APPLICATION

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

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Abstract

1. Assessing the quality of fit of a statistical model to data is a necessary step for conducting safe inference.
2. 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.

KEYWORDS
Arnason–Schwarz, capture–mark–recapture, Cormack–Jolly–Seber, model validation, `R2ucare`

1 | 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; Lebreton, Nichols, Barker, Pradel, & Spendelow, 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 (CJS) 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). Multi-state CR models, and the Arnason–Schwarz 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, Koons, & Ernest, 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 families of methods exist to perform goodness-of-fit (GOF) tests for CR models. First, an omnibus test of the null hypothesis that a given model fits the data adequately can be conducted using resampling methods and the deviance as a metric (White, 2002). However, when the null hypothesis is rejected, this omnibus approach does not inform about an alternative model that could be fitted. Second, specialized tests have been built to address biologically meaningful causes of departure from the null hypothesis. A global test for single- and multi-state CR models is decomposed into several interpretable components based on contingency tables, for example the presence of transients (Pradel, Hines, Lebreton, & Nichols, 1997; Pradel, Wintrebert, & Gimenez, 2003) or that for trap-dependence (Pradel, 1993; Pradel et al., 2003). These GOF tests are implemented in the Windows application U-CARE (Choquet, Lebreton, Gimenez, Reboulet, & Pradel, 2009; Choquet, Rouan, & Pradel, 2009).

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` provides 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 wolves in France for single-state models and geese in the United States for multi-state models.

2 | 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. More liberal models require more information to be fitted (there are more parameters to estimate) but also 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 assumptions. The implementation retained in `R2ucare` builds on the optimal approach originally devised by Pollock, Hines, and Nichols (1985) and later modified by Pradel (1993). It is based on contingency tables and aims at testing with chi-squared tests (and Fisher's exact tests when needed) for transients and trap-dependence. These aspects are examined specifically in two independent component tests called, respectively, `Test 3.SR` and `Test 2.CT`. The component tests directed at transients and trap-dependence actually address features of the data that are consequences of, respectively, the presence of transients and trap-dependence, so that these features may also be caused by other, completely different phenomena. They do verify, respectively, that:

- Newly encountered individuals have the same chance to be later reobserved as recaptured (previously encountered) individuals; this is the null hypothesis of `Test 3.SR`.
- Missed individuals have the same chance to be recaptured at the next occasion as currently captured individuals; this is the 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 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.

Interestingly, these two components provide formal tests for comparing the CJS model with more general models, namely a model with an interaction between age (2 classes) and time in the survival probability for `Test 3.SR` (Pradel et al., 1997) and a model allowing for a different recapture probability of individuals just released for `Test 2.CT` (Pradel, 1993).

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:

- Among those individuals seen again, when they were seen does not differ among previously and newly marked individuals; this is the null hypothesis of `Test 3.Sm`.

- There is no difference in the timing of reencounters between the individuals encountered and not encountered at occasion i, conditional on presence at both occasions i and $i + 2$; this is the null hypothesis of `Test 2.CL`.

Data are generally sparse for these components and scattered over many occasions. Despite the implementation of some automatic pooling (see Choquet, Reboulet, Lebreton, Gimenez, & Pradel, 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 solutions in most cases.

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

- Newly encountered individuals have the same chance to be later reobserved as recaptured (i.e. previously encountered) individuals; this is the null hypothesis of `Test 3.GSR` which is the exact equivalent of `3.SR`.
- Individuals currently in the same state, whether captured or missed, have the same chance to be recaptured in each state at the next occasion; this is the 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 observed state at the most recent capture; this is the 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 previously encountered, whereas `Test M.LTEC` contrasts missed and encountered individuals. Fortunately, these components play a secondary role as they are usually not significant alone.

For more details about the theory of GOF testing for CR models, we strongly encourage users to read Pradel, Gimenez, and Lebreton (2005) and Cooch and White (2006).
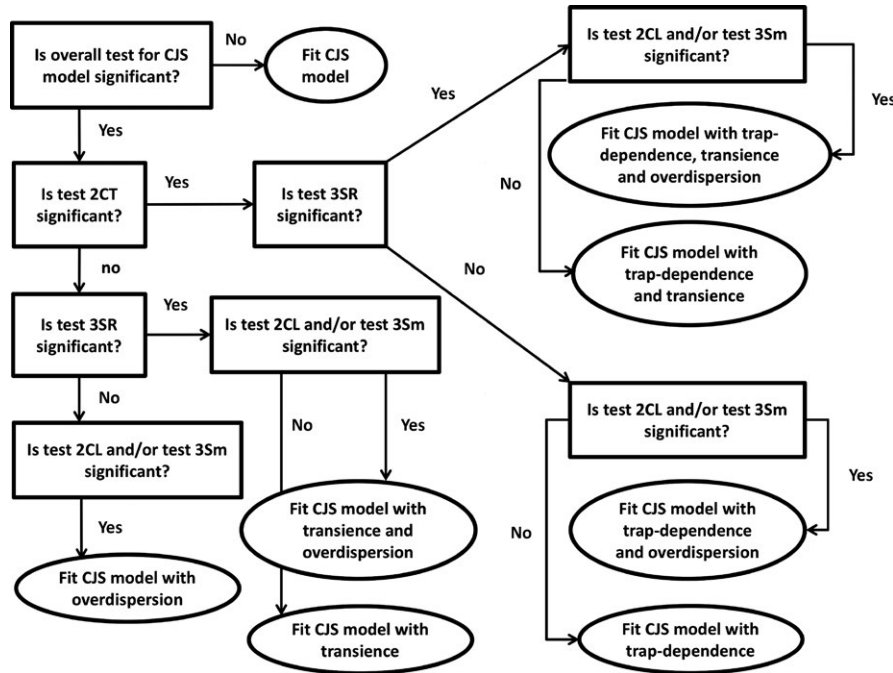
FIGURE 1 Decision tree to navigate towards testing the fit of single site/state capture–recapture models, with the Cormack–Jolly–Seber (CJS) model as a reference. Questions are in the rectangles, actions in the ellipses. We start by asking the question in the top-left corner. The coefficient of overdispersion 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, McCrea, Bregnballe, Frederiksen, and Pradel (2017) developed a formal test for the same purpose. Cubaynes, Lavergne, Marboutin, and Gimenez (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 trap-dependence or an effect of heterogeneity, we refer to Pradel et al. (1997), Pradel and Sanz-Aguilar (2012; see also Gimenez, Choquet, & Lebreton, 2003; Pradel, 1993) and Gimenez, Cam, and Gaillard (2018) respectively

3 | 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 possible with the `U-CARE` (Choquet, Lebreton , et al., 2009; Choquet, Rouan, 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, Johnson, & Conn, 2013) or to carry out simulations to assess statistical power (e.g. Bromaghin, McDonald, & Amstrup, 2013; Fletcher et al., 2012).

4 | GOODNESS-OF-FIT TESTS FOR SINGLE-SITE/STATE MODELS

We illustrate the use of `R2ucare` to assess the GOF of the CJS model to a dataset on wolves (*Canis lupus*) in France (e.g., Fletcher et al., 2012). Briefly, the data consist of capture histories for 160 individuals, partitioned into 35 3-month intervals (from spring 1995 to autumn 2003).

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 accommodate 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, Lebreton, et al., 2009; Choquet, Rouan, et al., 2009). The wolf dataset has the `MARK` format, therefore:

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

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 using the function `overall _ CJS`:

```
overall_CJS(ch,n)
##                          chi2 degree_of_freedom p_value
## Gof test for CJS model: 180.73              115       0
```

TABLE 1 The main functions of `R2ucare` and their description. See main text for more details

Function	Description
`marray`	build a m-array for single-site/state capture–recapture data
`multimarray`	build 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 into individual ones
`read_inp`	read MARK formatted files
`read_headed`	read E-SURGE formatted files
`test3sr`	implement `Test 3.SR` for single-site/state models (presence of transients)
`test3sm`	implement `Test 3.Sm` for single-site/state models
`test2ct`	implement `Test 2.CT` for single-site/state models (presence of trap-dependence)
`test2cl`	implement `Test 2.CL` for single-site/state models
`test3Gsr`	implement `Test 3.GSR` for multi-site/state models (presence of transients)
`test3Gsm`	implement `Test 3.GSm` for multi-site/state models
`test3Gwbwa`	implement `Test WBWA` for multi-site/state models (presence of memory)
`testMitec`	implement `Test M.ITEC` for multi-site/state models (presence of trap-dependence)
`testMltec`	implement `Test M.LTEC` for multi-site/state models

Clearly, the CJS model does not fit the data well (χ^2_{115}=180.73, $p<.01$). We then test for an effect of trap-dependence:

```
test2ct(ch,n,verbose = FALSE)
```

```
## $test2ct
##      stat       df     p_val sign_test
##    64.451   31.000     0.000    -5.641
```

`Test 2.CT` is significant ($\chi^2_{31} = 64.45$, $p<.01$). We also provide the signed square root (`sign_test`) of the Pearson chi-square statistic as a directional test of the null hypothesis (Pradel et al., 2005), which is negative when there is an excess of individuals encountered at a given occasion among the individuals encountered at the previous occasion.

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

```
test3sr(ch,n,verbose = FALSE)
```

```
## $test3sr
##      stat       df     p_val sign_test
##    65.414   29.000     0.000     5.037
```

`Test 3.SR` is also significant ($\chi^2_{29} = 65.41$, $p<.01$). We also provide the signed square root (`sign_test`) of the Pearson chi-square statistic (Pradel et al., 2005), which is positive when there is an excess of never seen again among the newly marked.

Navigating through the decision tree in Figure 1 suggests we should perform the two remaining tests:

```
test3sm(ch,n,verbose = FALSE)
```

```
## $test3sm
##      stat       df    p_val
##    22.977   25.000    0.579
```

```
test2cl(ch,n,verbose = FALSE)
```

```
## $test2cl
##      stat       df    p_val
##    27.888   30.000    0.576
```

Neither `Test 3.Sm` ($\chi^2_{25} = 22.98$, $p=.58$) nor `Test 2.CL` ($\chi^2_{30} = 27.89$, $p=.58$) is significant, therefore we recommend fitting a CJS model incorporating both a transience effect and a trap-dependence effect and start the analysis from there. In passing, it is possible to calculate a GOF test for this new model by removing the two components `Test 3.SR` and `Test 2.CT` to the overall GOF test (Pradel et al., 2005):

```
# substract the components 3SR and 2CT to the CJS test statistic
stat_new = overall_CJS(ch,n)$chi2 - (test3sr(ch, n)$test3sr[[1]]
                                    + test2ct(ch, n)$test2ct[[1]])
# calculate degree of freedom associated with the new test
    statistic
df_new = overall_CJS(ch,n)$degree_of_freedom -
    (test3sr(ch, n)$test3sr[[2]] + test2ct(ch, n)
        $test2ct[[2]])
# compute p-value
1 - pchisq(stat_new, df_new)
```

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

This new model incorporating transient and trap-dependence effects fits the wolf data well ($\chi^2_{55} = 50.87$, $p=.63$).

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`).

5 | GOODNESS-OF-FIT TESTS FOR THE ARNASON–SCHWARZ MODEL

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

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

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

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

```
ch = geese$encounter_histories
n = geese$sample_size
```

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

```
overall_JMV(ch,n)

##                                 chi2 degree_of_freedom p_value
## Gof test for JMV model: 982.594                   197        0
```

The null hypothesis that the Arnason -Schwarz provides an adequate fit to the data is clearly rejected (χ^2 197 = 982.59, P < .01.). In a second step, we further explore each component of the overall test:

```
test3Gsr(ch,n,verbose=FALSE) # transience

## $test3Gsr
##    stat     df   p_val
## 117.753  12.000  0.000

test3Gsm(ch,n,verbose=FALSE)

## $test3Gsm
##    stat     df   p_val
## 302.769 119.000  0.000

test3Gwbwa(ch,n,verbose=FALSE) # memory

## $test3Gwbwa
##    stat     df   p_val
## 472.855  20.000  0.000

testMitec(ch,n,verbose=FALSE) # short-term trap-dependence

## $testMitec
##   stat     df p_val
## 68.225 27.000 0.000

testMltec(ch,n,verbose=FALSE) # Long-term trap-dependence

## $testMltec
##   stat     df p_val
## 20.991 19.000 0.337
```

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(ch,n,verbose=TRUE)

## $test3Gsr
##    stat     df   p_val
## 117.753  12.000  0.000
##
## $details
##   occasion site        stat df       p_val  test_perf
## 1         2    1 3.894777e-03  1 9.502378e-01 Chi-square
## 2         2    2 2.715575e-04  1 9.868523e-01 Chi-square
## 3         2    3 8.129814e+00  1 4.354322e-03 Chi-square
## 4         3    1 1.139441e+01  1 7.366526e-04 Chi-square
## 5         3    2 2.707742e+00  1 9.986223e-02 Chi-square
## 6         3    3 3.345916e+01  1 7.277633e-09 Chi-square
## 7         4    1 1.060848e+01  1 1.125702e-03 Chi-square
## 8         4    2 3.533332e-01  1 5.522323e-01 Chi-square
## 9         4    3 1.016778e+01  1 1.429165e-03 Chi-square
## 10        5    1 1.101349e+01  1 9.045141e-04 Chi-square
## 11        5    2 1.292013e-01  1 7.192616e-01 Chi-square
## 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 transients in site 2.

6 | 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, Morgan, & Pradel, 2014) and residual-based diagnostics (Choquet, Carrie, Chambert, & Boulinier, 2013; Warton, Stoklosa, Guillera-Arroita, MacKenzie, & Welsh, 2017).

7 | AVAILABILITY

The current stable version of the package requires R 3.4.3 and is distributed under the GPL license. It can be installed from CRAN (https://cran.r-project.org/web/packages/R2ucare/) 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.

AUTHORS' CONTRIBUTIONS

O.G., J .- D.L. and R.P. conceived the ideas and designed methodology; O.G., J .- D.L., R.C. and R.P. wrote the code; O.G. and R.P. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

This article does not contain data

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REFERENCES

Bromaghin, J. F., McDonald, T. L., & Amstrup, S. C. (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. https://doi.org/10.4236/oje.2013.31002

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. https://doi.org/10.1890/12-1849.1

Choquet, R., Lebreton, J.-D., Gimenez, O., Reboulet, A.-M., & Pradel, R. (2009). U-CARE: Utilities for performing goodness of fit tests and manipulating CApture-REcapture data. *Ecography*, *32*, 1071–1074. https://doi.org/10.1111/j.1600-0587.2009.05968.x

Choquet, R., Reboulet, A.-M., Lebreton, J.-D., Gimenez, O., & Pradel, R. (2005). *U-CARE 2.2 user's manual*. Montpellier: CEFE, UMR 5175.

Choquet, R., Rouan, L., & Pradel, R. (2009). Program E–SURGE: A software application for fitting multievent models. In D. L. Thomson, E. G. Cooch, M. J. Conroy (Eds.), *Modeling demographic processes in marked populations* (Vol. 3, pp. 845–865). Berlin, Germany: Springer.

Cooch, E., & White, G. (2006). Program MARK: A gentle introduction. Retrieved from http://www.phidot.org/software/mark/docs/book/

Cubaynes, S., Lavergne, C., Marboutin, E., & Gimenez, O. (2012). Assessing individual heterogeneity using model selection criteria: How many mixture components in capture-recapture models? *Methods in Ecology and Evolution*, *3*, 564–573. https://doi.org/10.1111/j.2041-210X.2011.00175.x

Fletcher, D., Lebreton, J.-D., Marescot, L., Schaub, M., Gimenez, O., Slooten, E., & Dawson, S. (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. https://doi.org/10.1111/j.2041-210X.2011.00137.x

Gimenez, O., Cam, E., & Gaillard, J.-M. (2018). Individual heterogeneity and capture-recapture models: What, why and how? *Oïkos*, *127*, 664–686. https://doi.org/10.1111/oik.04532

Gimenez, O., Choquet, R., & Lebreton, J.-D. (2003). Parameter redundancy in multistate capture-recapture models. *Biometrical Journal*, *45*, 704–722. https://doi.org/10.1002/(ISSN)1521-4036

Guéry, L., Descamps, S., Pradel, R., Hanssen, S. A., Erikstad, K. E., Gabrielsen, G. W., ... Bêty, J. (2017). Hidden survival heterogeneity of three Common eider populations in response to climate fluctuations. *Journal of Animal Ecology*, *86*, 683–693. https://doi.org/10.1111/1365-2656.12643

Jeyam, A., McCrea, R. S., Bregnballe, T., Frederiksen, M., & Pradel, R. (2017). A test of positive association for detecting heterogeneity in capture for capture-recapture data. *Journal of Agricultural, Biological, and Environmental Statistics*, *23*, 1–9.

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., & 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. https://doi.org/10.1111/2041-210X.12065

Lebreton, J.-D., Burnham, K. P., Clobert, J., Anderson, D. R. (1992). Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. *Ecological Monographs*, *62*, 67–118. https://doi.org/10.2307/2937171

Lebreton, J. D., Nichols, J. D., Barker, R. J., Pradel, R., Spendelow, J. A. (2009). Modeling individual animal histories with multistate capture–recapture models. *Advances in Ecological Research*, *41*, 87–173.

McCrea, R. S., Morgan, B. J. T., & Pradel, R. (2014). Diagnostic goodness-of-fit tests for joint recapture and recovery models. *Journal of Agricultural, Biological, and Environmental Statistics*, *19*, 338–356. https://doi.org/10.1007/s13253-014-0174-1

Péron, G., Crochet, P. A. C., Choquet, R., Pradel, R., Lebreton, J.-D., & Gimenez, O. (2010). Capture-recapture models with heterogeneity to study survival senescence in the wild. *Oïkos*, *119*, 524–532.

Péron, G., Gaillard, J.-M., Barbraud, C., Bonenfant, C., Charmantier, A., Choquet, R., ... Gimenez, O. (2016). Evidence of reduced individual heterogeneity in adult survival of long-lived species. *Evolution*, *70*, 2909–2914. https://doi.org/10.1111/evo.13098

Pollock, K., Hines, J., & Nichols, J. (1985). Goodness-of-fit tests for open capture-recapture models. *Biometrics*, *41*, 399–410. https://doi.org/10.2307/2530865

Pradel, R. (1993). Flexibility in Survival analysis from recapture data: Handling trap–dependence. In J. D. Lebreton, P. M. North (Eds.), *Marked individuals in the study of bird population* (pp. 29–37). Basel, Switzerland: Birkhäuser Verlag.

Pradel, R., Gimenez, O., & Lebreton, J.-D. (2005). Principles and interest of GOF tests for multistate capture-recapture models. *Animal Biodiversity and Conservation*, *28*, 189–204.

Pradel, R., Hines, J. E., Lebreton, J.-D., & Nichols, J. D. (1997). Capture–recapture survival models taking account of transients. *Biometrics*, *53*, 60–72. https://doi.org/10.2307/2533097

Pradel, R., & Sanz-Aguilar, A. (2012). Modeling trap-awareness and related phenomena in capture-recapture studies. *PLoS ONE*, *7*, e32666. https://doi.org/10.1371/journal.pone.0032666

Pradel, R., Wintrebert, C. M. A., & Gimenez, O. (2003). A proposal for a goodness-of-fit test to the Arnason-Schwarz multisite capture-recapture model. *Biometrics*, *59*, 43–53. https://doi.org/10.1111/1541-0420.00006

R Development Core Team (2014). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Spendelow, J. A., Monticelli, D., Nichols, J. D., Hines, J. E., Nisbet, I. C. T., Cormons, G., ... Mostello, C. S. (2016). Roseate tern breeding dispersal and fidelity: Responses to two newly restored colony sites. *Ecosphere*, *7*, e01510. https://doi.org/10.1002/ecs2.1510

Supp, S. R., Koons, D. N., & Ernest, S. K. M. (2015). Using life history trade-offs to understand core-transient structuring of a small mammal community. *Ecosphere*, *6*, 187. https://doi.org/10.1890/ES15-00239.1

Warton, D. I., Stoklosa, J., Guillera-Arroita, G., MacKenzie, D. I., & Welsh, A. H. (2017). Graphical diagnostics for occupancy models with imperfect detection. *Methods in Ecology and Evolution*, *8*, 408–419. https://doi.org/10.1111/2041-210X.12761

White, G. C. (2002). Discussant: The use of auxiliary variables in capture-recapture modeling: An overview. *Journal of Applied Statistics*, *29*, 103–106. https://doi.org/10.1080/02664760120108476