A recent paper by Andy Royle and Jim Nichols explains how these data can be used to estimate the abundance of a species across the study area (Royle, J.A. and J.D. Nichols. 2003. Estimating abundance from repeated presence-absence data or point counts. Ecology 84(3):777-790). There are several assumptions of this model, but we are going to focus on the two that are the conceptual core, namely: (1) the spatial distribution of the animals across the survey sites follows some kind of prior distribution, such as the

Poisson distribution, and (2) the probability of detecting an animal at a site is a function of how many animals are actually at that site.

Note that the Royle-Nichols model can accommodate different kinds of distributions representing the spatial distribution of the target species, but that we will focus exclusively on the Poisson distribution in this exercise. We use the Poisson in our spreadsheet and, for simplicity, we may omit reference to the fact that the Poisson is simply one option for modeling spatial distribution. This should become clearer after we discuss these assumptions in depth. After that, we'll go through how the Royle-Nichols model is put together.

THE PRIOR DISTIBUTION

In the Royle-Nichols model, we must "specify" a "prior" spatial distribution of the abundance of our target species. The spatial distribution of animals is simply how many animals occur at each site within the study area. However they are distributed, each of the survey sites will contain some number of animals (some sites may contain 0 animals). That number, the site abundance, is a function of the mechanisms governing the distribution.

A prior distribution is specified, or chosen, based on how you think the animal species is really distributed. If you were in the planning stages of your survey and had not yet collected any data, you would ask yourself, "How are these animals distributed in space?" *Prior* to collecting any data, we specify the Poisson—we consider the Poisson to accurately represent the true spatial distribution of our target species. Alternatively, *prior* studies might suggest that the Poisson is an appropriate distribution to use. We choose the Poisson probability function to represent the mechanisms of the spatial distribution. The Poisson won't tell us exactly how many animals inhabit a site, but it will define the probability for any number you might choose to consider. Let's start by reviewing the Poisson Distribution, and then we can see how it is used in the Royle-Nichols model.

THE POISSON DISTRIBUTION

The Poisson distribution is used to model the number of certain randomly occurring events, like the number of car accidents in your home town, or the number of individuals of a species within each of your survey sites. In the car accident example, each accident is independent of every other accident and the number of accidents in any time period is random and independent of any other time period. The spatial distribution of animals can also meet these Poisson assumptions when the number of animals inhabiting one site is random and independent of the number of animals at other sites.

The Royle-Nichols model assumes that each of the R sites in your occupancy survey is home to some number of animals that can be modeled by a specified prior distribution like the Poisson. In essence, each site is home to a certain number of animals of your target species and that number is a function of the specified process. We also must assume this number does not change over the course of your study. The population must be demographically closed, meaning that the number of individuals at the site does not change across sampling periods. That is, no births, no deaths, no immigrants, no emigrants. This additional assumption means repeated sampling visits must be completed within a relatively short period of time.

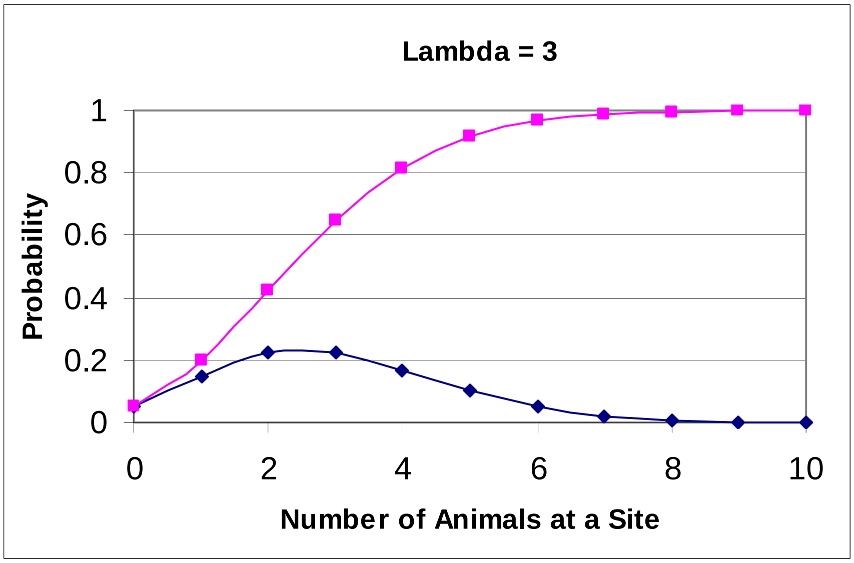
The Poisson distribution has a single parameter, λ ("lambda"), the mean. In this case, lambda is the mean abundance across the R sites. The Poisson distribution returns the probability of any level of abundance x from 0 to ∞ given some lambda. Suppose you win a huge grant ($$) and can accurately count the number of animals within your study area (instead of collecting presence-absence data). You can take this total abundance and divide it by the number of survey sites in the study area, R, and find that the mean abundance is 3 animals per site (lambda = 3). Suppose further, that you know (or assume) the number of animals in any site follows a Poisson distribution. Given this information, you can find the probability that a specific number of animals will occur at a given site. For example, when lambda = 3, the probability of a single site having an abundance of 5 is 0.10. Where does 0.10 come from? It is calculated with the probability density formula for the Poisson:

$$\boxed{f_x = \frac{e^{-\lambda}\lambda^x}{x!}}$$

where lambda is the mean of the Poisson distribution, and x is the "event" of interest, which in this case is the number of animals at a given site: x = 5. (Note: "f_x" is a generic term for any probability distribution. The term to the right of the equals sign is unique to the Poisson.) If you calculate this function for lambda = 3 and x = 5 animals, the result is a probability of 0.10.

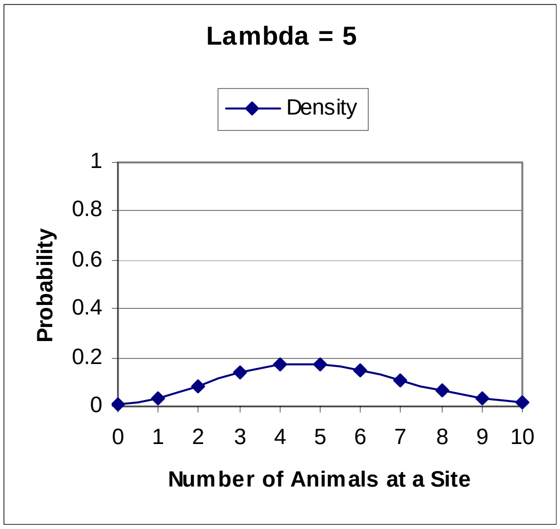
$$f_5 = \frac{\exp(-3)3^5}{5*4*3*2*1} = 0.10$$

The distribution of these Poisson probabilities over a range of values of x when λ = 3 looks like this:



The blue points (diamonds) show the probabilities of a given site being inhabited by x individuals when the lambda is 3. The graph would take a different shape if lambda were different. Notice that the peak of this blue curve is around 3. While it is possible to have x = 8 animals at a site when lambda = 3 animals, it isn't nearly as probable as having x = 3 animals. The pink curve (squares) shows the probabilities accumulating for each value of x. The pink point corresponding to x = 5 shows the probability of <u>5 or fewer</u> individuals inhabiting the site (the sum of the individual probabilities for x = 0 through 5). Since the mean is 3, most sites probably have abundances around 3 so the cumulative probability for x = 5 is quite high (0.92, in fact). It's easy to generate such probabilities in Excel with the POISSON function. In this function, you enter x and lambda, and then tell Excel whether you want the cumulative probability ("true") or individual probability ("false"). For example, we used "=Poisson(5,3,true)" to obtain the cumulative probability of 0.92 mentioned above.

Here are some more examples of interpretation of the Poisson distribution and its single parameter, lambda. Look again at the graph above. Lambda = 3 indicates that the average abundance for all sites is 3. Many sites will have 3 animals. When lambda = 3, x = 3 has the highest probability of occurrence. There will be quite a few sites with 0, 1, 2, 4, and 5 animals, and fewer sites with more than 5 animals.



If lambda = 5 (as shown to the left), probabilities are highest for site abundance between, say 3 and 7 animals. Relatively many sites may have 3, 4, 5, 6, or 7 animals. The probability of x = 1 or x = 9 is still above 0, but this probability is very small. There probably will be few sites with 1, 2, 8, or 9 animals, and very little chance of a site having 0 or 10+ animals. We could carry out the function for all values of x up to ∞, and the probabilities would just get smaller and smaller as we moved away from lambda. It wouldn't take long for them to be essentially 0. Consider that for lambda = 5 as in the graph above, the Poisson probability of x = 10 is 0.018. For x = 20 it is 0.00000027. It's very unlikely that a site would have 20 animals when lambda = 5.

The intent behind all of this is to "define" the function we will use to calculate the probability of a given level of abundance at any site. Why do we care? Because the Royle-Nichols model assumes that whether an animal is detected at a site is a function of site abundance (more on this in a bit). We need to know how likely one abundance is relative to another. Without specifying a prior distribution, we would be saying, in effect, "We think any number of animals at this site is as likely as any other number. A site abundance of 2 is as likely as 20." This is not only uninformative, it's totally unrealistic. Spatial distributions of organisms *do* follow mechanisms that can be represented by probability distributions. By specifying a prior distribution, we can quantify the probabilities of site abundance being 2 or 20. For the Poisson, we can do this provided we know the average abundance across all sites. In practice, we won't know true abundances, so lambda is one of the key parameters that is estimated by Royle-Nichols model.

PROBABILITY OF DETECTING AN ANIMAL AT A SITE

The second major assumption of the Royle-Nichols model is related to the first: the probability of detection of our target species at any site is a function of the abundance of animals there. But before we go there, let's step back for a moment and think about detection probability. All animals have some inherent detection probability that is independent of abundance. Some species are easy to find and locate, while others (cougars, for example) are just plain difficult to observe. Royle and Nichols call this inherent detection probability, r. This varies by species, but is constant for all individuals of a species. Cougars may have an r of 0.1, while black-throated blue warblers during the breeding season may have a detection probability of 0.8. A typical occupancy model such as the single-season model (MacKenzie et al. 2002) aims to estimate this detection probability in order to estimate the number of sites that were truly occupied even if there were no detections there.

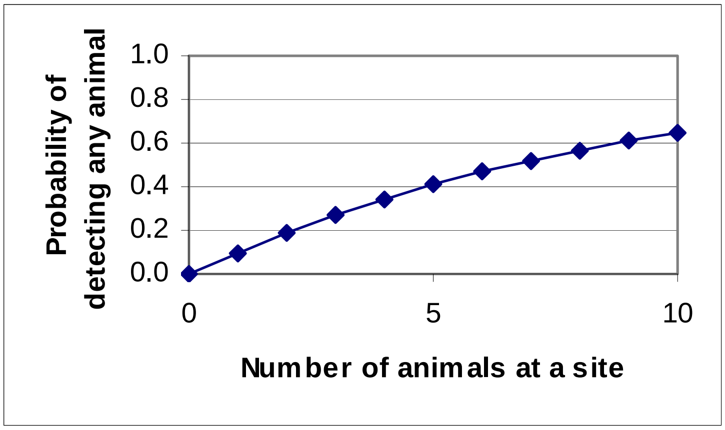
Royle and Nichols take this concept one step further. Recall that we are sampling sites, not individuals. Our detections will not purely reflect the r of the target species; they will follow a site detection probability that is a function of r *and* the site abundance.

For a given species detectability, r, it's easier to achieve detection when there are many animals at the site than when there are few. Even though cougars are inherently difficult to detect, you are more likely to observe cougar sign when a site is occupied by 10 cougars compared to 1. To record a detection for the site, you need only detect a single individual of those that are present. To fail to detect, you need to miss every individual. The more individuals are present, the more chances you have to detect them. Since you ensure that your surveys all fall within a period of time over which you can assume that the site abundance does not change (demographic closure), the probability of detection at the site follow this formula:

$$\boxed{p = 1 - (1 - r)^{N_i}}$$

This "site detection probability", p, is a function of the species inherent detection probability, r, and the site abundance, N_i. (NOTE: N_i is the abundance at site i.) We'll let N_{total} represent the total abundance across all sites. $N_{total} = \Sigma(N_i)$. The term (1-r) is the probability of missing a single individual occupying the site. The probability of missing all N_i individuals is $(1-r)^{N_i}$. Thus, the probability of detecting any animal at the site is one minus this term, or $1 - (1-r)^{N_i}$.

An example might make this clearer. Suppose a site is home to 10 animals, but the species has an r = 0.10 (intrinsically hard to detect). The probability of missing one individual is 1 - 0.10 = 0.90. The probability of missing all 10 animals is (1-0.10)^10 = 0.35. The probability of detecting an animal at this site is 1-(1-0.10)^10, or 0.65. If abundance was only 2 at that site, the probability of detecting an animal at this site is 1-(1-0.10)^2, or 0.19. Here is what this relationship looks like graphically, given that r = 0.10.



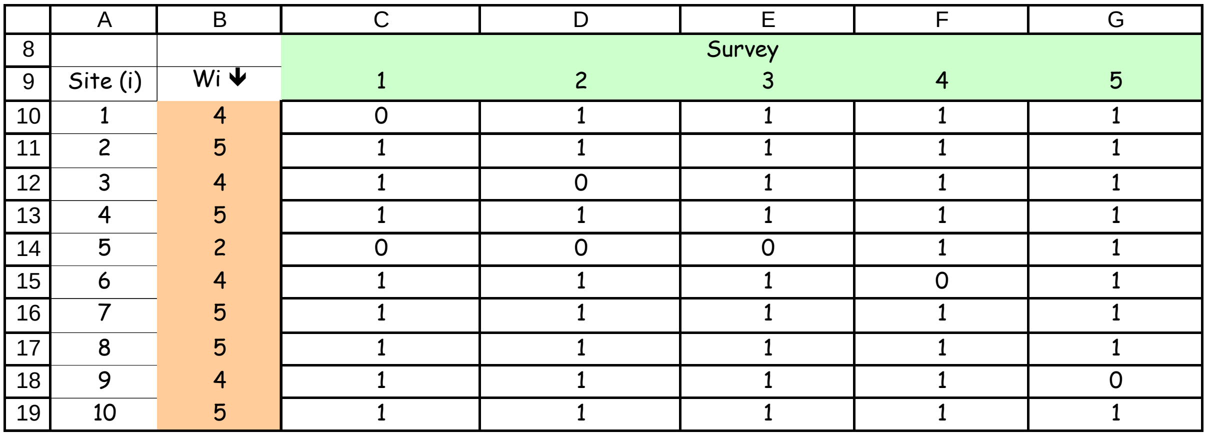
Considered in this light, differences in detection across sites will be a function of the site abundances. Again, if the site abundance is the same for every site, given that we assume no difference in detectability within the species, then you would expect the detections to be equal among the sites. Conversely, heterogeneous detectability (differences in the total detections per site) implies different site abundances.

KEY ASSUMPTIONS OF THE ROYLE-NICHOLS MODEL

OK, to recap: The key assumptions of the Royle-Nichols model are that (1) the number of animals at a particular site follows a Poisson probability distribution for which lambda indicates the mean abundance across all sites, and (2) the probability of detecting animals at each site is related to the species' r and the site abundance, N_i.

THE ROYLE-NICHOLS MODEL OVERVIEW

As with other occupancy models, repeated surveys are the cornerstone of data collection. For each site in your survey, you will get a series of 1's and 0's denoting detection or failure to detect at each visit. A site with detections in all of 5 visits will have a history of 11111. Another site may return a history of 10010. These can be summed, 5 and 2 respectively, to represent the total number of detections at the site over the whole survey. This is how data are summarized for this model. The total detections for site i being denoted as w_i. For example, here are some data for 10 sites, with w_i being the total number of times a species was detected at a site across surveys:



	A	B	C	D	E	F	G
8			Survey				
9	Site (i)	Wi ↓	1	2	3	4	5
10	1	4	0	1	1	1	1
11	2	5	1	1	1	1	1
12	3	4	1	0	1	1	1
13	4	5	1	1	1	1	1
14	5	2	0	0	0	1	1
15	6	4	1	1	1	0	1
16	7	5	1	1	1	1	1
17	8	5	1	1	1	1	1
18	9	4	1	1	1	1	0
19	10	5	1	1	1	1	1

To estimate abundance from this data, remember our two key assumptions: we assume that there is some number (it could be 0) of individuals actually inhabiting each site (N_i). We also assume that whether or not you detect the target at that site is going to be a function of the species-specific detection probability (r) according to this formula:

$$p = 1 - (1 - r)^{N_i}$$

We don't know r, but our assumption is that site-detection probability (p) is a function of r and N_i. We don't know Ni, but we assume that N_i follows a Poisson distribution across sites. The detection probability is "conditioned" on this Poisson-governed abundance, N_i. When detection is conditional, or dependent, on abundance, we can find abundance if we can estimate detection probability. If this conditional link weren't made - if we assumed detection at a site was independent of N_i - then we would have nowhere to go and should be looking for a different occupancy model.

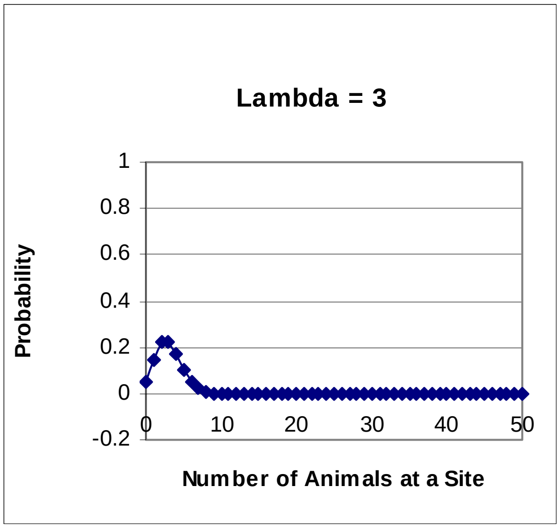
OK, we need to estimate r and N_i. These two parameters are combined in the site detection probability, p. But p depends on N_i and N_i is *unknown!* How can we even get started?

MIXTURE MODEL BASICS

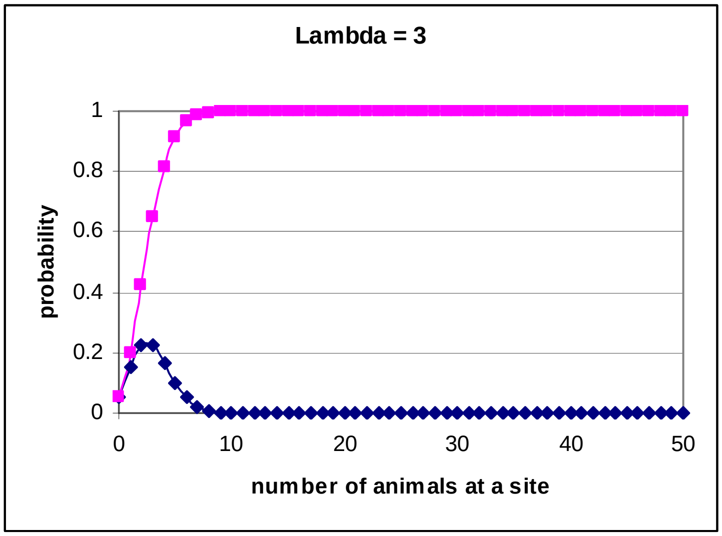
We'll have to "plug in" some numbers to take the place of N_i in the site detection probability formula. We will say, essentially, "Suppose that N_i is 0. Given r, what will p be? Okay, now what if N_i is 1? 2? 3?" etc. (Don't worry about the "given r" part just now. The spreadsheet will take care of this for us later. For now, just consider that any value of r will do.) We're going to do these "what-ifs" using a "stand-in", or index, of N_i. We'll call this "stand-in" k, the number of animals *potentially* at a site. N_i is the number of animals really at the site and we're just plugging in k's, so they are only potentially, or probably, the real abundance. We do this for a range of k's from 0 up to some maximum, K (capital K). K = 50 in this exercise, so we'll examine 51 different k scenarios.

How do you choose a value for K? Theoretically K = ∞, but we have to pick something smaller to work with. K must be large enough to include the range of realistically possible abundances, but sufficiently large that it covers nearly all possible abundances. To illustrate this, let's look again at the Poisson distribution.

Here is another illustration of Poisson probabilities, this time for lambda = 3 and ranging over a set of possible site abundances (k) from 0 to 50.



When lambda is 3, it's most probable that a site has 3 animals. It's highly improbable that number of animals that actually occurs at a site is above 10. If lambda = 3, what is the probability that actual abundance N_i = k = 9? We can compute this in Excel as =POISSON(9,3,FALSE). The answer is 0.0027, not a very high probability. What is the probability that actual abundance N_i = k = 4? The formula =POISSON(4,3,FALSE) gives the answer 0.1953. In other words, assuming that the variation in abundance across sites follows a Poisson distribution with a lambda = 3, it's more probable that the actual abundance at any given site is closer to lambda than further away from it.



Here is the same distribution including the cumulative probabilities (again, lambda = 3). Look at how for the higher values of k, little is contributed to the overall (cumulative) probability. Here, the cumulative probability is indistinguishable from 1 for k > 16. For a higher level of lambda, like lambda = 5, this happens around k > 20. We want the cumulative probability of K to be very close to 1, but we need some "wiggle room" since lambda is unknown. Consider K = 50 as a minimum. There is no penalty for a larger K. Andy Royle recommended we start out with K = 100 or 150, but we cut it down to make the spreadsheet simpler.

That just about covers the basic concepts. Let's jump to the big picture and see how it all goes together.

THE ROYLE-NICHOLS LIKELIHOOD OVERVIEW

Assuming you've worked through previous exercises in this book, our analysis will once again use maximum likelihood methods to find the most likely values for the two key parameters in the Royle-Nichols model, namely λ and r. We'll maximize the following equation:

$$L(w) = \prod_{i=1}^{R} \{ \sum_{k=0}^{K} \binom{T}{w_i} p_k^{w_i} (1 - p_k)^{T - w_i} f_k \}$$

where

$$p_k = 1 - (1 - r)^k$$

and

$$f_k = \frac{e^{-\lambda} \lambda^k}{k!}$$

This is the Royle-Nichols model. It's pretty daunting at first (in our humble experience). The formula computes the likelihood of **W** detections across the R sites, given T surveys, and it does so in a way that allows you to derive the abundance. The formula works on one site at a time, and computes the probability of observing w_i detections at the site given the site detection probability, p_k. We are using the potential site abundances, k, to calculate p_k. We do this for all levels of k and then mix these k-based probabilities together according to f_k, the probability that a given N_i = k.

HERE WE GO!

THE LIKELIHOOD FOR A SINGLE SITE

It's easiest to consider 1 site at a time, for which the likelihood is:

$$L(w_i \mid N_i = k) = \sum_{k=0}^{K} \binom{T}{w_i} p_k^{w_i} (1 - p_k)^{T - w_i} \; f_k$$

The symbols to the left of the equal sign reads "the likelihood of w_i (the total number of detections at site i), given that N_i equals k." The likelihood of the observed field data, w_i, is what we're interested in. The right side of the equal sign looks incredibly complex, but it is just the product of two probabilities: the binomial probability of observing w_i observations in T surveys, and the Poisson probability that there are k animals on the site.

Let's start with the binomial probability. Recall that the site-detection probability depends on the number of animals at the site—it is conditional on abundance. We calculate the site detection probability as a function of the species-detection probability, r, and the index of abundance, k, because N_i is unknown. We call this parameter p_k. Notice in the formula below, how k is replacing N_i in the earlier version of this formula.

$$p_k = 1 - (1 - r)^k$$

This function tells us the probability of seeing an animal at this site for a given level of k. Our data are the sums of the number of detections over T survey visits, w_i. The results of a survey occasion are binomial, a 1 or a 0, so detection at a site is a binomial probability. We want to find the probability of observing w_i detections over T surveys (in this case, 5), given the probability of a success is p_k. This is a binomial probability. A binomial probability formula for a series of detection surveys has the following three terms:

$$\boxed{\binom{T}{w_i} p_k^{\,w_i} (1 - p_k)^{T - w_i}}$$

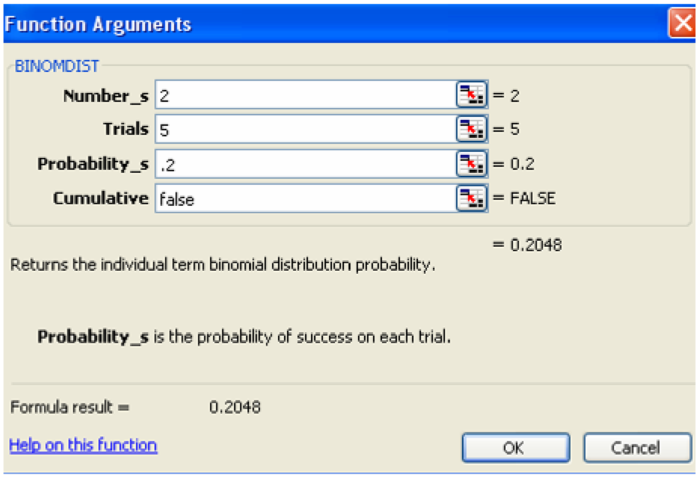
This is the binomial equation (see also http://mathworld.wolfram.com/BinomialDistribution.html). The first term (in brackets) counts the number of different combinations of w_i detections you can have in T visits. It reads, "T choose w_i" and is called the binomial coefficient. Suppose you conducted 5 surveys, and detected your target species on four surveys. There are 5 different ways in which this result can be realized: you could miss the animal on the first occasion, miss it on the second occasion, 3rd occasion, 4th occasion, or 5th occasion. Five choose 4 = 5 ways.

The second term, p_k^{wi}, is the joint likelihood of w_i detections at a site given the site detection probability, p_k. If $p_k = 0.6$, the probability of detecting a species on 4 out of 5 surveys is $0.6^4 = 0.1296$.

The final term, $(1-p_k)^{T-wi}$ is the likelihood associated with the occasions when nothing was detected. Failing to detect the target species at a site on a given visit is 1 minus p_k. Raising this to the power of T-w_i gives the joint probability of missing T-w_i detections on each of the visits where you saw nothing. If p_k = 0.6, the probability of missing a species in 1 out of 5 surveys is $0.4^1 = 0.4$.

$$\binom{T}{w_i} {p_k}^{w_i} (1 - p_k)^{T - w_i}$$

So, the portion of the likelihood pictured above describes the probability of detecting w_i animals in T surveys at a site, given p_k. If this formulation sickens you, just think of the words, BINOMIAL PROBABILITY, in place of it, where the number of binomial trials is T, the number of binomial successes is w_i, and the probability of a success is p_k. In Excel, the BINOMDIST function uses this same information to compute the binomial probability. For example, if T = 5, w_i = 2, and p_k = 0.2, the BINOMDIST function have the following arguments, with the final answer being 0.2048.



Function Arguments

BINOMDIST

Number_s 2 = 2

Trials 5 = 5

Probability_s .2 = 0.2

Cumulative false = FALSE

= 0.2048

Returns the individual term binomial distribution probability.

Probability_s is the probability of success on each trial.

Formula result = 0.2048

Now, let's go back the Royle-Nichols likelihood formula for a single site:

$$L(w_i \mid N_i = k) = \sum_{k=0}^{K} \binom{T}{w_i} p_k^{\,w_i} (1 - p_k)^{T - w_i} \; f_k$$

We just covered the binomial detection calculation. The next step is to multiply this by the term f_k. What's this, a derogatory term?! Not exactly. This is how we "adjust" the k-based probability of w_i detections to reflect how likely it is we would really have N_i animals at the site. So, f_k is the prior probability (for which we have specified the Poisson) that the site actually has an abundance of N_i.

$$f_k = \frac{e^{-\lambda} \lambda^k}{k!}$$

For a given site we will have one binomial probability of seeing w_i for each value of k. If we model 51 different values of k (k = 0 to 50), we have 51 binomial probabilities of w_i. Since each level of k is one possibility of the true site abundance, N_i, we need to "adjust" each probability of w_i for the probability that $k = N_i$. It's as if we're making a weighted average of the k-based probabilities and using the prior distribution of abundance to assign weights. This is a mixture model—we are mixing a set of probabilities (site detection; binomial) according to another set of probabilities (site abundance; Poisson). For a single site, the likelihood is this:

$$L(w_i \mid N_i = k) = \sum_{k=0}^{K} \binom{T}{w_i} p_k^{w_i} (1 - p_k)^{T - w_i} \; f_k$$

You should recognize the binomial probability of w_i based on p_k. The f_k term is the mixing probability—here, the Poisson prior distribution that k = N_i. The summation symbol tells us to mix all these together for the whole range of k for the w_i of this site. Is this making sense?

THE ROYLE-NICHOLS LIKELIHOOD FOR ALL SITES

The next step is to combine the site-likelihoods to get the likelihood over the whole survey (R sites):

$$L(w) = \prod_{i=1}^{R} \{ \sum_{k=0}^{K} \binom{T}{w_i} p_k^{wi} (1 - p_k)^{T - w_i} \; f_k \}$$

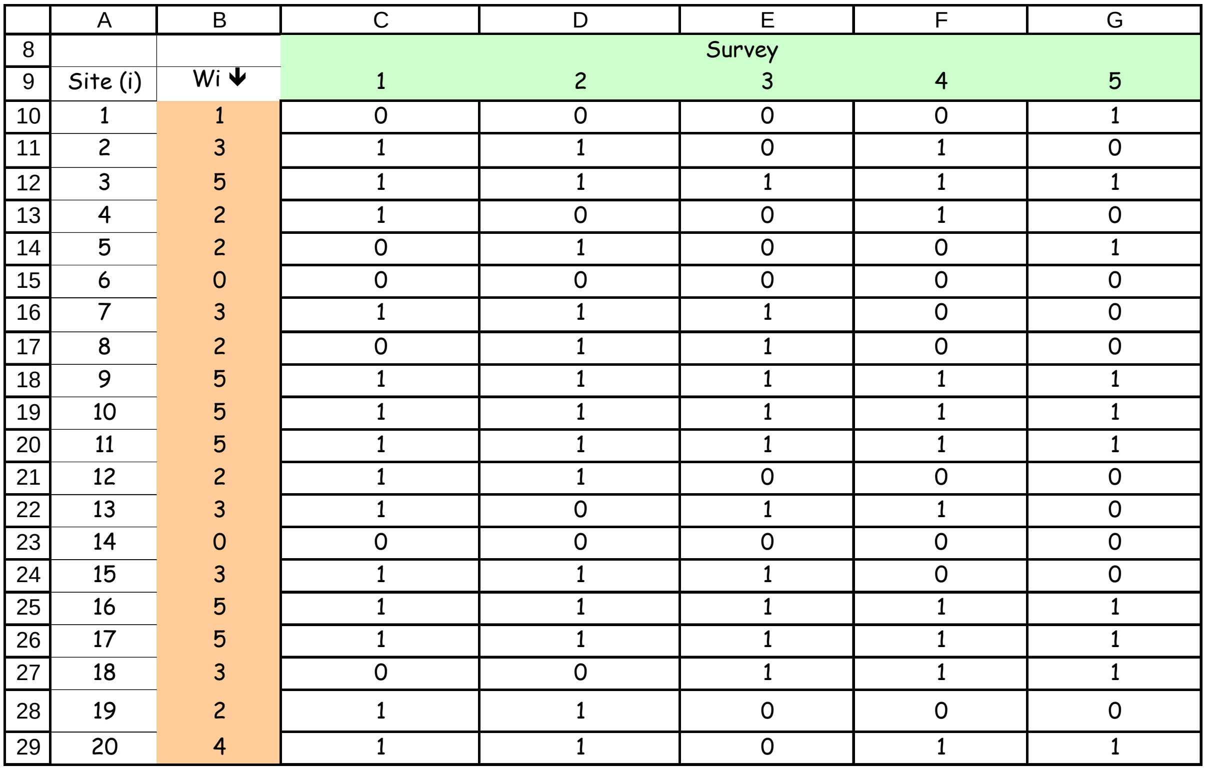
The big Π is telling you to take the product of the terms to the right for each site i from i = 1 to R. This is the product of all of the likelihoods for each site. This product is the likelihood of seeing this collection of w_i values for the whole survey area.

Since we are using the Poisson distribution of k to stand in for Ni, we now need to estimate lambda for this distribution. N_i has been removed from the formula. If we can estimate r and lambda from the data, we can then derive N. We will use Excel to find those combinations of r and lambda that maximize the overall likelihood. That's why you didn't need to worry about the "given r" and "given lambda" stuff before. Excel will just plug in values for these parameters and then tell us the values for each that maximize the overall likelihood.

That's it! Once you estimate r and lambda, you can calculate an estimate of N (study area abundance) and psi (the probability of occupancy). Let's go to the spreadsheets and see it work.

THE ROYLE-NICHOLS SPREADSHEET MODEL INPUTS

The table labeled "Survey" shows your detection data.

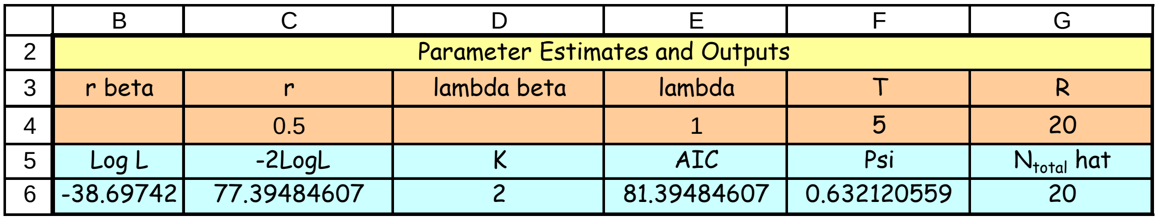


	A	B	C	D	E	F	G
8			Survey				
9	Site (i)	Wi ↓	1	2	3	4	5
10	1	1	0	0	0	0	1
11	2	3	1	1	0	1	0
12	3	5	1	1	1	1	1
13	4	2	1	0	0	1	0
14	5	2	0	1	0	0	1
15	6	0	0	0	0	0	0
16	7	3	1	1	1	0	0
17	8	2	0	1	1	0	0
18	9	5	1	1	1	1	1
19	10	5	1	1	1	1	1
20	11	5	1	1	1	1	1
21	12	2	1	1	0	0	0
22	13	3	1	0	1	1	0
23	14	0	0	0	0	0	0
24	15	3	1	1	1	0	0
25	16	5	1	1	1	1	1
26	17	5	1	1	1	1	1
27	18	3	0	0	1	1	1
28	19	2	1	1	0	0	0
29	20	4	1	1	0	1	1

Above is a picture of results from all 20 sites. The 20 sites are listed in the column on the left and the 5 periods run left to right. The first site had one detection, which occurred in the last survey (00001). The second site had detections in periods 1, 2, and 4 only. In the column "Wi" (B10:B29) are the total detections, w_i, for each site. Believe it or not, that's basically it in terms of data entry.

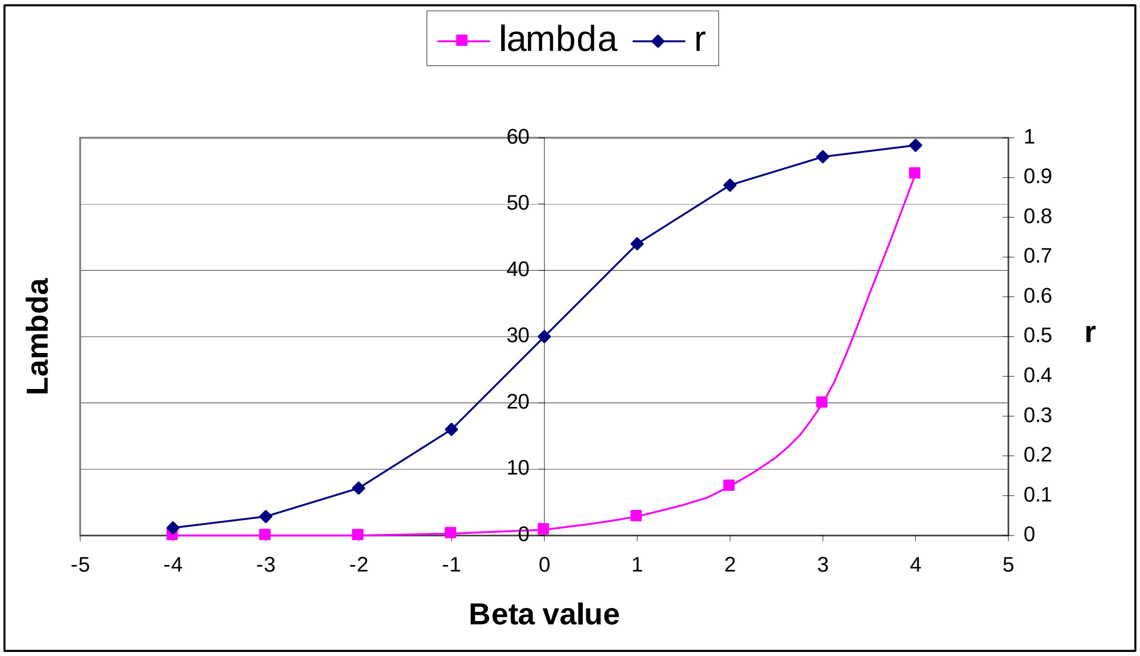
THE ROYLE-NICHOLS SPREADSHEET MODEL OUTPUTS

OK, now let's look at the outputs that will be generated by the model:



	B	C	D	E	F	G
2	Parameter Estimates and Outputs					
3	r beta	r	lambda beta	lambda	T	R
4		0.5		1	5	20
5	Log L	-2LogL	K	AIC	Psi	N_{total} hat
6	-38.69742	77.39484607	2	81.39484607	0.632120559	20

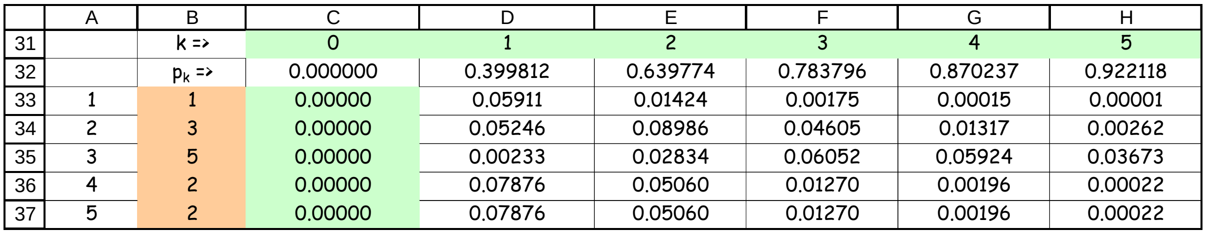
At the top of the sheet is a table titled, "Parameter Estimates and Outputs" (C2:G6). Remember that the primary goal is to estimate r and lambda. Hopefully, you remember that r is the species inherent detection probability (named r_ in the spreadsheet; click on cell C4 and the name "r_" will appear to the left of the formula bar), and that lambda is the parameter from the Poisson distribution that describes the mean abundance of animals across the sites. These are the two main parameters to be estimated in this model, and Solver will find them. But Solver won't find these directly…instead it will work on the betas that are linked to these estimates. As a very quick refresher, r is a probability that is bounded between 0 and 1, while lambda is a positive integer. If we plan to do some linear modeling (that is, constrain r or lambda to be a function of predictor variables, such as habitat, time of year, etc. within the model itself), we need to unbound these parameters so that they range from plus infinity to minus infinity. To achieve this, we use a logit transformation for r (which has the form exp(beta)/(1+exp(beta)) and we use the log transformation for lambda (which has the form exp(beta)). Thus, Solver will find a beta for r (cell B4) and a beta for lambda (cell D4), and then will back-transform these betas into a probability (r; cell C4) or into a positive integer (lambda; cell D4). The picture below shows how this works. On the x-axis are possible beta values. The transformed lambda values associated with each beta are shown in the squares (center axis), while the transformed r values associated with each beta are shown in the diamonds (right axis).



Note that, for lambda, beta values <0 correspond to lambda values close to 0. Note that, for r, beta values < -4 correspond to r = 0 while beta values >4 correspond to r = 1. T is the number of repeated visits and the value of T, cell F4, is named “t” in the spreadsheet. R is the total number of sites in the survey and is named _R in the spreadsheet (cell G4). The primary outputs of the model are given in the blue-shaded cells. In cell B6 is the Log Likelihood. This is the log of the total likelihood for all sites combined. We will estimate r and lambda by maximizing this cell. In cell C6 is the -2*Log Likelihood. K (cell D6) is the number of parameters being estimated (namely, r and λ) and is also used in calculating AIC. AIC is calculated in cell E6 as $-2\text{Log}_e L + 2K$. Psi (cell F6) is the probability of occupancy for a given site. It is derived from the Poisson function for the given lambda—the probability that a site is occupied is 1 minus the Poisson probability that the abundance is 0. N-hat is the estimated total abundance (cell G6). N-hat is derived, and is estimated as lambda*R, the mean site abundance times the number of sites. We'll revisit these outputs soon.

THE LIKELIHOOD FOR SITES, ONE AT A TIME

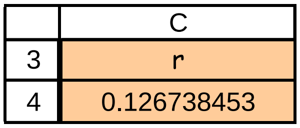
OK, now let's get to the analytical meat of the spreadsheet.



	A	B	C	D	E	F	G	H
31		k =>	0	1	2	3	4	5
32		p_k =>	0.000000	0.399812	0.639774	0.783796	0.870237	0.922118
33	1	1	0.00000	0.05911	0.01424	0.00175	0.00015	0.00001
34	2	3	0.00000	0.05246	0.08986	0.04605	0.01317	0.00262
35	3	5	0.00000	0.00233	0.02834	0.06052	0.05924	0.03673
36	4	2	0.00000	0.07876	0.05060	0.01270	0.00196	0.00022
37	5	2	0.00000	0.07876	0.05060	0.01270	0.00196	0.00022

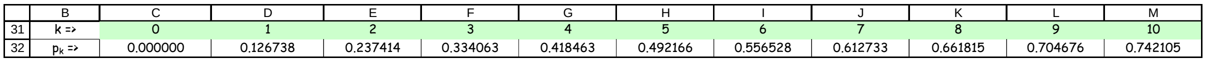
The table, "Likelihood w_i" (A30:BC53), is where we calculate the likelihood of our data, <u>given</u> r and lambda. In this spreadsheet, k ranges from 0 to 50 (row 31, green cells), so we are considering a mixture of 51 possible abundance values, k. For any given k, the site detection probability p_k is computed in row 32 with the formula =1-(1-r_)^k. Click on cell C32 and you should see the formula =1-(1-r_)^C31. Excel returns a 0 here because 1-(any number raised to the 0) is 0. This is good because if k = 0, the actual abundance is 0 and so the probability of detecting any animals should be 0.

Let's look at this from another angle. Suppose we enter the following estimates for r:



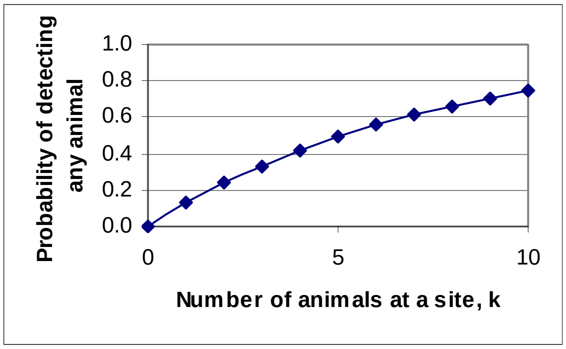
	C
3	r
4	0.126738453

Given this r, the probability of detecting 0, 1, 2, 3, …10 animals is computed in row 32:

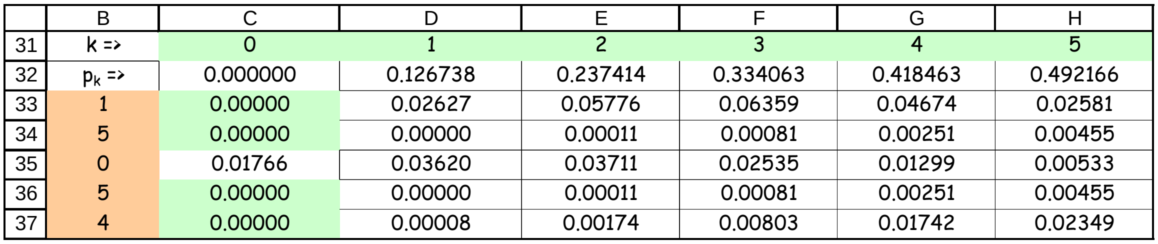


	B	C	D	E	F	G	H	I	J	K	L	M
31	k =>	0	1	2	3	4	5	6	7	8	9	10
32	p_k =>	0.000000	0.126738	0.237414	0.334063	0.418463	0.492166	0.556528	0.612733	0.661815	0.704676	0.742105

A graph of these values is also shown on the spreadsheet:



So, we now have estimates of p_k for each and every value of k. Now we get to the fun part…computing the likelihood of observing w_i detections at each site. In the diagram below you can see the likelihoods for the first five sites across values of k from 0 to 5.



	B	C	D	E	F	G	H
31	k =>	0	1	2	3	4	5
32	p_k =>	0.000000	0.126738	0.237414	0.334063	0.418463	0.492166
33	1	0.00000	0.02627	0.05776	0.06359	0.04674	0.02581
34	5	0.00000	0.00000	0.00011	0.00081	0.00251	0.00455
35	0	0.01766	0.03620	0.03711	0.02535	0.01299	0.00533
36	5	0.00000	0.00000	0.00011	0.00081	0.00251	0.00455
37	4	0.00000	0.00008	0.00174	0.00803	0.01742	0.02349

Each site is computed on a single row, and consists of the raw data (w_i; shaded orange) and the binomial and Poisson mixture: that is, the probability of observing w_i animals at the site, given k and p_k, multiplied by the Poisson probability that are k animals at the site. Notice that the orange column in this table (B33:B52) is identical to the orange column in the Survey table (B10:B29). These are the w_i values.

It's easiest to walk through a few specific examples so that you can see what's going on. Click on cell C33 and you should see the formula =IF(B33=0,1,0)*POISSON($C$31,lambda,FALSE). What does this do? It doesn't look like the equation:

$$L(w_i \mid N_i = k) = \sum_{k=0}^{K} \binom{T}{w_i} p_k^{w_i} (1 - p_k)^{T - w_i} \, f_k$$

Well, row C corresponds to the mixture: k = 0, p_k = 0. This is an odd-ball mixture because you would get Excel errors if you entered the above equation. When a site has no animals (k = 0), the probability of detecting 0 animals is 1, and the probability of detecting any animals is 0. So the first part of the formula in cell C33, =IF(B33=0,1,0), essentially takes care of the term p_k^{wi} $(1-p_k)^{T-wi}$ in the equation above. This result is then multiplied by the term POISSON($C$31,lambda,FALSE), which is the probability that 0 animals occur at a site, given lambda. That does it for the first mixture, where k = 0. This part wasn't obvious at first but with Andy Royle's generous help and some attitude adjustment from the Program PRESENCE help files, we were able to get this part of the model to work.

Now let's look at the next mixture for site 1: k = 1. Click on cell D33 and you should see the formula:

=BINOMDIST($B33,t,D$32,FALSE)*POISSON(D$31,lambda,FALSE),

$$L(w_i \mid N_i = k) = \sum_{k=0}^{K} \binom{T}{w_i} p_k^{w_i} (1-p_k)^{T-w_i} f_k$$

which describes the right hand side of the likelihood function:

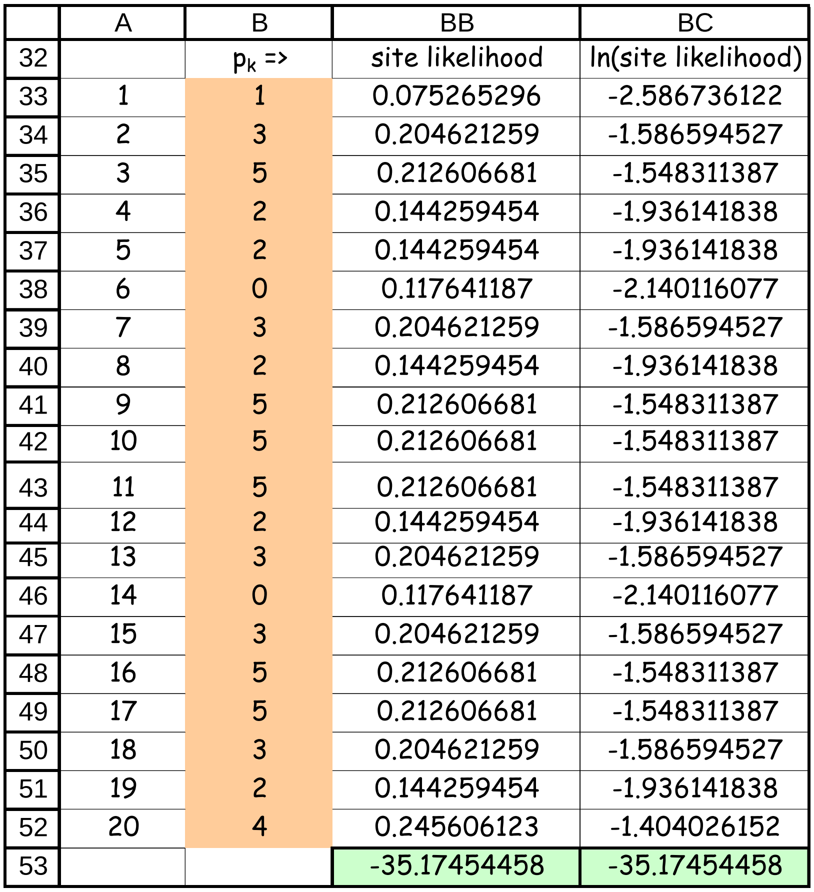
This is the probability mixture for k = 1…..it is a binomial probability (in red type) multiplied by a Poisson probability (in blue type). When k = 1, we first compute p_k as 1-(1-r)^1 (cell D32). Knowing k and p_k for this mixture, we now compute binomial probability of detecting w_i animals at site 1 with the binomial equation BINOMDIST($B33,t,D$32,FALSE), and then multiply this by the probability that the actual abundance at site 1 was really 1, given lambda POISSON(D$31,lambda,FALSE). Make sense? This formula is copied across for the other 49 mixtures for that site. The site likelihood for site 1

$$L(w_i \mid N_i = k) = \sum_{k=0}^{K} \binom{T}{w_i} p_k{}^{w_i} (1 - p_k)^{T-w_i} \; f_k$$

is computed in cell BB33 by adding the 51 k-based results together. If you've done the CJS models, the result is analogous to an encounter history probability for the site. Cell BC33 is the natural log of the site likelihood. Taking the natural log of a likelihood is a common practice to simplify calculations.

We then repeat this process for the other sites. So the likelihood equation for each site consists of 51 entries that are added together, and this happens for all 20 (R = 20) sites.

The end result is the likelihood and log likelihood for each of the 20 sites:



	A	B	BB	BC
32		p_k =>	site likelihood	ln(site likelihood)
33	1	1	0.075265296	-2.586736122
34	2	3	0.204621259	-1.586594527
35	3	5	0.212606681	-1.548311387
36	4	2	0.144259454	-1.936141838
37	5	2	0.144259454	-1.936141838
38	6	0	0.117641187	-2.140116077
39	7	3	0.204621259	-1.586594527
40	8	2	0.144259454	-1.936141838
41	9	5	0.212606681	-1.548311387
42	10	5	0.212606681	-1.548311387
43	11	5	0.212606681	-1.548311387
44	12	2	0.144259454	-1.936141838
45	13	3	0.204621259	-1.586594527
46	14	0	0.117641187	-2.140116077
47	15	3	0.204621259	-1.586594527
48	16	5	0.212606681	-1.548311387
49	17	5	0.212606681	-1.548311387
50	18	3	0.204621259	-1.586594527
51	19	2	0.144259454	-1.936141838
52	20	4	0.245606123	-1.404026152
53			-35.17454458	-35.17454458

Notice that these values change when you change r and lambda (cells C4:D4).

THE FULL LIKELIHOOD

The full likelihood (across R sites) for the entire study area is computed as:

$$L(w) = \prod_{i=1}^{R} \{ \sum_{k=0}^{K} \binom{T}{w_i} p_k^{\,wi} (1 - p_k)^{T - w_i} \; f_k \}$$

This can be done either by taking the natural log of the product of the site level likelihoods together (cell BB53) or by adding the site level log likelihoods together (cell BC53). We will maximize the log likelihood to estimate the parameters, r and λ, for our data across all sites.

Look carefully at the likelihoods (BB33:BB52) and notice that some are equal to others. Seeing that the site likelihoods are the same for these two sites tells us what? It tells us that they have the same w_i. All of the other parameters and variables are the same for calculating the likelihoods of the sites. Differences in the site likelihoods are caused by differences in w_i

RUNNING THE MODEL

The spreadsheet is set up to estimate r and lambda from the raw data in the Survey table (cells C10:G29). To do this, you run the Excel function, Solver, which we'll do in a moment. Solver will find the maximum log Likelihood by changing the values of r and lambda.

Before we begin, do two things. First, make sure the inputs on your spreadsheet match those shown below:

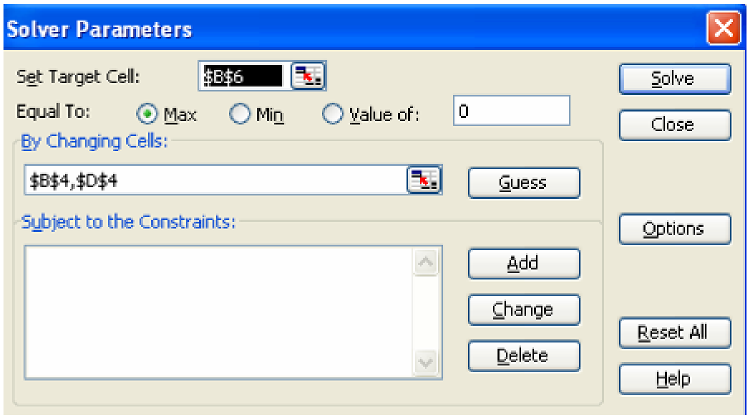
	C	D	E	F	G
10	0	1	0	0	0
11	1	1	1	1	1
12	0	0	0	0	0
13	1	1	1	1	1
14	1	1	1	0	1
15	0	1	0	0	0
16	0	0	1	1	0
17	1	1	1	1	1
18	0	0	0	0	0
19	1	1	1	1	1
20	0	1	1	1	0
21	0	0	0	0	0
22	1	0	0	1	0
23	1	0	1	1	1
24	1	1	1	1	0
25	1	0	1	1	1
26	1	0	1	1	1
27	1	0	1	0	1
28	0	1	1	1	1
29	1	1	1	1	1

Second, before running Solver, click the "Random Starters" button (around cell I2). Clicking this button puts copies random betas from cells I5:J6 and pastes them into the "r beta" and "lambda beta" cells (B4,D4). With some datasets we've had trouble getting Solver to run properly without "seeding" these cells.

So, hit "Random Starters" and you should see the r and lambda cells change. Look at the line graph up below the "Random Starters" as you hit this button a few times. The graph shows k (potential abundance) on the x-axis and p_k on the y-axis. Remember that p_k is a function of r, so the graph should change as r changes. Notice the steepness of the first portion of the curve when r is close to 1 (indicating the species intrinsically has a high detection probability). When r is close to 0, the slope of the first part of the line is very flat. In this case, the species is intrinsically difficult to detect, and there must be a lot of animals present at the site for site detection probability to be somewhat reasonable. For now, we are just looking at random betas and their associated r and lambda estimates…these are not the maximized estimates. Once we have our maximized estimates, though, we will refer back to this graph.

MAXIMIZING THE LIKELIHOOD

Okay, you have your random starters and you are ready to solve for the maximum likelihood estimates (MLE) of r and lambda. Go to Tools on the top menu bar and select Solver. When the Solver window opens set the target cell as B6, the Log Likelihood. You want Solver to find the maximum of the target cell by changing cells B4 and D4:



Solver Parameters

Set Target Cell: $B$6

Equal To: ● Max ○ Min ○ Value of: 0

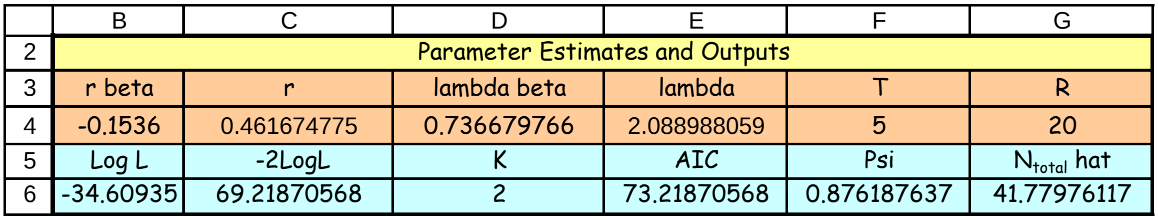
By Changing Cells: $B$4,$D$4

Subject to the Constraints:

Once that is all set, hit Solve and Solver will do its thing. If all goes well, you will get a window saying Solver converged on a solution. Accept this.

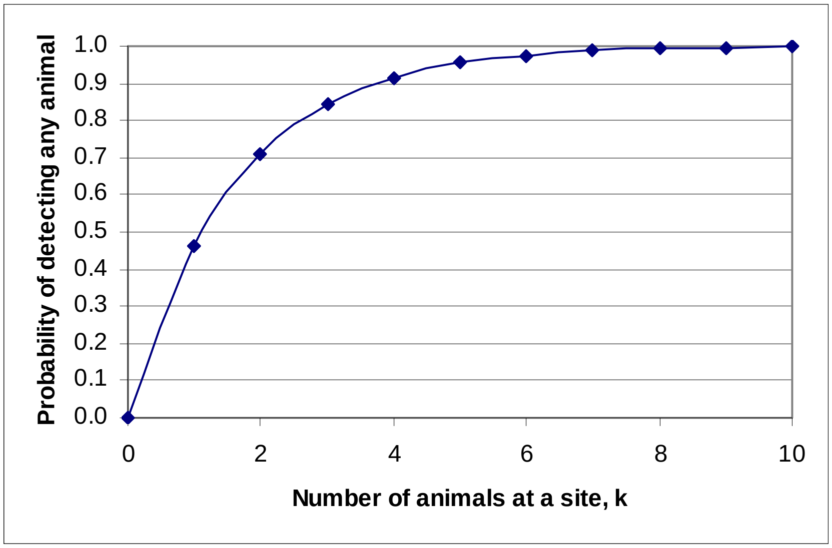
INTERPRETING THE MODEL OUTPUT

Now in the uppermost table you will have the MLE (r, lambda) plus the estimate of N derived from them.



	B	C	D	E	F	G
2	Parameter Estimates and Outputs					
3	r beta	r	lambda beta	lambda	T	R
4	-0.1536	0.461674775	0.736679766	2.088988059	5	20
5	Log L	-2LogL	K	AIC	Psi	N_{total} hat
6	-34.60935	69.21870568	2	73.21870568	0.876187637	41.77976117

For this dataset, r is estimated at 0.4617, and lambda was estimated at 2.0890. Given these parameters, the relationship between the number of animals at a site and site detection probability is shown below.



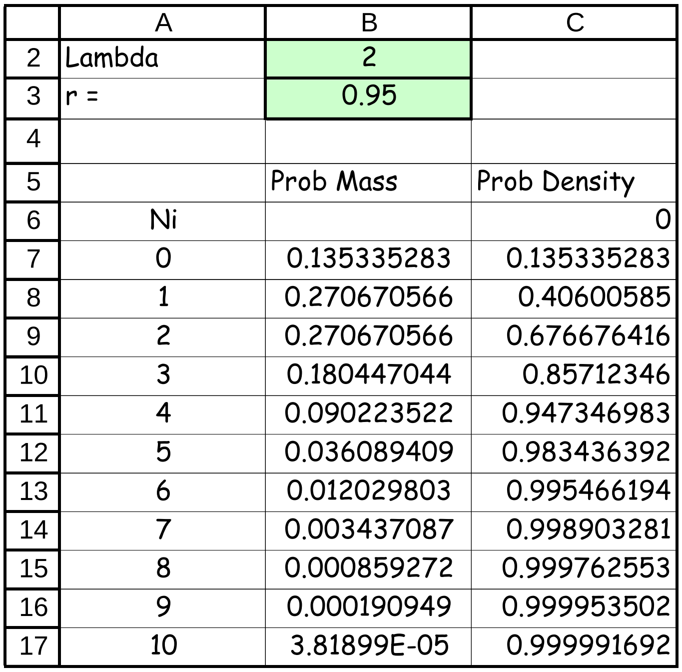
If there is only one animal present at a site, then the probability of detecting the species at that site is 0.46. If there are two animals present at a site, then the probability of detecting the species at that site is 0.71. You can find these values as the p_k for k = 1 and 2 (cells D32:E32).

N hat (cell G6) is computed as lambda*R. This is what we were after in the first place: the abundance of animals in our study sites, given R sites and T surveys. AIC is computed as $-2\text{Log}_e L$ *2*the number of parameters estimated in the model. In this model, there are two estimated parameters, r and lambda. Psi is the probability that a site is occupied. Now that we know lambda = 2.0890, we can compute the probability of getting 0 animals as POISSON(0,2.0890,FALSE), and 1 minus this is the probability of not getting a 0 (Psi). Those are the basic outputs in PRESENCE. We'll run this in PRESENCE soon.

SIMULATING DATA

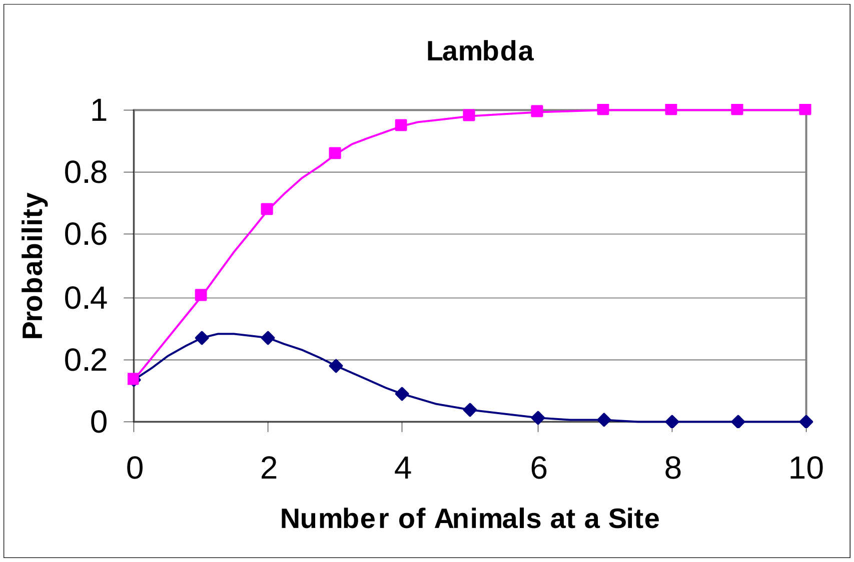
Before going on to PRESENCE, let's look at how the raw data are simulated. It quite simply takes the model and turns it inside out to generate the survey results. First a Poisson distribution is used to generate N_i for each site. Then you "flip a coin" a number of times for each visit to each site to see if any animals were detected.

Open the Simulate Data sheet. You can see the Poisson distribution function set up along the left side of the sheet in columns A:C.



	A	B	C
2	Lambda	2	
3	r =	0.95	
4			
5		Prob Mass	Prob Density
6	Ni		0
7	0	0.135335283	0.135335283
8	1	0.270670566	0.40600585
9	2	0.270670566	0.676676416
10	3	0.180447044	0.85712346
11	4	0.090223522	0.947346983
12	5	0.036089409	0.983436392
13	6	0.012029803	0.995466194
14	7	0.003437087	0.998903281
15	8	0.000859272	0.999762553
16	9	0.000190949	0.999953502
17	10	3.81899E-05	0.999991692

First, enter a lambda value in cell B2. This is the mean abundance of the population of interest. We entered 2, indicating that we will be simulating data for study sites in which the average abundance of animals across sites is 2. (We just saw that Solver found this lambda). Cells A7:A57 shows possible site abundances ranging from 0 to 50. Cells B7:B57 show the Poisson individual probabilities pertaining to each N_i and the value of lambda in cell B2. The formula in cell B7 is =POISSON(A7,$B$2,FALSE). This formula returns the probability that a site will contain 0 animals, given the lambda value in cell B2. Cells C7:C57 show the Poisson cumulative probabilities pertaining to each N_i and the value of lambda in cell B2. The formula returns the probability that a site will contain at least 0 animals, given the lambda value in cell B2. As you can see, the formulae are copied down the columns, providing the cumulative and mass probability functions:



In the table labeled Simulate Data, we first assign an abundance (N_i) to each site (cells E8:E27)

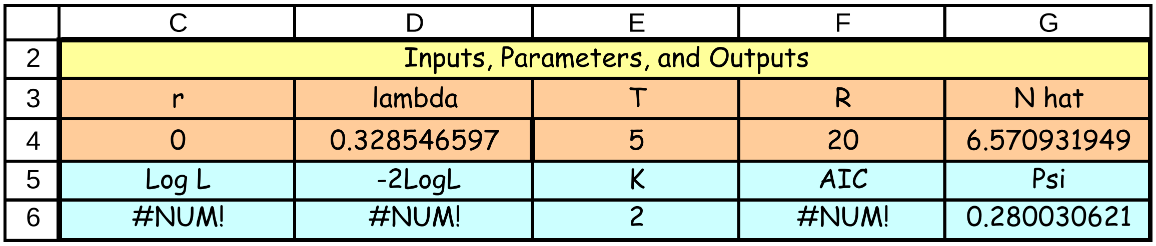
	D	E	F	G	H	I	J
4		**Simulate Data**					
5							
6					Survey		
7	Site	N	1	2	3	4	5
8	1	5	1	1	1	1	1
9	2	0	0	0	0	0	0
10	3	1	1	0	1	0	1
11	4	3	1	1	1	0	1
12	5	2	1	0	1	1	0
13	6	2	1	0	1	1	0
14	7	4	1	1	1	1	1
15	8	3	1	1	1	0	1
16	9	2	0	1	0	1	0
17	10	3	1	1	1	1	0
18	11	1	0	1	0	0	1
19	12	3	1	0	1	1	1
20	13	1	1	0	0	1	1
21	14	1	1	1	1	0	0
22	15	1	1	0	0	0	0
23	16	2	1	0	1	1	1
24	17	2	0	1	0	1	1
25	18	1	0	0	0	1	0
26	19	3	1	1	0	0	1
27	20	2	0	1	1	1	1

We do this by generating a random number (between 0 and 1) in each cell E8:E27 and comparing it to the cumulative Poisson probability distribution you just created. The site gets the N_i corresponding to the cumulative probability that the random number is closest to without going over. For instance, the equation in cell E8 is =LOOKUP(RAND(),$C$6:$C$57,$A$7:$A$57). This says look up a random number in the column of cumulative probabilities (C6:C57). Then, return the value from the column of abundances (A7:A57) for the interval where the random number falls. This function works because the cumulative Poisson probabilities are ordered from 0 to 1, and LOOKUP does not need to find an exact match for the random number. This formula is copied down for each site in cells E8:E27.

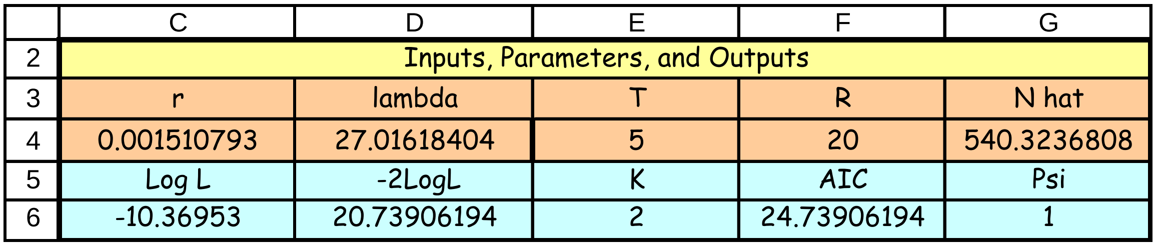
Now that we have assigned N_i to each site, we need to find out if we detect anything in each of our surveys. In other words, we'll now generate detection non-detection data for the site across the T surveys. Given the N_i, we compare another random number to the site detection probability based on r (cell B3). Here, we know N_i so we can directly calculate 1-the probability of missing all N_i animals at the site on that visit, $1-(1-r)^{Ni}$. The equation in cell F8 is =IF(RAND()<(1-((1-$B$3)^$E8)),1,0). This says: if the random number is less than the probability $1-(1-r)^{Ni}$, then a detection results, if not, a non-detection results. This is done in every survey cell (F8:J27). As you can see, the data we just explored in the Royle-Nichols spreadsheet exercise were simulated for lambda = 2 and r = 0.5. Solver estimated these parameters as 2.09 and 0.462, respectively. These estimates may or may not be biased because the data were, after all, simulated with stochasticity.

SOME ADDITIONAL THINGS TO PONDER

This spreadsheet model is sensitive to very low and very high values of r and lambda, especially r. This spreadsheet version of the model works well for 0.3 < r < 0.7. Outside of that, Solver may fail to converge. This often results in an error message and a parameter estimate at a limit, like r = 1. Even if Solver estimates parameters, they may be way off and inconsistent. For example, for a simulated dataset where r = 0.01 and lambda = 1, the following figures are from two runs of the exact same survey data but with different random starters.



	C	D	E	F	G
2	Inputs, Parameters, and Outputs				
3	r	lambda	T	R	N hat
4	0	0.328546597	5	20	6.570931949
5	Log L	-2LogL	K	AIC	Psi
6	#NUM!	#NUM!	2	#NUM!	0.280030621



	C	D	E	F	G
2	Inputs, Parameters, and Outputs				
3	r	lambda	T	R	N hat
4	0.001510793	27.01618404	5	20	540.3236808
5	Log L	-2LogL	K	AIC	Psi
6	-10.36953	20.73906194	2	24.73906194	1

Recall that r is the probability of detecting our target species and lambda is the mean abundance of that species across the sites. Data with a high r and lambda means lots of animals and lots of detections. The survey returns mostly 1's with few 0's. It becomes hard for the model to distinguish whether r or lambda is driving the pattern. Conversely, data with low r and low lambda result in surveys with mostly 0's. There is nothing for the model to work with here, so it fails to estimate parameters.

For more moderate, but slightly high and low, values of r, such as 0.8 and 0.3, you sometimes get estimates with Solver and other times you can't. The difference is how close the random seed is to the true value when you fire up Solver. Recall from Exercise 1 that a likelihood surface can be a complex surface and we are looking for the very top of this surface. The parameter values associated with the peak of the surface are the maximum likelihood estimates, telling us the best estimated values of the parameters. Solver alters the parameter estimates and monitors the resulting likelihood (or log-likelihood if you prefer). It "watches" the likelihood increase for changing values of the parameters and when the likelihood starts to decrease, Solver knows it has found the maximum likelihood. In many cases, there is a single maximum peak on the likelihood surface, and Solver can find it. But in other situations the likelihood surface has lots of little bumps and wiggles which are local maxima and minima, fine-scale highs and lows. The highest point over the whole profile is called the global maximum. In our case, unless the random seed is near the global maximum, Solver will stop when it finds any maximum—it doesn't know to look for the global one. So it stops when it finds whichever maximum is closest to where it began searching, the random starter. This will return poor estimates since they don't necessarily maximize the likelihood overall.

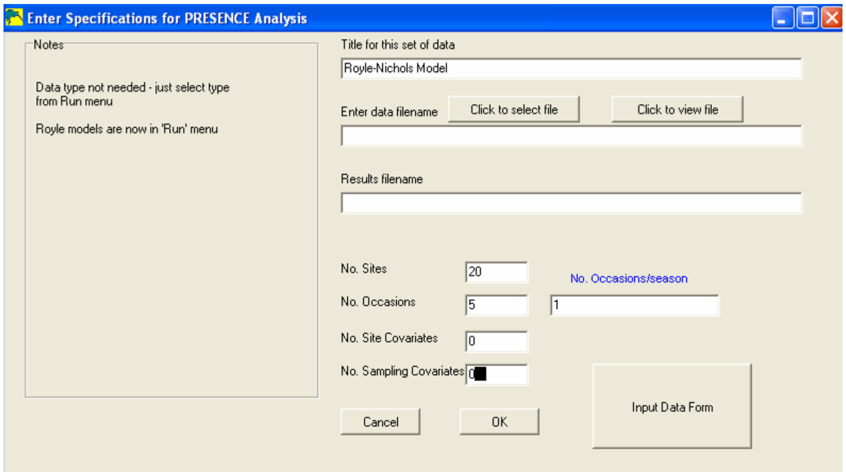
The instability in our estimates is not completely inherent in the spreadsheet model. One of the limitations here is the size of the survey. We could improve this spreadsheet version by adding more sites, but the improvement is not perfect. Royle and Nichols (2003) describe $r > 0.15$ as the lower limit for good estimation with this model, even when simulating a large number of sites ($R = 100$).

ROYLE-NICHOLS ABUNDANCE INDUCED HETEROGENEITY ANALYSIS IN PROGRAM PRESENCE

Hopefully you've worked through the spreadsheet Royle-Nichols Model by now. If you haven't done so, complete the spreadsheet exercise now.

GETTING STARTED

Open PRESENCE, and click File | New Project to begin a brand new data analysis.



Data type not needed - just select type from Run menu

Royle models are now in 'Run' menu

Title for this set of data: Royle-Nichols Model

No. Sites: 20

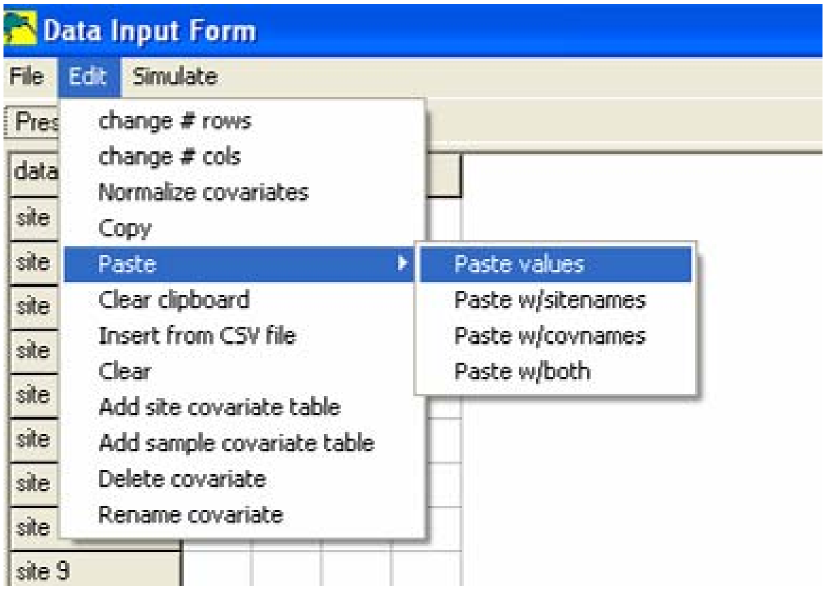
No. Occasions: 5

No. Occasions/season: 1

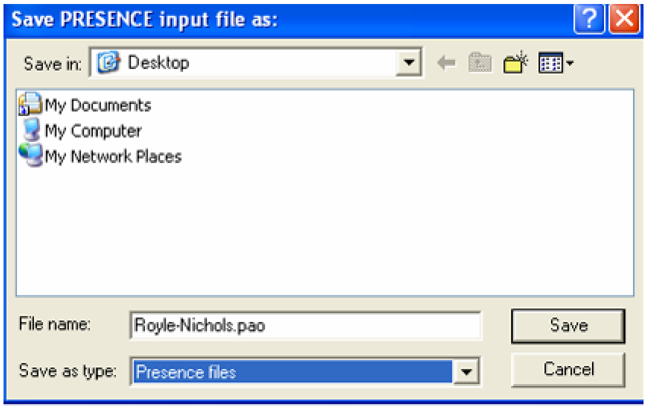
No. Site Covariates: 0

No. Sampling Covariates: 0

Enter a title for this set of data (e.g., Royle-Nichols Model). Enter 20 for the number of sites, and 5 for the No. Occasions, and then click on the Input Data Form button. Copy cells C10:G29, and then click on the first, blank data cell and go to Edit | Paste | Paste Values:



Then go to File | Save As and enter a file name for your new PRESENCE input file, and store it somewhere where you can retrieve it easily:

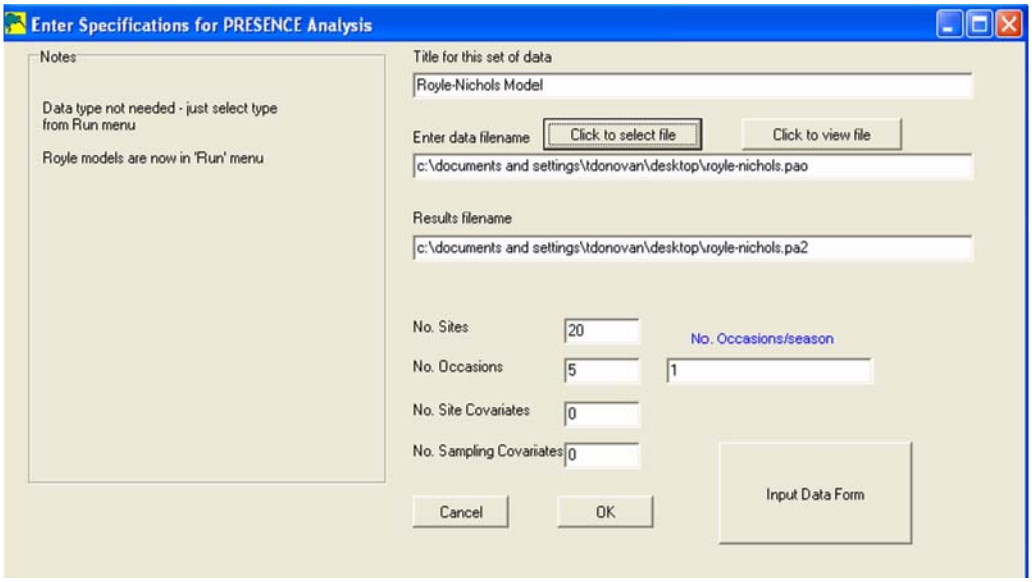


Save in: Desktop

File name: Royle-Nichols.pao

Save as type: Presence files

Now, return to the Enter Specifications form, click the button labeled "Click to Select File" and browse to your freshly created input file:



Notes

Data type not needed - just select type from Run menu

Royle models are now in 'Run' menu

Title for this set of data: Royle-Nichols Model

Enter data filename: c:\documents and settings\tdonovan\desktop\royle-nichols.pao

Results filename: c:\documents and settings\tdonovan\desktop\royle-nichols.pa2

No. Sites: 20

No. Occasions: 5

No. Occasions/season: 1

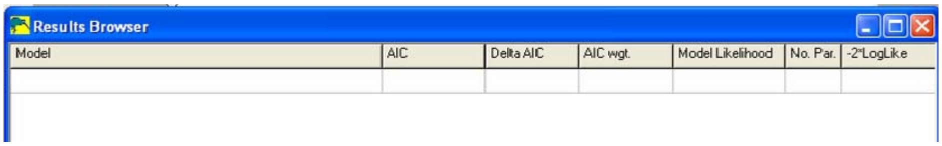
No. Site Covariates: 0

No. Sampling Covariates: 0

Press OK and you're ready to run your first (and only) model.

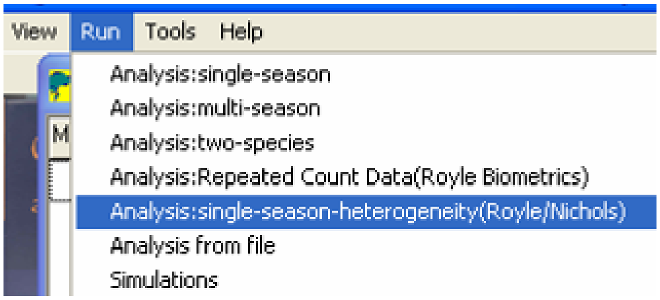
RUNNING THE ROYLE-NICHOLS MODEL

You should get the main PRESENCE page with a results browser over it. It looks a lot like the results browser in MARK.

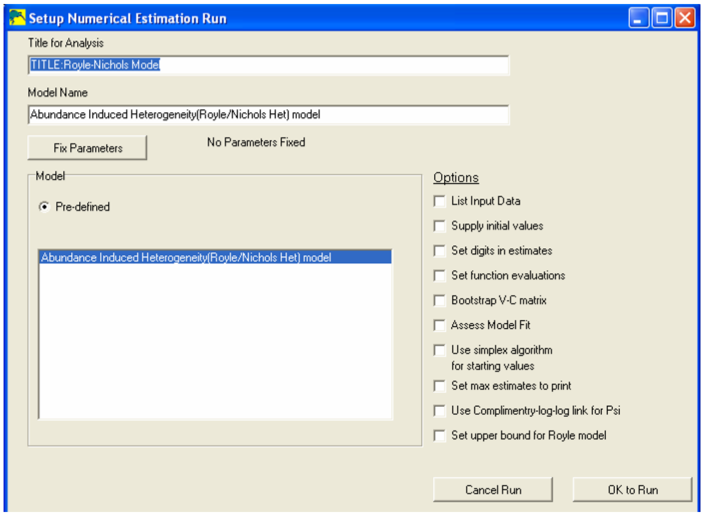


Model	AIC	Delta AIC	AIC wgt.	Model Likelihood	No. Par.	-2*LogLike

The results browser is empty since we haven't run any models yet. Select Run from the upper menu bar and on the drop-down menu, select the "Analysis: single-season-heterogeneity(Royle/Nichols)" model.



You'll get a new window where you can name the analysis, name the model, and customize the running of the model. Note that, at the moment, there is only one option for running this model, which is the pre-defined model where lambda and r will be estimated. The title and model name shown are the default names. You can change these if you want to. Then, click "OK to Run".



Title for Analysis: TITLE:Royle-Nichols Model

Model Name: Abundance Induced Heterogeneity(Royle/Nichols Het) model

No Parameters Fixed

Model

● Pre-defined

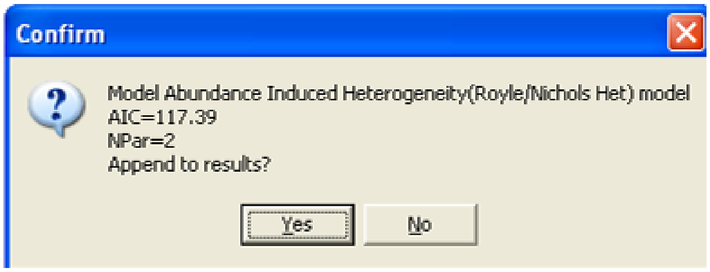
Abundance Induced Heterogeneity(Royle/Nichols Het) model

Options

☐ List Input Data
☐ Supply initial values
☐ Set digits in estimates
☐ Set function evaluations
☐ Bootstrap V-C matrix
☐ Assess Model Fit
☐ Use simplex algorithm for starting values
☐ Set max estimates to print
☐ Use Complimentry-log-log link for Psi
☐ Set upper bound for Royle model

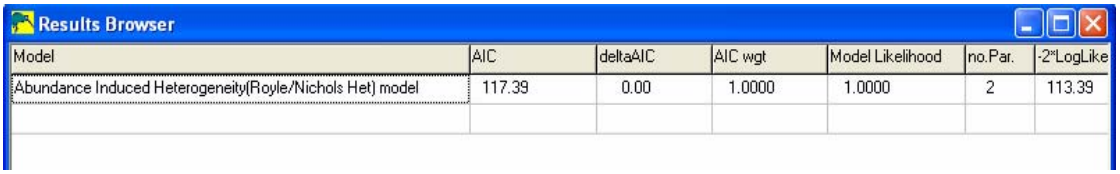
THE ROYLE-NICHOLS OUTPUT

In a moment you are prompted that results have been found and asked if you want to append results to the browser.



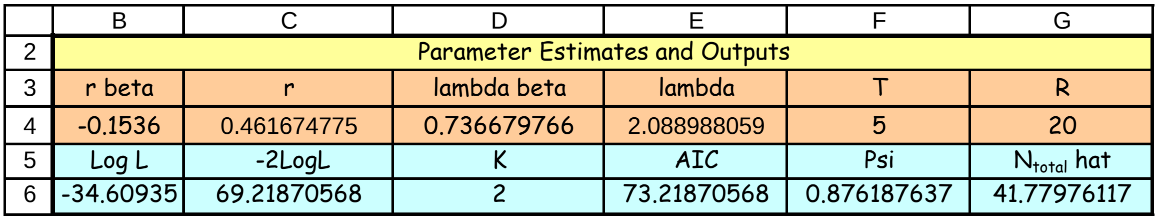
Model Abundance Induced Heterogeneity(Royle/Nichols Het) model
AIC=117.39
NPar=2
Append to results?

Click "yes", and then the Results Browser will appear:



Model	AIC	deltaAIC	AIC wgt	Model Likelihood	no.Par.	-2*LogLike
Abundance Induced Heterogeneity(Royle/Nichols Het) model	117.39	0.00	1.0000	1.0000	2	113.39

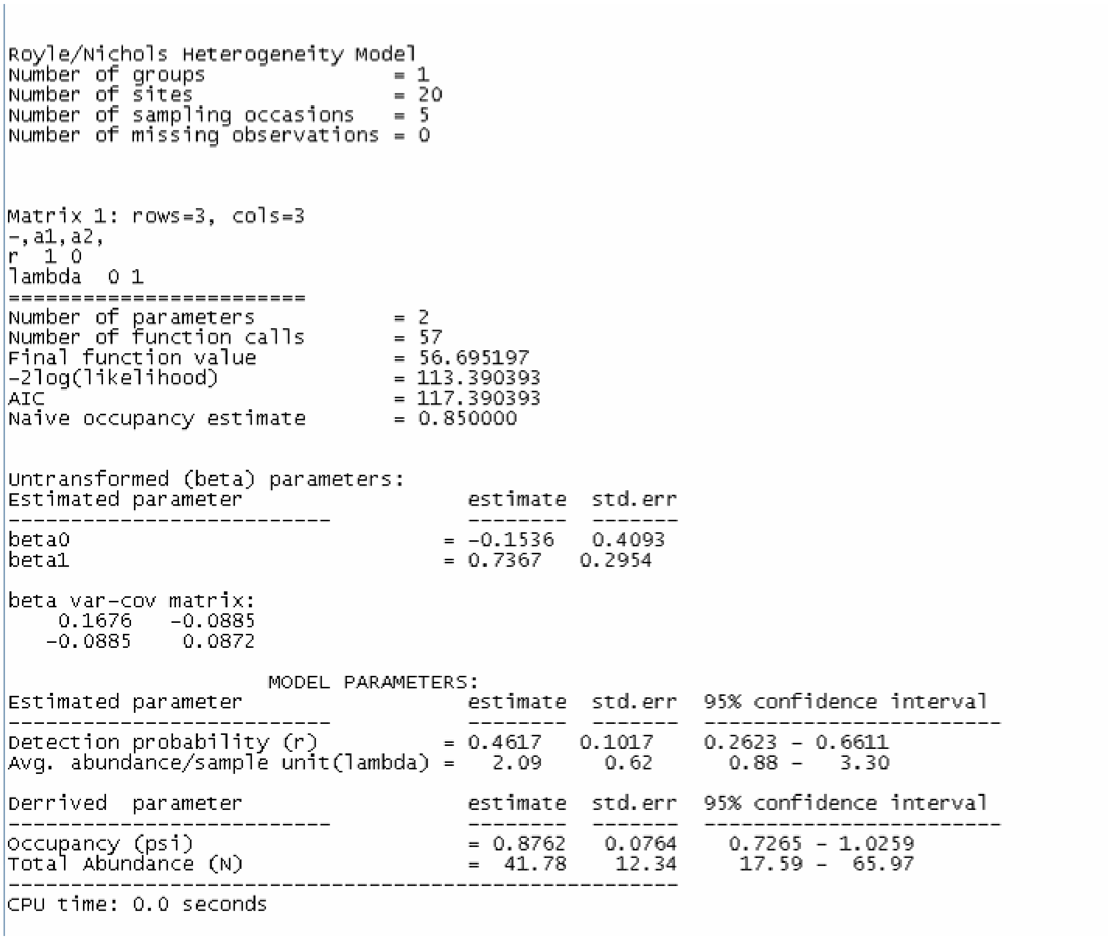
Here are the spreadsheet results for the same data:



	B	C	D	E	F	G
2	Parameter Estimates and Outputs					
3	r beta	r	lambda beta	lambda	T	R
4	-0.1536	0.461674775	0.736679766	2.088988059	5	20
5	Log L	-2LogL	K	AIC	Psi	N_{total} hat
6	-34.60935	69.21870568	2	73.21870568	0.876187637	41.77976117

Right away you should notice that the PRESENCE AIC value doesn’t match our spreadsheet. The difference is due to the fact that PRESENCE does not compute a constant combinatorial term in the binomial portion of the likelihood, which saves some computer time, but doesn't affect the final estimates. Thus, the Log_eL will be different, and hence the AIC scores will be different. However, these differences do not affect inference from the model, and the parameter estimates match.

In the results browser, right click on the model itself and select “view model output”. This will open a page in notepad with the results of the model.



```
Royle/Nichols Heterogeneity Model
Number of groups              = 1
Number of sites               = 20
Number of sampling occasions   = 5
Number of missing observations = 0


Matrix 1: rows=3, cols=3
-,a1,a2,
r  1 0
lambda  0 1
========================
Number of parameters          = 2
Number of function calls       = 57
Final function value           = 56.695197
-2log(likelihood)              = 113.390393
AIC                            = 117.390393
Naive occupancy estimate       = 0.850000


Untransformed (beta) parameters:
Estimated parameter                  estimate  std.err
--------------------------           --------  -------
beta0                              = -0.1536   0.4093
beta1                              = 0.7367   0.2954

beta var-cov matrix:
    0.1676   -0.0885
   -0.0885    0.0872

                     MODEL PARAMETERS:
Estimated parameter                  estimate  std.err  95% confidence interval
--------------------------           --------  -------  ------------------------
Detection probability (r)          = 0.4617   0.1017    0.2623 - 0.6611
Avg. abundance/sample unit(lambda) =   2.09     0.62      0.88 -   3.30

Derrived  parameter                  estimate  std.err  95% confidence interval
--------------------------           --------  -------  ------------------------
Occupancy (psi)                      = 0.8762   0.0764    0.7265 - 1.0259
Total Abundance (N)                  =  41.78    12.34     17.59 -  65.97
------------------------------------------------------
CPU time: 0.0 seconds
```

You should see that the following are correctly estimated in the spreadsheet: r, lambda, psi, and N. PRESENCE also reports the beta estimates and their standard errors, and also the real estimated (r and lambda), their standard errors, and the 95% confidence intervals. As you can see, the confidence intervals are quite large, most likely due to the very small number of sites used in the analysis. The derived parameters, psi and total abundance, also match the spreadsheet, and also have quite large confidence intervals.