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A new method for estimating animal abundance with two sources of data in capture–recapture studies

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Summary

1. Mark–recapture studies are often used to estimate population size based on a single source of individual identification data such as natural markings or artificial tags. However, with the development of molecular ecology, multiple sources of identification can be obtained for some species and combining them to obtain population size estimates would certainly provide better information about abundance than each survey can provide alone.

2. We propose an extension of the Jolly–Seber model to infer abundance by combining two sources of capture–recapture data. The need to merge both sources of data was motivated by studies of humpback whales in which both photo-identification and DNA from skin biopsy samples are often collected. As whales are not necessarily available by both sampling methods on any given occasion, they can appear twice in the combined data set if no combined sampling ever occurred during the survey, i.e. being photographed and genotyped on the same occasion. Our model thus combines the two sources of information by estimating the possible overlap. Monte Carlo simulations are used to assess the properties of the present estimator that is then used to estimate the size of the humpback whale population in New Caledonia. The new open-population estimator is also compared with classic closed-population estimators incorporating either temporal and/or individual heterogeneity in the capture probability: the purpose was to evaluate which approach (closed or open population) was the least biased for an open population with individual heterogeneous capture probabilities.

3. When all assumptions are met, the estimator is unbiased as long as the probability of being double-tagged (e.g. photographed and biopsied on the same occasion) on every occasion is above 0·2.

4. The humpback whale case study in New Caledonia shows that our two-source Jolly–Seber (TSJS) estimator could be more efficient in estimating population size than models based only on one type of data. For monitoring purposes, the proposed method provides an efficient alternative to the existing approaches and a productive direction for future work to deal with multiple sources of data to estimate abundance.

5. R-codes formatting the data and implementing the TSJS model are provided in Resource S5.

Key-words: abundance, humpback whales, joint modelling, Jolly–Seber model, open population, two-source Jolly–Seber model

Introduction

Methods for estimating abundance of wild animal populations have been of growing interest in ecology, and a large number of such methods have been developed (Williams, Nichols, & Conroy 2002; Amstrup, McDonald, & Manly 2005). The use of capture–recapture methods with tagging methods such as photo-identification and genetic sampling, in particular, is increasing (Smith *et al.* 1999; Pearse *et al.* 2001; Mowat & Paetkau 2002; Garrigue *et al.* 2004; Bellemain *et al.* 2005; Lukacs & Burnham 2005; Forcada & Robinson 2006;

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Yoshizaki *et al.* 2009). Joint photo-identification and DNA fingerprinting (i.e. microsatellite genotyping) from skin biopsy samples are especially widely used to survey marine mammals, as more individuals can be sampled and more information gained that way about the population than using the traditional method of photo-identification alone. Using these methods in combination, researchers typically end up with two data sets that, currently, are analysed separately to estimate abundance (e.g. Garrigue *et al.* 2004). We suggest a sensible solution where the two sources of information are combined to estimate abundance. The use of multiple sampling methods is potentially a relevant sampling design to minimize bias by maximizing effectively the number of catchable animals (e.g. Barker, Burnham, & White 2004). Using this approach, the heterogeneity in individual capture probabilities could be reduced, decreasing the negative bias in the population size estimates usually associated with heterogeneity (Cubaynes *et al.* 2010) without having to dilute the sampling effort over a large area or a long period of time.

Open-population models have been developed to overcome the violation of the closure assumption when using closed-population models over an extended period. In terms of population size estimation, they can also provide useful information on trends in abundance as they provide an estimate for every capture occasion. However, open-population models with time variation on both survival and capture probability, like the Cormack–Jolly–Seber (CJS) model, have been mostly used to estimate biological parameters such as survival and capture probabilities (Lebreton *et al.* 1992). Although it is possible to estimate abundance with the CJS model using a Horvitz–Thompson-like estimator after estimating the capture probabilities (McDonald & Amstrup 2001; Cubaynes *et al.* 2010), currently only the Jolly–Seber (JS) model leads to a direct estimate of population size (Jolly 1965; Seber 1965).

We propose here an extension of the JS estimator to obtain estimates of population abundance by combining two sources of capture–recapture data (e.g. from photo-identification and genotyping) from the same population at the same time where there is an unknown degree of overlap between the data sets. This overlap results from the same animal appearing in both data sets but – never having been caught by both methods – being treated as two separate animals. Fusing the data sets enables us to get a larger sample size to get a more reliable estimate of population size than could be achieved by analysing the two data sources separately. First, we introduce the data structure and our extension of the JS model, referred to as the two-source Jolly–Seber (TSJS) model, with the corresponding notation and assumptions. Then, we compare the new estimator to existing closed-population estimators in various scenarios of individual heterogeneity in the capture probability. Finally, we illustrate its use in the context of a humpback whale's study where two kinds of data are available: a photographic catalogue and a genotype data base.

Materials and methods

DATA STRUCTURE

In the present sampling situation, there are three kinds of capture histories that need to be distinguished as individuals of a population can be sampled by a method '1' or by a method '2' or by both simultaneously designated as method '3' at any capture occasion. Therefore, we denote by x_l the capture history l of an individual only captured by method 1, by y_m the capture history m of an individual (possibly the same individual) only captured by method 2 and by w_n the capture history n of an individual that has been simultaneously captured by both sampling methods at least once during the study period. For instance, possible capture histories for a 6-year study include $x_l = 001011$, $y_m = 200000$ and $w_n = 023100$. These sequences mean that the animal with history l, captured by method 1 only, has been caught at time 3, 5 and 6, that the animal with history m, captured by method 2 only, has been caught at time 1 and that individual n that has been simultaneously captured by both sampling methods at time 3 has also been captured by method 2 at time 2 and by method 1 at time 4. The main issue comes from the individuals that have never been sampled by method 3 (i.e. simultaneously by methods 1 and 2) but have been captured separately by methods 1 and 2 on different occasions. For example, histories x_l and y_m might be from the same individual. These individuals have a capture history in data set 1 and another distinct one in data set 2. The possible histories of captured animals can be seen more clearly in Fig. 1, the set of all possible histories of captured animals.

Thus, the number of animals actually caught by method 1 is the number of animals in B∪G∪E∪F, by method 2 the number of animals in C∪D∪E∪F and by both methods simultaneously, method 3, the number of animals in A∪B∪C∪E. However, when lists 1 and 2 are put together, i.e. combined, for joint analysis, the resulting list will be too large by the number in E∪F. Those animals in E will be easily

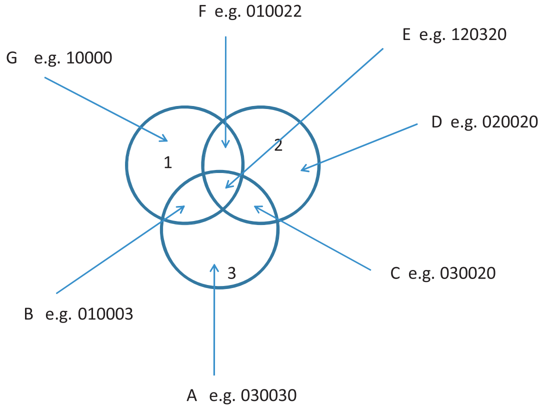

Fig. 1. A Venn diagram showing the possible theoretical types of capture histories (with examples) for captured animals in a mark–recapture experiment where two capture methods can be used separately (methods 1 and 2) or simultaneously (method 3) on any occasion: A is the set of individuals captured only by method 3, B the set of individuals captured at least once by methods 1 and 3, C the set of individuals captured at least once by methods 2 and 3, D the set of individuals captured only by method 2, E the set of individuals captured by methods 1, 2 and 3 and F the set of individuals captured by methods 1 and 2 during the study. In the capture histories, '1' refers to a capture by method 1, '2' to a capture by method 2, '3' to a capture by both methods simultaneously and '0' to the animal not being caught on the occasion.

identified and corrected thanks to the information provided by the simultaneous capture, but those in F will not because they have never been captured by both methods simultaneously.

So the unrecorded overlap (individuals in F, see Fig. 1) needs to be estimated to avoid counting the individuals in F twice.

THE EXTENSION OF THE JOLLY–SEBER MODEL: THE TWO-SOURCE JOLLY–SEBER MODEL

In this section, we describe the development of the TSJS model. The notation used is given in Table 1. The modification of the JS model and details about the approximation used in the TSJS model to estimate the overlap between the two data sets are provided. In what follows, by 'record' we imply capture history over the survey period.

POPULATION SIZE ESTIMATION

As in the JS model, the population size estimate does not appear directly in the likelihood and we use the traditional capture–recapture formula where the ratio of the number of marked individuals over the total population size is constant over time:

$$\frac{m'_i}{n_i} = \frac{\hat{M}_i}{\hat{N}_i} \qquad \text{eqn 1}$$

which leads to:

$$\hat{N}_i = \frac{n_i \hat{M}_i}{m'_i} \qquad \text{eqn 2}$$

with

$$n_i = m'_i + U'_i \qquad \text{eqn 3}$$

where the number of marked individuals m'_i captured at time i is the sum of the number of individuals captured by each of the three sampling methods

$$m'_i = m^*_{i,3} + (m^*_{i,1} + m^*_{i,2})I_{\mathrm{id}} \qquad \text{eqn 4}$$

and U'_i the number of unmarked individuals captured at time i is the sum of the number of unmarked individuals captured by each of the three sampling methods

$$U'_i = U^*_{i,3} + (U^*_{i,1} + U^*_{i,2})I_{\mathrm{id}} \qquad \text{eqn 5}$$

The rate of true identity I_{id} is used for m'_i and U'_i to avoid counting some individuals twice (i.e. individuals in F, see Fig. 1).

Following the method in the JS model, the estimation of $\hat{M}_i$, the total number of marked individuals in the population immediately before time i, is carried out by estimating the size of two different groups of animals in the population:

1. the group $M_i - m'_i$ of marked animals not seen at time t,
2. the group n_i of animals seen at time i, marked and released for subsequent recaptures.

Table 1. Notation in the two-source Jolly–Seber model and corresponding definition

Notation	Definition
I_{id}	Probability of true identity, i.e. given that an animal has only been captured by method 1 or 2, the probability it has never also been captured respectively by methods 2 and 1
$m^*_{i,1}$	Number of marked animals captured at occasion i by method 1 given that they were never captured simultaneously during the survey period
$m^*_{i,2}$	Number of marked animals captured at occasion i by method 2 given that they were never captured simultaneously during the survey period
$m^*_{i,3}$	Number of marked animals captured at occasion i given that they have at least one simultaneous capture (i.e. by method 3) in their record
m'_i	Number of marked animals captured at time i
M_i	Total number of marked animals captured and alive just before occasion i
$\hat{M}_i$	Estimate of the total number of marked individuals (by either method) at time i
n_i	Total number of animals, marked and unmarked, captured at occasion i
$\hat{N}_i$	Estimate of abundance at time i
$r'_{i,1}$	Number of animals captured at occasion i by method 1, given that they were never captured simultaneously during the survey period, that are captured again by method 1
$r'_{i,2}$	Number of animals captured at occasion i by method 2, given that they were never captured simultaneously during the survey period, that are captured again by method 2
$r'_{i,3}$	Number of animals captured at occasion i given that they have at least one simultaneous capture in their record, that are captured again
r'_i	Total number of animals captured at occasion i that are captured again later
U'_i	Total number of unmarked animals captured at occasion i
$z'_{i,1}$	Number of animals captured by method 1 before i, not captured at i and captured by method 1 again later given that they were never captured simultaneously during the survey period
$z'_{i,2}$	Number of animals captured by method 2 before i, not captured at i and captured by method 2 again later given that they were never captured simultaneously during the survey period
$z'_{i,3}$	Number of animals captured before i, not captured at i and captured again later, given that they have at least one simultaneous capture in their record
z_i	Number of animals captured before i, not captured at i and captured again later

Taking z_i and r'_i as members of, respectively, $M_i - m'_i$ and n_i, which are seen at least once again after time i, this leads, under the assumption of equal catchability, to the ratios of $\frac{z_i}{M_i - m'_i}$ and $\frac{r'_i}{n_i}$ being approximately equal:

$$\frac{z_i}{M_i - m'_i} \approx \frac{r'_i}{n_i} \approx \frac{r'_{i,3} + (r'_{i,1} + r'_{i,2})I_{\mathrm{id}}}{n_i} \qquad \text{eqn 6}$$

Similarly to U'_i and m'_i, r'_i and z_i can be decomposed into the sum of three components based, respectively, on the number of animals captured at time i and recaptured again later by each method and on the number of animals captured before i, not captured at i and captured again later such that

$$z_i = z'_{i,3} + (z'_{i,1} + z'_{i,2})I_{\mathrm{id}} \qquad \text{eqn 7}$$

Again, we use I_{id} in z_i to avoid double-counting because of possible duplicates (i.e. individuals in F, see Fig. 1).

Consequently, an estimator of M_i is given by:

$$\hat{M}_i = m'_i + \frac{U'_i z_i}{r'_i} \qquad \text{eqn 8}$$

After i capture occasions, capture histories (records) are available for each individual caught at least once during the survey and the data set used is the one combining all capture histories from methods 1, 2 and 3, thus, all the x_l, y_m and w_n defined earlier. We define the following events:

$$\ell_1 = \{\text{animal } i \text{ belongs to list } 1\} = \mathrm{B} \cup \mathrm{G} \cup \mathrm{E} \cup \mathrm{F}$$

$$\ell_2 = \{\text{animal } i \text{ belongs to list } 2\} = \mathrm{C} \cup \mathrm{D} \cup \mathrm{E} \cup \mathrm{F}$$

$$\ell_3 = \{\text{animal } i \text{ belongs to list } 3\} = \mathrm{A} \cup \mathrm{B} \cup \mathrm{C} \cup \mathrm{E}$$

and the complement of event ℓ_3:

$$\bar{\ell}_3 = \{\text{animal } i \text{ does not belong to list } 3\} = \mathrm{G} \cup \mathrm{F} \cup \mathrm{D}$$

It is assumed that:

1. membership of the lists is independent: the probability of an individual being included in the first list does not depend on whether it was included in the other lists,

2. there is homogeneity in the probability of inclusion on a list that does not vary from individual to individual.

In what follows, we reason conditionally on detection with $P_1 = \mathrm{P}(\ell_1)$, $P_2 = \mathrm{P}(\ell_2)$ and $P_3 = \mathrm{P}(\ell_3)$. Given events ℓ_1 and ℓ_2 are independent (conditionally on detection), events ℓ_1 and ℓ_2, i.e. $(\ell_1 \cap \ell_2)$ is equivalent to (E∪F) in Fig. 1 and:

$$\mathrm{P}(\ell_1 \cap \ell_2) = P_1 P_2 \qquad \text{eqn 9}$$

The probability of belonging to list 1 and list 2 given the animal was sampled on some occasions can be written as the sum of two probabilities:

1. the probability of belonging to list 1 and list 2 separately and being acknowledged to belong to both list 1 and list 2, P(E), and

2. and the probability of belonging to list 1 and list 2 separately and not being acknowledged as belonging to both list 1 and list 2, P(F), such that

$$\mathrm{P}(\ell_1 \cap \ell_2) = \mathrm{P}((\ell_1 \cap \ell_2) \cap \ell_3) + \mathrm{P}((\ell_1 \cap \ell_2) \cap \bar{\ell}_3) \qquad \text{eqn 10}$$

Therefore,

$$\mathrm{P}(\ell_1 \cap \ell_2) = P_1 P_2 P_3 + P_1 P_2 (1 - P_3) \qquad \text{eqn 11}$$

And the probability of the unknown overlap between list 1 and list 2, i.e. the probability that an individual has an entry in list 1 and an entry in list 2 but is not acknowledged as being in both lists, i.e. P(F), is

$$\mathrm{P}((\ell_1 \cap \ell_2) \cap \bar{\ell}_3) = P_1 P_2 (1 - P_3) \qquad \text{eqn 12}$$

It follows that the probability that an individual has a single entry in the combined list is

$$I_{\mathrm{id}} = 1 - \mathrm{P}((\ell_1 \cap \ell_2) \cap \bar{\ell}_3) = 1 - P_1 P_2 (1 - P_3) \qquad \text{eqn 13}$$

.

In a real data set, the probabilities P_1, P_2, P_3 can be approximated as being:

$$\hat{P}_1 = \frac{\text{Number of individuals with a capture by method 1 on at least one occasion}}{\text{Total number of individuals in the combined data set}} = \hat{\mathrm{P}}(\ell_1) \qquad \text{eqn 14}$$

$$\hat{P}_2 = \frac{\text{Number of individuals with a capture by method 2 on at least one occasion}}{\text{Total number of individuals in the combined data set}} = \hat{\mathrm{P}}(\ell_2) \qquad \text{eqn 15}$$

$$\hat{P}_3 = \frac{\text{Number of individuals with a capture by both methods on at least one occasion}}{\text{Total number of individuals in the combined data set}} = \hat{\mathrm{P}}(\ell_3) \qquad \text{eqn 16}$$

However, such estimators are biased, as the total number of capture histories has not been corrected for the undetected duplicates. The total number of capture histories used as a denominator to calculate those probabilities is likely to be overestimated because of the unknown number of individuals appearing twice in the combined data set. Hence, it will result in overestimation of the I_{id} parameter. The primary purpose of using I_{id} is to correct the population size estimate for duplicated, 'phantom', individuals when using two data sets, so it seems legitimate to use it as well to correct the total number of individuals. To correct for the potential overestimation of the total number of individuals, the total number of individuals in the calculation of $\hat{P}_1$, $\hat{P}_2$, $\hat{P}_3$ is multiplied by the previous value of the parameter. In the second step of the iteration, the $\hat{I}_{\mathrm{id}}$ parameter then becomes:

$$I^*_{\mathrm{id}} = 1 - \left(\frac{1}{I^{*2}_{\mathrm{id}}} \hat{P}_1 \hat{P}_2 - \frac{1}{I^{*3}_{\mathrm{id}}} \hat{P}_1 \hat{P}_2 \hat{P}_3 \right) \qquad \text{eqn17}$$

The iteration should continue substituting the previous value of $\hat{I}_{\mathrm{id}}$ calculated to get the next one until convergence. However, the present iteration method resulted in unstable estimates where the iteration did not converge. The reason for nonconvergence is that if the $\hat{I}_{\mathrm{id}}$ estimate overshoots the true value and goes too small, then because of the reciprocal of high powers of $\hat{I}_{\mathrm{id}}$, the estimate gets massively inflated and the process starts again. We tried to fix the instability by using the mean of the two previous values and weighted means (with a variety of weighting schemes) and produce convergence, but with no success. Thus, an alternative approach was developed. The idea here is to find the root(s) of $f(\hat{I}_{\mathrm{id}})$ with $f(\hat{I}_{\mathrm{id}}) = I^*_{\mathrm{id}}$, which would be equivalent to the value of $\hat{I}_{\mathrm{id}}$ reached at the convergence point (Ross Ihaka, pers.com.). We solved this for I_{id} by getting the root of the equation (see Resource S1 for details):

$$1 - \left(\frac{1}{I_{\mathrm{id}}^{*2}}\hat{P}_1\hat{P}_2 - \frac{1}{I_{\mathrm{id}}^{*3}}\hat{P}_1\hat{P}_2\hat{P}_3\right) - I^{*}_{\mathrm{id}} = 0 \qquad \text{eqn 18}$$

Then, the same unbiased formulae as in the JS are used for $\hat{M}_i$ and $\hat{N}_i$:

$$\hat{N}_i = \frac{(n_i + 1)\hat{M}_i}{m'_i + 1} \qquad \text{eqn 19}$$

and

$$\hat{M}_i = \frac{z_i(n_i + 1)}{r'_i + 1} + m'_i \qquad \text{eqn 20}$$

The variance for $\hat{N}_i$ is given by the same formulas as in Pollock *et al.* (1990):

$$\mathrm{Var}(\hat{N}_i|N_i) = N_i\{N_i - E(n_i)\} \times \left[\frac{M_i - E(m'_i) + n_i}{M_i}\left\{\frac{1}{E(r'_i)} - \frac{1}{n_i}\right\} + \frac{N_i - M_i}{N_i \times E(m'_i)}\right] \qquad \text{eqn 21}$$

Assumptions are similar to those of the JS model: the capture probabilities are the same across individuals within each capture method, all animals have the same probability of survival between occasion i and occasion $i + 1$, marked animals do not lose their mark and marks are not overlooked, sampling periods are short enough to avoid death during sampling period, emigration is permanent, and capture probabilities are independent of each other. The TSJS model also relies on three additional assumptions: there is no loss on capture, i.e. animals are returned to the population following a capture; having a capture by one method in the capture history does not depend on also having or not captures by the other methods; Individuals cannot be caught separately by methods 1 and 2 on any capture occasion unless the capture is a simultaneous capture (method 3), i.e. any overlap between methods 1 and 2 on any capture is known.

BIAS ESTIMATION

A simulation study was carried out to investigate the performances of the TSJS model (see Resource S2 for details on the simulation). Bias can be described by many measures of difference. In this paper, the performance of the model will be discussed in terms of mean relative error (MRE) on capture occasion i:

$$\mathrm{MRE}_i = \frac{\sum_{j=1}^{\alpha}\frac{\hat{N}_{ij} - N_{ij}}{N_{ij}}}{\alpha} = \frac{1}{\alpha}\sum_{j=1}^{\alpha}\frac{\hat{N}_{ij}}{N_{ij}} - 1, \qquad \text{eqn 22}$$

i.e. the expected value of the estimate as a proportion of the true value, minus 1. It is therefore a measure of bias where $\hat{N}_j$ is the predicted population size given by the model, for simulation run j on capture occasion i, N_j is the observed, true population size, for simulation run j, α is the number of simulation runs. We also chose to measure the performance, the overall error, of the TSJS estimator in terms of root mean–squared relative error (RMSRE):

$$\mathrm{RMSRE}_i = \sqrt{\frac{\sum_{j=1}^{\alpha}\frac{(\hat{N}_{ij} - N_{ij})^2}{N_{ij}^2}}{\alpha}} \qquad \text{eqn 23}$$

The important difference between the two indices, MRE and RMSRE, is that the MRE provides information on the average error (i.e. the bias of the proportion), while the RMSRE measures the bias and the random variation around the expected value. The RMSRE can be seen as a measure of overall utility of the method and could be large even in the absence of bias.

Finally, confidence intervals are one of the most effective ways to measure precision. Assuming $\hat{N}_i$ is log-normally distributed, the log-normal approximation for the confidence interval (CI) is obtained at each occasion such that $\mathrm{CI} = (\hat{N}_i/C; \hat{N}_i \times C)$ where (Buckland *et al.* 1993)

$$C = \exp\left\{2\sqrt{\log(1 + \frac{Var(\hat{N}_i)}{\hat{N}_i^2})}\right\} \qquad \text{eqn 24}$$

Here, the coverage rate of the confidence intervals (CI coverage rate) will be calculated as the ratio of the number of times that the true value falls between the bounds of the estimated log-normal 95% confidence interval over the total number of simulation runs. Results are based on 200 simulation runs.

COMPARISON WITH EXISTING CLOSED- AND OPEN-POPULATION MODELS

Multiple-recapture models handling heterogeneity in capture probabilities, i.e. $\mathrm{M_h}$ and $\mathrm{M_{th}}$ by Chao (Chao 1988; Chao & Lee 1992) and $\mathrm{M_t}$ by Darroch (Darroch 1958), and the JS model were coded to be used in the simulations. This choice was based upon the closed-population models used in abundance assessment of many animal populations such as polar bears, whales and sharks, even though the population may be thought of as open (Calambokidis *et al.* 1990; Derocher & Stirling 1995; Cerchio 1998; Meekan *et al.* 2006; Parra, Corkeron, & Marsh 2006). It is of interest to compare, in the presence of heterogeneity in capture probability, the results of the TSJS model, the JS model and the closed-population models that are commonly used even with open populations: $\mathrm{M_h}$, $\mathrm{M_{th}}$ and $\mathrm{M_t}$. The objective here is to see in which case the assumption of closure is more important than the assumption of equal capture probability and if using two data sets could overcome the systematic underestimation in the JS estimates in presence of heterogeneity in capture probability among individuals (Carothers 1973, 1979; Hwang & Chao 1995). To compare the closed- and the open-population estimates, we averaged the open-population estimates and all related values (standard errors, MRE, RMSRE, true population size) across occasions.

In the case study, we estimated the population size using the TSJS and JS models and the following closed-population models: the modified Chapman (1951), $\mathrm{M_t}$ by Darroch, $\mathrm{M_h}$ and $\mathrm{M_{th}}$ by Chao. We used program CAPTURE included in the option 'closed capture' in program MARK for the multi-occasion closed-population estimates (White & Burnham 1999).

Results

In what follows, Pr(capture) refers to capture probabilities, whereas method-specific capture probabilities, i.e. probabilities of sampling by any of the methods, refer to the percentage of captured individuals caught by any one specific method (e.g. sampling scenario 20-40-40 = percentage of double-sampling-percentage of sampling by method 1-percentage of sampling by method 2) (see Resource S2 for details).

RESULTS OF THE TSJS ESTIMATOR WITH NO VIOLATION OF ASSUMPTIONS

The first issue of interest was the behaviour of the model estimates for different probabilities of simultaneous double-tagging (i.e. caught by method 3). The simultaneous double captures allowed the correct identification of the unknown duplicate entries in the capture history matrix. The probabilities of sampling by each method separately were set equal, the population set at 500 individuals at the start of the 10-occasion simulation experiment. If the probability of a capture being a simultaneous tagging was below 0·2, the TSJS estimator gave negatively biased estimates (see Resource S3 for details).

For the following, we investigated the bias of the TSJS model for a minimum probability of double-sampling of 0·2 (that was 20% of all captures should be by method 3). Above this value, the TSJS estimator seemed to be fairly reliable so long as the overall capture probability on an occasion was

Table 2. Mean relative error (MRE), root mean squared relative error (RMSRE), mean estimate and true value of the population size over the simulation runs, and standard errors (SE) of the estimated values and log-normal CI coverage rates at each capture occasion of a 10-year study for different capture probabilities for a starting population of 500 individuals with sampling scenario 20-40-40

Capture probability	Mean estimate	Mean true value	MRE	Mean estimated SE	RMSRE	Log-normal CI coverage rate (%)
Pr(c) = 0·05						
$\hat{N}_2$	391	627	−0·38	259	0·56	81
$\hat{N}_3$	546	653	−0·16	323	0·62	84
$\hat{N}_4$	670	695	−0·04	372	0·89	86
$\hat{N}_5$	778	719	0·08	419	1·1	83
$\hat{N}_6$	873	748	0·17	466	1·3	87
$\hat{N}_7$	734	766	−0·04	396	0·61	88
$\hat{N}_8$	805	799	0·01	432	0·8	83
$\hat{N}_9$	653	834	−0·22	351	0·69	77
Pr(c) = 0·1						
$\hat{N}_2$	643	627	0·03	194	0·63	74
$\hat{N}_3$	696	656	0·06	186	0·4	86
$\hat{N}_4$	785	694	0·13	203	0·46	87
$\hat{N}_5$	803	719	0·12	204	0·44	88
$\hat{N}_6$	817	745	0·1	205	0·39	88
$\hat{N}_7$	880	762	0·15	220	0·45	84
$\hat{N}_8$	834	794	0·05	209	0·42	86
$\hat{N}_9$	937	829	0·13	234	0·77	75
Pr(c) = 0·2						
$\hat{N}_2$	648	626	0·04	78	0·28	67
$\hat{N}_3$	678	653	0·04	77	0·19	79
$\hat{N}_4$	713	692	0·03	80	0·17	86
$\hat{N}_5$	755	718	0·05	85	0·18	85
$\hat{N}_6$	769	743	0·03	87	0·17	84
$\hat{N}_7$	801	762	0·05	91	0·17	81
$\hat{N}_8$	820	793	0·03	94	0·16	87
$\hat{N}_9$	860	828	0·04	100	0·24	74
Pr(c) = 0·5						
$\hat{N}_2$	619	627	−0·01	14	0·07	54
$\hat{N}_3$	652	654	0	16	0·04	35
$\hat{N}_4$	698	694	0	20	0·04	60
$\hat{N}_5$	727	720	0·01	22	0·04	70
$\hat{N}_6$	750	744	0	24	0·04	79
$\hat{N}_7$	764	763	0	25	0·04	69
$\hat{N}_8$	793	795	0	27	0·04	73
$\hat{N}_9$	809	830	−0·02	29	0·06	56
Pr(c) = 0·8						
$\hat{N}_2$	623	625	0	2	0·02	27
$\hat{N}_3$	662	651	0·02	4	0·02	35
$\hat{N}_4$	711	693	0·03	7	0·03	31
$\hat{N}_5$	740	716	0·03	8	0·04	26
$\hat{N}_6$	768	743	0·03	10	0·04	30
$\hat{N}_7$	783	761	0·03	11	0·03	47
$\hat{N}_8$	808	792	0·02	12	0·03	75
$\hat{N}_9$	823	827	0	13	0·02	90

Pr(c) = occasion-specific capture probability; $\hat{N}_2$, …, $\hat{N}_9$ = population size estimate at time 2, …, 9.

above 0·1. For capture probabilities smaller than 0·1, TSJS estimates could be severely biased with values of the MRE reaching −0·38 on the second capture occasion for a capture probability of 0·05 (see Table 2 and Resource S3). If we ignored the estimates based on animals marked in the first and last occasions of sampling and concentrated on the intermediate estimates that were based on more information, TSJS estimates were quite reasonable even at relatively small probability of simultaneous tagging (≥0·2) and low capture probabilities (> 0·05). Concerning the magnitude of the overall relative variation represented by the RMSRE, it followed the evolution of the MRE: it varied between 0·4 and 1·3 for capture probabilities smaller than 0·1 and then stabilized at small values (< 0·2) above this capture probability.

As expected, the standard error decreased with an increase in the value of the capture probability and it increased with the capture occasion. For capture probabilities smaller than 0·1, the standard errors were large (in the order of 50% of the estimated population size), while, for large capture probabilities, the standard error was generally much smaller. Consequently, the CI coverage rate was better for small capture probabilities (< 0·1), generally above 80%, than for very high capture probabilities (0·8), where although the SE was small the small bias causes poor coverage. In this case, coverage could be as small as 25%. However, the confidence intervals at small capture probabilities were too wide for the model to be useful (recapture rates were too low for reliable estimates). Standard errors and coverage rates of confidence intervals for capture probability above 0·2 (even though they are too liberal) still suggested that the estimation method worked reasonably well. A smaller CI coverage rate was also usually observed for the second and the ninth capture occasions.

COMPARISON OF ESTIMATORS

Table 3 shows that $\hat{N}_{\mathrm{TSJS}}$ was the best estimator when the heterogeneity (see Resource S2 for details on the structure of the heterogeneity in the simulations) was small and/or the capture probabilities high (cases 1, 5 and 6) with respect to MRE, RMSRE and CI coverage. In presence of moderate or high individual heterogeneity in capture probabilities (cases 2, 3 and 4), the TSJS estimator was generally better than the JS estimator, although less good in terms of CI coverage rate because the TSJS method usually produced smaller standard errors. In moderate and high cases of heterogeneity, closed-population estimators performed better: in cases 2 and 3, $\hat{N}_{\mathrm{t}}$ produced the best estimates with more than 87% of CI coverage rate. However, in case 3, $\hat{N}_{\mathrm{TSJS}}$ and $\hat{N}_{\mathrm{h}}$ seemed similar in RMSRE and absolute value of MRE ($\hat{N}_{\mathrm{TSJS}}$ underestimates while $\hat{N}_{\mathrm{h}}$ overestimates) and $\hat{N}_{\mathrm{TSJS}}$ even appeared slightly better than $\hat{N}_{\mathrm{h}}$ in case 3, in terms of CI coverage rate: log-normal CI coverage rate was of 44% while being 32% for $\hat{N}_{\mathrm{h}}$.

All the estimators were expected to underestimate the true parameter when capture probabilities vary among individuals (Carothers 1973; Otis *et al.* 1978; Pollock *et al.* 1990; Hwang & Chao 1995) but most of the closed-population estimators $\hat{N}_{\mathrm{t}}$, $\hat{N}_{\mathrm{h}}$, $\hat{N}_{\mathrm{th}}$ presented a positive error (MRE > 0·1) for most cases of heterogeneity ($\hat{N}_{\mathrm{t}}$, $\hat{N}_{\mathrm{h}}$, $\hat{N}_{\mathrm{th}}$ in cases 1, 2, 3, 5 and 6 and $\hat{N}_{\mathrm{th}}$ in case 4). When the heterogeneity was high (case 4), $\hat{N}_{\mathrm{h}}$ and $\hat{N}_{\mathrm{th}}$ provided a very good CI coverage. The JS estimator led to estimates systematically more negatively biased than the ones given by the TSJS estimator but better CI coverage rates in cases 2, 3 and 4 (see Resource S4 for details on the bias of the TSJS estimator per capture occasion under the six cases of heterogeneity).

CASE STUDY

The TSJS model was applied to capture–recapture data of humpback whales in New Caledonia between 1996 and 2001. Two sampling methods were used to gather data during the breeding season, from July to September: photo-identification and skin biopsy. However, on some occasions, some whales did not fluke so could not be photographed or could not be approached closely enough to be genotyped by skin biopsy. Thus, combining data from photo-identification and genotyping during the survey offered the opportunity to produce more efficient abundance estimates for the humpback whale population in New Caledonia. See Garrigue *et al.* (2004) for further details.

The 1996–2001 data set comprised 373 captures and 273 recapture histories: 62 whales have been genotyped only, 34 photographed only and 177 simultaneously genotyped and photographed at least once (Table 4).

As a comparison to the TSJS model results on the combined data set, the JS and some closed-population models were applied separately on the photographic data set 1996–2001 and on the genetic data set 1996–2001. The results are given in Table 5.

From this example, the variety of models and the resulting large range of abundance estimates led to two questions in the absence of a way to use both data set in one abundance model: which model to believe and which data set to use? Indeed of the six models, four gave similar results but models $\mathrm{M_h}$ and $\mathrm{M_{th}}$ produced estimates twice as large as the other four models, both with the photo-identification data set alone [respectively 624 (SE = 100·87) and 628 (SE = 94·16)] and with the genetic data set alone [respectively 730 (SE = 110·96) and 720 (SE = 108·33)]. Moreover, results given by models estimating population size from the genetic data set were also systematically larger than those based on the photo-identification data set.

On a population that was clearly open like the humpback whale population here over 6 years, the closed-population estimates cannot be interpreted like the open-population one: the closed-population estimates could only be interpreted as a superpopulation (Kendall 1999), i.e. the total number of individuals ever present in the population between 1996 and 2001. Therefore, these models were of limited use for monitoring the population.

Both the JS model and the TSJS model suggested an increase in the population every year, with the results based on the TSJS estimator [from 167 (SE = 33) in 1997 to 366

Table 3. Comparison of mean relative error (MRE), root mean squared relative error (RMSRE), mean estimate and true value of the population size and standard errors of the estimated values and log-normal CI coverage rates over the simulation runs, under six cases of heterogeneity in capture probabilities, with closed-population and Jolly–Seber (JS) models and the two-source Jolly–Seber (TSJS) model under scenario 20-40-40, over 10 occasions and with a starting population of 500 individuals

Heterogeneity case	Mean estimate	Mean true value	MRE	Mean estimated SE	RMSRE	Log-normal CI coverage rate (%)
Case 1						
CV = 0·14						
$\bar{\mathrm{P}}\mathrm{r}(c)_g = 0.2$						
$\hat{N}_{\mathrm{TSJS}}$	709	728	−0·03	82	0·19	79
$\hat{N}_{JS}$	689		−0·06	113	0·27	76
$\hat{N}_{\mathrm{t}}$	962		0·33	75	0·36	2
$\hat{N}$h	1053		0·46	82	0·48	0
$\hat{N}_{\mathrm{th}}$	1073		0·46	68	0·66	0
Case 2						
CV = 0·37						
$\bar{\mathrm{P}}\mathrm{r}(c)_g = 0.2$						
$\hat{N}_{\mathrm{TSJS}}$	585	728	−0·2	66	0·25	46
$\hat{N}_{JS}$	566		−0·22	92	0·32	51
$\hat{N}$t	799		0·11	69	0·16	92
$\hat{N}$h	871		0·21	72	0·24	27
$\hat{N}_{\mathrm{th}}$	847		0·17	52	0·19	50
Case 3						
CV = 0·43						
$\bar{\mathrm{P}}\mathrm{r}(c)_g = 0.2$						
$\hat{N}_{\mathrm{TSJS}}$	583	727	−0·2	67	0·26	44
$\hat{N}_{JS}$	561		−0·23	92	0·33	48
$\hat{N}$t	802		0·11	70	0·16	87
$\hat{N}$h	877		0·22	75	0·25	32
$\hat{N}_{\mathrm{th}}$	866		0·18	55	0·2	31
Case 4						
CV = 0·68						
$\bar{\mathrm{P}}\mathrm{r}(c)_g = 0.2$						
$\hat{N}_{\mathrm{TSJS}}$	411	728	−0·44	37	0·45	1
$\hat{N}_{JS}$	401		−0·45	54	0·47	7
$\hat{N}$t	628		−0·13	55	0·16	49
$\hat{N}$h	700		−0·03	66	0·11	100
$\hat{N}_{\mathrm{th}}$	761		0·06	48	0·1	85
Case 5						
CV = 0·23						
$\bar{\mathrm{P}}\mathrm{r}(c)_g = 0.64$						
$\hat{N}_{\mathrm{TSJS}}$	677	727	−0·07	13	0·07	20
$\hat{N}_{JS}$	558		−0·23	20	0·24	0
$\hat{N}$t	1068		0·48	44	0·5	0
$\hat{N}$h	1159		0·61	42	0·63	0
$\hat{N}_{\mathrm{th}}$	1275		0·74	37	0·75	0
Case 6						
CV = 0·26						
$\bar{\mathrm{P}}\mathrm{r}(c)_g = 0.7$						
$\hat{N}_{\mathrm{TSJS}}$	731	729	0	11	0·04	55
$\hat{N}_{JS}$	581		−0·2	18	0·21	0
$\hat{N}$t	1214		0·68	43	0·7	0
$\hat{N}$h	1310		0·61	38	0·83	0
$\hat{N}_{\mathrm{th}}$	1412		0·93	35	0·93	0

CV = coefficient of variation;
$\hat{N}_{\mathrm{TSJS}}$, $\hat{N}_{JS}$,$\hat{N}$t, $\hat{N}$h, $\hat{N}_{\mathrm{th}}$ = population size estimate for the TSJS model, JS model, $\mathrm{M_t}$ by Darroch, $\mathrm{M_h}$ by Chao, $\mathrm{M_{th}}$ by Chao.

(SE = 69) in 2000] systematically in between the estimates given by the JS estimator on the photographic [from 139 (SE = 33) in 1997 to 227 (SE = 43) in 2000] and genetic data [from 216 (SE = 51) in 1997 to 484 (SE = 116) in 2000]. Given that more than 20% of the individuals sampled on any occasion between 1996 and 2001 were caught by both methods simultaneously (Table 4), the probability of true identity $\hat{I}_{\mathrm{id}}$ was high ($\hat{I}_{\mathrm{id}}$ = 0·98) and the TSJS estimator was within the

Table 4. Number of whales captured by genetic, photographic and simultaneous sampling between 1996 and 2001 in New Caledonia

	1996	1997	1998	1999	2000	2001
Number of whales genotyped only	4	3	10	11	16	35
Number of whales photographed only	12	18	13	3	6	11
Number of whales photographed and genotyped	43	33	36	24	33	62
Total number of captures	59	54	59	38	55	108

Table 5. Humpback whale population size in New Caledonia between 1996 and 2001 using the two-source Jolly–Seber model on the combined data set, the Jolly–Seber and closed-population models separately on the photo-identification (photo) and the genetic (genet) data sets

Model	Type	1997 (SE)	1998 (SE)	1999 (SE)	2000 (SE)	2001
Two-source Jolly–Seber model	Open	167 (33)	205 (40)	262 (41)	366 (69)	
Jolly–Seber model						
Photo	Open	139 (33)	138 (30)	170 (25)	227 (43)	
Genet		216 (51)	273 (67)	298 (65)	484 (116)	
Modified Chapman						
Photo	Closed	193 (35)	162 (27)	466 (214)	186 (58)	295 (72)
Genet		253 (75)	216 (58)	563 (261)	299 (97)	612 (179)
Model M_t Darroch						
Photo	Closed			357 (27)		
Genet				474 (42)		
Model M_h Chao						
Photo	Closed			624 (101)		
Genet				730 (111)		
Model M_{th} Chao						
Photo	Closed			628 (94)		
Genet				720 (108)		

appropriate range of sampling probabilities as suggested by the simulations. However, heterogeneity in capture probability was most likely present among the individuals of this population as it is the case in other humpback whale populations (Hammond 1990; Smith *et al*. 1999; Garrigue *et al*. 2004), and therefore, the population sizes given by the TSJS model may be underestimated. Nevertheless, with the evidence provided by the present TSJS model, the humpback whale population of New Caledonia was estimated at less than 400 individuals in 2000 [i.e. 366 (SE = 69)], and these results emphasized the potential vulnerability of this population. This also suggested that if the hunt really ended 30 years ago and if the New Caledonia population was recovering, as suggested by the TSJS model, the rate of recovery may be far less than the 10% observed for some other populations (Zerbini, Clapham, & Wade 2008).

Discussion

Multiple sampling methods are nowadays commonly jointly used in mark–recapture surveys, and these sampling schemes are arguably good approaches to maximize the number of catchable animals without having to dilute the sampling effort over a large area. In doing so, one might also expect to decrease the heterogeneity in capture probabilities among individuals, hence minimizing the bias in the population size estimates. However, a drawback of using multiple sampling methods is the potential overlap that can arise between the sampling methods. This can prevent the joint use of the data from the different sampling methods if this overlap is unknown. Our objective was thus to develop an analytical framework allowing for the combination of two overlapping sources of data in an open-population model to provide a robust abundance estimator. We adopted an *ad hoc* approach based on an extension of the JS model. While classical approaches in mark–recapture models are typically based on the likelihood, presence of two overlapping sources of capture currently limits the development of a likelihood approach to closed-population models (Madon 2010). Theoretically, for open populations, other solutions could be considered for a more parsimonious modelling of parameters: an extension of the Crosbie–Manly–Arnason–Schwarz framework (Crosbie & Manly 1985; Schwarz & Arnason 1996), or the use of multinomial models based on the latent history approach of Link & Barker (2010) are appealing. However, the approach would consist in enumerating the complete list of possible latent histories, and even for short studies, it would require a rather powerful computer.

Correlation between the sampling methods is an important consideration (Boulanger *et al*. 2008) that could be a limiting factor in the TSJS model. Here, the reasoning is based on the assumption that the sampling methods are independent conditionally on detection. In the case study and in the simulations (see Resource S2), the sampling methods are therefore not assumed unconditionally independent on occasion but they are assumed independent providing the animal was detected. Furthermore, in the TSJS model, we assume that having a capture by one method in the capture history does not depend on also having captures by the other methods, i.e. capture events are independent across occasions. This assumption is only justified asymptotically as the number of periods goes to infinity, as the incidence of a capture by one method reduces the number of trials available for the other methods.

Our simulations demonstrate that the TSJS estimator's bias is negligible when the capture probability is reasonably high. These results are similar to those of Gilbert's (1973) on the JS model. As in the study by Gilbert (1973), the bias is not $> 10\%$ of the true population size when the capture probability is $> 0{\cdot}2$ and additionally the probability of simultaneous sampling is above 0·2. The comparison with closed-population estimators highlights that in presence of small heterogeneity in individual capture probability, although negatively biased, the TSJS estimator remains more robust than closed-population estimators handling heterogeneous capture probabilities.

The assumption of population closure is most likely violated in the humpback whale study given the length of study (6 years) and the migratory behaviour of the animals. In other cases, the closure assumption might alternatively be violated because of sampling design, such as small grid size or inappropriate grid placement. When the assumption of closure is not met, closed-population estimators become hard to interpret. Yet closed-population estimators offer the advantage of being able to incorporate heterogeneity in capture probabilities between individuals and/or over time. Among humpback whales in New Caledonia, heterogeneity in individual capture probability is likely (Smith *et al.* 1999; Garrigue *et al.* 2004). It is therefore important to determine what results in the least biased estimate: a closed-population estimator that addresses heterogeneity in capture but whose closure assumption is violated, or the TSJS, which acknowledges the open nature of the population but assumes homogeneous capture probabilities? The violation of the closure assumption generally biases closed-population estimators upward, because it inflates the number of marked animals and negatively biases capture probabilities (Boulanger & McLellan 2001). In contrast, capture heterogeneity among individuals usually induces a downward bias in these estimators, even though such heterogeneity is ostensibly accounted for (Otis *et al.* 1978). We argue that this makes closed-population estimators difficult to interpret in many real-world circumstances. Although our simulations indicate that the TSJS estimator suffers from negative bias when heterogeneity in capture probabilities is present, we feel it outperforms available closed-population estimators by providing more interpretable estimates. It also offers more information for population monitoring by estimating abundance at each time period.

We provide a valid *ad hoc* open-population size estimator, the TSJS model, that allows researchers to combine two sources of capture–recapture data to estimate population size and therefore holds great promise in monitoring by providing researchers and managers with a method allowing for a diversity of sampling protocols. Furthermore, extension of this methodology to closed-population models handling heterogeneity in capture should also prove useful for short studies or closed populations. R-codes formatting the data and implementing the TSJS model are provided in Resource S5.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Resource S1. Function approach.

Resource S2. Simulation experiment.

Resource S3. Graphical representation of the evolution of the bias of the TSJS estimator.

Resource S4. Results of the TSJS estimator with heterogeneity.

Resource S5. Two-source-Jolly–Seber user's guide.