R2ucare: An R package to perform goodness-of-fit tests for capture-recapture models

³ Olivier Gimenez, Jean-Dominique Lebreton, Rémi Choquet, Roger Pradel

4 CEFE UMR 5175, CNRS—Université de Montpellier—Université Paul-Valéry Montpellier—EPHE, 1919 Route de

⁵ *Mende*, 34293 *Montpellier cedex 5, France*

6 Summary:

7 1. Assessing the quality of fit of a statistical model to data is a necessary step for conducting
 8 safe inference.

We introduce R2ucare, an R package to perform goodness-of-fit tests for open single- and
 multi-state capture-recapture models. R2ucare also has various functions to manipulate
 capture-recapture data.

3. We remind the basics and provide guidelines to navigate towards testing the fit of capture recapture models. We demonstrate the functionality of R2ucare through its application to
 real data.

4. The R2ucare package will be of use to ecologists interested in estimating demographic parameters under imperfect detection of individuals.

Keywords: Arnason-Schwarz, capture-mark-recapture, Cormack-Jolly-Seber, model validation,
 R2ucare

19 Introduction

Capture-recapture (CR) models have become a central tool in population ecology for estimating
demographic parameters under imperfect detection of individuals (Lebreton et al. 1992; 2009).
These methods rely on the longitudinal monitoring of individuals that are marked (or identifiable)
and then captured or sighted alive over time.

Single-state CR models, and the Cormack-Jolly-Seber model in particular (Lebreton et al. 1992),
have been used to assess the effect of climate change (e.g. Guéry et al. 2017) or study senescence
(e.g. Péron et al. 2016). The extension of single-state models to situations where individuals are detected in several geographical sites or equivalently states (e.g. breeding/non-breeding or sane/ill)
are called multi-state CR models (Lebreton et al. 2009). Multistate CR models, and the ArnasonSchwarz model in particular (Lebreton et al. 2009), are appealing for addressing various biological

questions such as metapopulation dynamics (e.g. Spendelow et al. 2016) or life-history trade–offs
 (e.g. Supp et al. 2015).

A necessary step for correct inference about demographic parameters is to assess the fit of single- and multi-state models to CR data, regardless of whether a Bayesian or a frequentist framework is adopted.

Two family of methods exist to perform goodness-of-fit (GOF) tests for CR models. First, an 35 omnibus test of the null hypothesis that a given model fits the data adequately can be conducted 36 using resampling methods and the deviance as a metric (White 2002). However when the null 37 hypothesis is rejected, this omnibus approach does not inform about an alternative model that 38 could be fitted. Second, specialized tests have been built to address biologically meaningful causes 39 of departure from the null hypothesis. A global test for single- and multi-state CR models is 40 decomposed into several interpretable components based on contingency tables, for example the 41 presence of transients (Pradel et al., 1997; Pradel et al. 2003) or that for trap-dependence (Pradel, 42 1993; Pradel et al. 2003). These GOF tests are implemented in the Windows application U-CARE 43 (Choquet et al. 2009). 44

Here, we introduce the R (R Development Core Team 2014) package R2ucare to perform GOF tests for single- and multi-state CR models. R2ucare also includes various functions to help manipulate CR data. As a package in the CRAN database, R2ucare allows to take full advantage of R's many features (e.g. simulations, model fitting), while being multi-platform. We go through the theory first, then illustrate the use of R2ucare with an example on wolf in France for single-state models and geese in the U.S. for multi-state models.

51 Theory

Once a model has been specified, GOF testing is the procedure that controls model assumptions. GOF testing and model fitting are two complementary procedures that share and compete for the information contained in the data. The more liberal is a model, the more information it requires to be fitted (there are more parameters to estimate) but also the fewer assumptions need to be verified. For instance, the time-dependent CJS model is merely content with the numbers of individuals captured at each occasion and the numbers never seen again from those released at each

occasion when it comes to estimating its parameters. These summary statistics leave much of the
 details of the capture histories available to test its assumptions.

There are several ways in which this remaining information may be exploited to test the as-60 sumptions. The implementation retained in R2ucare builds on the optimal approach originally de-61 vised by Pollock et al. (1985) and later modified by Pradel (1993). It is based on contingency tables 62 and aims at testing with power for transients and trap-dependence. These aspects are examined 63 specifically in two independent component tests called respectively Test 3.SR and Test 2.CT. 64 Truly, the component tests directed at transients and trap-dependence actually address features of 65 the data that are consequences of respectively the presence of transients and trap-dependence, so 66 that these features may also be caused by other, completely different phenomena. They do verify 67 respectively that: 68

Newly encountered individuals have the same chance to be later reobserved as recaptured
 (previously encountered) individuals (null hypothesis of Test 3.SR).

• Missed individuals have the same chance to be recaptured at the next occasion as currently
 captured individuals (null hypothesis of Test 2.CT).

Although these components are often called 'test of transience' and 'test of trap-dependence',
when it comes to interpretation, one should should keep in mind that transience and trap-dependence
are just two specific reasons why the tests respectively called 3.SR and 2.CT might be significant.
Beyond these two oriented components, the remaining information is distributed and structured into two additional components: Test 3.Sm and Test 2.CL. Those examine long-term features of the data:

Have newly encountered not immediately recaptured individuals the same timing of reen counters as previously captured not immediately recaptured individuals (null hypothesis of
 Test 3.Sm)?

Have missed not immediately recaptured individuals the same timing of reencounters as
 currently captured not immediately recaptured individuals (null hypothesis of Test 2.CL)?

⁸⁴ Data are generally sparse for these components and scattered over many occasions. Despite

the implementation of some automatic pooling (see Choquet et al. 2005 for more details about the
pooling rules), they are rarely significant alone.

Although many situations can lead to similar test results, we propose here a decision tree (Figure 1) that should lead to reasonable, if not perfect, solutions in most cases.

The theory for the GOF test of the multistate Arnason-Schwarz model was developed along 89 similar lines as for the CJS model (Pradel et al. 2003). This test has yet more components and some 90 components have a more complex structure (hence our non attempt to build a decision tree as for 91 the CJS model), but for all that concerns us, the reasoning remains very similar. Truth be told, the 92 test implemented in R2ucare is actually a test of the Jolly-Move model, a slightly more general 93 model than the Arnason-Schwarz model in that it allows detection parameters to depend on the 94 previous state occupied. This is a weird idea in most common situations, so that we may reason 95 as if we were examining the Arnason-Schwarz model. Components here have been designed 96 to detect transients, trap-dependence, and - this is new - the memory of past states. This last 97 point means that the component examines whether transitions to a new state depend on previous 98 states beyond the current one. The corresponding components are respectively Test 3.GSR, Test 99 M. ITEC, and Test WBWA. Like for the CJS case, they actually examine features of the data, namely 100 that: 101

Newly encountered individuals have the same chance to be later reobserved as recaptured
 (i.e. previously encountered) individuals (null hypothesis of Test 3.GSR which is the exact
 equivalent of 3.SR).

• Missed individuals have the same chance to be recaptured in each state at the next occasion
 as currently captured individuals in the same state (null hypothesis of Test M.ITEC).

Individuals currently captured in the same state have the same chance to be next reobserved
 in the different states independently of their most recent observed state (null hypothesis of
 Test WBWA).

These interpretable components are complemented by two composite components with no clearly identified interpretation, Test 3.GSm and Test M.LTEC. We do not attempt to give a description of these; let it suffice to say that Test 3.GSm is concerned with comparing newly and

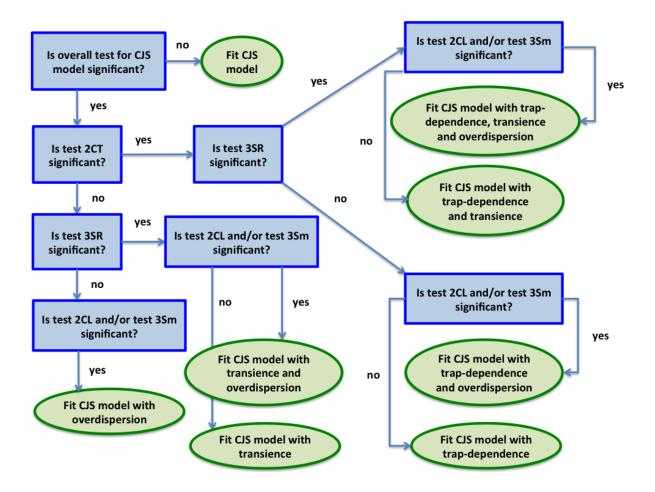


Figure 1: Decision tree to navigate towards testing the fit of single site/state capture-recapture models, with the Cormack-Jolly-Seber (CJS) model as a reference. Questions are in the blue rectangles, actions in the green ellipses. We start by asking the question in the top-left corner. The coefficient of overdispersion is calculated as the ratio of the goodness-of-fit test statistic over the number of degrees of freedom (Pradel et al. 2005). Remark 1: we begin by testing for the presence of trap-dependence, then that of transience; these steps could be permuted without affecting the final outcome. *Remark* 2: the overall goodness-of-fit test may be significant while none of the four sub-components is; in this situation, we recommend fitting the CJS model and correcting for overdispersion. Remark 3: we do not cover the issue of heterogeneity for which a formal test does not exist. When both the tests for the presence of transience and trap-dependence are significant, and only them, there is suspicion of heterogeneity in detection (Péron et al. 2010). Péron et al. (2010) implemented an approximate procedure to assess the presence of heterogeneity in the detection process, and Jeyam et al. (2017) developed a formal test for the same purpose. Cubaynes et al. (2012) recommended using the Akaike Information Criterion (AIC) to compare models with and without heterogeneity. Remark 4: To account for the presence of transience, that of trapdependence or an effect of heterogeneity, we refer to Pradel et al. (1997), Pradel and Sanz-Aguilar (2012; see also Pradel 1993 and Gimenez et al. 2003) and Gimenez et al. (2017) respectively.

previously encountered, while Test M.LTEC contrasts missed and encountered individuals. Fortunately, these components play a secondary role as they are most time not significant alone.
For more details about the theory of GOF testing for CR models, we refer to Pradel et al. (2005)
and Cooch and White (2006).

117 The R2ucare package

The R2ucare package contains R functions to perform GOF tests for CR models as well as various
functions to manipulate CR data (see Table 1 and the vignette of the package named vignette_R2ucare).
It ensures reproducibility which was not allowed with the U-CARE (Choquet et al. 2009) Windows
standalone application. Besides, it can be used in combination with other R packages for fitting
CR data like RMark (Laake 2013) or marked (Laake et al. 2013) or to carry out simulations to assess
statistical power (e.g. Bromaghin et al. 2013; Fletcher et al. 2012).

Table 1: The main functions of R2ucare and their description	
--	--

Function	Description
marray	builds a m-array for single-site/state capture-recapture data
multimarray	builds a m-array for multi-site/state capture-recapture data
group_data	pool together individuals with the same encounter capture-recapture
	history
ungroup_data	split encounter capture-recapture histories in individual ones
read_inp	read MARK formated files
read_headed	read E-SURGE formated files
test3sr	in single-site/state models, test for the presence of transients, the null
	hypothesis being that there is no difference in the probability of being later
	reencountered between new and old individuals encountered at occasion i
test3sm	in single-site/state models, test the null hypothesis that there is no
	difference in the expected time of first reencounter between the new and
	old individuals encountered at occasion <i>i</i> and seen again at least once

Function	Description
test2ct	in single-site/state models, test for the presence of trap-dependence, the
	null hypothesis being that there is no difference in the probability of being
	reencountered at occasion $i + 1$ between those encountered and not
	encountered at occasion <i>i</i> conditional on presence at both occasions
test2cl	in single-site/state models, test the null hypothesis that there is no
	difference in the expected time of next reencounter between the
	individuals encountered and not encountered at occasion <i>i</i> conditional on
	presence at both occasions i and $i + 2$
test3Gsr	in multi-site/state models, test the null hypothesis that there is no
	difference in the probability of being later reencountered between new and
	old individuals encountered at occasion i in state l
test3Gwbwa	in multi-site/state models, test for the presence of memory, the null
	hypothesis being that there is no difference in the expected state of next
	reencounter among the individuals previously encountered in the different
	states
testMitec	in multi-site/state models, test the null hypothesis that there is no
	difference in the probabilities of being reencountered in the different states
	at $i + 1$ between the animals in the same state at occasion i whether
	encountered or not encountered at this date, conditional on presence at
	both occasions
testMltec	in multi-site/state models, test the null hypothesis that there is no
	difference in the expected time and state of next reencounter between
	individuals in the same state at occasion <i>i</i> that were not encountered at
	occasion $i + 1$ whether encountered or not encountered at occasion i
	conditional on presence at both occasions i and $i + 2$
test3Gsm	in multi-site/state models, this component is a composite test (several null
	hypotheses) that gathers what remains of the global test after the other
	components have been isolated (Pradel et al. 2005)

124 Goodness-of-fit tests for single-site/state models

¹²⁵ We illustrate the use of R2ucare to assess the GOF of the CJS model to a dataset on wolves (Canis

126 lupus) in France (e.g., Fletcher et al. 2012). Briefly, the data consist of capture histories for 160

¹²⁷ individuals, partitioned into 35 3-month intervals (from spring 1995 to autumn 2003).

¹²⁸ We first load the R2ucare package:

library(R2ucare)

Then we read in the wolf data that is provided with the package. To do so, R2ucare contains two functions that accomodate the most frequent CR formats: read_inp deals with the MARK format (Cooch and White 2006) while read_headed deals with the E-SURGE format (Choquet et al. 2009). The wolf dataset has the MARK format, therefore:

```
wolf = system.file("extdata", "wolf.inp", package = "R2ucare")
wolf = read_inp(wolf)
```

¹³³ We then get the matrix and number of CR encounter histories:

```
ch = wolf$encounter_histories
n = wolf$sample_size
```

Following the procedure described in Figure 1, we first assess the overall fit of the CJS model by using the function overall_CJS:

```
overall_CJS(ch,n)
```

136	##		chi2 degree	chi2 degree_of_freedom p_valu		
137	## Gof te	est for CJS model:	180.73	115	0	

¹³⁸ Clearly, the CJS model does not fit the data well ($\chi^2_{115} = 180.73$, P < 0.01). We then test for an ¹³⁹ effect of trap-dependence:

test2ct(ch,n,verbose = FALSE)

\$test2ct 140

141	##	stat	df	p_val	sign_test
142	##	64.451	31.000	0.000	-5.641

Test 2.CT is significant (χ^2_{31} = 64.45, P < 0.01). We also provide the signed square root 143 (sign_test) of the Pearson chi-square statistic as a directional test of the null hypothesis (Pradel 144 et al. 2005), which is negative when there is an excess of individuals encountered at a given 145 occasion among the individuals encountered at the previous occasion. 146

Note that, by default, the GOF functions in R2ucare returns all the contingency tables that 147 compose the test under scrutiny, which might not be of immediate use and rather cumbersome 148 on screen, hence the use of verbose=FALSE in the call to the test2ct function above. Now we ask 149 whether there is a transient effect: 150

test3sr(ch,n,verbose = FALSE)

151	##	\$test3sr			
152	##	stat	df	p_val	sign_test
153	##	65.414	29.000	0.000	5.037

Test 3.SR is also significant ($\chi^2_{29} = 65.41$, P < 0.01). We also provide the signed square root 154 (sign_test) of the Pearson chi-square statistic (Pradel et al. 2005), which is positive when there is 155 an excess of never seen again among the newly marked. 156

Navigating through the decision tree in Figure 1 suggests we should perform the two remain-157 ing tests: 158

test3sm(ch,n,verbose = FALSE)

\$test3sm 159

stat df p_val 160

22.977 25.000 0.579 161

test2cl(ch,n,verbose = FALSE)

162 ## \$test2cl

163 ## stat df p_val

164 ## 27.888 30.000 0.576

¹⁶⁵ Neither Test 3.Sm ($\chi^2_{25} = 22.98$, P = 0.58) nor Test 2.CL ($\chi^2_{30} = 27.89$, P = 0.58) is significant, ¹⁶⁶ therefore we recommend fitting a CJS model incorporating both a transience effect and a trap-¹⁶⁷ dependence effect and start the analysis from there. In passing, it is possible to calculate a GOF ¹⁶⁸ test for this new model by removing the two components Test 3.SR and Test 2.CT to the overall ¹⁶⁹ GOF test (Pradel et al. 2005):

```
170 ## [1] 0.6332861
```

This new model incorporating transient and trap-dependence effects fits the wolf data well $(\chi^2_{55} = 50.87, P = 0.63).$

To date, no GOF test exists for models with individual covariates (unless we discretize them and use groups), individual time-varying covariates (unless we treat them as states) or temporal covariates; therefore, these covariates should be removed from the dataset before using R2ucare. For groups, we recommend treating the groups separately (see e.g. the example in the help file for overall_CJS).

Goodness-of-fit tests for the Arnason-Schwarz model 178

We now wish to assess the GOF of the Arnason-Schwarz model to a dataset on Canada Geese 179 (Branta canadensis) (Pradel et al. 2005). Briefly, the data consist of capture histories for 28,849 180 individuals marked and re-observed at wintering locations in the US between 1984 and 1986. 181

We first read in the geese data that are provided with the package: 182

```
geese = system.file("extdata", "geese.inp", package = "R2ucare")
geese = read_inp(geese)
```

We then get the matrix and number of CR encounter histories: 183

```
geese.hist = geese$encounter_histories
geese.freq = geese$sample_size
```

Then we assess the quality of fit of the Arnason-Schwarz model to the geese CR data with 184 the overall_JMV function. Beware that it takes a minute or so to run the test because an iterative 185 optimization procedure is involved to perform Test M.ITEC and Test M.LTEC (Pradel et al. 2003) 186 that is repeated several times to try and avoid local minima. 187

overall_JMV(geese.hist,geese.freq)

188	##			chi2	degree_of_freedo	om p_value	э
189	## Gof	test for	JMV model:	982.589	19	97 (С

The null hypothesis that the Arnason-Schwarz provides an adequate fit to the data is clearly 190 rejected ($\chi^2_{197} = 982.59$, P < 0.01). In a second step, we further explore each component of the 191 overall test: 192

test3Gsr(geese.hist,geese.freq,verbose=FALSE) # transience

\$test3Gsr 193

195

df stat 194 p_val ## 117.753 12.000 0.000

test3Gsm(geese.hist,geese.freq,verbose=FALSE)

- 196 ## \$test3Gsm
- 197 ## stat df p_val
- 198 ## 302.769 119.000 0.000

test3Gwbwa(geese.hist,geese.freq,verbose=FALSE) # memory

- 199 ## \$test3Gwbwa
- 200 ## stat df p_val
- 201 ## 472.855 20.000 0.000

testMitec(geese.hist,geese.freq,verbose=FALSE) # short-term trap-dependence

- 202 ## \$testMitec
- 203 ## stat df p_val
- 204 ## 68.233 27.000 0.000

testMltec(geese.hist,geese.freq,verbose=FALSE) # long-term trap-dependence

- 205 ## \$testMltec
- 206 ## stat df p_val
- 207 ## 20.982 19.000 0.338

It appears that all components are significant but the test for a long-term trap-dependence effect. By setting the verbose argument to TRUE (by default argument), one could closely examine the individual contingency tables and better understand the reasons for the departure to the null hypotheses. For example, let us redo the test for transience Test 3.GSR:

test3Gsr(geese.hist,geese.freq,verbose=TRUE)

212 ## \$test3Gsr

213 ## stat df p_val

214 ## 117.753 12.000 0.000

215 ##

216 ## \$details

217	##		occasion	site	stat	df	p_val	test_perf
218	##	1	2	1	3.894777e-03	1	9.502378e-01	Chi-square
219	##	2	2	2	2.715575e-04	1	9.868523e-01	Chi-square
220	##	3	2	3	8.129814e+00	1	4.354322e-03	Chi-square
221	##	4	3	1	1.139441e+01	1	7.366526e-04	Chi-square
222	##	5	3	2	2.707742e+00	1	9.986223e-02	Chi-square
223	##	6	3	3	3.345916e+01	1	7.277633e-09	Chi-square
224	##	7	4	1	1.060848e+01	1	1.125702e-03	Chi-square
225	##	8	4	2	3.533332e-01	1	5.522323e-01	Chi-square
226	##	9	4	3	1.016778e+01	1	1.429165e-03	Chi-square
227	##	10	5	1	1.101349e+01	1	9.045141e-04	Chi-square
228	##	11	5	2	1.292013e-01	1	7.192616e-01	Chi-square
229	##	12	5	3	2.978513e+01	1	4.826802e-08	Chi-square

By inspecting the data.frame containing the details of the test, we see that there is no transientsin site 2.

232 Future directions

R2ucare allows evaluating the quality of fit of standard capture-recapture models for open populations. Future developments will focus on implementing goodness-of-fit tests for models combining different sources of data (McCrea et al. 2014) and residual-based diagnostics (Choquet et
al. 2013, Warton et al. 2017).

237 Availability

The current stable version of the package requires R 3.3.3 and is distributed under the GPL license.
It can be installed from CRAN and loaded into a R session as follows:

```
install.packages("R2ucare",dependencies=TRUE)
library("R2ucare")
```

The repository on GitHub https://github.com/oliviergimenez/R2ucare hosts the development version of the package, it can be installed as follows:

```
if(!require(devtools)) install.packages("devtools")
library("devtools")
install_github("oliviergimenez/R2ucare")
```

We also maintain a forum at https://groups.google.com/forum/#!forum/esurge_ucare to which questions can be asked.

244 Acknowledgments

Replication files (paper and code) are available on the first author's Github account (https://github.com/oliviergimenez).
This work was supported by a grant from the French National Research Agency, reference ANR-16-CE020007. We warmly thank E. Marboutin and J. Hestbeck for sharing the wolf and geese datasets, respectively.

248 Authors' contributions

OG, JDL and RP conceived the ideas and designed methodology; OG, JDL, RC and RP wrote the code; OG
and RP led the writing of the manuscript. All authors contributed critically to the drafts and gave final
approval for publication.

252 References

- Bromaghin, J. F., T. L. McDonald, and S. C. Amstrup (2013) Plausible combinations: An improved method to
 evaluate the covariate structure of Cormack-Jolly-Seber mark-recapture models. *Open Journal of Ecology*3: 11-22.
- Choquet, R., Reboulet, A.-M., Lebreton, J.-D., Gimenez, O., and R. Pradel. (2005). U-CARE 2.2 user's
 manual. CEFE, UMR 5175, Montpellier.
- ²⁵⁸ Choquet, R., Lebreton, J.-D., Gimenez, O., Reboulet, A.-M., and R. Pradel. (2009). U-CARE: Utilities for
- ²⁵⁹ performing goodness of fit tests and manipulating CApture-REcapture data. *Ecography* **32**: 1071-1074.

- ²⁶⁰ Choquet, R., Rouan, L., Pradel, R. (2009). Program E–SURGE: A software application for fitting multievent
- ²⁶¹ models. Modeling Demographic Processes in Marked Populations. D. L. Thomson, E. G. Cooch and M.
- J. Conroy. Berlin, Germany, Springer. 3: 845-865.
- ²⁶³ Choquet, R., Carrie, C., Chambert, T. & Boulinier, T. (2013). Estimating transitions between states using
- measurements with imperfect detection: application to serological data. *Ecology* **94**: 2160-2165.
- ²⁶⁵ Cubaynes, S., C. Lavergne, E. Marboutin, and O. Gimenez (2012). Assessing individual heterogeneity us-
- ing model selection criteria: How many mixture components in capture-recapture models? *Methods in*
- *Ecology and Evolution* **3**: 564-573.
- ²⁶⁸ Fletcher, D., Lebreton, J.-D., Marescot, L., Schaub, M., Gimenez, O., Slooten, E. and S. Dawson (2012). Bias
- in estimation of adult survival and asymptotic population growth rate caused by undetected capture
- heterogeneity. *Methods in Ecology and Evolution* **3**: 206-216.
- Gimenez O., Choquet R. and J.-D. Lebreton (2003). Parameter redundancy in multistate capture-recapture
 models. *Biometrical Journal* 45: 704-722.
- Gimenez, O., Cam, E., and J.-M. Gaillard (2017). Individual heterogeneity and capture-recapture models: what, why and how? *Oikos*. In press. doi: 10.1111/oik.04532.
- 275 Guéry, L., Descamps, S., Pradel, R., Hanssen, S. A., Erikstad, K. E., Gabrielsen, G. W., Gilchrist, H. G. and

²⁷⁶ Bêty, J. (2017). Hidden survival heterogeneity of three Common eider populations in response to climate

- fluctuations. Journal of Animal Ecology 86: 683–693.
- ²⁷⁸ Jeyam, A., R. S. McCrea, T. Bregnballe, M. Frederiksen, and R. Pradel (2017). A test of positive association
- for detecting heterogeneity in capture for capture-recapture data. Submitted to *Journal of Agricultural*, *Biological*, and *Environmental Statistics*.
- Laake, J. L. (2013). RMark: An R Interface for Analysis of Capture-Recapture Data with MARK. AFSC
 Processed Rep 2013-01, 25p. Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way
 NE, Seattle WA 98115.
- Laake, J. L., Johnson, D. S. and Conn, P. (2013). marked: An R package for maximum-likelihood and MCMC
 analysis of capture-recapture data. *Methods in Ecology and Evolution* 4: 885-890.
- Lebreton, J.-D. et al. (1992). Modeling survival and testing biological hypotheses using marked animals: a
 unified approach with case studies. *Ecological Monographs* 62: 67-118.
- 288 McCrea, R. S., B. J. T. Morgan, R. Pradel (2014). Diagnostic Goodness-of-Fit Tests for Joint Recapture and

- 289 Recovery Models. Journal of Agricultural, Biological, and Environmental Statistics 19: 338-356.
- Péron, G., Crochet, P.A.C., Choquet, R., Pradel, R., Lebreton, J.-D. and O. Gimenez. (2010). Capture-
- recapture models with heterogeneity to study survival senescence in the wild. *Oikos* **119**: 524-532.
- 292 Péron, G., J.-M. Gaillard, C. Barbraud, C. Bonenfant, A. Charmantier, R. Choquet, T. Coulson, V. Grosbois,
- A. Loison, G. Marzolin, N. Owen-Smith, D. Pardo, F. Plard, R. Pradel, C. Toïgo, O. Gimenez (2016).
- Evidence of reduced individual heterogeneity in adult survival of long-lived species. *Evolution* **70**: 2909 2914.
- Pollock, K., J. Hines, J. Nichols (1985). Goodness-of-Fit Tests for Open Capture-Recapture Models. *Biomet- rics* 41: 399-410.
- ²⁹⁸ Pradel, R. (1993). Flexibility in Survival analysis from recapture data: Handling trap-dependence. Pages
- 299 29–37 in Lebreton & North, editors. *Marked individuals in the study of bird population*. Birkhaüser Verlag,
 300 Basel, Switzerland.
- Pradel, R., Hines, J. E., Lebreton, J.–D. & Nichols, J. D. (1997). Capture–recapture survival models taking
 account of transients. *Biometrics* 53: 60–72.
- Pradel R., Wintrebert C.M.A. and Gimenez O. (2003). A proposal for a goodness-of-fit test to the Arnason Schwarz multisite capture-recapture model. *Biometrics* 59: 43-53.
- Pradel, R., Gimenez O. and J.-D. Lebreton (2005). Principles and interest of GOF tests for multistate capture recapture models. *Animal Biodiversity and Conservation* 28: 189–204.
- Pradel R, Sanz-Aguilar A (2012) Modeling Trap-Awareness and Related Phenomena in Capture-Recapture
 Studies. *PLoS ONE* 7: e32666.
- R Development Core Team (2014) *R: A Language and Environment for Statistical Computing*. R Foundation for
 Statistical Computing, Vienna, Austria.
- 311 Spendelow, J. A., D. Monticelli, J. D. Nichols, J. E. Hines, I. C. T. Nisbet, G. Cormons, H. Hays, J. J. Hatch,
- and C. S. Mostello (2016). Roseate Tern breeding dispersal and fidelity: responses to two newly restored
- colony sites. *Ecosphere* **7**: e01510.
- Supp, S. R., D. N. Koons, and S. K. M. Ernest (2015). Using life history trade-offs to understand coretransient structuring of a small mammal community. *Ecosphere* 6: 187.
- ³¹⁶ Warton, D. I., J. Stoklosa, G. Guillera-Arroita, D. I. MacKenzie and A. H. Welsh (2017). Graphical diagnostics

- for occupancy models with imperfect detection. *Methods in Ecology and Evolution* **8**: 408-419.
- 318 White, G. C. (2002). Discussant: The Use of Auxiliary Variables in Capture-Recapture Modeling: An
- ³¹⁹ Overview. *Journal of Applied Statistics* **29**: 103-106.