



0 **Estimating the abundance of burrow-nesting species through the statistical analysis of combined playback and visual surveys** 53

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15 The conservation of elusive species relies on our ability to obtain unbiased estimates of their abundance trends. Many species live or breed in cavities, making it easy to define the search units (the cavity) yet hard to ascertain their occupancy. One such example is that of certain colonial seabirds like petrels and shearwaters, which occupy burrows to breed. In order to increase the chances of detection for these types of species, their sampling can be done using two independent methods to check for cavity occupancy: visual inspection, and acoustic response to a playback call. 70

20 This double-detection process allows us to estimate the probability of burrow occupancy by accounting for the probability of detection associated with each method. Here we provide a statistical framework to estimate the occupancy and population size of burrow-dwelling species. We show how to implement the method using both maximum likelihood and Bayesian approaches, and test its precision and bias using simulated datasets. We subsequently illustrate how to extend the method to situations where two different species may occupy the burrows, and apply it to a dataset on wedge-tailed shearwaters *Puffinus pacificus* and tropical shearwaters *P. bailloni* on Aride Island, Seychelles. 75

25 The simulations showed that the single-species model performed well in terms of error and bias except when detection probabilities and occupancies were very low. The two-species model applied to shearwaters showed that detection probabilities were highly heterogeneous. The population sizes of wedge-tailed and tropical shearwaters were estimated at 13 716 (95% CI: 12 909–15 874) and 25 550 (23 667–28 777) pairs respectively. 80

30 The advantages of formulating the call-playback sampling method statistically is that it provides a framework to calculate uncertainty in the estimates and model assumptions. This method is applicable to a variety of cavity-dwelling species where two methods can be used to detect cavity occupancy. 85

35 Estimating abundance is central to most ecological studies. In the context of conservation, abundance estimates provide baseline information about the status of a population (Sutherland et al. 2004, Bibby et al. 2012). They allow the tracking of temporal changes and the study of habitat preferences, and help assess the impact of environmental and land use changes (Gregory et al. 2004). To meet this need, a plethora of field and statistical methods have been devised to improve abundance estimates, adapted to the habits of a variety of species. Central to this exercise is accounting for the widespread problem of imperfect detection (Borchers et al. 2002, Royle et al. 2005, Scott et al. 2009). 90

45 For the vast majority of populations, be it due to logistical constraints or species elusiveness, it is impossible to directly count all the individuals present at a given time. Unbiased estimates of population abundance therefore require estimating the probability of detection of individuals present in the population (MacKenzie et al. 2005). This can be estimated from a variety of sampling designs like double observer counts (Forcey et al. 2006), distance sampling (Buckland et al. 2001), repeated counts (Royle and Nichols 2003, Kéry et al. 2005) or capture–mark–recapture (McCrea and Morgan 2014). Modern statistical methods can use these designs to jointly estimate species detection probabilities and abundance, thus accounting for the uncertainty of both estimates. Despite this, it is not uncommon for practitioners to independently estimate the detection probability using a subset of data, and later apply it as a correction factor to individual counts (Azuma et al. 1990, Zielinski and Stauffer 1996, Bodkin and Udevitz 1999, Burger and Lawrence 2001, Thompson 2002, Kissling et al. 2006, Soanes et al. 2012). This ad hoc application of correction factors, however, makes it difficult to produce abundance confidence intervals that account for the uncertainty in the detection factor estimation. In the worst cases, ignoring uncertainty in correction factors can lead to grossly misleading conclusions, such as was illustrated in a recent re-analysis of tiger recovery (Gopalaswamy et al. 2015). Even more problematic is the 100 105

0 fact that these corrections assume constant detection probabilities over time and space. If that is not the case, this will strongly hinder spatiotemporal comparisons.

1 In species that inhabit dens or burrows, estimates of population densities rely on our ability to infer the proportion of those cavities that are inhabited by a breeding pair. This is the case for burrow nesting seabirds, which have a tradition of correcting for detectability through ad hoc application of correction factors (Warham 1996, Ratcliffe et al. 1998, Burger and Lawrence 2001, Scott et al. 2009). For example, some studies have used multiple visits to ascertain occupancy in a subsample of burrows, calculated an average occupancy rate and applied it to the total number of burrows of the sample area (Rayner et al. 2007, Whitehead et al. 2014). Other studies use the playback method, which combines visual and acoustic detection, and calculate a playback response rate which, applied to the number of burrows with undetected birds in it, gives an estimate of the proportion of apparently empty burrows that contained an unresponsive bird (James and Robertson 1985, Burger and Lawrence 2001). While some studies use both visual and acoustic detection methods only on a subset of data to later apply the calculated playback response rate to surveys using only acoustic sampling (James and Robertson 1985), others use both detection methods for all burrows (Burger and Lawrence 2001). In the first case, the number of occupied burrows is calculated as:

$$\widehat{N} = n_R p_R \quad (1)$$

where n_R is the number of burrows in which a bird responded to the playback call, and p_R is the response rate calculated from the subsample as the proportion of visible birds that responded to the playback (James and Robertson 1985). When both methods are used for all burrows, the total number of occupied burrows N is subsequently estimated using the following formula:

$$\widehat{N} = n_V + n_0 \frac{n_{R_0}}{n_{VR}} \quad (2)$$

where n_V is the total number of birds seen, n_0 is the number of burrows with undetected birds (not seen nor heard), n_{R_0} is the number of birds that responded but were not seen, and n_{VR} is the number of birds that were seen and responded.

While the above methods address the bias in our estimates of burrow occupancy by accounting for imperfect detection, they do not provide measures of uncertainty in the estimate and do not overcome the problem that population changes are confounded by changes in detection probability over time and space. Because uncertainty and the ability to make spatiotemporal comparisons in population estimates are key to the management of species, it is clearly desirable to formalize the joint estimation of detection and abundance probabilities in a formal statistical framework.

The aim of this article is to provide a statistical framework for the analysis of playback census. First, we derive the necessary likelihood functions. Second, we will implement them on simulated data using both maximum likelihood and Bayesian approaches, in order to assess the bias and precision of the occupancy estimates. Third, we extend the approach to cases where a burrow can be occupied by two different species. Finally, we implement the approach using data on two species of burrow-nesting seabirds, the

wedge-tailed *Puffinus pacificus* and the tropical shearwater *P. bailloni*, breeding on Aride Island, an Important Bird Area of the Seychelles (Rocamora and Skerrett 2001). Although particularly useful for the sampling of burrow-nesting seabirds, the approach is applicable to any species where two independent methods of detection (e.g. passive sighting and active luring) can be applied to estimate the occupancy of an animal's dwelling (e.g. crabs in burrows, fish in shelters, or woodpeckers in tree-holes).

Material and methods

Statistical framework

Consider a set of m burrows that may be occupied by the species of interest. For each burrow, the detection procedure occurs by two independent methods with different detection probabilities: visual examination and playback. The data is arranged in a matrix X of m rows and two columns, whereby for each burrow i , elements $x_{i,1}$ and $x_{i,2}$ contain a 0 or 1 depending on whether an individual was detected or not with either the first (visual) or second (playback) method respectively. For example, an individual (or pair) that was not seen but heard on burrow i , will correspond to $x_{i,\cdot} = \{0,1\}$. If we denote the probability of occupancy of the burrow Ψ , the probability of visual detection p_V , and the probability of playback response p_R , the likelihood of all four possible outcomes is given in Table 1. The total likelihood of the data X is therefore:

$$L(X | \Psi, p_V, p_R) = \prod_{i=1}^m \{ \Psi [p_V x_{i,1} + (1 - p_V)(1 - x_{i,1})] [p_R x_{i,2} + (1 - p_R)(1 - x_{i,2})] + (1 - \Psi)(1 - x_{i,2} x_{i,2}) \} \quad (3)$$

Note that for this to be true, we must make the following biological assumptions. First, we assume that each burrow can only be occupied by a single individual (or pair). Second, we assume independence of the two detection methods: in other words, visual inspection does not affect the probability of response nor vice-versa. In order to ensure this is fulfilled, it is recommendable to use the potentially more disturbing method last (e.g. playback should be done after visual inspection, to ensure birds do not change their behaviour in ways that affect their visibility). Third, it assumes that unoccupied burrows represent the absence of a breeding bird, rather than a temporary absence (e.g. to forage). To ensure this, it is important to time the sampling during the appropriate stage in the breeding cycle and during the animal's inactive period of the day, which will depend on the target species (e.g. at night for *P. bailloni* and *P. pacificus*). The latter assumption

Table 1. Likelihood of each possible data scenario in a single species case (Ψ : probability of occupancy; p_V : probability of visual detection; p_R : probability of playback response).

Scenario		Data $x_{i,\cdot}$	Likelihood $L(x_{i,\cdot} \Psi, p_V, p_R)$
Sighting	Response		
Yes	Yes	{1,1}	$\Psi p_V p_R$
Yes	No	{1,0}	$\Psi p_V (1 - p_R)$
No	Yes	{0,1}	$\Psi (1 - p_V) p_R$
No	No	{0,0}	$\Psi (1 - p_V) (1 - p_R) + (1 - \Psi)$

0 can be relaxed by the use of repeated observations through
 1 time. Note that the illustrated estimate refers to the number
 2 of burrows that are occupied at the time of sampling. While
 3 burrow occupation of non-breeding individuals is rare, the
 4 tropical shearwater is known to breed throughout the year,
 5 and thus a proper breeding census would require including
 6 samples throughout the year, rather than a single time point
 7 as in our example.

8 The estimation of parameters ψ , p_S , and p_R can proceed
 9 by maximum likelihood or Bayesian methods. For the latter,
 10 it will be necessary to define priors. Since all three parameters
 11 are probabilities we will use a uniform distribution bounded
 12 between 0 and 1 as recommended in Royle and Dorazio
 13 (2008). The total number of individuals in a sampling unit
 14 can be estimated as $\hat{N} = \psi m$.

[AQ2]

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Simulated datasets and performance comparison

16 In order to evaluate the performance of both maximum
 17 likelihood and Bayesian methods, we simulated a series of
 18 datasets. All datasets represented a plot with 30 burrows
 19 (representative of the number of burrows found in a typical
 20 plot for the shearwater case study described below). Data
 21 was generated using binomial trials for three-way combina-
 22 tions of the following parameter values. For both detection
 23 probabilities p_V and p_R we used {0.1, 0.2, 0.3, 0.4, 0.5, 0.6,
 24 0.7, 0.8, 0.9}. The occupancy probabilities ψ used were {0.1,
 25 0.3, 0.5, 0.7, 0.9}. For each combination, we performed a
 26 total of 20 simulations.

27 Maximum likelihood estimation was performed in pro-
 28 gram R 3.1.2 (R Core Team), using function `mle2` in package
 29 `bbmle` (Bolker 2014). Bayesian estimation was implemented
 30 in JAGS 3.4.0 (Plummer 2003). As uninformative priors for
 31 all parameters (ψ , p_V , p_R) we used a uniform distribution
 32 from 0 to 1. For each estimation we ran 2000 chains with a
 33 burnin of 500.

[AQ3]

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36 We evaluated the performance of the estimation by
 37 calculating the average error and bias in estimating the total
 38 number of occupied burrows, the most likely measure of
 39 interest. As a measure of error we used the root mean squared
 40 error (RMSE):

$$RMSE = \sqrt{\frac{(\hat{N} - N)^2}{n}} \quad (4)$$

41 where N is the known population size, \hat{N} is its estimate,
 42 and n is the expected number of occupied burrows (number
 43 of burrows $\times p_{oc}$). The results are presented in standardized
 44 units by subtracting the mean RMSE for a given parameter
 45 combination and dividing by its standard deviation (Fig. 1).

46 We calculated relative bias as the proportional difference
 47 between estimated and known population size $\frac{(\hat{N} - N)}{N}$.

48 Models performed better when the probability of occu-
 49 pancy increased, both in terms of bias (Fig. 1) and error
 50 (Fig. 2). This is because higher occupancies imply larger sam-
 51 ple sizes to estimate detection probabilities. Only plots with
 52 $\psi = 0.1$ (an average of 3 out of 30 occupied burrows) showed
 53 considerable levels of error and bias. Expectedly, the models
 54 also performed better when the probabilities of detection
 55 increased. Note that the two probabilities of detection (here
 56 visual detection and response to a playback call) are mathematically
 57 interchangeable in the simulation. The likelihood
 58 framework performed better under low occupancy rates and
 59 very different detection probabilities among both methods
 60 (e.g. the probability of visual detection being high and the
 61 probability of response being low).

Extension to two species

62 It is not uncommon for burrows and other types of refuge
 63 to be suitable for more than one species. In the example of

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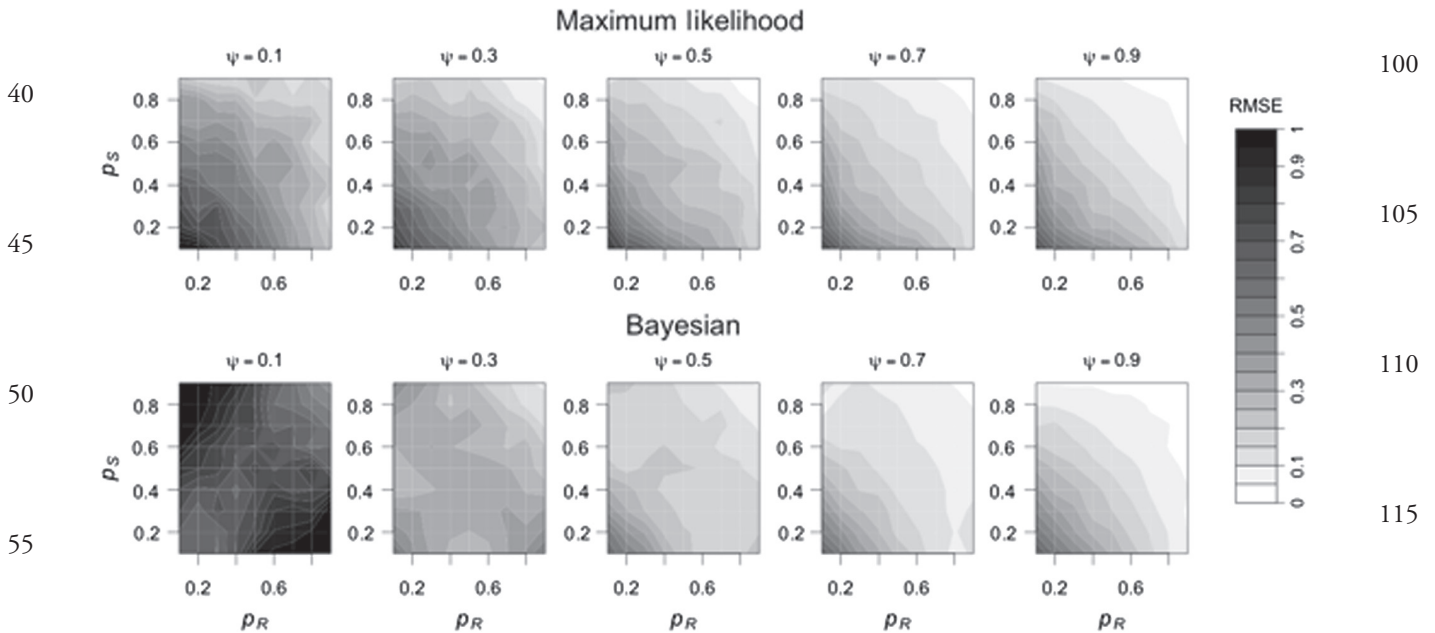
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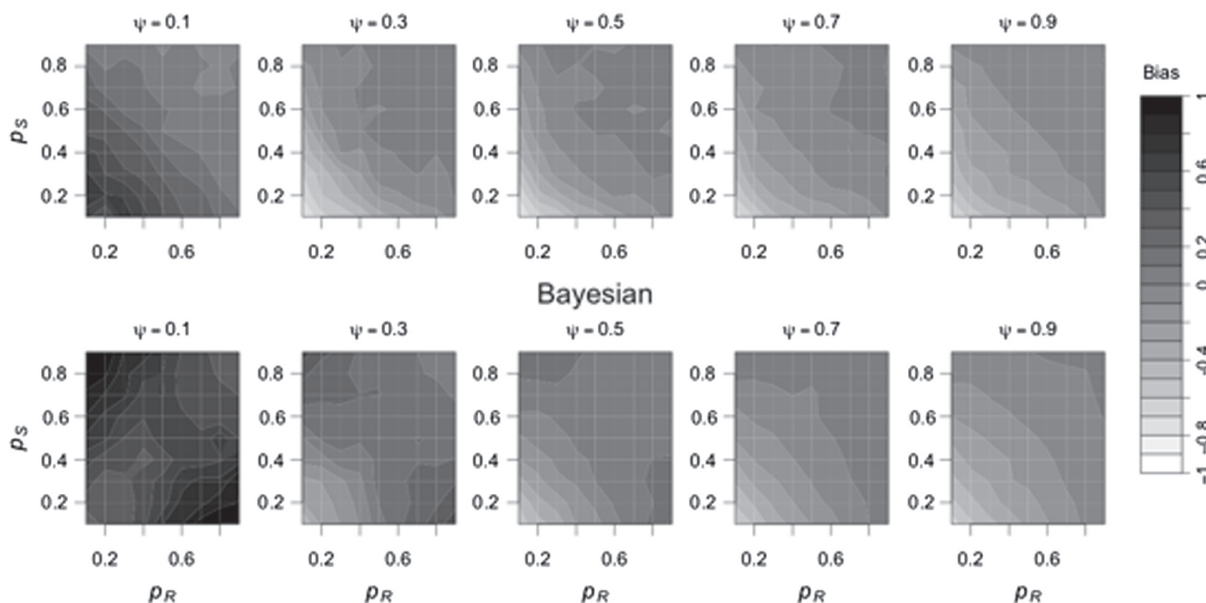
[AQ6] 60 Figure 1. Standardized root mean squared error (RMSE) of estimates of population size for maximum likelihood and Bayesian estimation for the simulated plots under a variety of parameters.

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Maximum likelihood

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[AQ6] Figure 2. Relative bias of estimates of population size for maximum likelihood and Bayesian estimation for the simulated plots under a variety of parameters.

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25 a two-species scenario where the burrow can be occupied
 by either species A or B alternately it is straightforward to
 extend the model. We do so by assuming species-specific
 occupancies (Ψ_A, Ψ_B) and detection probabilities ($p_{VA}, p_{VB},$
 p_{RA}, p_{RB}). If we assume that it is only possible to find an
 30 individual (or pair) of one or the other species (not both),
 we need to constrain the model so that $\Psi_A + \Psi_B \leq 1$. Table
 2 specifies the likelihood for all possible data outcomes. Note
 that in this case, the way to code the data is similar to the
 one-species case, but with 1 or 2 representing detection of
 35 species A or B respectively. For example, if species B is seen
 but not heard in burrow i , $x_i = \{2, 0\}$. The total data like-
 likelihood is again the product of likelihoods for all burrows.
 Table A3 in the Supplementary material Appendix 1 shows the
 results of simulations to evaluate the performance of the
 40 two-species model under a Bayesian framework, applied in
 the case-study below.

Case study: estimating shearwater densities on aride island

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We here present the application of the two-species model
 to the estimation of the size of a mixed colony on Aride

Island (Seychelles) with two breeding shearwaters: the
 wedge-tailed *Puffinus pacificus* and tropical shearwater
P. bailloni. Aride Island Nature Reserve comprises 73 ha
 and is suspected to harbor the largest colony of *P. bailloni*
 in the world (Rocamora and Skerrett 2001). Both species
 90 breed in the same type of natural burrow on the hill-
 sides of the island. While *P. pacificus* is a seasonal breeder
 found mainly from September to February, *P. bailloni*
 has no clear breeding season in Seychelles, and incubat-
 ing birds may be found all year round (Skerrett et al.
 95 2001).

To carry out the sampling analysed here, we followed the
 playback census protocol described in Betts (1998). In each
 plot, we noted all potentially suitable burrows (between 1
 and 38 burrows per plot, 267 in total) and inspected them
 100 visually with a head torch for the presence of a nesting
 bird of either species. We played recorded male–female
 duet calls for both species (Rocamora et al. 2000) in the
 case of unknown content, and for the observed species when
 the bird was visible. We played the call at the opening of
 105 the burrow and noted whether the bird responded by the
 end of the recordings (1:24 min for *P. bailloni* and, 1.58 for
P. pacificus).

Table 2. Likelihood for all possible scenarios in a 2 species case. Ψ_A (resp. Ψ_B): probability of occupancy by species A (resp. B); p_{VA} (resp. p_{VB}): probability of visual detection of species A (resp. B); p_{RA} (resp. p_{RB}): probability of playback response of species A (resp. B).

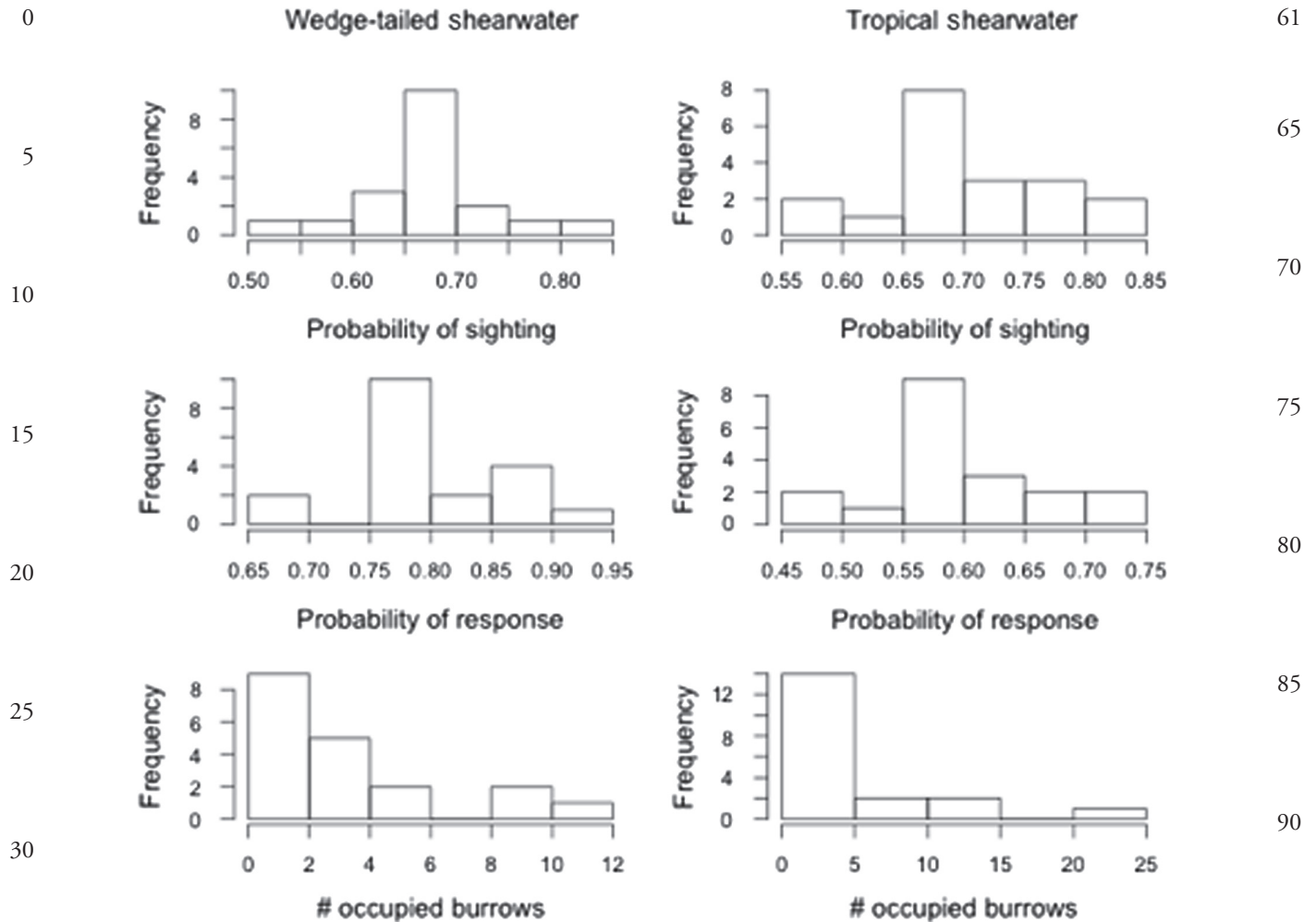
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Sighting	Scenario		Data X_i .	Likelihood $L(x_i, \cdot p_{ocA}, p_{ocB}, p_{VA}, p_{VB}, p_{RA}, p_{RB})$
	Response	Species		
Yes	Yes	A	{1,1}	$\Psi_A p_{VA} p_{RA}$
55 Yes	No	A	{1,0}	$\Psi_A p_{VA} (1 - p_{RA})$
No	Yes	A	{0,1}	$\Psi_A (1 - p_{VA}) p_{RA}$
Yes	Yes	B	{2,2}	$\Psi_B p_{VB} p_{RB}$
Yes	No	B	{2,0}	$\Psi_B p_{VB} (1 - p_{RB})$
No	Yes	B	{0,2}	$\Psi_B (1 - p_{VB}) p_{RB}$
60 No	No		{0,0}	$\Psi_A (1 - p_{VA})(1 - p_{RA}) + \Psi_B (1 - p_{VB})(1 - p_{RB}) + (1 - \Psi_A - \Psi_B)$

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[AQ6] Figure 3. Histograms of estimated probabilities of sighting p_V , probabilities of response p_R and number of occupied burrows for the 19 sampled plots.

Although *P. bailloni* is a year-round breeder, in this illustrative application, we did only one round of sampling for both species, in November 2011. We surveyed 19 circular plots of 100 m² randomly selected in 1996 for a previous survey (Betts 1998). All surveys occurred at night between 20:00 h and 23:00 h once every sampling month.

We used the two-species model specified above to estimate the average number of occupied burrows per unit area by dividing the average number of occupied burrows per plot by the area of a plot (100 m²). This number was then multiplied by the area of suitable habitat on the island (51 100 m²) to estimate the densities of shearwaters on the island. In order to account for plot-variation in occupancy and produce estimates of average island densities, we modelled species-specific occupancy probabilities ψ as a random effect. That is, rather than estimating plot-specific occupancy probabilities, given plot i and species S the probabilities of occurrence followed a logit-normal distribution:

$$\text{logit}S, i \sim \text{NS}, S$$

We evaluated the importance of heterogeneity in detection probabilities by comparing models that differed on whether the detection probabilities ($p_{VA}, p_{VB}, p_{VA}, p_{VB}$) were fixed or randomly (logit-normally) varying across plots. As a measure of model performance we used the deviance information criterion, DIC (Spiegelhalter et al. 2002; Supplementary material Appendix 1, Table A1).

Parameters were estimated using a Bayesian framework. We specified the following uninformative parameter priors for the random variables:

$$\begin{aligned} N(0,10) \\ \text{Unif}(0,10) \end{aligned}$$

When probabilities were set as constant across plots, we used a uniform prior ranging from 0 to 1.

We ran three independent MCMC chains with 10 000 iterations each, a burnin of 5000 and thinning of every 10 samples. Convergence was considered achieved when the Gelman–Rubin statistic (Gelman and Rubin 1992) for all parameters was lower than 1.1.

0 Results

Simulated datasets and performance comparison

5 Figure 1 and 2 show the standardized root mean squared error (RMSE) and bias, respectively, for the estimation of shearwater densities in the simulated plots. Models performed better when the probability of occupancy increased, both in terms of error (Fig. 1) and bias (Fig. 2). This is because higher occupancies imply larger sample sizes to estimate detection probabilities. Only plots with $\psi = 0.1$ (and therefore an average of 3 out of 30 occupied burrows) showed considerable levels of error and bias. As expected, the models also performed better when the probabilities of detection are interchangeable. The Bayesian framework performed worse under low occupancy rates and very different detection probabilities among both methods (i.e. one being high and the other low).

20 Case study: estimating shearwater densities on aride island

[AQ7] Table 3 shows the performance of two-species shearwater models varying in assumptions of detection heterogeneity. The model with heterogeneity in all probabilities of detection was clearly superior ($\Delta\text{DIC} = 24.08$). The parameter estimates using the best model are shown in Table 4.

25 Total population sizes were estimated at 25 550 pairs (95% CI: 23 667–28 777) for *P. bailloni* and 13 716 pairs (12 909–15 874) for *P. pacificus*. This is considerably lower than previous estimates using a correction factor approach, particularly for the *P. bailloni* (estimated at 98 000 pairs in 2006–2007, Sampson and Sampson 2007). However, it is important to note that previous estimates were obtained using correction factors rather than the statistical method we here propose.

40 Discussion

We have described a simple statistical framework to estimate the abundance of cavity-dwelling species when cavities are easy to detect and count. In these species, abundance estimation reduces to a problem of occupancy, where the key quantity to estimate is the probability of an individual (or breeding pair) being present in the cavity. This is analogous to the estimation of species occurrence in occupancy models (MacKenzie et al. 2005).

45 While species occupancy models typically use multiple site visits and a single detection method to estimate detection probabilities, some studies have extended them to incorporate multiple detection methods (Coggins et al. 2014). Nichols et al. (2008) provide a general framework for analysing multiple-method data on species occurrence. The method we presented is closely related to the special case of single site visits, yet applied to the estimation of abundance, rather than presence, when the species inhabits discrete units such as burrows and can be extended to other cavity-dwelling species.

61 Our formulation bears some implicit assumptions to be considered when interpreting the density estimates. The first one is that all birds are present in their burrow at the time of the survey. If individuals are absent foraging at the time of sampling, or their breeding attempt has ended before sampling, they will not be accounted for. This problem is minimized during egg-laying, incubation, or chick brooding, when at least one bird (one of the adults or the chick) stays behind in the burrow at all times. If this issue, however, is deemed important for the species at hand, the design can be extended to performing multiple visits per burrow in an analogous way to Nichols et al. (2008). In the case of shearwaters, performing the surveys at night, when birds return to their burrows can minimize the risk of sampling when individuals are absent. Moreover, the subset of data we analyze in this article represents a single snapshot of the population in time. Estimation of the year-round population size would require sampling at different times of the year. Design considerations such as how often to sample in order to have a representative sample of breeding attempts will depend on the biological details of the species. In our case, this will be particularly important for *P. bailloni*, which breeds year round. A second important assumption is that both detection methods (visual and playback) are independent of each other (i.e. the use of one does not affect the other). In our case, we decided to always first inspect burrows before playing the call, in order to avoid the call affecting the activity level, and thus visibility, of the bird. Finally, our model also assumes an accurate count of burrows per unit area, which we believe is justifiable given the terrain and dimensions of our plots. However, surveys in areas of more difficult access might require the explicit incorporation of burrow count error through repeated measurements.

95 Extensions of the model may be developed to adapt to the idiosyncrasies of different species and surveys. For example, while uncommon in our study, burrows may be occupied by more than one individual, potentially requiring detection probabilities to be modeled as dependant on the number of individuals present.

100 Other possible extensions to the method include modeling the dependence of occupancy or detection probabilities on habitat characteristics (e.g. soil depth, aspect, etc.), as has been done in studies with a single detection method (Pearson et al. 2013, Oppel et al. 2014). This may be important to yield reliable predictions at larger scales that include a variety of environments.

110 Although we have illustrated an application to the study of shearwaters, the method we outline is applicable to any cavity-dwelling species that may be sampled non-invasively using two detection methods. This may include, not only a variety of burrow-nesting birds such as shearwaters, petrels, penguins or burrowing owls, for which playback detection is commonly used (Haug and Didiuk 1993, Jouventin and Aubin 2002, Conway et al. 2008); but also a variety of other animals like den-living mammals and burrowing crabs or spiders. For example, den occupancy might be estimated using a combination of camera traps and the presence of tracks. Populations of burrowing crabs or spiders might be estimated with a combination of visual burrow inspection

- 0 and luring the animal, or checking whether a piece of lint
placed in the entrance is destroyed, as illustrated by Pombo
and Turra (2013).
- One advantage of our proposed method is that it does
not require destructive sampling to yield reliable estimates
5 of burrow occupancy. Destructive methods such as burrow
excavation have been used to calibrate imperfect methods of
detection (Lawton et al. 2006, Newman et al. 2009 for sea-
birds; Pombo and Turra 2013 for crabs). These approaches
raise ethical and conservation issues. Simultaneous use of
10 two imperfect methods allows the estimation of occupancy
without the need to ascertain it destructively.
- Accurately representing uncertainty in our estimates
of species population densities is of central importance to
effective and sustainable management (Ludwig et al. 1993).
15 This is the main advantage of our proposed method over
other methods used to estimate densities of cavity-dwelling
species. While these other methods aim to account for
detection bias through application of correction factors, they
do not calculate the uncertainty caused by imperfect detec-
20 tion (James and Robertson 1985, Warham 1996, Ratcliffe
et al. 1998, Gusset and Burgener 2005, Scott et al. 2009,
Oppel et al. 2014). Moreover, they do not account for
possible spatial heterogeneity in the probabilities of detec-
tion. Conway et al. (2008), for example, showed that the
25 detection of burrowing owls (visual and playback response)
depends on factors such as ambient temperature. In our
application, the best models for both species incorporated
variation in both visual and acoustic detection probabilities.
The problem of correction and calibration factors extends
30 beyond studies of burrow occupancy. Gopalaswamy et al.
(2015) showed that using ad hoc calibration indexes relat-
ing track-counts to camera-trap-based population estimates
resulted in a deceptive overestimation of Indian tiger recov-
ery. This highlights the importance of jointly estimating
35 observation and occurrence in our estimation of animal
abundances.
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