

**multimark**: an R package for analysis of  
capture-recapture data consisting of multiple  
“non-invasive” marks

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RUNNING HEAD: **multimark** mark-recapture package

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## Summary

1. I describe an open source R package, **multimark**, for estimation of survival and abundance from capture-mark-recapture data consisting of multiple “non-invasive” marks. Non-invasive marks include natural pelt or skin patterns, scars, and genetic markers that enable individual identification in lieu of physical capture, and thus apply to any species that can be individually identified from visual or genetic sampling surveys. **multimark** provides a means for combining and jointly analyzing encounter histories from multiple non-invasive sources that otherwise cannot be reliably matched (e.g. left- and right-sided photos of bilaterally asymmetrical individuals).
2. **multimark** is currently capable of fitting open population Cormack-Jolly-Seber (CJS) and closed population abundance models with up to two mark types using Bayesian Markov chain Monte Carlo (MCMC) methods. Although originally motivated by the challenges posed by multiple non-invasive marks, **multimark** can also be used for Bayesian analyses of conventional capture-recapture data consisting of a single mark type.
3. Some package features include: (i) general model specification using formulas already familiar to most R users, (ii) ability to include temporal, behavioural, cohort, and individual heterogeneity effects in detection and survival probabilities, (iii) Bayesian multimodel inference using reversible jump MCMC, and (iv) data simulation capabilities for power analyses and assessing model performance.
4. I demonstrate use of **multimark** using left- and right-sided encounter histories for bobcats (*Lynx rufus*) collected from remote single-camera stations in southern Cal-

ifornia. In this example, there is evidence of a behavioural effect (i.e. trap “happy” response) that is otherwise indiscernible using traditional single-sided analyses.

5. The package will be most useful to ecologists seeking stronger inferences by combining different sources of mark-recapture data that are difficult (or impossible) to reliably reconcile, particularly with the sparse datasets typical of rare or elusive species for which non-invasive sampling techniques are most commonly employed. Addressing deficiencies in currently available software, **multimark** also provides a user-friendly interface for performing Bayesian multimodel inference using capture-recapture data consisting of a single conventional mark or multiple non-invasive marks.

**Key-words** Bayesian multimodel inference, capture-recapture, Cormack-Jolly-Seber (CJS), latent multinomial, mark-recapture, Markov chain Monte Carlo (MCMC), multiple lists, population size

## 1 Introduction

“Non-invasive” capture-recapture sampling techniques are becoming commonplace for monitoring animal populations (e.g. Hammond 1990; Lukacs & Burnham 2005; O’Connell *et al.* 2010). Examples of non-invasive marks include natural pelt or skin patterns, scars, and genetic markers that enable individual identification in the absence of physical capture. Capture-recapture methods based on non-invasive marks have been applied to diverse taxa, including sharks (e.g. Holmberg *et al.* 2008), reptiles (e.g. Nair *et al.* 2012), ursids (e.g. Dreher *et al.* 2007), felids (e.g. Karanth & Nichols 1998; Ruell *et al.* 2009), and marine mammals (e.g. Hammond 1990; Wilson

10 *et al.* 1999; Madon *et al.* 2011). While non-invasive capture-recapture methods have  
11 many advantages related to financial cost and animal welfare, they also pose new  
12 difficulties such as animal misidentification (Wright *et al.* 2009; Yoshizaki *et al.* 2009;  
13 Link *et al.* 2010; Morrison *et al.* 2011) and the complexity of multiple types of marks  
14 (Corkrey *et al.* 2008; Madon *et al.* 2011; Bonner & Holmberg 2013; McClintock *et al.*  
15 2013).

16 Multiple marks can arise from sighting or camera surveys of species with natu-  
17 ral mark patterns that are bilaterally asymmetrical (e.g. cetaceans, felids) or from  
18 multiple sources of non-invasive capture-recapture data being collected concurrently  
19 (e.g. faecal DNA sampling and visual surveys). With multiple marks, an encounter  
20 history is produced for each individual and mark type, but there is typically no reli-  
21 able means to match them (unless each mark type is simultaneously observed at least  
22 once for every encountered individual). Because the number of unique individuals  
23 encountered must be known for standard capture-recapture analyses of population  
24 abundance (or related demographic parameters), the typical approach is to conduct  
25 separate analyses for each mark type and compare the results (e.g. Wilson *et al.*  
26 1999; Berrow *et al.* 2012; Nair *et al.* 2012). However, given that sample sizes (and  
27 precision) may be considerably reduced, this is not as efficient as conducting an inte-  
28 grated analysis utilizing encounter histories arising from all mark types (McClintock  
29 *et al.* 2013). Additional costs of conducting separate analyses for each mark type  
30 include a limited ability to explore models with behavioural or cohort effects, and, for  
31 capture-recapture models that condition on first encounter, a forfeiting of informa-  
32 tion from histories with the (apparent) first encounter occurring on the last sampling  
33 occasion. These limitations can be particularly important for the sparse datasets

34 typical of rare and elusive populations for which non-invasive sampling techniques  
35 are most commonly employed.

36 Bonner & Holmberg (2013) and McClintock *et al.* (2013) recently developed meth-  
37 ods for performing integrated analyses of capture-recapture data consisting of mul-  
38 tiple non-invasive marks. However, to my knowledge, their approaches have yet  
39 to be applied by practitioners. This is certainly not due to a lack of appropriate  
40 data (e.g. Wilson *et al.* 1999; Holmberg *et al.* 2008; Madon *et al.* 2011; Berrow  
41 *et al.* 2012; Nair *et al.* 2012), and is likely attributable to the mathematical and  
42 computational complexity of the models, as well as a lack of user-friendly software  
43 for implementing them. Generalized software for performing Bayesian multimodel  
44 inference with capture-recapture data has also been lacking, thereby leaving these  
45 procedures largely inaccessible to non-statisticians (e.g. Brooks *et al.* 2000; Durban  
46 & Elston 2005; King & Brooks 2008; Royle 2008). These software needs were the  
47 motivation for **multimark**, an R (R Core Team 2013) package for Bayesian analysis  
48 of capture-recapture data consisting of multiple non-invasive marks.

49 After providing some additional background on capture-recapture with multiple  
50 marks, I briefly describe the models implemented in **multimark**. These currently in-  
51 clude open population Cormack-Jolly-Seber (CJS) and closed population abundance  
52 models (e.g. Williams *et al.* 2002) with up to two mark types. Although originally  
53 motivated by the challenges posed by multiple non-invasive marks, **multimark** can  
54 also be used for analyses of conventional capture-recapture data consisting of a single  
55 mark type. Using real and simulated data for illustration, I provide an overview of  
56 the workflow for the package and a new analysis of left- and right-sided encounter  
57 histories for bobcats (*Lynx rufus*) collected from remote single-camera stations in

southern California. Additional information, including help files, data, examples, and package usage is available by downloading the `multimark` package from CRAN (<http://cran.r-project.org>) or github (<https://github.com/bmcclintock/multimark>).

## 2 Description

### 2.1 Background

Capture-recapture data are typically represented by a collection of encounter histories  $\mathbf{Y} = \{\mathbf{y}_1, \mathbf{y}_2, \dots, \mathbf{y}_n\}$ , where each element of  $\mathbf{y}_i = (y_{i,1}, y_{i,2}, \dots, y_{i,T})$  indicates whether individual  $i$  was detected ( $y_{i,t} = 1$ ) or not detected ( $y_{i,t} = 0$ ) on each of  $t = 1, \dots, T$  sampling occasions. Typical analyses then proceed by formulating a likelihood conditional on the  $n$  unique individuals encountered (e.g. Williams *et al.* 2002). With two mark types, we instead have  $\tilde{\mathbf{Y}}_m = \{\tilde{\mathbf{y}}_{m_1}, \tilde{\mathbf{y}}_{m_2}, \dots, \tilde{\mathbf{y}}_{m_{n_m}}\}$  for  $m \in \{1, 2\}$ , where each element of  $\tilde{\mathbf{y}}_{m_i} = (\tilde{y}_{m_i,1}, \tilde{y}_{m_i,2}, \dots, \tilde{y}_{m_i,T})$  indicates individual  $i$  was detected ( $\tilde{y}_{m_i,t} = m$ ) or not detected ( $\tilde{y}_{m_i,t} = 0$ ), and  $n_m$  is the number of unique individuals encountered for mark type  $m$ . We focus on situations where it is difficult (or impossible) to reliably match individuals from  $\tilde{\mathbf{Y}}_1$  and  $\tilde{\mathbf{Y}}_2$ . In this case, although we know  $n \leq n_1 + n_2$ ,  $n$  is nevertheless unknown and standard capture-recapture analysis methods cannot be reliably used for simultaneous inference using both sources of data.

Depending on the mark types, it may sometimes be possible to observe both marks simultaneously. In this case, some of the encounter histories from  $\tilde{\mathbf{Y}}_1$  and  $\tilde{\mathbf{Y}}_2$  can be matched to unique individuals with certainty. For example, suppose images were collected during vessel-based line transect surveys of surfacing whales, where mark type 1 corresponds to patch patterns on the left side and mark type 2 corresponds

to patterns on the right side. If an individual happens to be photographed on both sides simultaneously on at least one sampling occasion, then the true encounter history for this individual would be known (i.e. left- and right-sided images could be matched). This results in an additional set of  $n_{known}$  observed encounter histories,  $\tilde{\mathbf{Y}}_{known} = \{\tilde{\mathbf{y}}_{known_1}, \tilde{\mathbf{y}}_{known_2}, \dots, \tilde{\mathbf{y}}_{known_{n_{known}}}\}$ , consisting of histories that are known with certainty (Table 1).

In essence, **multimark** facilitates the joint analysis of type 1 ( $\tilde{\mathbf{Y}}_1$ ), type 2 ( $\tilde{\mathbf{Y}}_2$ ), and known encounter histories ( $\tilde{\mathbf{Y}}_{known}$ ) while accounting for uncertainty in the number of unique individuals encountered using extensions of the methodology proposed by Bonner & Holmberg (2013) and McClintock *et al.* (2013). While the mathematical and computational details are complicated (and generally of little interest to ecologists), **multimark** performs these operations in the background and requires only simple data formatting and model specification formulas familiar to most R users.

## 2.2 Models

**multimark** currently includes open population Cormack-Jolly-Seber (CJS) and closed population abundance models (e.g. Williams *et al.* 2002). These Bayesian implementations are similar in spirit to the CJS model of Royle (2008) and the abundance model of King *et al.* (2015). Given the latent encounter histories ( $\mathbf{Y}$ ) that generated the observed encounter histories ( $\tilde{\mathbf{Y}}_1, \tilde{\mathbf{Y}}_2, \tilde{\mathbf{Y}}_{known}$ ), the likelihood for the CJS model with two mark types is

$$[\mathbf{Y} \mid \mathbf{p}, \boldsymbol{\delta}, \alpha, \phi, \mathbf{Z}] \propto \prod_{i=1}^n \prod_{t=C_i+1}^T \pi_{i,t} \quad (1)$$

**Table 1.** Latent encounter histories  $\mathbf{y}$  and the recorded histories  $(\tilde{\mathbf{y}}_1, \tilde{\mathbf{y}}_2, \tilde{\mathbf{y}}_{known})$  they generate for  $T = 2$  sampling occasions and two mark types, where  $\mathbf{y} = (y_1, y_2)$  for  $y_t \in \{0, 1, 2, 3, 4\}$ . Latent encounter histories are indexed by  $j = 1 + \sum_{t=1}^T y_t 5^{T-t}$ , where the encounter types indicate non-detection ( $y_t = 0$ ), type 1 encounter ( $y_t = 1$ ), type 2 encounter ( $y_t = 2$ ), non-simultaneous type 1 and type 2 encounter ( $y_t = 3$ ), and simultaneous type 1 and type 2 encounter ( $y_t = 4$ ). If simultaneous encounters are possible, these result in some  $\mathbf{y}$  being completely observable (as indicated by  $\tilde{\mathbf{y}}_{known}$ ).

$j$	$\mathbf{y}$	$\tilde{\mathbf{y}}_1$	$\tilde{\mathbf{y}}_2$	$\tilde{\mathbf{y}}_{known}$
1	00	..	..	..
2	01	01	..	..
3	02	..	02	..
4	03	01	02	..
5	04	..	..	04
6	10	10	..	..
7	11	11	..	..
8	12	10	02	..
9	13	11	02	..
10	14	..	..	14
11	20	..	20	..
12	21	01	20	..
13	22	..	22	..
14	23	01	22	..
15	24	..	..	24
16	30	10	20	..
17	31	11	20	..
18	32	10	22	..
19	33	11	22	..
20	34	..	..	34
21	40	..	..	40
22	41	..	..	41
23	42	..	..	42
24	43	..	..	43
25	44	..	..	44



$$\pi_{i,t} = \begin{cases} (1 - p_{i,t}) \phi_{i,t-1} q_{i,t} + (1 - \phi_{i,t-1}) (1 - q_{i,t}) & \text{if } y_{i,t} = 0 \text{ and } q_{i,t-1} = 1 \\ p_{i,t} \delta_1 \phi_{i,t-1} & \text{if } y_{i,t} = 1 \\ p_{i,t} \delta_2 \phi_{i,t-1} & \text{if } y_{i,t} = 2 \\ p_{i,t} (1 - \delta_1 - \delta_2) (1 - \alpha) \phi_{i,t-1} & \text{if } y_{i,t} = 3 \\ p_{i,t} (1 - \delta_1 - \delta_2) \alpha \phi_{i,t-1} & \text{if } y_{i,t} = 4 \\ 1 & \text{otherwise} \end{cases}$$

where  $C_i \in \{1, \dots, T\}$  is the time of first capture for individual  $i$ ,  $p_{i,t}$  is the detection probability for individual  $i$  during sampling occasion  $t$ ,  $\delta_m$  is the conditional probability of a type  $m$  encounter (given detection),  $\alpha$  is the conditional probability of a simultaneous type 1 and type 2 encounter (given both mark types detected),  $\phi_{i,t-1}$  is the survival probability between times  $t-1$  and  $t$ , and  $q_{i,t}$  is an indicator for whether individual  $i$  was alive ( $q_{i,t} = 1$ ) or not ( $q_{i,t} = 0$ ) during sampling occasion  $t$ . For added flexibility,  $p$  and  $\phi$  are modeled using the probit link function:

$$\Phi(p_{i,t}) = \mathbf{x}_t^{p'} \boldsymbol{\beta}^p + z_i^p$$

$$\Phi(\phi_{i,t}) = \mathbf{x}_t^{\phi'} \boldsymbol{\beta}^\phi + z_i^\phi$$

where  $\Phi()$  the cumulative distribution function of the standard normal density,  $\mathbf{x}_t^p$  and  $\mathbf{x}_t^\phi$  are row  $t$  of the design matrices for  $p$  and  $\phi$ ,  $\boldsymbol{\beta}^p$  and  $\boldsymbol{\beta}^\phi$  are the corresponding regression coefficients, and  $z_i^p \sim \mathcal{N}(0, \sigma_{z^p}^2)$  and  $z_i^\phi \sim \mathcal{N}(0, \sigma_{z^\phi}^2)$  are individual-level effects. The probit link is implemented for CJS models in `multimark` because it facilitates a Gibbs sampler in the spirit of Albert & Chib (1993) and Laake *et al.* (2013). We note that this model reduces to that of Laake *et al.* (2013) for conventional capture-recapture data with a single mark type when  $\delta_1 = 1$  and  $\delta_2 = 0$  for  $y_{i,t} \in \{0, 1\}$ .

Similarly, the likelihood for the closed population abundance model with two

110 mark types is

$$[\mathbf{Y} \mid \mathbf{p}, \boldsymbol{\delta}, \alpha, N] \propto \frac{1}{(p^*)^n} \prod_{i=1}^n \prod_{t=1}^T \pi_{i,t} \times \text{Binomial}(n; N, p^*) \quad (2)$$

$$\pi_{i,t} = \begin{cases} (1 - p_{i,t}) & \text{if } y_{i,t} = 0 \\ p_{i,t} \delta_1 & \text{if } y_{i,t} = 1 \\ p_{i,t} \delta_2 & \text{if } y_{i,t} = 2 \\ p_{i,t} (1 - \delta_1 - \delta_2) (1 - \alpha) & \text{if } y_{i,t} = 3 \\ p_{i,t} (1 - \delta_1 - \delta_2) \alpha & \text{if } y_{i,t} = 4 \\ 1 & \text{otherwise} \end{cases}$$

where  $N$  is the population size, and  $p^*$  is the probability that a randomly selected individual is detected at least once. As before, this model reduces to that for conventional capture-recapture data with a single mark type when  $\delta_1 = 1$  and  $\delta_2 = 0$  for  $y_{i,t} \in \{0, 1\}$ . For added flexibility,  $p$  is modeled using the logit link function:

$$\text{logit}(p_{i,t}) = \mathbf{x}_t^{p'} \boldsymbol{\beta}^p + z_i^p$$

such that

$$p^* = 1 - \int_{-\infty}^{\infty} \prod_{t=1}^T \left( 1 - \frac{1}{1 + \exp(-(\mathbf{x}_t^{p'} \boldsymbol{\beta}^p + z^p))} \right) \mathcal{N}(z^p; 0, \sigma_{z^p}^2) dz^p$$

111 Although a Gibbs sampler has been proposed for closed population models using the  
 112 probit link and a complete data likelihood (McClintock *et al.* 2014), this does not  
 113 apply to the “semi-complete” data likelihood in Eq. 2 (hence the traditional logit  
 114 link is used). The primary utility of **multimark** is finding the set of latent encounter  
 115 histories that are feasible given the observed encounter histories (sensu Link *et al.*  
 116 2010; Bonner & Holmberg 2013; McClintock *et al.* 2013, 2014). Given a feasible set  
 117 of latent encounter histories ( $\mathbf{Y}$ ), fitting capture-recapture models such as Eqs. 1 or

**Table 2.** Summary of three different types of multiple-mark data. The data differ in terms of the latent encounter types ( $y_t$ ) that are possible based on the conditional probability of a simultaneous type 1 and type 2 encounter,  $\alpha = \Pr(y_t = 4 | y_t = 3 \text{ or } y_t = 4)$ .

Data type	$y_t$	Constraints
“never”	$\{0, 1, 2, 3\}$	$\alpha = 0$
“sometimes”	$\{0, 1, 2, 3, 4\}$	$0 < \alpha < 1$
“always”	$\{0, 1, 2, 4\}$	$\alpha = 1$

118 2 is relatively straightforward.

## 119 3 Workflow

### 120 3.1 Multiple non-invasive marks

#### 121 3.1.1 Data formatting

122 There are three types of multiple-mark data that can be analyzed with `multimark`.  
123 These are the “never”, “sometimes”, and “always” data types, and they are named  
124 based on their respective probabilities of a simultaneous type 1 and type 2 encounter  
125 (Table 2). An example of the “never” data type is provided with `multimark` and  
126 includes 23 left-sided ( $\tilde{\mathbf{Y}}_1$ ) and 23 right-sided ( $\tilde{\mathbf{Y}}_2$ ) encounter histories for bobcats  
127 (*Lynx rufus*) collected from remote single-camera stations in southern California over  
128  $T = 8$  sampling periods between July 2006 and January 2007 (McClintock *et al.* 2013;  
129 Alonso *et al.* 2015).

130 `multimark` expects observed encounter history data to be a matrix with rows  
131 corresponding to individuals and columns corresponding to sampling occasions. Be-  
132 cause the bobcat data were collected from single-camera stations, simultaneous left-  
133 and right-sided encounters were not possible; hence  $\alpha = 0$  and the rows consist of  
134 either 0’s and 1’s or 0’s and 2’s:

```
> library(multimark)
> data(bobcat)
> head(bobcat)
```

	occ1	occ2	occ3	occ4	occ5	occ6	occ7	occ8
ID2	0	0	0	0	0	1	1	0
ID3	0	0	1	0	1	0	0	0
ID4	0	0	0	0	1	0	0	0
ID6	1	0	0	0	0	0	0	0
ID7	0	0	1	0	0	0	0	1
ID8	0	1	0	0	0	0	0	0

```
> tail(bobcat)
```

	occ1	occ2	occ3	occ4	occ5	occ6	occ7	occ8
ID49	0	0	2	0	0	0	0	0
ID50	0	0	2	0	0	0	0	0
ID51	0	0	0	2	0	0	0	0
ID52	0	0	0	0	2	0	0	0
ID53	0	0	0	0	0	2	0	0
ID54	0	0	0	0	0	0	2	0

135 The ordering of the rows is unimportant; the package automatically recognizes which  
 136 histories belong to  $\tilde{\mathbf{Y}}_1$ ,  $\tilde{\mathbf{Y}}_2$ , and, if applicable,  $\tilde{\mathbf{Y}}_{known}$ .

137 The `multimark` function `processdata()` performs all additional data formatting.  
 138 The basic inputs are the matrix of observed encounter histories (*Enc.Mat*) and the  
 139 data type (*data.type*):

```
> bobcatsetup <- processdata(Enc.Mat=bobcat,data.type="never")
```

140 This creates an object of class *multimarksetup* that includes everything needed for  
 141 model fitting and further analysis. In particular, `processdata()` calculates all of the  
 142 necessary ingredients for identifying the feasible set of latent encounter histories (for  
 143 technical details see Bonner & Holmberg 2013; McClintock *et al.* 2013). There is  
 144 also a feature enabling designation of individual encounter histories as known with

145 certainty despite no simultaneous type 1 and type 2 detections (i.e.  $y_{i,t} \neq 4 \forall t$ ),  
 146 a situation that can arise from a previous physical capture or concurrent telemetry  
 147 study (e.g. McClintock *et al.* 2013).

### 148 3.1.2 Model fitting

149 The package currently includes functions *multimarkCJS()* and *multimarkClosed()*  
 150 for fitting CJS and closed population models, respectively, with two mark types.  
 151 Use of these functions is perhaps best explained by example. To fit a simple closed  
 152 population model assuming constant detection probability using the default settings:

```
> bobcat.dot <- multimarkClosed(mms=bobcatsetup,  
+                               mod.p=~1)
```

153 Equivalently, *Enc.Mat* and *data.type* can be provided in lieu of the *mms* argument.

154 In this case, *processdata()* is called from within *multimarkClosed()*:

```
> bobcat.dot <- multimarkClosed(Enc.Mat=bobcat,data.type="never",  
+                               mod.p=~1)
```

155 This creates a list, *bobcat.dot*, containing the MCMC output for the model  
 156 (*bobcat.dot\$mcmc*). The MCMC output is of class *mcmc*, which should be familiar  
 157 to users of the R package *coda* (Plummer *et al.* 2006):

```
> summary(bobcat.dot$mcmc)

Iterations = 2001:12000
Thinning interval = 1
Number of chains = 1
Sample size per chain = 10000
```

1. Empirical mean and standard deviation for each variable,  
plus standard error of the mean:

Mean	SD	Naive SE	Time-series SE
------	----	----------	----------------

```

pbeta[(Intercept)] -1.2819 0.25944 0.0025944      0.02259
N                  35.4325 5.28704 0.0528704      0.30073
delta_1             0.4108 0.07927 0.0007927      0.01192
delta_2             0.4271 0.07923 0.0007923      0.01182

```

2. Quantiles for each variable:

```

                2.5%    25%    50%    75%   97.5%
pbeta[(Intercept)] -1.8239 -1.4505 -1.2746 -1.0989 -0.8016
N                  28.0000 32.0000 35.0000 38.0000 48.0000
delta_1             0.2518  0.3563  0.4138  0.4664  0.5590
delta_2             0.2671  0.3726  0.4304  0.4831  0.5752

```

```
> coda::effectiveSize(bobcat.dot$mcmc)
```

```

pbeta[(Intercept)]          N          delta_1          delta_2
      131.88674      309.07930      44.21238      44.90002

```

158 Here we can see posterior summaries for the default monitored parameters ( $\beta^p$ ,  $N$ ,  $\delta_1$ ,  $\delta_2$ ).

159 Based on the effective sample sizes, it's clear that the default chain length is inadequate for this example; a typical "rule of thumb" is effective sample sizes  $> 4000$  for  
 160 all quantities of interest.  
 161

162 Other common models for detection probability can be easily specified using  
 163 formulas for *mod.p*, including shorthands for time variation (*mod.p*=*~time*), temporal trends (*mod.p*=*~Time*), behavioural response to first capture (*mod.p*=*~c*),  
 164 and individual heterogeneity (*mod.p*=*~h*). Additive or interaction terms can be included (e.g. *mod.p*=*~time+c+h*, *mod.p*=*~Time+I(Time^2)*, *mod.p*=*~time\*c*). User-  
 165  
 166 specified temporal covariates in detection probability can also be used:  
 167

```

> dummy <- rnorm(ncol(bobcat)) # some fake temporal covariates
> bobcatsetup <- processdata(Enc.Mat=bobcat,data.type="never",
+                           covs=data.frame(cov1=dummy))
> bobcat.dummy_h <- multimarkClosed(mms=bobcatsetup,
+                                  mod.p=~cov1+h,
+                                  parms=c("pbeta","N","delta","sigma2_zp"))

```

168 The *covs* argument is a data frame used to enter discrete- or continuous-valued  
 169 temporal covariates, and *parms* specifies the parameters to monitor.

170 There are currently two options for specifying models for  $\delta$ , the default *mod.delta*=*~type*  
 171 (i.e.  $\delta_1 \neq \delta_2$ ), and *mod.delta*=*~1* (i.e.  $\delta_1 = \delta_2$ ). There are many additional arguments  
 172 for specifying the number (*nchains*) and length (*iter*) of chains, including burn-in  
 173 and adaptive periods. For potential improvements in mixing, the number of “moves”  
 174 used to update the feasible set of latent encounter histories at each iteration can be  
 175 user specified (*maxnumbasis*; see Appendix S1). The default priors are “uninforma-  
 176 tive”, but user-specified priors can be used for each parameter. Initial values can be  
 177 automatically generated or user specified for each parameter.

178 The function *multimarkCJS()* works in exactly the same fashion, with the only  
 179 notable difference being specification of models for  $\phi$  (in addition to  $p$  and  $\delta$ ). Al-  
 180 though CJS-specific data are not included with *multimark*, data can be simulated  
 181 using the *simdataCJS()* function (or *simdataClosed()* for closed populations):

```
> CJSdata <- simdataCJS(N=100,noccas=7,pbeta=-0.25,phibeta=1,delta_1=0.2,
+                        delta_2=0.5,alpha=0.5,sigma2_zphi=0.25,data.type="sometimes")
> Enc.Mat <- CJSdata$Enc.Mat
> head(Enc.Mat)
```

	[,1]	[,2]	[,3]	[,4]	[,5]	[,6]	[,7]
[1,]	2	0	4	0	0	0	0
[2,]	1	0	0	0	0	0	0
[3,]	1	0	0	0	0	0	0
[4,]	4	3	0	0	0	0	0
[5,]	1	0	0	0	0	0	0
[6,]	3	2	0	0	2	2	4

```
> CJSsetup <- processdata(Enc.Mat=Enc.Mat,data.type="sometimes")
> CJS.dot.h <- multimarkCJS(mms=CJSsetup,
+                            mod.p=~1,mod.delta=~type,mod.phi=~h,
+                            parms=c("pbeta","delta","alpha","phibeta","sigma2_zphi"),
```

```
+          nchains=2,iter=45000,burnin=5000)
> summary(CJS.dot.h$mcmc)
```

```
Iterations = 5001:45000
Thinning interval = 1
Number of chains = 2
Sample size per chain = 40000
```

1. Empirical mean and standard deviation for each variable,  
plus standard error of the mean:

	Mean	SD	Naive SE	Time-series SE
pbeta[(Intercept)]	-0.15140	0.13359	0.0004723	0.004430
phibeta[(Intercept)]	1.36590	0.28271	0.0009995	0.011139
alpha	0.41376	0.11629	0.0004111	0.002977
sigma2_zphi	0.03509	0.07353	0.0002600	0.003850
delta_1	0.19499	0.04631	0.0001637	0.001644
delta_2	0.61160	0.05175	0.0001829	0.001156

2. Quantiles for each variable:

	2.5%	25%	50%	75%	97.5%
pbeta[(Intercept)]	-0.400914	-0.244114	-0.1554	-0.06250	0.1200
phibeta[(Intercept)]	0.903728	1.167340	1.3335	1.52943	2.0162
alpha	0.206999	0.329973	0.4067	0.49071	0.6579
sigma2_zphi	0.002623	0.006893	0.0139	0.03306	0.2093
delta_1	0.109283	0.162635	0.1934	0.22540	0.2902
delta_2	0.508181	0.576891	0.6124	0.64722	0.7103

182 An additional feature for *multimarkCJS()* is simple specification of “age” and cohort  
183 effects for  $p$  ( $mod.p = \sim age$  and  $mod.p = \sim cohort$ ) and  $\phi$  ( $mod.phi = \sim age$  and  $mod.phi = \sim cohort$ ),  
184 which can be useful for investigating structure related to time since first capture and  
185 time of initial capture, respectively. These variables by default include a level for  
186 each unique age or cohort, but they can be binned to reduce the number of levels  
187 using additional arguments.



## 188 3.2 Single mark type

189 For conventional capture-recapture data consisting of a single mark type, encounter  
190 histories are formatted the same way but now consist solely of 1's (detections) and  
191 0's (non-detections). The package currently includes the functions *markCJS()* and  
192 *markClosed()* for fitting conventional CJS and closed population models, respec-  
193 tively. These functions are essentially wrappers that “trick” *multimarkCJS()* and  
194 *multimarkClosed()* to fit models with a single mark type. The functions *simdat-*  
195 *aCJS()* and *simdataClosed()* can also be used to simulate encounter history data  
196 with a single mark type by setting the arguments *delta\_1=1* and *delta\_2=0*. For  
197 example, to simulate CJS data and fit a model with constant detection probability  
198 and individual heterogeneity in survival:

```
> singleCJSdata <- simdataCJS(delta_1=1,delta_2=0,  
+                             pbeta=-0.25,phibeta=1,sigma2_zphi=0.25)  
> Enc.Mat <- singleCJSdata$Enc.Mat  
> singleCJS.dot.h <- markCJS(Enc.Mat=Enc.Mat,mod.p=~1,mod.phi=~h,  
+                             parms=c("pbeta","phibeta","sigma2_zphi"),  
+                             nchains=2,iter=45000,burnin=5000)
```

199 There are fewer arguments for *markCJS()* and *markClosed()* because there is only  
200 one mark type (e.g., the arguments *mms* and *mod.delta* are no longer needed), but  
201 the remaining arguments are specified exactly as for *multimarkCJS()* and *multimark-*  
202 *Closed()*.

## 203 3.3 Further analysis

204 While the *coda* package can be used to summarize, plot, and assess convergence  
205 of MCMC samples from *markClosed()*, *multimarkClosed()*, *markCJS()*, and *multi-*  
206 *markCJS()*, several additional functions are available for further analysis of model

207 output. Because link functions are used for  $p$  and  $\phi$ , the functions *getprobsClosed()*  
 208 and *getprobsCJS()* provide estimates on the real scale:

```
> bobcat.c <- multimarkClosed(mms=bobcatsetup,mod.p=~c)
> pc <- getprobsClosed(bobcat.c)
> summary(pc[,c("p[1]", "c[2]")])
```

```
Iterations = 2001:12000
Thinning interval = 1
Number of chains = 1
Sample size per chain = 10000
```

1. Empirical mean and standard deviation for each variable,  
plus standard error of the mean:

	Mean	SD	Naive SE	Time-series SE
p[1]	0.1406	0.05481	0.0005481	0.004992
c[2]	0.2510	0.05481	0.0005481	0.004678

2. Quantiles for each variable:

	2.5%	25%	50%	75%	97.5%
p[1]	0.05674	0.09906	0.1338	0.1750	0.2673
c[2]	0.15111	0.21231	0.2487	0.2876	0.3642

209 Here, p[1] and c[2] refer to the probabilities of capture and recapture at times  $t = 1$   
 210 and  $t = 2$ , respectively.

211 Based on Barker & Link (2013), Bayesian multimodel inference using reversible  
 212 jump MCMC is implemented through the functions *markClosed()*, *multimarkClosed()*,  
 213 *markCJS()*, and *multimarkCJS()*. Using this approach, models are first run individ-  
 214 ually and a Gibbs sampler explores the model space using the individual model  
 215 MCMC output. All that must be provided to the multimodel inference functions is a  
 216 list containing the output from at least two models. The models must have the same

217 number and length of MCMC chains, and all model parameters must be monitored  
 218 (this is accomplished by setting *parms*="all"):

```
> bobcat.dot <- multimarkClosed(mms=bobcatsetup,mod.p=~1,parms="all")
> bobcat.c <- multimarkClosed(mms=bobcatsetup,mod.p=~c,parms="all")
> bobcat.time <- multimarkClosed(mms=bobcatsetup,mod.p=~time,parms="all")
> bobcat.h <- multimarkClosed(mms=bobcatsetup,mod.p=~h,parms="all")
> modlist <- list(mod1=bobcat.dot,mod2=bobcat.c,
+               mod3=bobcat.time,mod4=bobcat.h)
> bobcat.M <- multimodelClosed(modlist=modlist)
```

219 The list `bobcat.M` includes RJMCMC output (`bobcat.M$rjmc`) for parameters  
 220 common to all models (which can be specified using the argument *monparms*) and  
 221 posterior model probabilities (`bobcat.M$pos.prob`). Other arguments for *multimod-*  
 222 *elClosed()* and *multimodelCJS()* include prior model probabilities (*modprior*) and  
 223 user-specified proposal distributions for moving between models.

## 224 4 Example

225 I will now provide results from a new closed population analysis of the bobcat data  
 226 performed in `multimark`. Previous analyses of these data include McClintock *et al.*  
 227 (2013), who performed an integrated analysis but for a limited model set that did not  
 228 include behavioural or individual effects, and Alonso *et al.* (2015), who performed  
 229 standard single-sided analyses that could not investigate behavioural effects to first  
 230 capture. Using `multimark`, it is possible to conduct a more complete analysis using  
 231 both left- and right-sided encounter histories that includes no effects, temporal effects,  
 232 behavioural effects, and individual effects in detection probability. I also investigated  
 233 two models for  $\delta$  ( $\delta_1 \neq \delta_2$  and  $\delta_1 = \delta_2$ ) because it is reasonable to suspect that the  
 234 conditional probabilities of left- and right-sided encounters are similar.

235 Fitting all possible additive combinations yielded 16 models using the default  
 236 “non-informative” priors for *multimarkClosed()*:

$$\begin{aligned}
 \beta^p &\sim \mathcal{N}(0, 1.75) \\
 \boldsymbol{\delta} &\sim \begin{cases} \text{Beta}(1, 1) & \text{if } \delta_1 = \delta_2 \\ \text{Dirichlet}(1, 1, 1) & \text{if } \delta_1 \neq \delta_2 \end{cases} \\
 z_i^p &\sim \mathcal{N}(0, \sigma_{z^p}^2) \\
 \sigma_{z^p} &\sim \text{half-Cauchy}(25) \\
 N &\propto \frac{1}{N}
 \end{aligned}$$

237 With 2 chains each consisting of 2 million iterations (with thinning every 20 iterations  
 238 to reduce memory requirements), the simplest models required 12 mins on a computer  
 239 running Windows 7 (3.4GHz Intel Core i7, 16GB RAM), while the more complicated  
 240 models including time variation required at most 2 hrs. These relatively fast run times  
 241 are attributable to **multimark**’s parallel processing of MCMC algorithms written in  
 242 the C programming language (Kernighan & Ritchie 1988). Bayesian multimodel  
 243 inference was performed with *multimodelClosed()* using the default equal prior model  
 244 weights, where 300000 iterations for each chain required 2.6 hrs. The longer run time  
 245 for *multimodelClosed()* owes to the number of models and the RJMCMC algorithm  
 246 being written entirely in R.

247 Models including a positive behavioural response to first capture accounted for  
 248 0.51 of the posterior model weight, while models including  $\delta_1 = \delta_2$  accounted for 0.78  
 249 of posterior model weight (Table 3). Model-averaged posterior modes were  $N = 35$   
 250 (HPDI: 26-101; Fig. 1) for population abundance,  $p = 0.15$  (HPDI: 0.04-0.27) for  
 251 capture probability, and  $c = 0.21$  (HPDI: 0.07-0.33) for recapture probability. With

$\delta_1 = \delta_2 = 0.41$  (HPDI: 0.30-0.50) based on the model with the highest posterior probability, both-sided encounters were relatively infrequent for these data ( $1 - \delta_1 - \delta_2 = 0.18$ ; HPDI: 0.00-0.39).

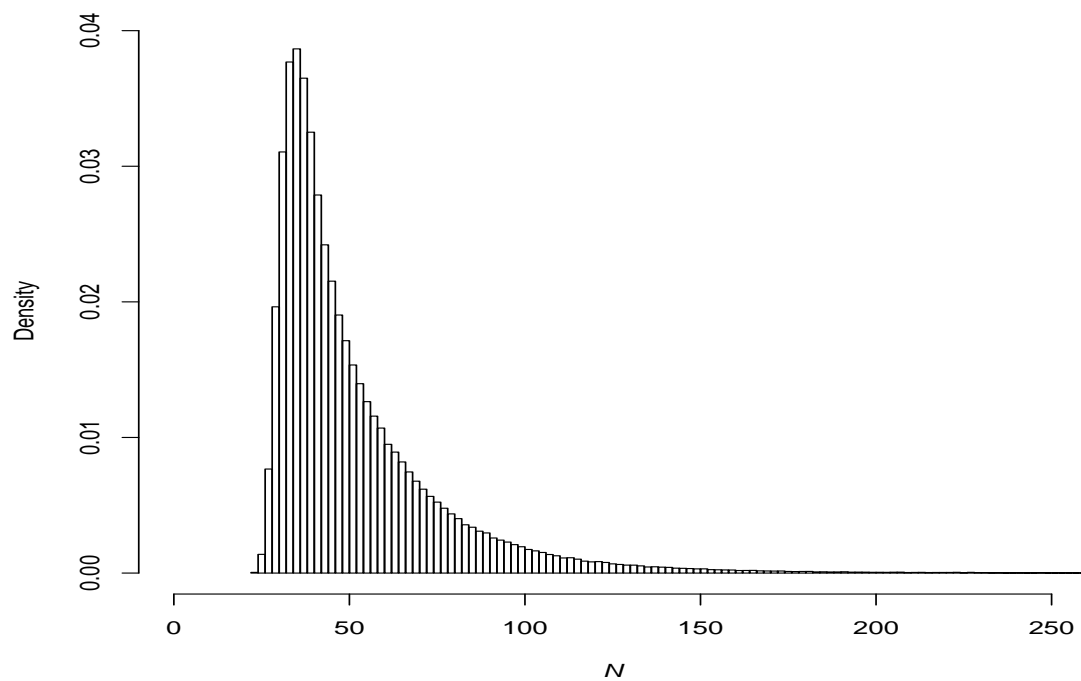
Model	PMM	$N$	HPDI	ESS	GRB
p(~c)delta(~1)	0.30	38	27-91	38944	1.00
p(~1)delta(~1)	0.22	33	26-46	54696	1.00
p(~h)delta(~1)	0.16	46	29-114	11685	1.00
p(~c + h)delta(~1)	0.09	50	29-145	18544	1.00
p(~c)delta(~type)	0.09	38	27-90	35054	1.00
p(~1)delta(~type)	0.06	33	26-46	53961	1.00
p(~h)delta(~type)	0.05	48	29-113	12099	1.00
p(~c + h)delta(~type)	0.03	51	29-146	17276	1.00
p(~time + h)delta(~1)	0.00	47	28-115	14414	1.00
p(~c + time + h)delta(~1)	0.00	45	28-116	21473	1.00
p(~time)delta(~1)	0.00	33	26-45	47781	1.00
p(~c + time)delta(~1)	0.00	33	25-78	35169	1.00
p(~time + h)delta(~type)	0.00	50	29-118	13882	1.00
p(~c + time + h)delta(~type)	0.00	46	27-115	21337	1.00
p(~time)delta(~type)	0.00	33	26-45	49425	1.00
p(~c + time)delta(~type)	0.00	32	25-78	35360	1.00

**Table 3.** Posterior model probabilities (PMM) and abundance estimates for the bobcat data. Summaries include posterior modes ( $N$ ), 95% highest posterior density intervals (HPDI), effective sample sizes (ESS), and Gelman-Rubin-Brooks diagnostics (GRB) for  $N$ . Models for detection probability (p) included no effects (~1), behavioural effects (~c), time effects (~time), and individual effects (~h). Models for the conditional probability of a left- or right-sided encounter (delta) included  $\delta_1 = \delta_2$  (~1) and  $\delta_1 \neq \delta_2$  (~type).

254

## 255 5 Discussion

256 I have described some of the key features of **multimark**, a new R package for the  
 257 analysis of capture-recapture data consisting of a single conventional mark or multiple  
 258 non-invasive marks. The package currently includes open population CJS and closed



**Figure 1.** Model-averaged posterior distribution of population abundance ( $N$ ) for the bobcat data.

259 population models, with functions for derived parameters (e.g.  $\phi$ ,  $p$ ) and multimodel  
 260 inference. It adds to the growing toolbox of freely-available software for the analysis  
 261 of non-spatial (e.g. White & Burnham 1999; Choquet *et al.* 2009; Laake 2013; Laake  
 262 *et al.* 2013) and spatial (e.g. Gopalaswamy *et al.* 2012; Efford 2015) capture-recapture  
 263 data, but it is the first to combine otherwise irreconcilable encounter histories arising  
 264 from multiple mark types. Although initially developed for integrated analyses of  
 265 left- and right-sided images for bilaterally asymmetrical species, the package can be  
 266 used to jointly analyze data arising from any two types of marks. For example,  
 267 **multimark** could be used to integrate an analysis of encounter histories arising from  
 268 genetic (e.g. hair or faecal) and visual (e.g. photo-ID) detections (sensu Madon *et al.*  
 269 2011; but see Bonner 2013). **multimark** is also the first capture-recapture software  
 270 to implement generalized Bayesian multimodel inference based on the RJMCMC  
 271 algorithm proposed by Barker & Link (2013).

272 Relative to previous applications using multiple marks (Bonner & Holmberg 2013;  
 273 McClintock *et al.* 2013), the relatively fast computation times of the package are at-  
 274 tributable to its use of “semi-complete” data likelihoods (King *et al.* 2015), parallel  
 275 processing, and MCMC algorithms written in C (instead of R). Because parallel pro-  
 276 cessing relies on the **parallel** package (R Core Team 2013), first-time Windows and  
 277 OS X users can expect a firewall pop-up dialog box asking if an R process should  
 278 accept incoming connections. Memory requirements are minimized by condition-  
 279 ing on the observed encounter histories when identifying the feasible set of latent  
 280 encounter histories. To facilitate better mixing, **multimark** improves the MCMC  
 281 algorithms proposed by Bonner & Holmberg (2013) and McClintock *et al.* (2013,  
 282 2014) by avoiding latent encounter history proposals with negative frequencies in a

283 manner that requires no proposal tuning (see Appendix S1 for details).

284 Many potentially desirable extensions to **multimark** are possible. These include  
285 a broader suite of capture-recapture models, such as multi-state and robust design  
286 models (e.g. Williams *et al.* 2002). In addition to individual-level heterogeneity,  
287 “random effect” distributions for temporal or user-specified covariates could also be  
288 incorporated (e.g. Laake *et al.* 2013). More general modelling formulae for  $\delta$  and  $\alpha$   
289 would allow additional hypotheses related to detection to be explored. The package  
290 could also be extended to accomodate >2 mark types and additional link functions.  
291 Although many individual covariates tend to be difficult (or impossible) to observe  
292 with non-invasive sampling, some (e.g. sex) may be easily discernable for each mark  
293 type. For these cases, it would be relatively straightforward to extend **multimark**  
294 to accommodate individual covariates. Other extensions include spatially-explicit  
295 models (e.g. Royle 2015) and allowing for partial overlap in the sampling periods  
296 for each mark type. Practitioners interested in such extensions are encouraged to  
297 contact the author.

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