

An open-population hierarchical distance sampling model

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Abstract. Modeling population dynamics while accounting for imperfect detection is essential to monitoring programs. Distance sampling allows estimating population size while accounting for imperfect detection, but existing methods do not allow for estimation of demographic parameters. We develop a model that uses temporal correlation in abundance arising from underlying population dynamics to estimate demographic parameters from repeated distance sampling surveys. Using a simulation study motivated by designing a monitoring program for Island Scrub-Jays (*Aphelocoma insularis*), we investigated the power of this model to detect population trends. We generated temporally autocorrelated abundance and distance sampling data over six surveys, using population rates of change of 0.95 and 0.90. We fit the data generating Markovian model and a mis-specified model with a log-linear time effect on abundance, and derived post hoc trend estimates from a model estimating abundance for each survey separately. We performed these analyses for varying numbers of survey points. Power to detect population changes was consistently greater under the Markov model than under the alternatives, particularly for reduced numbers of survey points. The model can readily be extended to more complex demographic processes than considered in our simulations. This novel framework can be widely adopted for wildlife population monitoring.

Key words: *Aphelocoma insularis; demography; distance sampling; Island Scrub-Jay; Markov model; population trend estimation; power analysis; Santa Cruz Island, California, USA; temporal autocorrelation.*

INTRODUCTION

Monitoring population dynamics is a key component of wildlife conservation and management (Nichols and Williams 2006). One of the most common methods for estimating the demographic parameters governing population dynamics is through the use of open-population capture–recapture models (see Pollock et al. 1990). These models, however, require the identification of individuals over the course of the study. This usually requires expensive and often logistically challenging methodologies like live-capture or genetic sampling.

An alternative to estimating demographic parameters directly is to estimate abundance and monitor its trends. Distance sampling (Buckland 2001) is widely used to estimate population size because it only requires recording the perpendicular distance of an animal to the observer (or transect), rather than individual identification. Repeated visits to sites are not necessary as the probability of detecting an individual (p) is assumed to be a decreasing function

of distance, with p assumed to equal 1 on the transect. Further assumptions include that animals are distributed uniformly with respect to the transect, distance is recorded accurately, animals are recorded at their initial location, and animals are not double counted (Buckland 2001).

The distance sampling framework has been expanded to allow for modeling spatial variation in abundance as a function of site-specific covariates (e.g., Hedley and Buckland 2004, Royle et al. 2004). The hierarchical model developed by Royle et al. (2004) for distance sampling is analogous to that applied in N -mixture models (Royle 2004), where repeated visits to a collection of survey sites are used to make inference about detection probability and abundance. We employ this model structure in the present paper and refer to it as hierarchical distance sampling (HDS).

Traditional distance sampling models, including HDS, limit our ability to model population dynamics because they assume that the sampled populations are closed to additions or losses during the course of the study. Thomas et al. (2004) present a framework for inference about population dynamics from distance sampling repeated over time, allowing for losses or gains between sampling periods, by modeling estimates of N (e.g., Buckland et al. 2004, 2007). Their approach,

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PLATE 1. Island Scrub-Jay (*Aphelocoma insularis*) harvesting acorn from an island scrub oak (*Quercus pacifica*) on Santa Cruz Island, California, USA. Photo credit: Colin Woolley.

however, relies on post hoc analyses of abundance estimates, rather than integrating distance sampling with a model describing population dynamics. Such an integrated approach is suggested by Thomas et al. (2004), but not implemented. A second option is to integrate distance sampling counts with a model of population dynamics to formulate a HDS model including a time effect in the log-linear predictor of site-specific abundance (e.g., Moore and Barlow 2011). An alternative approach is to acknowledge that number of individuals in a given replicate (e.g., year) is typically a function of the number in the previous replicate, and that this function is governed by demographic parameters. Dail and Madsen (2011) presented such an extension for N -mixture models, where abundance in the initial time period is estimated as in the standard N -mixture model; but, in subsequent surveys, it is modeled as the sum of survivors from the previous survey and new individuals recruited into the site-specific population. This model has become increasingly applied in ecological studies (e.g., Chandler and King 2011, Zipkin et al. 2013), because of its ability to estimate demographic parameters from unmarked populations.

In this paper, we combine the Dail and Madsen (2011) process model with a distance sampling observation model to provide a coherent framework

for studying spatial and temporal variation in abundance from multiple-survey distance sampling data. This integrated approach further opens an avenue for ecologists to combine large scale distance sampling surveys with high-intensity, smaller scale surveys that yield direct information on some demographic parameters (for example, mark-resighting surveys) in the framework of integrated population models (e.g., Schaub and Abadi 2011). The study was motivated by the challenge of developing a long-term monitoring plan for the Island Scrub-Jay (*Aphelocoma insularis*, see Plate 1). This bird species is endemic to Santa Cruz Island, California, USA, and is of conservation concern due to its restricted range, small population size, and susceptibility to emerging threats, such as climate change and disease (Morrison et al. 2011, Sillett et al. 2012). Our work was motivated by the need to determine more efficient methods for detecting population trends due to the logistic and financial difficulty in sampling the entire island. We show, with a simulation study, that our model returns unbiased estimates of population trends. We further explore whether explicitly modeling temporal autocorrelation in counts caused by demographic processes increases power to detect population trends compared to a log-linear trend model (as in Moore and Barlow

2011), and a post hoc calculation of population trends based on independent abundance estimates. Given the broad applicability of distance sampling in abundance estimation, the open-population HDS model developed here should be useful for studying and monitoring wildlife population dynamics.

METHODS

Open-population hierarchical distance sampling model

In hierarchical distance sampling (HDS; Royle et al. 2004), abundance at spatially independent survey locations is assumed to come from a discrete-positive distribution. We present a hierarchical distance sampling model development using the Poisson distribution, but note that the model is conceptually equivalent for other distributions, such as the negative binomial (which we use in the simulation study). Variation in the expected value of abundance (λ) can be modeled on the log scale as a function of site-specific covariates, X :

$$N_j \sim \text{Poisson}(\lambda_j)$$

$$\log(\lambda_j) = \alpha + \beta' X_j$$

where N_j is the latent abundance at site j , α is the intercept, and β are the coefficients related to the site-specific habitat covariates X_j . The detection probability of an individual (p) is a function of the individual's distance to the observer (d). For example, using a half-normal detection function, the observation model is

$$p = \exp\left(-\frac{d^2}{2\sigma^2}\right)$$

The scale parameter σ can be modeled, on the log scale, as a function of site-specific covariates (e.g., Marques and Buckland 2003, Sillett et al. 2012):

$$\log(\sigma_j) = \alpha_\sigma + \beta'_\sigma X_j.$$

Observations are often binned into discrete distance classes, because of inaccuracy in estimating distance to the observer, with some maximum detection distance, generally defined a priori. Let the vector b be the break points of the K distance categories. Then, for sampling points (as opposed to transects), detection probability in k , p_k , is the integral of the detection function over k , divided by the area of k , A_k :

$$p_k = \frac{2\pi \int_{b_k}^{b_{k+1}} \exp\left(-\frac{x_k^2}{2\sigma^2}\right) dx}{A_k}. \quad (1)$$

Assuming that animals are distributed uniformly around a sampling point, the distribution of distances is triangular rather than uniform because area increases with distance. Specifically, the probability of an individual being in a particular distance band, Ψ_k , corresponds to A_k divided by the total sampled circle. Then, the number of observed individuals in each

distance band follow a multinomial distribution with cell probabilities π , where $\pi_k = p_k \Psi_k$, and $\pi_{k+1} = 1 - \sum \pi_k$, i.e., the probability of not being detected at all. The multinomial sample size at site j is the (latent) population size N_j .

To extend this model to an open population, consider that distance sampling surveys are repeated over T primary occasions. Site specific abundances are assumed to be static within each occasion, but we expect changes in N_j between occasions. Abundance at time $t = 1$ is described by the static abundance model used in the single-survey distance sampling model. To describe abundance in subsequent years, we parameterize explicit dynamics to allow for survival and recruitment. Specifically, N at $t > 1$ is composed of (apparent) survivors ($S_{j,t}$) from $t = 1$, with (apparent) survival probability ϕ ; and of recruits ($R_{j,t}$). We cannot differentiate between recruitment from birth or immigration without additional information. Here, we approximate recruitment with a process that also depends on $t - 1$ and a per capita recruitment rate, v :

$$S_{j,t} \sim \text{Binomial}(N_{j,t-1}, \phi)$$

$$R_{j,t} \sim \text{Poisson}(N_{j,t-1} v)$$

$$N_{j,t} = S_{j,t} + R_{j,t}.$$

The dependency of R on N at $t - 1$ implies that animals reproduce, then survive, which is a standard assumption in matrix population models (e.g., Caswell 2001). A very similar model can be expressed in terms of a population rate of change (γ), which can be thought of as the sum of ϕ and v . Under this formulation

$$N_{j,t} \sim \text{Poisson}(N_{j,t-1} \gamma). \quad (2)$$

This formulation is more parsimonious and yields adequate results when the monitoring focus is on population trend. It does, however, assume a different variance for $N_{j,t}$. Note that, for the sake of model development, we chose a simple model of population dynamics, which may not be adequate for many biological situations. Specifically, demographic parameters are unlikely to be constant in space and time, and the present framework allows for the modeling of these parameters as functions of covariates, or in the form of factors or random effects. We consider alternative models in *Discussion*. The distance sampling observation model remains as described for the single-survey model, conditional on $N_{j,t}$. The detection parameter (σ) can either remain constant or be allowed to vary with time (linearly, categorically, or randomly).

Dail and Madsen (2011) implement the open-population N -mixture model in a likelihood framework. With its Markovian structure on latent variables, however, the model is readily implemented in a Bayesian framework and can easily be described using the BUGS language (Gilks et al. 1994). We adopt a

Bayesian implementation of the open-population distance sampling model using appropriate uniform (i.e., uninformative) prior distributions for all model parameters (see Supplement 1 for model code). Note, however, that knowledge of demographic parameters could be incorporated directly in the form of informative priors to improve estimates of abundance. Because the integral in Eq. 1 has no closed form, we approximated it using the rectangular rule. We evaluated the detection function at the distance category midpoints and multiplied by the distance width in order to calculate category-specific detection probabilities. For implementation, we opted for a relatively coarse approximation (wide intervals) in order to improve computational efficiency. This, however, will produce a numerically less precise evaluation of the integral. See Supplement 2 for a simulation-based evaluation of the approximation, as well as alternative implementations of the detection function.

SIMULATION STUDY

Our simulation study builds upon surveys of intensive, island-wide surveys of Island Scrub-Jays conducted in 2008 and 2009 (Sillett et al. 2012). These surveys required helicopter transport of observers to sampling locations due to the rugged terrain on Santa Cruz Island. The Nature Conservancy and Channel Islands National Park, joint owners and managers of the island, seek a cost-effective monitoring protocol for the Island Scrub-Jay population, estimated at less than 2500 individuals, that involves a subset of the 307 survey points used by Sillett et al. (2012). Thus, we used a simulation study to evaluate the power of different monitoring designs.

We based data generation on the fall-season distance sampling model for Island Scrub-Jays by Sillett et al. (2012). We simulated abundance for six hypothetical years for each of the 307 sampling points. Point abundance at $t = 1$ at survey location j was generated from

$$N_{j1} \sim \text{Negative Binomial}(\lambda_j, r)$$

$$\log(\lambda_j) = \alpha + \beta_1 \times \text{Chap}_j + \beta_2 \times \text{Elevation}_j + \beta_3 \times \text{Chap}_j^2$$

where Chap is percent cover that is chaparral (an oak-dominated, shrubland plant community), and r is the dispersion parameter of the negative binomial distribution. Input values were $\alpha = 0.83$, $\beta_1 = 1.43$, $\beta_2 = -0.23$, and $\beta_3 = -0.38$. Each generated N refers to a circle with a 300 m radius surrounding a survey location. This model generates an expected number of 889.66 individuals in the area covered by all point count circles.

We generated data from the model parameterized in terms of survival (ϕ) and recruitment (v). To reflect population declines of 5% and 10%, we set ϕ to be constant at 0.6, and v at either 0.35 or 0.30, which corresponds to $\gamma = 0.95$ and 0.90, respectively. We stress

that this is an unlikely description of the Island Scrub-Jay population, but we chose this parameterization for ease of presentation. We generated distance sampling data from the simulated point abundances by placing individuals (i) at random distances (d_i) between 0 and 300 m from the survey point, assuming a uniform distribution of individuals. We generated individual observations, $y_{i,j}$, using the fall observation model from Sillett et al. (2012):

$$p_j = \exp\left(-\frac{d^2}{2\sigma_j^2}\right)$$

$$\log(\sigma_j) = \alpha_\sigma + \beta_\sigma \times \text{Chap}_j.$$

Individual observations were aggregated into counts per $k = 3$ 100-m distance class. Input values were $\alpha_\sigma = 4.68$ and $\beta_\sigma = -0.20$.

We analyzed these data using the model parameterization in terms of γ (Eq. 2), rather than ϕ and v , to make results comparable with those from a log-linear and a post hoc trend model. We refer to this model as the Markov model. We performed these simulations using all 307 sampling points, as well as random subsets of 200 and 100 points.

To assess the gain in power of detecting a downward population trend of this novel model, we analyzed the data generated under the Markov model with a log-linear trend model:

$$\begin{aligned} \log(\lambda_{j,t}) = & \alpha + \beta_1 \times \text{Chap}_j + \beta_2 \times \text{Elevation}_j \\ & + \beta_3 \times \text{Chap}_j^2 + \beta_4(t-1). \end{aligned} \quad (3)$$

Here, β_4 is a log-linear time effect, corresponding to $\log(\gamma)$ from the Markov model. We assessed the baseline performance of the log-linear trend model when specified correctly with a simulation study analogous to the one described for the Markov model (Appendix A). Finally, we compare performance of the Markov model to the performance of post hoc trend estimates, obtained by estimating abundance separately for each year, and deriving a population trends as the average over $\sum_j N_{j,t}/\sum_j N_{j,t-1}$. We included this last scenario because it represents the approach commonly used in practice (e.g., Norvell et al. 2003, Friday et al. 2013). To perform a fair comparison, however, we maintained log-linear coefficients on abundance constant across years, so that the abundance model becomes:

$$\log(\lambda_{j,t}) = \alpha_t + \beta_1 \times \text{Chap}_j + \beta_2 \times \text{Elevation}_j + \beta_3 \times \text{Chap}_j^2.$$

We further generated data with the log-linear trend model and analyzed it with the Markov model to evaluate sensitivity to mis-specification. Details and results can be found in Appendix B.

For all scenarios, we generated and analyzed 100 data sets using R version 2.15.2 (R Core Team 2012). We implemented the models using the software JAGS version 3.2.0 (Plummer 2003), accessed through R with the package rjags version 3-5 (Plummer 2011). We ran

TABLE 1. Simulation results for estimating population rate of change (γ) from temporally correlated (Markov) data, analyzed with different models and using different numbers of sampling points.

Model and number of points	True value	Mean	RMSE	Bias	CI coverage	Sig. (%)
Markov model						
307 points	0.90	0.897	0.022	-0.003	95	98
	0.95	0.949	0.022	-0.001	97	54
200 points	0.90	0.898	0.028	-0.002	97	93
	0.95	0.950	0.022	<0.001	100	35
100 points	0.90	0.903	0.040	0.003	97	60
	0.95	0.948	0.038	-0.002	98	21
Log-linear trend model						
307 points	0.90	0.900	0.027	<0.001	99	89
	0.95	0.952	0.025	0.002	99	25
200 points	0.90	0.902	0.031	0.002	100	70
	0.95	0.946	0.028	-0.004	99	15
100 points	0.90	0.902	0.040	0.002	100	39
	0.95	0.945	0.041	-0.005	100	9
Post hoc trend model						
307 points	0.90	0.909	0.026	0.010	91	94
	0.95	0.959	0.027	0.009	87	45
200 points	0.90	0.913	0.036	0.015	90	79
	0.95	0.965	0.031	0.016	91	24
100 points	0.90	0.938	0.069	0.042	86	33
	0.95	0.984	0.061	0.036	87	6

Notes: Results of 100 simulations are given in the form of the mean parameter estimate (mean), root mean square error (RMSE), relative bias (Bias), 95% Bayesian confidence interval coverage (BCI coverage) of the true (input) parameter, and percentage of simulations where population rate of change was significant (Sig(%)), defined as the 95% BCI not overlapping 1). The 100- and 200-point scenarios use a random subset of the full set of 307 points. The log-linear trend model is parameterized in terms of a log-linear time effect on abundance; we exponentiated estimates of β_4 so that it is on the same scale as the population rate of change estimated in the other two models.

three parallel Markov chains with 30 000 iterations and a burn-in of 10 000, thinning chains by 10. We assessed model convergence using the Gelman-Rubin statistic (Gelman et al. 2004). A value close to 1 indicates convergence of parallel chains; the Gelman-Rubin statistic was <1.1 for all parameters in all models. We report the average parameter estimates with root mean square error (RMSE), average relative bias, 95% Bayesian credible interval (BCI) coverage of the true (input) value, and, for population rate of change, γ (Markov model) and the equivalent $\exp(\beta_4)$ (log-linear time effect in trend model) and the number of times the downward population trend was deemed significant, defined as the 95% BCI not overlapping 1. We interpret this significance rate as an index of power to detect population trends. Results for estimates of abundance and detection parameters are given in Appendix C.

RESULTS

The open-population HDS model with a Markovian structure of abundance returned unbiased and precise estimates of the population rates of change (γ) under all simulated scenarios, and consistently outperformed the other models (Table 1). When using all 307 sampling points in the Markov model, γ was significantly below 1 in more than 50% of the simulations for $\gamma = 0.95$, and in almost 100% of the simulations for $\gamma = 0.90$. The post hoc calculated

trends had comparable significance rates (94% and 45% for $\gamma = 0.90$ and 0.95, respectively). The log-linear model only produced significant outcomes for the same rates of population decline in 25% and 89% of the simulations, respectively (Table 1). These rates are comparable to the performance of the log-linear trend model with log-linear trend data (Appendix A: Table A1). The Markov model estimated population trends with high precision, with relative RMSE (RMSE/mean estimate) of 0.023 and 0.024 for $\gamma = 0.95$ and 0.90, respectively (Table 1). Both the log-linear trend model and the post hoc trend estimates were similarly precise (Appendix A: Table A1). Bias in estimates of population rate of change under the Markov and the log-linear trend model was consistently below 1%. With a bias of 1–3%, the post hoc trend estimates were still very accurate. Power to detect downward population trends declined with reduced number of sampling points, to 21% and 60% under the Markov model, to 9% and 39% under the log-linear trend model, and to 6% and 33% under the post hoc model, for 100 survey points and $\gamma = 0.95$ and 0.9, respectively. Bias of γ remained <1% with decreasing survey points for the Markov and the log-linear trend model, while bias increased to 4% in the post hoc trend estimates (Table 1).

The Markov model produced estimates of the parameters related to abundance and detection that

were mostly unbiased (relative bias < 5%; Appendix C: Tables C1–C3). Bias in parameters increased with decreasing number of sampling points. Parameter estimates from the log-linear trend model had comparable or stronger bias (Appendix C: Tables C4–C6).

DISCUSSION

We developed a hierarchical distance sampling model of spatial and temporal variation in abundance that allows practitioners to make use of a well-developed survey technique for population monitoring. By taking into account the Markovian nature of populations over time, our HDS model greatly improves the power of monitoring programs to detect population trends, especially when survey points are limited. For most long-lived species, a correlation structure where abundance at year t depends on abundance the previous year, $t - 1$, is biologically realistic. Such a model should have more power to detect population declines, because abundance estimates at any given year are also informed by the data from the previous year. Indeed, we found that, using a Markov model, distance sampling had higher power to detect population declines, as compared to a log-linear trend model, or post hoc calculation of trends based on independent annual abundance estimates (Table 1). This was not caused by model misspecification, as the log-linear trend model showed similar power when used with data generated from the log-linear trend model (Appendix A). Because the underlying model of point abundances was a negative binomial, the number of birds varied substantially at any given site across years, which likely led to the low level of precision in estimates of population decline.

All models had higher power to detect larger population declines, but the gain in power from using the Markov over the other approaches was stronger for a smaller population decline. The same pattern emerged for changing numbers of survey points; power decreased for all models, but more strongly for the log-linear trend and the post hoc approach (Table 1). The post hoc model uses data from all years to estimate constant habitat parameters, and we expect the power to detect trends, as well as accuracy and precision of estimates, to decrease, if all parameters were estimated separately. Using the correlation in abundance, thus, becomes particularly important for smaller surveys, or when detecting small population declines is a priority.

We used a fairly restrictive model of recruitment in the simulation; once N at a site j reached 0, it remained 0 because of the sole dependence of N_t on N_{t-1} (Eq. 2). Biologically, this is equivalent to no immigration. Consequently, the Markov model performed poorly when used with log-linear trend data; estimates of population rate of change showed a negative bias of 3.3% and 3.8% ($\gamma = 0.9$ and 0.95, respectively), and parameters associated with abundance and detection were heavily biased and had low credible interval

coverage (Appendix B: Table B1). In the data generated under the log-linear trend model, recolonizations of sites with many individuals were common (Appendix A), so that the Markov model overestimates abundance at $t = 1$ (Appendix B: Table B1) to reconcile the model structure with high local abundances observed at $t > 1$. Dail and Madsen (2011) suggest a less restrictive formulation of the recruitment process:

$$R_{j,t} \sim \text{Poisson}(\gamma_{j,t})$$

$$\log(\gamma_{j,t}) = \omega_0 + \omega_1 \log(N_{j,t-1})$$

where $R_{j,t}$ is the number of recruits at j and t (for $t > 1$), ω_0 is the recruitment component not linked to N_j at $t - 1$, and ω_1 is the recruitment component linked to N_j at $t - 1$. Although this formulation seems ecologically more adequate, mathematically, $\gamma_{j,t}$ will still be undefined when $N_{j,t-1} = 0$. This might not pose a problem for data sets where site-specific populations are larger than in the present example, but we frequently realize $N = 0$ for our analysis with small local population sizes. One option to avoid this absorbing state is to include a time-specific, log-normal error term, ε_t , in the Markov model (Appendix B), which allows sites to be recolonized after extinction. This simple approach represents a random immigration model and greatly improved performance of the (generalized) Markov model when used to analyze log-linear time trend data (Appendix B: Table B2). Given the sensitivity of the Markov model to misspecification, we suggest employing Bayesian measures of model fit (e.g., Bayesian P value; Gelman et al. 1996) when analyzing data with this model.

The model of population dynamics used in the present simulation study is overly simplistic for real, natural systems. In addition to modeling demographic parameters as functions of covariates, the model is readily extended to more complex demographic processes. Recruitment, for example, could be modeled as a function of previous year's abundance at site j and neighboring locations. Parameters can be estimated for different life stages (age, sex), or the model could contain sub-processes of survival (e.g., harvest; Buckland et al. 2004, 2007). Additional information may be required to fit more complex models. Our study focused on the power to detect downward population trends, but other studies might be more concerned with false detections of trends or population increases. Exploring the performance of the open-population HDS model in other circumstances was beyond the scope of this report.

In our simulation study, we opted for an open-population distance sampling model parameterized in terms of the population rate of change γ . Survival and recruitment parameters generated by the Dail and Madsen (2011) model can be confounded in cases where data do not conform to the model's parametric assumptions. Ongoing mark–recapture and telemetry studies of Island Scrub-Jays could inform stage-structured survival parameters and dispersal, allowing for

estimation of both the Markovian and the immigration component of recruitment with an open-population HDS model. This approach would be applicable to many other monitoring programs, where marking animals and distance sampling can be combined, and warrants further exploration.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–C and Supplements 1 and 2 are available online: <http://dx.doi.org/10.1890/14-1625.1.sm>