

**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

March 27, 2015

## 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 two mark types using Bayesian Markov chain Monte Carlo (MCMC) methods.
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 California. 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 to combine 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.

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

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 multi-  
38 ple non-invasive marks. However, to my knowledge, their approaches have yet to be  
39 applied by practitioners. This is certainly not due to a lack of appropriate data (e.g.,  
40 Wilson *et al.*, 1999; Holmberg *et al.*, 2008; Madon *et al.*, 2011; Berrow *et al.*, 2012;

41 Nair *et al.*, 2012), and is likely attributable to the mathematical and computational  
 42 complexity of the models, as well as a lack of user-friendly software for implementing  
 43 them. This is the motivation for **multimark**, an R (R Core Team, 2013) package for  
 44 the analysis of capture-recapture data consisting of multiple non-invasive marks.

45 After providing some additional background on capture-recapture with multiple  
 46 marks, I briefly describe the models implemented in **multimark**. These currently  
 47 include open population Cormack-Jolly-Seber (CJS) and closed population abun-  
 48 dance models (e.g., Williams *et al.*, 2002) with two mark types. Using real and  
 49 simulated data for illustration, I provide an overview of the workflow for the pack-  
 50 age and a new analysis of left- and right-sided encounter histories for bobcats (*Lynx*  
 51 *rufus*) collected from remote single-camera stations in southern California. Addi-  
 52 tional information, including help files, data, examples, and package usage is avail-  
 53 able by downloading the **multimark** package from CRAN (<http://cran.r-project.org>)  
 54 or github (<https://github.com/bmcclintock/multimark>).

## 55 **2 Description**

### 56 **2.1 Background**

57 Capture-recapture data are typically represented by a collection of encounter histo-  
 58 ries  $\mathbf{Y} = \{\mathbf{y}_1, \mathbf{y}_2, \dots, \mathbf{y}_n\}$ , where each element of  $\mathbf{y}_i = \{y_{i,1}, y_{i,2}, \dots, y_{i,T}\}$  indicates  
 59 whether individual  $i$  was detected ( $y_{i,t} = 1$ ) or not detected ( $y_{i,t} = 0$ ) on each  
 60 of  $t = 1, \dots, T$  sampling occasions. Typical analyses then proceed by formulat-  
 61 ing a likelihood conditional on the  $n$  unique individuals encountered (e.g., Williams  
 62 *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  
 63  $m \in \{1, 2\}$ , 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

64  $i$  was detected ( $\tilde{y}_{m_i,t} = m$ ) or not detected ( $\tilde{y}_{m_i,t} = 0$ ), and  $n_m$  is the number of  
 65 unique individuals encountered for mark type  $m$ . We focus on situations where it is  
 66 difficult (or impossible) to reliably match individuals from  $\tilde{\mathbf{Y}}_1$  and  $\tilde{\mathbf{Y}}_2$ . In this case,  
 67 although we know  $n \leq n_1 + n_2$ ,  $n$  is nevertheless unknown and standard capture-  
 68 recapture analysis methods cannot be reliably used for simultaneous inference using  
 69 both sources of data.

70 Depending on the mark types, it may sometimes be possible to observe both marks  
 71 simulateneously. In this case, some of the encounter histories from  $\tilde{\mathbf{Y}}_1$  and  $\tilde{\mathbf{Y}}_2$  can  
 72 be matched to unique individuals with certainty. For example, suppose images were  
 73 collected during vessel-based line transect surveys of surfacing whales, where mark  
 74 type 1 corresponds to patch patterns on the left side and mark type 2 corresponds  
 75 to patterns on the right side. If an individual happens to be photographed on both  
 76 sides simultaneously on at least one sampling occasion, then the true encounter  
 77 history for this individual would be known (i.e., left- and right-sided images could be  
 78 matched). This results in an additional set of  $n_{known}$  observed encounter histories,  
 79  $\tilde{\mathbf{Y}}_{known} = \{\tilde{\mathbf{y}}_{known1}, \tilde{\mathbf{y}}_{known2}, \dots, \tilde{\mathbf{y}}_{knownn_{known}}\}$ , consisting of histories that are known  
 80 with certainty (Table 1).

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

**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

## 88 2.2 Models

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

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

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

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  $z_{i,t}$  is an indicator for whether individual  $i$  was alive ( $z_{i,t} = 1$ ) or not ( $z_{i,t} = 0$ ) during sampling occasion  $t$ . For added flexibility,  $p$  and  $\phi$  are modeled using the probit link function:

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

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



95 where  $\Phi()$  the cumulative distribution function of the standard normal density,  $\mathbf{x}_t^p$   
 96 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  
 97 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  
 98 effects. The probit link is implemented for CJS models in `multimark` because it  
 99 facilitates a Gibbs sampler in the spirit of Albert & Chib (1993) and Laake *et al.*  
 100 (2013).

101 Similarly, the likelihood for the closed population abundance model with two  
 102 mark types is

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

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

where  $N$  is the population size, and  $p^*$  is the probability that a randomly selected individual is detected at least once. 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

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

103 Although a Gibbs sampler has been proposed for closed population models using the  
 104 probit link and a complete data likelihood (McClintock *et al.*, 2014), this does not

**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”	$\{0, 1, 2, 4\}$	$\alpha = 1$

105 apply to the “semi-complete” data likelihood in Eq. 2 (hence the traditional logit  
 106 link is used). The primary utility of **multimark** is finding the set of latent encounter  
 107 histories that are feasible given the observed encounter histories (sensu Link *et al.*,  
 108 2010; Bonner & Holmberg, 2013; McClintock *et al.*, 2013, 2014). Given a feasible set  
 109 of latent encounter histories, fitting capture-recapture models such as Eqs. 1 or 2 is  
 110 relatively straightforward.

## 111 3 Workflow

### 112 3.1 Data formatting

113 There are three types of multiple-mark data that can be analyzed with **multimark**.  
 114 These are the “never”, “sometimes”, and “always” data types, and they are named  
 115 based on their respective probabilities of a simultaneous type 1 and type 2 encounter  
 116 (Table 2). An example of the “never” data type is provided with **multimark** and  
 117 includes 23 left-sided ( $\tilde{\mathbf{Y}}_1$ ) and 23 right-sided ( $\tilde{\mathbf{Y}}_2$ ) encounter histories for bobcats  
 118 (*Lynx rufus*) collected from remote single-camera stations in southern California over  
 119  $T = 8$  sampling periods between July 2006 and January 2007 (McClintock *et al.*,  
 120 2013; Alonso *et al.*, 2015).

121 **multimark** expects observed encounter history data to be a matrix with rows

corresponding to individuals and columns corresponding to sampling occasions. Because the bobcat data were collected from single-camera stations, simultaneous left- and right-sided encounters were not possible; hence  $\alpha = 0$  and the rows consist of 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

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

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

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

131 This creates an object of class *multimarksetup* that includes everything needed for  
 132 model fitting and further analysis. In particular, *processdata()* calculates all of the  
 133 necessary ingredients for identifying the feasible set of latent encounter histories (for  
 134 technical details see Bonner & Holmberg, 2013; McClintock *et al.*, 2013). There is  
 135 also a feature enabling designation of individual encounter histories as known with  
 136 certainty despite no simultaneous type 1 and type 2 detections (i.e.,  $y_{i,t} \neq 4 \forall t$ ),  
 137 a situation that can arise from a previous physical capture or concurrent telemetry  
 138 study (e.g., McClintock *et al.*, 2013). This feature can also be used to “trick” the  
 139 package to perform analyses with traditional capture-recapture data with a single  
 140 mark type.

## 141 3.2 Model fitting

142 The package currently includes functions *multimarkCJS()* and *multimarkClosed()*  
 143 for fitting CJS and closed population models, respectively. Use of these functions is  
 144 perhaps best explained by example. To fit a simple closed population model assuming  
 145 constant detection probability using the default settings:

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

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

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

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

148 This creates a list, *bobcat.dot*, containing the MCMC output for the model  
 149 (*bobcat.dot\$mcmc*). The MCMC output is of class *mcmc*, which should be familiar  
 150 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)]	-1.3632	0.25177	0.0025177	0.015807
N	35.5843	5.29665	0.0529665	0.247142
delta_1	0.3768	0.07704	0.0007704	0.008827
delta_2	0.3935	0.07748	0.0007748	0.008153

2. Quantiles for each variable:

	2.5%	25%	50%	75%	97.5%
pbeta[(Intercept)]	-1.8588	-1.5329	-1.3626	-1.1870	-0.8876
N	27.0000	32.0000	35.0000	39.0000	48.0000
delta_1	0.2316	0.3231	0.3762	0.4291	0.5313
delta_2	0.2467	0.3398	0.3925	0.4459	0.5489

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

	N	delta_1	delta_2
pbeta[(Intercept)]	253.70774	459.31285	76.16803
			90.32521

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

152 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  
153 all quantities of interest.

155 Other common models for detection probability can be easily specified using  
156 formulas for  $mod.p$ , including shorthands for time variation ( $mod.p=\sim time$ ), temporal trends ( $mod.p=\sim Time$ ), behavioural response to first capture ( $mod.p=\sim c$ ),  
157

158 and individual heterogeneity ( $mod.p=\sim h$ ). Additive or interaction terms can be in-  
 159 cluded (e.g.,  $mod.p=\sim time+c+h$ ,  $mod.p=\sim Time+I(Time^2)$ ,  $mod.p=\sim time*c$ ). User-  
 160 specified temporal covariates in detection probability can also be used:

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

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

163 There are currently two options for specifying models for  $\delta$ , the default  $mod.delta=\sim type$   
 164 (i.e.,  $\delta_1 \neq \delta_2$ ), and  $mod.delta=\sim 1$  (i.e.,  $\delta_1 = \delta_2$ ). There are many additional argu-  
 165 ments for specifying the number (*nchains*) and length (*iter*) of chains, including  
 166 burn-in and adaptive periods. For potential improvements in mixing, the number of  
 167 “moves” used to update the feasible set of latent encounter histories at each iteration  
 168 can be user specified (*maxnumbasis*; see Appendix S1). The default priors are “un-  
 169 informative”, but user-specified priors can be used for each parameter. Initial values  
 170 can be automatically generated or user specified for each parameter.

171 The function *multimarkCJS()* works in exactly the same fashion, with the only  
 172 notable difference being specification of models for  $\phi$  (in addition to  $p$  and  $\delta$ ). Al-  
 173 though CJS-specific data are not included with *multimark*, data can be simulated  
 174 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,]	0	1	0	0	0	0	0
[2,]	4	1	0	1	0	0	0
[3,]	1	0	0	1	1	0	0
[4,]	0	0	0	0	1	1	0
[5,]	1	0	0	0	0	0	0
[6,]	2	0	0	0	0	0	0

```
> 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)]	-0.3114	0.11386	0.0004025	0.0027095
phibeta[(Intercept)]	1.2668	0.19871	0.0007026	0.0056590
alpha	0.5101	0.10517	0.0003718	0.0017993
sigma2_zphi	0.3381	1.96565	0.0069496	0.2490295
delta_1	0.2455	0.04684	0.0001656	0.0009793
delta_2	0.5218	0.05137	0.0001816	0.0007298

2. Quantiles for each variable:

	2.5%	25%	50%	75%	97.5%
pbeta[(Intercept)]	-0.531093	-0.389086	-0.31272	-0.23533	-0.08282
phibeta[(Intercept)]	0.909615	1.136389	1.25806	1.38734	1.68459
alpha	0.309685	0.436888	0.50911	0.58177	0.71768
sigma2_zphi	0.002876	0.007975	0.01665	0.04837	3.16274
delta_1	0.157869	0.213062	0.24398	0.27639	0.34106
delta_2	0.420641	0.487297	0.52198	0.55657	0.62187

175 An additional feature for *multimarkCJS()* is simple specification of cohort effects for  
 176  $p$  (*mod.p*= $\sim age$ ) and  $\phi$  (*mod.phi*= $\sim age$ ), which is useful for investigating structure  
 177 related to age (or time of first capture).

### 178 3.3 Further analysis

179 While the `coda` package can be used to summarize, plot, and assess convergence  
 180 of MCMC samples from *multimarkClosed()* and *multimarkCJS()*, several additional  
 181 functions are available for further analysis. Because link functions are used for  $p$  and  
 182  $\phi$ , the functions *getprobsClosed()* and *getprobsCJS()* provide estimates on the real  
 183 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]	0.1317	0.05434	0.0005434	0.004925
c[2]	0.2519	0.05510	0.0005510	0.004527

2. Quantiles for each variable:

	2.5%	25%	50%	75%	97.5%
p[1]	0.03909	0.09228	0.1253	0.1656	0.2501
c[2]	0.15227	0.21297	0.2496	0.2884	0.3641

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



Based on Barker & Link (2013), Bayesian multimodel inference using reversible jump MCMC is implemented through the functions *multimodelClosed()* and *multimodelCJS()*. Using this approach, models are first run individually and a Gibbs sampler explores the model space using the individual model MCMC output. All that must be provided to the multimodel inference functions is an object of class *multimarksetup* and a list containing the output from at least two models. The models must have the same number and length of MCMC chains, and all model parameters must be monitored (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(mms=bobcatsetup,modlist=modlist)
```

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

## 4 Example

I will now provide results from a new closed population analysis of the bobcat data performed in *multimark*. Previous analyses of these data include McClintock *et al.* (2013), who performed an integrated analysis but for a limited model set that did not include behavioural or individual effects, and Alonso *et al.* (2015), who performed

204 standard single-sided analyses that could not investigate behavioural effects to first  
 205 capture. Using **multimark**, it is possible to conduct a more complete analysis using  
 206 both left- and right-sided encounter histories that includes no effects, temporal effects,  
 207 behavioural effects, and individual effects in detection probability. I also investigated  
 208 two models for  $\delta$  ( $\delta_1 \neq \delta_2$  and  $\delta_1 = \delta_2$ ) because it is reasonable to suspect that the  
 209 conditional probabilities of left- and right-sided encounters are similar.

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

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

212 With 2 chains each consisting of 2 million iterations (with thinning every 20 iterations  
 213 to reduce memory requirements), the simplest models required 12 mins on a machine  
 214 running Windows 7 (3.4GHz Intel Core i7, 16GB RAM), while the more complicated  
 215 models including time variation required at most 2 hrs. These relatively fast run times  
 216 are attributable to **multimark**’s parallel processing of MCMC algorithms written in  
 217 the C programming language (Kernighan & Ritchie, 1988). Bayesian multimodel  
 218 inference was performed with *multimodelClosed()* using the default equal prior model  
 219 weights, where 300000 iterations for each chain required 3 hrs. The longer run time  
 220 for *multimodelClosed()* owes to the number of models and the RJMCMC algorithm

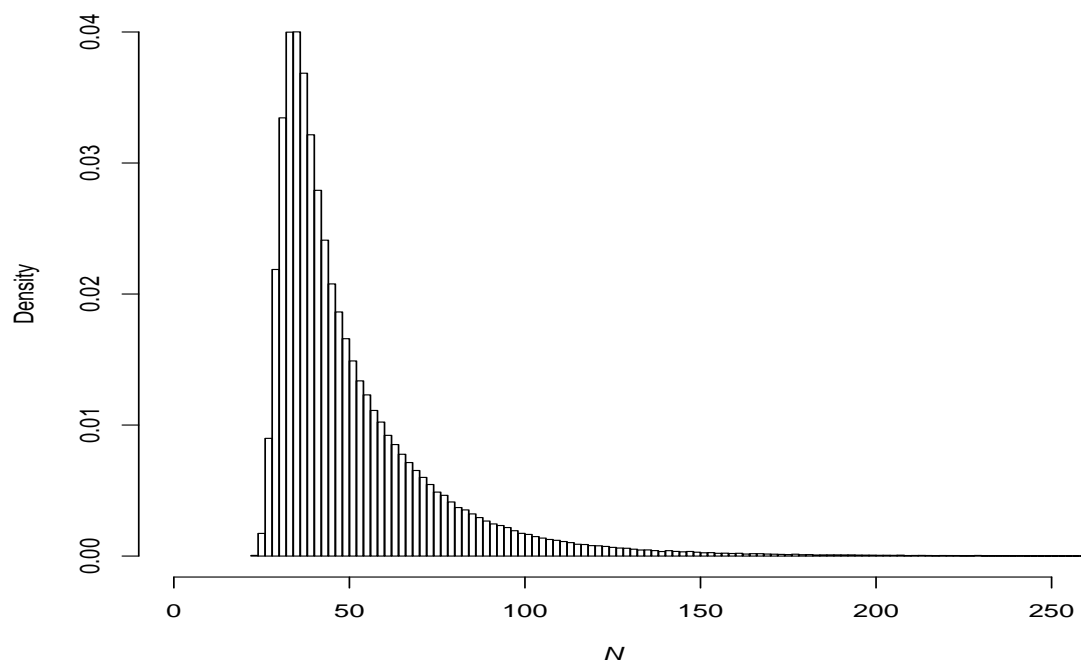
221 being written entirely in R.

222 Models including a positive behavioural response to first capture accounted for  
223 0.51 of the posterior model weight, while models including  $\delta_1 = \delta_2$  accounted for 0.78  
224 of posterior model weight (Table 3). Model-averaged posterior modes were  $N = 34$   
225 (HPDI: 25-99; Fig. 1) for population abundance,  $p = 0.15$  (HPDI: 0.04-0.28) for  
226 capture probability, and  $c = 0.21$  (HPDI: 0.07-0.33) for recapture probability. With  
227  $\delta_1 = \delta_2 = 0.41$  (HPDI: 0.31-0.5) based on the model with the highest posterior  
228 probability, both-sided encounters were relatively infrequent for these data ( $1 - \delta_1 -$   
229  $\delta_2 = 0.17$ ).

## 230 5 Discussion

231 I have described some of the key features of **multimark**, a new R package for the  
232 analysis of capture-recapture data with multiple non-invasive marks. The package  
233 adds to the growing toolbox of freely-available software for the analysis of non-spatial  
234 (e.g., White & Burnham, 1999; Choquet *et al.*, 2009; Laake, 2013; Laake *et al.*, 2013)  
235 and spatial (e.g., Gopalaswamy *et al.*, 2012; Efford, 2015) capture-recapture data,  
236 but it is the first to combine otherwise irreconcilable encounter histories arising from  
237 multiple mark types. Although initially developed for integrated analyses of left- and  
238 right-sided images for bilaterally asymmetrical species, the package can be used to  
239 jointly analyze data arising from any two types of marks. For example, **multimark**  
240 could be used to integrate an analysis of encounter histories arising from genetic  
241 (e.g., hair or faecal) and visual (e.g., photo-ID) detections (sensu Madon *et al.* 2011;  
242 but see Bonner 2013).

243 **multimark** currently includes open population CJS and closed population models,



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

Model	PMM	$N$	HPDI	ESS	GRB
p(~c)delta(~1)	0.30	37	27-89	38769	1.00
p(~1)delta(~1)	0.23	33	27-46	51133	1.00
p(~h)delta(~1)	0.15	48	28-113	12795	1.00
p(~c + h)delta(~1)	0.09	49	28-144	19192	1.00
p(~c)delta(~type)	0.09	38	27-89	37853	1.00
p(~1)delta(~type)	0.07	33	27-46	52354	1.00
p(~h)delta(~type)	0.04	46	28-113	13214	1.00
p(~c + h)delta(~type)	0.03	49	29-143	19525	1.00
p(~time + h)delta(~1)	0.00	48	28-115	14781	1.00
p(~time)delta(~1)	0.00	32	25-44	42386	1.00
p(~c + time + h)delta(~1)	0.00	45	27-115	20273	1.00
p(~c + time)delta(~1)	0.00	33	24-76	36202	1.00
p(~time + h)delta(~type)	0.00	47	28-115	12824	1.00
p(~c + time + h)delta(~type)	0.00	44	28-115	20761	1.00
p(~time)delta(~type)	0.00	33	26-44	42781	1.00
p(~c + time)delta(~type)	0.00	33	24-76	35808	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).

with functions for derived parameters (e.g.,  $\phi$ ,  $p$ ) and Bayesian multimodel inference. Relative to previous applications using multiple marks (Bonner & Holmberg, 2013; McClintock *et al.*, 2013), the relatively fast computation times of the package are attributable to its use of “semi-complete” data likelihoods (King *et al.*, 2015), parallel processing, and MCMC algorithms written in C (instead of R). Because parallel processing relies on the `parallel` package (R Core Team, 2013), first-time Windows and OS X users can expect a firewall pop-up dialog box asking if an R process should accept incoming connections. Memory requirements are minimized by condi-

tioning on the observed encounter histories when identifying the feasible set of latent encounter histories. To facilitate better mixing, **multimark** extends the MCMC algorithms proposed by Bonner & Holmberg (2013) and McClintock *et al.* (2013, 2014) by avoiding latent encounter history proposals with negative frequencies in a manner that requires no proposal tuning (see Appendix S1 for details).

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

## Acknowledgments

P. Boveng, P. Conn, and J. Laake for helpful comments on earlier drafts. D. Johnson for helpful discussions. The findings and conclusions in the manuscript are those of the author(s) and do not necessarily represent the views of the National Marine Fisheries Service, NOAA. Any use of trade, product, or firm names does not imply

276 an endorsement by the US Government.

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