



Comparing Groups

Traditionally, capture-recapture analysis was motivated by the desire to estimate parameters such as survival rate, or population size. However, biologists are frequently less interested in the precise numerical value of these parameters than they are in assessing whether differences exist in one or more parameters among different groups of interest (e.g., males versus females, control versus treatments). One of the strengths of SURGE is that it makes comparisons among groups very easy to implement. In fact, as we will see, it involves only slightly more work than the model comparisons within group we saw in Chapter 4.

In this chapter, we will introduce the procedure for using SURGE to test among groups by using a data set from a study of the swift (*Apus apus*), from a 7 year study of 2 different colonies in southern France. These data are found in the examples (file AA.REL). One of the two colonies was believed to be of “poorer” quality than the other colony for a variety of reasons, and the purpose of the study was to determine if these perceived differences between the two colonies (hereafter, P - “poor”, and G - “good”) were reflected in differences in either survival or recapture rate. The data for both the P and G colonies are both in AA.REL - use RELTOSUR (see Chapter 2) to create the SURGE-format files P.SUR and G.SUR, (for “good” and “poor”, respectively).

- In this example, we will analyze the data in terms of the following 2 factors: colony (G or P), and time. Thus, this example is very similar to the one presented in Chapter 4, except that we have added one more factor, colony. As such, the number of possible models is increased from $2^2 = 4$ (Fig. 4.1) to $4^2 = 16$ models (Fig. 5-1) - survival and recapture could vary with colony, time or both. With an increasing number of factors, the number of possible models that may need to be tested increases geometrically. Here we have a 7 year study, considering only 2 primary factors (colony and time), and there are at least 16 possible models to test (in fact, we will see in subsequent chapters there are potentially many more). One of the things that you will quickly realize with capture-recapture analysis is

that it can be time-consuming, given the large number of models you might have to test. Obviously, it will pay to become proficient at using SURGE!

Models	
ϕ_{c*t}, p_{c*t}	ϕ_t, p_{c*t}
ϕ_{c*t}, p_c	ϕ_t, p_c
ϕ_{c*t}, p_t	ϕ_t, p_t
ϕ_{c*t}, p	ϕ_t, p
ϕ_c, p_{c*t}	ϕ, p_{c*t}
ϕ_c, p_c	ϕ, p_c
ϕ_c, p_t	ϕ, p_t
ϕ_c, p	ϕ, p

Fig. 5.1

- First, we should make sure you understand the syntax of the model representations in Fig. 5.1 (which follow the approach recommended in Lebreton *et al.* 1992). Remember, that the subscripts for the two parameters (ϕ and p) reflect the structure of the model. The most general model in Fig. 5.1 is model ϕ_{c*t}, p_{c*t} . The “c*t” subscript means we have a ‘full’ model (for both survival and recapture), including both the main effects (colony and time) and the interaction of the two (i.e., ‘c*t’ = c + t + c.t + error). By ‘interaction’, we are referring to the statistical meaning of the word - that colony and time interact, such that the relationship between survival or recapture and time can differ depending upon the colony (or conversely, the relationship between survival or recapture and colony can differ depending upon the time interval). In Fig. 5.1, this model is the most general, since any of the other models listed can be derived by removing one or

more factors (a simple comparison of the “complexity” of the subscribing for both survival and recapture among the various models will confirm this).



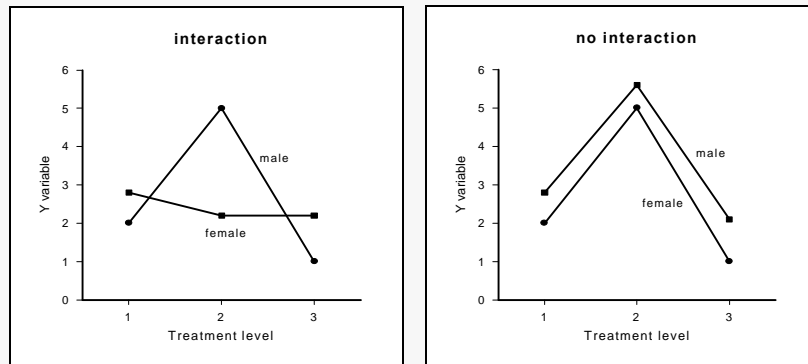
So remind me again what an interaction term is? Well, think back to your basic biometrics classes, where you studied multifactorial designs (either as factorial ANOVA, or analysis of covariance - ANCOVA). Consider a simple 2-factor ANOVA, with factors SEX and TRT (for treatment). Assume there are 2 sexes, and 3 levels of the TRT factor. Thus, written in a linear model context (assuming both effects are fixed treatments), the variate Y_{ijk} is the k th item in the subgroup representing the i th group of SEX and the j th group of treatment TRT. It can be written as:

$$Y_{ijk} = m + a_i + b_j + (ab)_{ij} + e_{ijk}$$

Using a simpler notation, we can also write

$$Y = \text{SEX} + \text{TRT} + \text{SEX}.\text{TRT} + \text{error}$$

The term $(ab)_{ij}$ or equivalently SEX.TR, represents the “interaction” of SEX and TRT - in other words, the magnitude of Y varies as a function of the particular combination of SEX and TRT (lines “cross” statistically - no interactions means lines are either coincident or statistically parallel).



- So, as we saw in the preceding chapter, the basic approach will be to start from the most general model, and using one or more selection criterion, try to find the most parsimonious acceptable model containing the factor of interest (in this case, we are interested in comparing the colonies), and then, using a LRT, formally tests for a difference between the colonies.
- Lebreton *et al.* (1992) begin their analysis of these data with program RELEASE. First, as noted in Chapter 3, the first step in CMR analysis must be testing the GOF of your starting model(s). GOF testing using RELEASE is covered briefly in the Appendix. Second, TEST 1 in RELEASE is an “overall” or “omnibus” test of differences between groups, using the CJS time-dependent model. TEST 1 does not tell you whether the difference occurs in survival or recapture, or both - merely that there is an “overall” difference.
- We can do precisely the same test in SURGE. Can you think of how? Read the preceding paragraph again - a simple overall test for colony differences. In other words, a simultaneous test of a colony effect on both survival and recapture. In model notation, this means we would compare model $\phi_{c,*},p_{c,*}$ with model $\phi_{t,p}$, using a LRT. As we can see, these models are nested (model $\phi_{t,p}$ is nested within model $\phi_{c,*},p_{c,*}$).
- Let’s rewrite this another way, using the simpler notation presented in the box in the preceding column on this page. First for survival, we are comparing $\phi_{c,*}$ with ϕ_t . We could write this as

$$\begin{array}{l} \phi = \text{COLONY} + \text{TIME} + \text{C.T} + \text{error} \\ \text{versus } \phi = \frac{\text{TIME}}{\text{COLONY}} + \text{error} + \text{C.T} \end{array}$$

- In other words, the difference between the two models is the difference in the terms of the two “equations” - in this case, the terms COLONY and the interaction of colony and time, C.T. If the LRT test is significant (in other words, if the differences in the model fits is significantly large, given the change in the number of parameters between the two models), then we interpret this as saying that

COLONY and the interaction of colony and time (C.T) contribute significantly to the variation in survival.

- The same thing applies to recapture rate.

$$\begin{array}{l} p = \text{COLONY} + \text{TIME} + \text{C.T} + \text{error} \\ \text{versus } p = \frac{\text{TIME}}{\text{COLONY}} + \text{C.T} + \text{error} \end{array}$$

- Thus, comparing model ϕ_t, p_t with model ϕ_{c*t}, p_{c*t} is the same test as TEST 1 in RELEASE - is there an *overall* effect of COLONY on variation in survival and recapture rate.
- Let's see how we do this with SURGE.

Model ϕ_{c*t}, p_{c*t} versus model ϕ_t, p_t

- Start program SURGE, and enter the file name you want to direct the results to. For this example, call the file SWIFT1.LST.
- Now, we need to enter the title we want to give to our first analysis. At this point, you should be starting to be familiar with the basic convention we've been following. Since we are testing model $\phi_{c,t}, p_{c,t}$ versus model ϕ_t, p_t , we write "Phi(c*t),p(c*t)". This is our starting model.
- SURGE then asks us for the number of data sets we want to include in our analysis. Previously, we have used SURGE to analyze only one particular data set. However, we are now interested in comparing two colonies - therefore, 2 data sets. As noted on the first page of this chapter, the two data sets are contained in files G.SUR and P.SUR, for the "good" and "poor" colonies, respectively. So, we enter the number 2, and then, when prompted, enter each of the file names in turn. It is a good idea for you to keep track of which data set you enter first (G.SUR or P.SUR).
- Once you've completed the data input screen, you will be presented with the model specification menu for the survival parameter (Fig. 5.2).

```

M* MODEL CHOICE : SURVIVAL PROBABILITIES

M*          AGE DEPENDENCE           = 1
M*          TIME DEPENDENCE          = 2
M*          CONSTANCY OVER AGE AND TIME = 3
M*          USER DEFINED MODEL       = 4
M*          TIME DEPENDENCE, DEP. ON EXT.UAR. = 5
M*          2 AGE CLASSES 1=TIME DEP. 2=TIME DEP. = 6
M*          1=TIME DEP. 2=EXT.UAR. = 7
M*          1=EXT.UAR. 2=TIME DEP. = 8
M*          1=EXT.UAR. 2=EXT.UAR. = 9

M* OPTION FOR DATA SET g.sur ? 2
M* SAME PARAM. VALUES ACROSS DATA SETS ? n
M* SAME PARAM. STRUCTURE ACROSS DATA SETS ? y
  
```

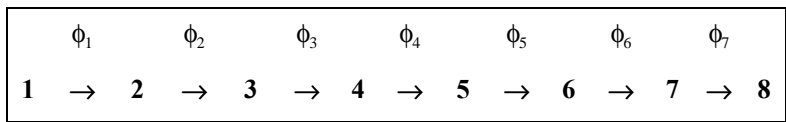
Fig. 5.2

- Now, we need to examine the series of queries and responses in Fig. 5.2 *VERY* carefully. This is one of the **most important** lessons we will need to learn to understand how to use SURGE.
- It's so important we'll say it a second time! It is also one of the steps in using SURGE that can sometimes be confusing.
- Start with the first step. In the menu, we see the now-familiar list of "built in" model options SURGE gives you. Since we are interested in fitting model ϕ_{c*t}, p_{c*t} we are obviously interested in a "time-dependent model", for both survival and recapture. At the moment, we are defining the model for survival. There doesn't seem to be any option on the menu for "colony" or group, but there is obviously an option for time dependency, which we have previously used - choice 2. So, the first thing we do is enter the number "2", and hit the <enter> key.
- Now, for the "tricky part". Actually it's easy, if you think carefully about what the questions are asking, in the context of what we are trying to do. The next question asks you if you want to use the same parameter values across data sets - yes or no? What does this mean?
- Well, the first thing to remember is that we are using 2 data sets: G.SUR, and P.SUR. So, SURGE is clearly asking us if we want



something to be the “same” or “different” between these 2 data sets. What is it that can either be the same or different? The “parameter values”! In this case, the parameter is the survival rate, ϕ . So, in other words, SURGE is asking us if we want to use the same survival rate for both G.SUR (the good colony data) and P.SUR (the poor colony data). If we were to answer “yes” then this is saying that we want SURGE to constrain the estimate of survival such that it is the same for both colonies. However, if we answer “no” - we do NOT want the same parameter values, then we are telling SURGE we want it to estimate survival rates for each group.

- For model ϕ_{c^*t}, p_{c^*t} , we want to follow survival to potentially vary as a function of both colony and time. We already “let it” vary as a function of time by using option 2 from the menu. Now, we also want to allow it to vary between colonies. So, we answer “no” - do NOT use the same parameter values across data sets.
- The next question then asks us if we want to use the same parameter structure across data sets? What is our parameter structure? Well, we defined the parameter structure when we selected choice 2 from the menu - we selected a time-dependent model for the good colony. Thus, SURGE is now asking you if you want to use a time-dependent model for the remaining colony as well (i.e., both data sets). The answer to this question is clearly “yes”. We want time-dependence for both colonies.
- Now, before we go much further, let’s step back and look at the logic of what we just did. This time, let’s consider the sequence of questions and answers in a ‘symbolic’ or ‘schematic’ fashion. These schematic representations of the parameter structures are often very useful to ‘keep track’ of what is going on. First, we told SURGE we wanted to use a time-dependent model (choice 2 from the menu). For 8 occasions (1 initial release occasion followed by 7 subsequent recapture occasions), this corresponds to the following structure:

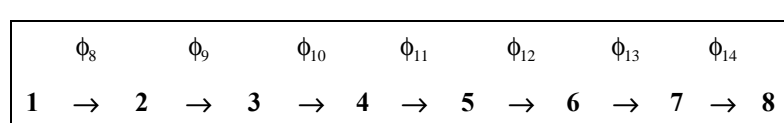


- Recall from the last chapter that this representation is not entirely complete, since it does not index the “cohort” or release group of the individuals in the sample - i.e., it ignores individuals newly captured on occasions 2 through 7 (see Fig. 4.13 in the preceding chapter). However, for present purposes it is sufficient to represent the time-dependent structure survival.
- Now that we have defined the basic model structure for survival, SURGE asks us if we want to use the same parameter values across data sets (i.e., between colonies). If we were to answer “no”, and then “yes” to the next question (same time-dependent structure for both groups), this is the same as allowing the indexing of the ϕ_i values to differ among data sets. In other words:

good colony

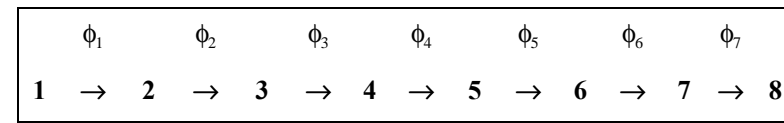


poor colony



- In contrast, if we had answered “yes” to this question, we would have told SURGE we want to use the same indexing across data sets. In other words:

good colony



1	2	3	4	5	6	7
	2	3	4	5	6	7
		3	4	5	6	7
			4	5	6	7
				5	6	7
					6	7
						7

- Since we have told SURGE that we want the same parameter structure, but different parameter values between the two colonies, we would in fact have 2 matrices for survival (one for each group). Remember that SURGE determines the parameter indexing for survival first, then recapture. Thus, a total of 14 “survival parameters”, 7 for each colony.

survival matrices

1	2	3	4	5	6	7
	2	3	4	5	6	7
		3	4	5	6	7
			4	5	6	7
				5	6	7
					6	7
<i>good colony</i>						7

8	9	10	11	12	13	14
	9	10	11	12	13	14
		10	11	12	13	14
			11	12	13	14
				12	13	14
					13	14
<i>poor colony</i>						14

- Since we used precisely the same overall parameter structure for recaptures, we will have two similar matrices for recaptures, one for each colony. The indexing for the recaptures begins where the survival indexing stopped:

recapture matrices

15	16	17	18	19	20	21
	16	17	18	19	20	21
		17	18	19	20	21
			18	19	20	21
				19	20	21
					20	21
<i>good colony</i>						21

22	23	24	25	26	27	28
	23	24	25	26	27	28
		24	25	26	27	28
			25	26	27	28
				26	27	28
					27	28
<i>poor colony</i>						28

- Thus, we have 28 total parameters: 14 each for survival and recapture, respectively. Are they all estimable? Let’s wait until we have run our analyses before we address that question.
- If you tell SURGE to show you the model structure, by entering “-1” at the prompt, it is these matrices you will see printed on the screen (and, ultimately, to the output file SWIFT1.LST).
- Once you have looked at the models, you can proceed with the rest of the SURGE queries. By now, they should be starting to look a bit familiar. First, SURGE will ask you if you want to fix any of the parameters. Again, at this stage, we do not want to fix any of the parameters, so we accept the default (“no”) by simply hitting the <enter> key.
- Next, SURGE will present the initial estimates for both survival and recapture, and will offer you the opportunity to change any of these starting values and/or to drop the logit transform. This is something you will almost never want to do, and it is probably safe to get in the habit of simply accepting the default (“no change”) by hitting the <enter> key, twice each for survival and recapture estimates respectively.
- Once you’ve gotten past the initial estimates screens, you will be ready to “run the analysis”. Again, you have several options at this point. Let’s look at the progress of the iterations by entering “-5”. At this point we don’t need to see the variance-covariance matrix, so we

answer “no” (Fig. 5.4).

```

O* OUTPUT OF ITERATIVE CALCULATIONS

O* DISPLAY RESULTS EVERY X ITERAT.<0=no display>
  <back to M =-2; back to C =-3; back to I =-4> : -5
O* PRINT VAR-COVAR MATRIX? <YES=<—>> : no
  
```

Fig. 5.4

- SURGE will indicate it has finished its estimation by printing an unformatted table of the final parameter estimates and function gradient, and the final model deviance (Fig. 5.5). A reminder that at the top of this unformatted table is a sequence of 3 numbers, separated by a space. As long as the final number is “1”, you can feel confident SURGE hasn’t had any real “problems” with the estimation. Also, although the deviance is printed at the bottom, remember that SURGE will output this value, as well as the estimates themselves, to the output file.

```

74 80 1
0.3397054454863780D+03
0.6931472D+00 0.5108256D+00 0.6931472D+00 0.1252763D+01 -0.4519851D+00
0.6931472D+00 -0.2119354D+00 0.2876386D+01 0.1050244D+01 0.1282616D+01
0.1220279D+01 0.9094224D+00 0.1061426D+01 0.4572957D+00 0.3250150D+02
0.6931472D+00 -0.4054651D+00 -0.1791759D+01 0.2876821D+00 0.5123818D+02
-0.2119354D+00 0.1696449D+01 -0.1086847D+01 0.1854032D+00 0.1311071D+01
0.2504709D+01 0.1852384D+01 0.4572957D+00
0.2481227D-09 -0.5300106D-08 -0.3370133D-08 0.2632624D-08 0.3816527D-09
-0.4019386D-08 0.9167697D-11 0.3386758D-08 0.3604254D-08 0.1151162D-07
0.3379797D-08 -0.1251355D-07 -0.7706001D-08 -0.1611109D-08 0.1554312D-13
0.4183907D-08 0.6549840D-08 0.1521470D-08 0.5649171D-08 0.0000000D+00
0.9167697D-11 0.7413736D-09 -0.1512622D-08 0.1874338D-07 0.7007719D-08
-0.8093002D-09 -0.4406847D-08 -0.1611109D-08
DEVIANC = 0.3397054D+03
strike <—> to continue
  
```

Fig. 5.5

- Once we’ve finished this run, and hit the <enter> key, we’re back at the “final” screen (e.g., Fig. 5.6). However, at this point, we don’t want to quit SURGE - we want to run another analysis, for the second model we’re testing: ϕ_t, p_t . To do this, we want to go back to the model selection screen (denoted by the character mnemonic **M***). This is choice “2” on the menu, so we simply type in “2”, and press the <enter> key.

```

D* DATA INPUT 1
M* MODEL CHOICE 2
C* CONSTRAINING PARAMETERS 3
I* INITIAL VALUES AND LOGISTIC TRANSF. 4
QUIT SURGE 5

OPTION # ? 2
  
```

Fig 5.6

- SURGE will then give you the option of entering a new title. Since we’re now going to fit a different model, we want to enter an appropriate title for this new model. So, for model ϕ_t, p_t we enter “Phi(t),p(t)”. Again, remember that in this model, we are “dropping” the colony effect from both parameters simultaneously.
- As soon as we’ve entered the title, SURGE presents us with the model specification screen for the survival parameters (e.g., Fig. 5.2).
- Now we come to the second half of the “tricky part” we introduced on pp. 5-3-5-5.
- The next question SURGE asks you is “do you want to use the same parameter values across data sets?”. Recall that we have 2 data sets: G.SUR (for the good colony), and P.SUR (for the poor colony). What SURGE wants to know is “do you want to ignore colony differences during the estimation?”.
- If we answer “no”, which is what we did for the first model (see p. 5-5), we are in effect saying “OK...estimate survival, but allow the survival to differ between colonies - in other words, estimate survival separately for each colony”.
- But what if we answer “yes”? Answering “yes” tells SURGE to ignore colony differences. And, if you think about it, this is exactly what we want to do. We want to estimate for a model which just has time-dependence (ϕ_t), but not a colony difference ($\phi_{c,t}$). Remember, we are trying to construct an LRT for model ϕ_{c^*t}, p_{c^*t} versus model ϕ_t, p_t . So, we enter “yes” (or “y”), and hit the <enter> key (Fig. 5.7).



- Now, at this point you should notice several things. First, the number of total parameters in the model has been reduced by half: from 28 total in model ϕ_{c^*t}, p_{c^*t} to 14 in model ϕ_t, p_t . Remember, not all of these parameters are individually identifiable (more on this in a moment), but it is clear that the total number has been reduced. Why? Well, because we have eliminated “colony” as a factor. There are 2 different colonies (good and poor), so the number of total parameters is reduced by a factor of 2.
- So, what we are now faced with is a test of a full model against a nested, reduced parameter model. If the LRT is significant, then this suggests strongly that “colony” has a significant effect. If the LRT is not significant, then we conclude that we are unable to demonstrate a colony effect (and thus accept the null hypothesis). Since the two models are clearly nested, we can use a likelihood ratio test. For completeness, we will also calculate the AIC.

Model	deviance	# parameters	AIC
ϕ_{c^*t}, p_{c^*t}	339.705	26	391.705
ϕ_t, p_t	354.945	13	380.945
	$\Delta = 15.24$		

- This table shows several things. First, as we know has to be true, the model with fewer parameters fits lets well than the more general model - indicated by the larger model deviance. Is this difference (15.24) significant? The difference in the number of estimable parameters between the two models is $26 - 13 = 13$. Thus, we have 13 degrees of freedom for our LRT. Our observed difference in deviance (15.24) is not significantly larger than would be expected by random chance ($P=0.293$). Thus, we conclude that there is not statistically significant overall difference in survival and recapture (considered simultaneously) between the 2 colonies.
- However, this is a rather unsatisfying analysis, since it tells us

nothing about survival or recapture rate independently. Obviously, there are a large number of other model tests we could try. Many of these are listed in Table 14 in Lebreton *et al.* (1992). We will examine one more of them, to reinforce what we have just learned.

- However, before we do so, we need to address 2 issues. First, the technical consideration of how to count the number of parameters. In this particular case, the answer is very easy, since we already made a start on this particular model in Chapter 4. Recall that in Chapter 4, we looked at a standard time-dependent (CJS) model. Recall also that the only “trick” to counting parameters for the time-dependent CJS model was that the final product of survival and recapture rate ($\phi_{k-1}p_k$ for k occasions) is not individually identifiable, and was denoted as the parameter β_k . So, for k occasions, there are $(2k-3)$ identifiable parameters (see Lebreton *et al.* 1992 - Table 7, and pp. 4-13 to 4-16 in Chapter 4). In this example, we again have the standard CJS model, but with 2 groups. In essence, fitting model ϕ_{c^*t}, p_{c^*t} is equivalent to fitting the CJS model separately to each data set. You could actually run SURGE twice, once with each data set, fitting the CJS model. Then, the 2 deviances obtained would sum to 339.705 - which is the deviance for model ϕ_{c^*t}, p_{c^*t} . Thus, to count parameters for model ϕ_{c^*t}, p_{c^*t} , you simply count parameters for one group alone (which is functionally model ϕ_t, p_t), and double it to account for 2 groups. For any one of the groups, or the two groups pooled, we have 8 occasions. So, one terminal β_8 term, and 12 other parameters: 6 survival estimates (ϕ_1 to ϕ_6), and 6 recapture estimates (p_2 to p_7). Thus, a total of 13 parameters for either colony alone, or both colonies pooled. $2 \times 13 = 26$ parameters for the model with parameters for both time and colony.
- The second issue is a bit more complex, but is **very important** to understand to use SURGE effectively. We started by saying that this particular model comparison was analogous to TEST 1 from RELEASE. A simultaneous test of an overall “colony” effect.
- However, did we really just test for the effect of “colony”? To understand this question, let’s reconsider 2 things. First, look back at the “question box” on p. 5-2 of this chapter - where we briefly reintroduced the concept of a statistical interaction.
- As noted, interpreting the statistical significance of “main effects” is



not always possible if there is a significant interaction of main effects, since the “significance” of the effect will depend on the particular combination of the various effects in the model.

- Why? Well, recall what an interaction means - an interaction means the response variable (in this case, survival rate) varies as a function of the particular combination of the main effects - COLONY and TIME. If there is significant interaction, then whether one colony has a higher survival rate than the other depends upon the time interval in question.
- In the example in the ‘question box’ on p. 5-2, we had two factors, SEX and TRT. In the left hand diagram at the bottom of the box, we show a representation typical of a significant interaction of the main effects. If we go left to right (along the TRT axis) we see that males and females may or may not differ significantly for TRT level 1 (the values are close), with females having a slightly larger average Y than males. However, at TRT level 2, males have a larger average Y than females. At TRT level 3, the male and female values are again similar, and again, females are slightly larger. So, whether or not females have greater Y than males, or the other way around, depends on the particular level of the TRT factor.
- So, clearly, the first thing we would want to do is test for the statistical significance of the interaction term. Did we do this?
- To answer this question, look carefully at the model representation for the survival. The same logic clearly applies to the recapture rate.

$$\begin{array}{l} \phi = \text{COLONY} + \text{TIME} + \text{C.T} + \text{error} \\ \text{versus } \phi = \frac{\text{TIME} + \text{error}}{\text{COLONY} + \text{C.T}} \end{array}$$

- If you look closely, you’ll realize this is precisely the analysis we just did. We started with the “full rank” model, with both of the main effects (COLONY and TIME, and the interaction (C.T), and the error term). This is the survival half of model $\phi_{c*t,p_{c*t}}$. This model was compared to a model with just TIME - i.e., the survival half of model

ϕ_{t,p_t} . We used a LRT to compare these two models.

- However, look closely at the difference between the two models. It is not simply COLONY alone, but COLONY plus the interaction term C.T. This is an important point, since it forces us to consider one of the way SURGE constructs models. As we will see, it is easy to use SURGE to construct either model $\phi_{c,t,p_{c,t}}$ or model ϕ_{t,p_t} , or any of the models in Fig. 5.1. However, there is, in fact, an “intermediate” model we have left out of the process. It is model

$$\phi \text{ (or } p) = \text{COLONY} + \text{TIME} + \text{error}$$

- This model, referred to as the “additive” model, is intermediate between model $\phi_{c*t,p_{c*t}}$ and model ϕ_{t,p_t} - it is a “main effects only” model. We denote the additive model using the following shorthand: $\phi_{c+t,p_{c+t}}$ - using the “+” sign to denote the additivity of main effects.
- Strictly speaking, we should use the following sequence of model tests to look for a significant “colony” effect. To make the notation simpler, we’ll consider only survival.

1. compare model $\phi_{c,t}$ versus model ϕ_{c+t}

$$\begin{array}{l} \phi = \text{COLONY} + \text{TIME} + \text{C.T} + \text{error} \\ \text{versus } \phi = \frac{\text{TIME} + \text{error}}{\text{C.T}} \end{array}$$

This is a formal test of the significance of the interaction term, (C.T)

2. if C.T not significant, then test main COLONY effect

$$\begin{array}{l} \phi = \text{COLONY} + \text{TIME} + \text{error} \\ \text{versus } \phi = \frac{\text{TIME} + \text{error}}{\text{COLONY}} \end{array}$$

This is a formal test of the significance of the COLONY main effect.

- Thus, we clearly have “missed a step” in the process. However, part of our purpose was to simply demonstrate the mechanics of

comparing groups.

- How do you build “additive models”. Unfortunately, SURGE does not make building additive models as easy as selecting an option from the menu. It requires the building of an external constraints file (which, as you’ll see is completely analogous to constructing linear models using dummy coding variables). However, this topic is so important, and has so many other uses besides additive models, we will give it its own chapter!
- For the moment, we’ll accept that we can test such “additive” or “main effects only” models, and, in fact, we should do so as one of the logical steps in our model testing. To some degree, this is not emphasized enough in Lebreton *et al.* (1992). We will therefore do so here.
- For the moment, let’s have one more practice run, ignoring the complication of additive models, using another example of a test presented in Table 14 of Lebreton *et al.* (1992).

Model ϕ_c, p_t versus model ϕ, p_t

- By now, you should be reasonably comfortable interpreting the syntax of this model notation. Consider the first model: ϕ_c, p_t . In this model, we have a possible colony difference in survival, but no time dependence, and time dependence in recaptures, but no colony term.
- What does this mean? Simply, it means that for survival rate, we’re using a model where survival rate is constant through time, but that the constant value may differ between the colonies.
- The recapture structure (p_t) should be familiar - we’re allowing for time variation in recapture rates, but telling SURGE to combine both colonies (i.e., the recapture rate at a given occasion is assumed to be the same for both colonies).
- You should also have a pretty good idea what the parameter structure SURGE uses looks like. If not, here they are, for survival and recapture, respectively (assuming we entered the “good” data set first):

1	1	1	1	1	1	1
	1	1	1	1	1	1
		1	1	1	1	1
			1	1	1	1
				1	1	1
<i>survival</i>					1	1
<i>good</i>						1

2	2	2	2	2	2	2
	2	2	2	2	2	2
		2	2	2	2	2
			2	2	2	2
				2	2	2
<i>survival</i>					2	2
<i>poor</i>						2

3	4	5	6	7	8	9
	4	5	6	7	8	9
		5	6	7	8	9
			6	7	8	9
				7	8	9
<i>recapture</i>					8	9
<i>good</i>						9

3	4	5	6	7	8	9
	4	5	6	7	8	9
		5	6	7	8	9
			6	7	8	9
				7	8	9
<i>recapture</i>					8	9
<i>poor</i>						9

- So, let’s now run SURGE to fit this model. For our title, we used “phi(c),p(t)”. Again, we are using 2 data sets: G.SUR, and P.SUR.
- Once you have completed the data entry questions, you will be faced with the model specification screens, starting with survival. We are trying to fit model ϕ_c, p_t . So, as we have just seen, we want a model where survival is constant over time. This is choice 3 from the menu.
- Then SURGE asks you if you want to use the same parameter values across data sets? What is the answer? The answer for this model is “no” - we want to estimate survival separately for the 2 colonies.
- Then, SURGE wants to know if we want the same parameter structure across data sets. What is the answer this time? The answer is “yes” - for both colonies (i.e., both data sets), we want survival to have the same model structure - constant.
- Next, we have the menu for the recapture model. For recaptures, we

have time-dependence, but no colony effect (i.e., survival rate is the same between colonies, but it can vary over time). So, clearly, we select choice 2 from the menu, for time-dependence. We want full time-dependence, so we simply hit the <enter> key to accept the default.

- Then, SURGE wants to know if we want the same parameter values across the data sets. Here, the answer is “yes”. We want the same parameter values, since we are ignoring colony.



It might be helpful to remember the following: if you want to include “group” in your model (where “group” is some classification factor other than “time” or “cohort” - e.g., sex, breeding status, or in this example, colony), you answer “no” when asked if you want the same parameter values across data sets. If you want to drop “group” from your model, you answer “yes”.

- We have no constraints, so we accept the default of no constraints by hitting the <enter> key.
- We don’t want to fix any parameters - again, simply hit the <enter> key.
- We do not want to change either the starting values or the logit transformation for either survival or recapture, so we again accept the defaults by hitting the <enter> key enough times until we are at the output screen. Enter “-5” (to have the reduced output print every 5 iterations), and then enter “no” for the variance covariance matrix.
- Once finished, hit the <enter> key, and you’ll be at the final menu. We want to run the second model, using the same data sets, so we select option 2.
- Our second model is ϕ, p_t . So, what we are doing is testing a model where there are two constant survival rates, one per colony (our first model) versus one where there is no colony difference in survival. The recapture structure is the same for both models. So, here, we are clearly looking at just colony differences in survival alone. This is different from our earlier example where we tested for

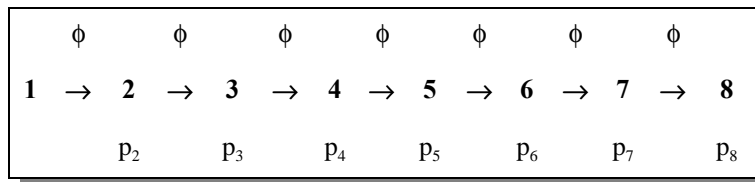
colony differences in both survival and recapture simultaneously.

- Enter the title for this model: “ $\phi(), p(t)$ ”, and proceed to the model menus. For survival, we want a model with constant survival, but no differences between colonies. So, we start by selecting option 1 - constant model.
- Then, we are asked whether we want the same parameter values across data sets. Clearly, the answer this time is “yes”.
- For recaptures, we want time dependence, so we select option 2. We again want full time-dependence, so we accept the default by hitting the <enter> key.
- When asked if we want the same parameter values across data sets, we again answer “yes”, since we want the same time-dependent estimates for both colonies.
- No constraints are needed, nor do we want to fix any variables. We also accept the starting estimates and the use of the logit link function. Proceed to run the analysis.
- Here are the results (from the output file):

Model	deviance	# parameters	AIC
ϕ_c, p_t	350.870	9	368.870
ϕ, p_t	356.488	8	372.488
	$\Delta = 5.618$		

- We see that the difference between the model fits is 5.618. Since the difference in the number of parameters between the two models is 1, this is a single degree of freedom LRT. The probability for this difference in deviance is 0.0178. So, there is a significant decrease in model fit with the elimination of the colony effect from survival. This could be interpreted as evidence of a significant colony difference in survival. In fact, the estimates from this model are consistent with this interpretation: $\phi_{\text{good}} = 0.77$, $\phi_{\text{poor}} = 0.58$.

- You should remember that this is a test of survival differences, not recapture. Why? Because p_i is in both models.
- The AIC values are consistent with the results from the LRT. Even though the second model has fewer parameters, the AIC value is larger. Based on the AIC criterion alone, we would have selected the more general model.
- The only remaining question here is how we derived the number of parameters. The answer is shown schematically in the following:



- In this diagram, we see the structure of the model ϕ, p_i . Remember that in fully time-dependent models (e.g., CJS), we had the problem of the terminal product - the β term - which could not be individually estimated. However, when one or both of the parameters in a model is constant, we don't have this problem. Why? Well, because we have information from all the other occasions with which to estimate the parameter - see p. 4-15. Thus, in Fig. 5.11, we have 8 parameters: 1 survival rate, which we estimate over all 7 time intervals, and 7 recapture rates.
- For the model ϕ_c, p_i , we have essentially the same thing, except that we have 2 survival parameters: 1 for each colony. So, 2 survival rates, 7 identifiable recapture rates = parameters.

That's the end of Chapter 5! We're not done with the swift example (not even close...), but we're finished with the introduction of comparing groups. We've covered a lot of important ground in this chapter, so make sure you have a good feel for it now. In the next chapter, we will introduce the concept of constraints. As you'll see, SURGE allows you to quickly and easily build all sorts of linear constraints into your analytical model. It is this feature which allows you to translate freely from the ideas and concepts of analysis of variance to analysis of mark-recapture data. As you'll see, there is a simple and logical connection between the two.

