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Hierarchical distance-sampling models to estimate population size and habitat-specific abundance of an island endemic

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Abstract. Population size and habitat-specific abundance estimates are essential for conservation management. A major impediment to obtaining such estimates is that few statistical models are able to simultaneously account for both spatial variation in abundance and heterogeneity in detection probability, and still be amenable to large-scale applications. The hierarchical distance-sampling model of J. A. Royle, D. K. Dawson, and S. Bates provides a practical solution. Here, we extend this model to estimate habitat-specific abundance and rangewide population size of a bird species of management concern, the Island Scrub-Jay (*Aphelocoma insularis*), which occurs solely on Santa Cruz Island, California, USA. We surveyed 307 randomly selected, 300 m diameter, point locations throughout the 250-km^2 island during October 2008 and April 2009. Population size was estimated to be 2267 (95% CI 1613–3007) and 1705 (1212–2369) during the fall and spring respectively, considerably lower than a previously published but statistically problematic estimate of 12 500. This large discrepancy emphasizes the importance of proper survey design and analysis for obtaining reliable information for management decisions. Jays were most abundant in low-elevation chaparral habitat; the detection function depended primarily on the percent cover of chaparral and forest within count circles. Vegetation change on the island has been dramatic in recent decades, due to release from herbivory following the eradication of feral sheep (*Ovis aries*) from the majority of the island in the mid-1980s. We applied best-fit fall and spring models of habitat-specific jay abundance to a vegetation map from 1985, and estimated the population size of *A. insularis* was 1400–1500 at that time. The 20–30% increase in the jay population suggests that the species has benefited from the recovery of native vegetation since sheep removal. Nevertheless, this jay's tiny range and small population size make it vulnerable to natural disasters and to habitat alteration related to climate change. Our results demonstrate that hierarchical distance-sampling models hold promise for estimating population size and spatial density variation at large scales. Our statistical methods have been incorporated into the R package *unmarked* to facilitate their use by animal ecologists, and we provide annotated code in the Supplement.

Key words: Aphelocoma insularis; *biodiversity conservation; California Channel Islands; distance sampling; hierarchical models.*

INTRODUCTION

Wildlife management and conservation require unbiased information about population size and about how abundance is shaped by environmental factors and human activity. Such knowledge is especially important for managing rare and vulnerable species to ensure that actions aimed at addressing apparent population declines or protecting important habitats are well informed (Buckland et al. 2008). Erroneous inferences about population status can waste limited conservation resources or prevent managers from recognizing when populations are threatened. Inaccurate estimates of abundance are principally due to two causes: failure to design surveys to sample the appropriate range of habitats and conditions, and biased counts resulting from imperfect detection of individuals present within a survey area (Yoccoz et al. 2001, Buckland et al. 2008). Thoughtful study design (see Greenwood and Robinson 2006) can minimize the first problem. Imperfect detection can be addressed by methods based on distance sampling (Buckland et al. 2001) or capture–mark–recapture protocols (Borchers et al. 2002, Williams et al. 2002, Royle and Dorazio 2008) that use empirical modeling to "correct" raw counts with estimated detection probability and thereby produce estimates of true abundance (Kéry et al. 2005, Kéry and Royle 2010).

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Distance sampling is perhaps the most widespread framework for estimating abundance of vertebrate populations. This approach is efficient because it requires only one round of counts for each biologically relevant interval, such as season or year. In addition, individuals do not need to be captured, marked, and recaptured. However, conventional distance-sampling models (Buckland et al. 2001) do not explicitly consider the relationships between covariates and population density. Consequently, such analyses have limited utility in advancing our understanding of how ecological mechanisms determine the abundance of natural populations, and for predicting how populations will respond to habitat change. Several recent papers have advanced distance-sampling methods to include the modeling of environmental covariates on abundance (e.g., Hedley and Buckland 2004, Royle et al. 2004, Johnson et al. 2010, Niemi and Fernández 2010).

Here, we extend the hierarchical distance-sampling models of Royle et al. (2004) to include covariate effects on both detection and abundance, and apply this model to counts of Island Scrub-Jays (*Aphelocoma insularis*), a species of management concern endemic to Santa Cruz Island, off the coast of southern California, USA (Curry and Delaney 2002). Kelsey and Collins (2000) estimated a total population size of 12 500, but this number was extrapolated from estimated territory sizes of a small number of birds, not derived from counts across the full range of jay habitat. Concerns about the viability of *A. insularis* became acute in 2006 when researchers (C. T. Collins and K. A. Corey, *personal communication*) noticed an apparent negative population trend on their long-term study plot in the central valley of the island. A preliminary analysis of these data suggested a decline over the preceding decade in the number of breeding territories and in population growth rate, which was estimated to be below that required for persistence of the species (P. R. Doherty, *unpublished data*). These findings coupled with the species' highly restricted range, and with emerging threats from West Nile virus (Reisen et al. 2004) and climate change, motivated The Nature Conservancy and the U.S. National Park Service, which jointly own and manage Santa Cruz Island, to convene a meeting of conservation professionals in February 2008 to develop a monitoring and management plan for *A. insularis*. A key recommendation from this workshop was to produce reliable estimates of the jay's rangewide population size based on the best available field and analysis methods.

Our purpose in this paper is four-fold. First, we present a unified framework for density estimation and modeling from distance-sampling data obtained at a collection of point transect surveys. Second, we apply this framework to a large-scale, distance-sampling data set to produce the first statistically rigorous estimates of population size of *A. insularis*. Third, we map patterns of habitat-specific abundance of *A. insularis* based on vegetation coverage data from the time of our island-wide survey and from the mid-1980s, just prior to the eradication of feral sheep from much the island. Fourth, we facilitate the use of our models by integrating them into the *unmarked* package (Fiske and Chandler 2011) for program R (R Development Core Team 2010), where they are freely available to researchers interested in estimating total population size and modeling spatial variation in abundance over some study region.

METHODS

Study site

Santa Cruz Island (34°0′ N, 119°45′ W) is 250 km^2 and located 40 km from Santa Barbara, California. The island is characterized by two, east-west-oriented mountain ranges and a large central valley. It has a mediterranean climate with warm dry summers, cool wet winters, and a mean annual precipitation of 50 cm in the central valley (Fischer et al. 2009). Slopes tend to have either a north-facing aspect with dense chaparral woodland dominated by scrub oaks (*Quercus pacifica*) and *Ceanothus* spp., or a south-facing aspect with woody vegetation interspersed by grass and *Artemisia* spp. (Parkes et al. 2010). From the 1840s until the 1980s, the island was managed as a livestock ranch. Decades of overgrazing by sheep (*Ovis aries*) and cattle (*Bos taurus*) and rooting by thousands of introduced, feral pigs (*Sus scrofa*) severely degraded chaparral and scrub habitats and greatly limited plant regeneration (Van Vuren and Coblentz 1987). Nonnative ungulates have been completely removed over the past three decades (Morrison 2011), which has allowed native vegetation to slowly recover (Klinger et al. 1994, Peart et al. 1994). Scrub-jay territories are distributed in oak chaparral and pine woodland along hillsides and in larger canyons (Caldwell 2010).

Field methods

We conducted island-wide surveys from 6 to 13 October 2008 and 6 to 18 April 2009 to quantify population size and habitat-specific abundance of *A. insularis*. We selected our survey points from 369 relevé plot locations randomly distributed across the island as part of an intensive vegetation study (A. K. McEachern, *unpublished data*). To meet logistical and cost constraints, we subsampled from this set. We removed points in close proximity to each other, excluding either points with greater percent cover of annual grasslands, or if grassland proportion was equal, dropping points randomly, until all remaining points were >300 m apart. Annual grasslands were overrepresented in the relevé plots and we expected little use of annual grasslands by scrub-jays. Our final sample size was 307 points (Fig. 1), which were surveyed with a distance-sampling design. A key design constraint was to cover the entire island each season in a 1–2 week interval in which the population was both relatively conspicuous (October, the non-breeding season when jays actively harvest and cache acorns; April, the breeding season when females

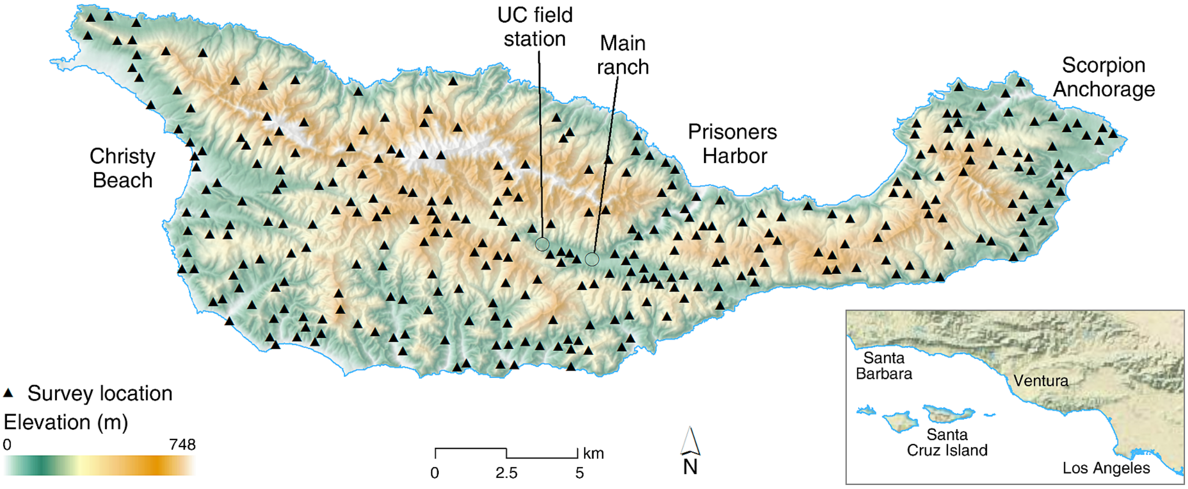

FIG. 1. Map of Santa Cruz Island, California, USA showing the 307 survey locations. The inset map displays the northern Channel Islands and the adjacent California mainland.

incubate eggs and parents feed nestlings) and closed with respect to recruitment and mortality. Because of the time limitation and the rugged, steep terrain on Santa Cruz Island, a small helicopter transported field technicians to locations 50–100 m from survey points. Jays quickly returned to their normal behaviors after the helicopter departed. Upon arrival at survey locations, which typically took >5 minutes after the helicopter drop-off due to dense vegetation and rugged terrain, technicians conducted 300 m radius point count surveys for 6 minutes in October and 10 minutes in April. Distance to jays seen or heard was measured with laser rangefinders or estimated by eye. Whenever possible, technicians kept track of repeat detections of individual jays at each survey plot. Repeat detections were discarded for statistical analyses.

Habitat data sets

We used vegetation cover data sets to describe island vegetation structure and to model habitat-specific abundance of jays (Table 1). Vegetation cover at the time of our island-wide surveys was represented by a classification from 2005 (Fig. 2a; see also Nature Conservancy 2007). A 1985 classification (Fig. 3a; see also Jones et al. 1993) represented vegetation conditions near the time that feral sheep were eliminated from 90% of the island in 1989 (Schuyler 1993). For each 300 m radius point count circle, we used GIS, a digital elevation model of the island, and the habitat data sets to estimate average elevation, the percent cover of four habitat categories (chaparral, predominantly scrub oak; forest, predominantly bishop pine *Pinus muricata* and tall stands of coast live oak *Q. agrifolia*; grass/bare, composed of native and nonnative grasses and forbs, including fennel *Foeniculum vulgare*; and shrubs, i.e., coastal sage scrub), and vegetation height (not available for the 1985 classification). Jays are largely confined to chaparral and forest (Curry and Delaney 2002, Caldwell 2010). Therefore, we only used these two habitat categories as covariates in abundance modeling.

Statistical methods

We extended the hierarchical distance-sampling model of Royle et al. (2004) to include submodels that describe how both the abundance process and the detection process vary as functions of environmental covariates, i.e., elevation and the chaparral and forest habitat categories. In the abundance component of the model, spatial variation in the number of jays at each plot (N_i) was treated as a Poisson or negative binomial random variable with expectation $E[N_i] = \lambda_i$ and dispersion parameter α in the negative binomial case. We note that although this formulation allows us to model spatial variation in density among point count plots, it assumes that density is constant *within* each

TABLE 1. Summaries of the distributions of covariates used to model jay abundance and detection probability.

			Percentile				
Variable	Scale	Year	0%	25%	50%	75%	100%
Chaparral	island	1985	0.00	0.02	0.11	0.28	0.95
	island	2005	0.00	0.06	0.20	0.39	0.98
	points	2005	0.00	0.07	0.22	0.43	0.94
Forest	island	1985	0.00	0.00	0.01	0.04	0.64
	island	2005	0.00	0.00	0.00	0.06	1.00
	points	2005	0.00	0.00	0.01	0.06	0.81
Grass	island	1985	0.02	0.58	0.78	0.92	1.00
	island	2005	0.00	0.04	0.14	0.34	1.00
	points	2005	0.00	0.06	0.20	0.39	1.00
Elevation (m)	island		0.00	115	200	306	698

Notes: Covariates were measured island-wide when sheep were still present (1985) and after their removal (2005). Vegetation variables are expressed as proportion of cover at two scales: island-wide or within 300 m radius circles centered at point count locations.

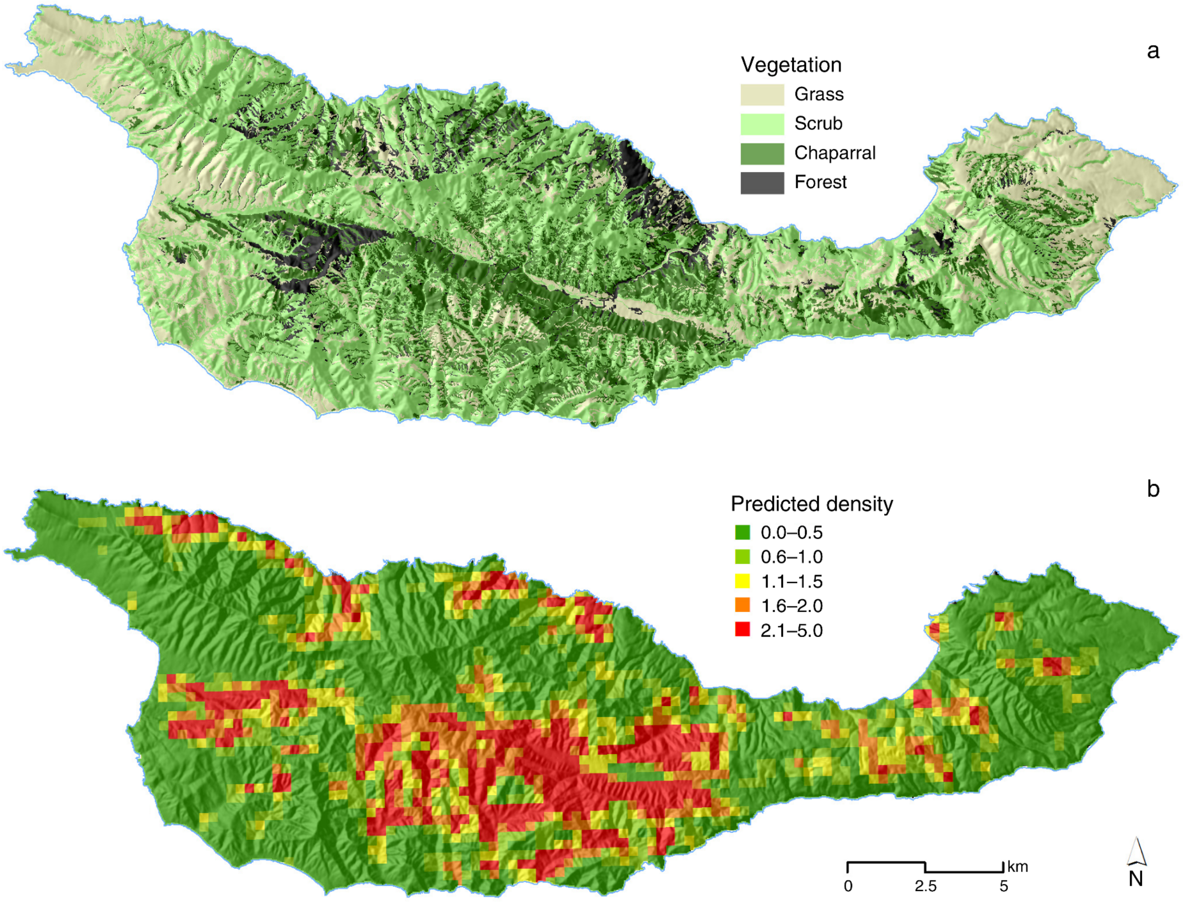

FIG. 2. (a) Vegetation map of Santa Cruz Island from 2005. See *Methods* for details of vegetation categories. (b) Predicted fall 2008 density of Island Scrub-Jays (individuals/9 ha) from the model $\lambda(\text{chap}^2 + \text{elev})\ \sigma(\text{chap})\ \alpha$ (see Table 2 for parameter definitions and model details).

plot. That is, if three jays were present at a plot, we assumed they could have occurred anywhere within that plot.

The detection process in our model is based upon the classical distance-sampling likelihood for point transect data (Buckland et al. 2001). We expected that detection probability would decrease monotonically with distance from the observer and modeled this process using the half-normal detection function, $g(r) = \exp -(r^2/2\sigma_i^2)$, where r is the radial distance and σ_i is the half-normal scale parameter at point i. Environmental covariates of λ_i and σ_i were accommodated using a log link function.

Distances were recorded on a continuous scale but we discovered a noticeable lumping of observations. We carried out exploratory analyses using 30-m distance intervals up to 300 m yielding 10 distance classes. Inspection of distance histograms suggested substantial movement of individuals toward the observer (evident by a spike in the first distance class) in the spring 2009 survey. This movement appeared to occur primarily by birds within 50 m and therefore we elected to use 100-m distance classes in the analysis to eliminate any movement effects. As such, we used three 100-m distance classes. Let y_{ij} be the number of individuals detected at plot i in distance class $j = 1, 2, 3$, and $\mathbf{y}_i = (y_{i1}, y_{i2}, y_{i3}, y_{i0})$ denote the vector of observations at plot i; the last element of the vector, y_{i0}, is the number of individuals present but not detected. Under the distance-sampling model, the vector $\mathbf{y}_i$ has a multinomial distribution

$$\mathbf{y}_i \sim \text{Multinomial}(N_i, \boldsymbol{\pi}_i)$$

where $\boldsymbol{\pi}_i$, the vector of cell probabilities, is the product of the probability that an individual occurs in distance class j (ψ_j) and the detection probability (p_{ij}). The final multinomial cell probability is the probability of not detecting an individual in any of the distance intervals, $\pi_{i0} = 1 - \sum_{j=1}^{j=3} \pi_{ij}$. In distance-sampling models for point transect data, individuals are assumed to be uniformly distributed around a point; therefore, ψ_j is simply the proportion of the plot area in distance class j. The detection probabilities were derived by integrating $g(r, \sigma_i)$, over the j distance classes defined by the distance break points $\mathbf{b} = 0, 100, 200, 300$:

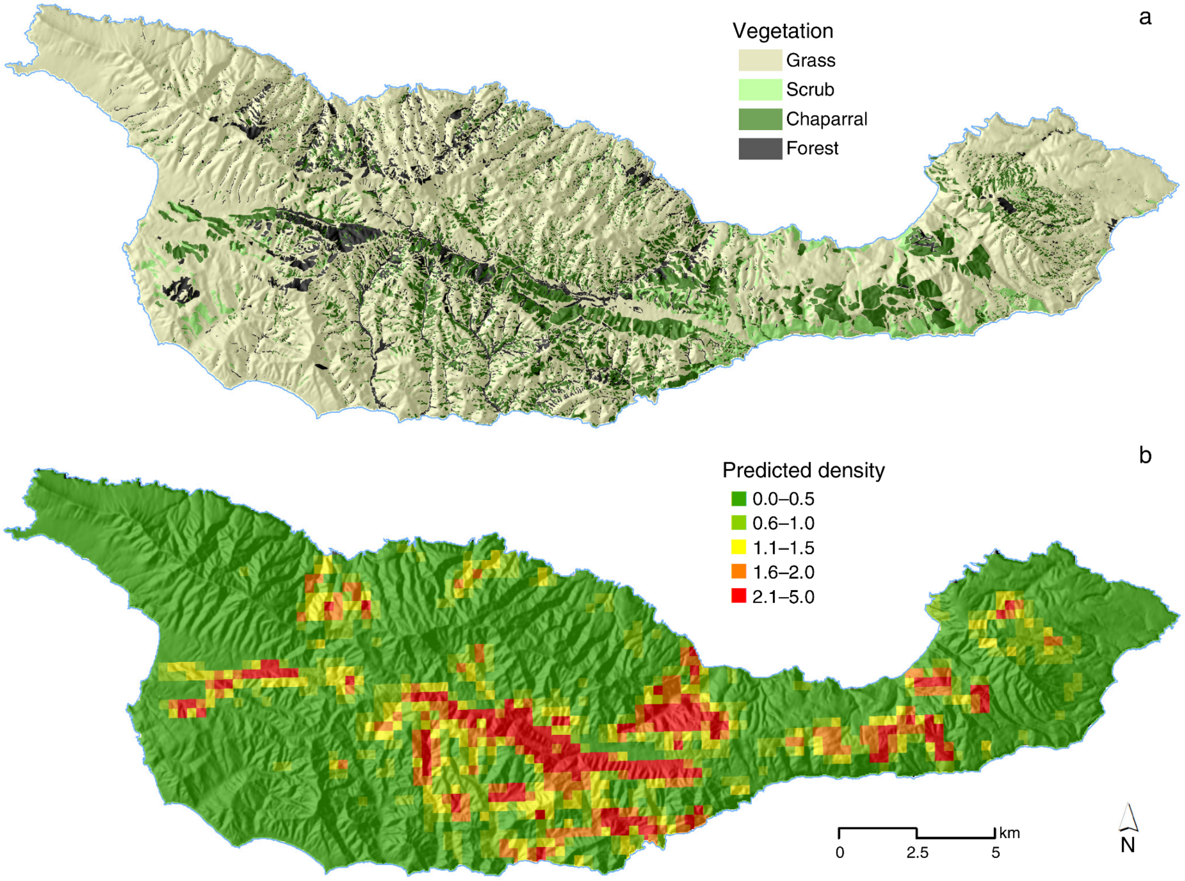

FIG. 3. (a) Vegetation map of Santa Cruz Island from 1985. See *Methods* for details of vegetation categories. (b) Predicted fall 1985 density of Island Scrub-Jays (individuals/9 ha) from the model $\lambda(\text{chap}^2 + \text{elev})\ \sigma(\text{chap})\ \alpha$ (see Table 2 for parameter definitions and model details).

$$p_{ij} = \frac{2\pi \int_{r=b_j}^{r=b_{j+1}} g(r, \sigma_i) r \, dr}{A_j}$$

where A_j is the area of distance class j.

Model selection, evaluation, and prediction

Given the known habitat associations of Island Scrub-Jays, we considered a maximum model consisting of the following covariates of $\log(\lambda_i)$: percent cover of forest (forest), percent cover of chaparral (chap), and elevation (elev). We included a quadratic effect of each covariate, resulting in six abundance effects in total. Because habitat structure could have influenced the ease with which jays were detected, we further considered forest and chaparral as effects on the $\log(\sigma_i)$ parameter of the detection function. We fitted each model containing only a single effect, resulting in eight models, and then combined important effects as indicated by Akaike's information criteria (AIC) to arrive at a final model set. Model development was carried out separately for the fall 2008 and spring 2009 data sets.

We used parametric bootstrapping to evaluate the goodness-of-fit of the best model for each season. We simulated 200 data sets from our model and each time refit the model to these "perfect" data and computed a fit statistic. We then compared the value of the fit statistic for the observed data set to the reference distribution obtained from the simulated data sets. For a model to fit, the observed value should not be too extreme, i.e., beyond the 0.05 percentile of the reference distribution. We used the Freeman-Tukey fit statistic to quantify the fit of a model to a data set, i.e., $D(\mathbf{x}; \boldsymbol{\theta}) = \sum_j (\sqrt{x_j} - \sqrt{e_j})^2$ (Brooks et al. 2000), where x_j is the observed value of observation j and e_j its expected value. In contrast to a chi square discrepancy, the Freeman-Tukey statistic removes the need to pool cells with small expected values.

We used the resulting AIC best model to predict jay abundance on each of 2787 9-ha grid cells on the island with the habitat characteristics computed by GIS for that cell based on habitat maps from both 1985 and 2005. We used the sum of the expected abundance values over all cells as the estimate of total population size. The uncertainty in this estimate was computed with a

TABLE 2. Akaike information criterion (AIC) values for models of jay abundance (λ) and the shape parameter of a half-normal detection function (σ).

Model	Number of parameters	AIC
Fall 2008		
$\lambda(\text{chap}^2 + \text{elev})\ \sigma(\text{chap})\ \alpha$	7	695.4
$\lambda(\text{chap}^2 + \text{elev})\ \sigma(\cdot)\ \alpha$	6	704.7
$\lambda(\text{chap}^2)\ \sigma(\cdot)\ \alpha$	5	705.2
$\lambda(\text{chap}^2 + \text{elev})\ \sigma(\text{forest})\ \alpha$	7	706.7
$\lambda(\text{chap}^2 + \text{forest}^2)\ \sigma(\cdot)\ \alpha$	7	708.2
$\lambda(\text{chap})\ \sigma(\cdot)\ \alpha$	4	714.3
$\lambda(\cdot)\ \sigma(\cdot)\ \alpha$	3	728.9
$\lambda(\text{forest}^2)\ \sigma(.)\ \alpha$	5	730.0
$\lambda(\text{elev})\ \sigma(\cdot)\ \alpha$	4	730.1
$\lambda(\text{forest})\ \sigma(\cdot)\ \alpha$	4	730.7
$\lambda(\cdot)\ \sigma(\text{forest})\ \alpha$	4	730.8
$\lambda(\cdot)\ \sigma(\text{chap})\ \alpha$	4	730.8
$\lambda(\text{elev}^2)\ \sigma(\cdot)\ \alpha$	5	731.3
$\lambda(\cdot)\ \sigma(\cdot)$	2	868.9
Spring 2009		
$\lambda(\text{chap}^2 + \text{elev}^2)\ \sigma(\text{forest})\ \alpha$	8	750.9
$\lambda(\text{chap}^2 + \text{elev}^2)\ \sigma(\cdot)\ \alpha$	7	753.3
$\lambda(\text{chap}^2 + \text{elev})\ \sigma(\cdot)\ \alpha$	6	757.5
$\lambda(\text{chap}^2)\ \sigma(\cdot)\ \alpha$	5	759.4
$\lambda(\text{chap})\ \sigma(\cdot)\ \alpha$	4	764.2
$\lambda(\cdot)\ \sigma(\text{chap})\ \alpha$	4	766.7
$\lambda(\text{elev}^2)\ \sigma(\cdot)\ \alpha$	5	768.5
$\lambda(\cdot)\ \sigma(\text{forest})\ \alpha$	4	773.0
$\lambda(\cdot)\ \sigma(\cdot)\ \alpha$	3	776.4
$\lambda(\text{elev})\ \sigma(\cdot)\ \alpha$	4	776.7
$\lambda(\text{forest})\ \sigma(\cdot)\ \alpha$	4	778.4
$\lambda(\text{forest}^2)\ \sigma(\cdot)\ \alpha$	5	780.1
$\lambda(\cdot)\ \sigma(\cdot)$	2	822.1

Notes: Models with a negative binomial distribution on N_i include the overdispersion parameter α; Poisson models do not. Quadratic effects are represented by superscript 2 and include both linear and squared terms. Covariates are percent cover of forest (forest), percent cover of chaparral (chap), and elevation (elev).

parametric bootstrap. Sample R scripts for reproducing the analyses are given in the Supplement.

RESULTS

Model selection and goodness of fit

Model sets for the fall and spring data were generally similar (Table 2). In both cases, the negative binomial distribution for abundance received more support than the Poisson, indicating that the spatial variation in abundance was greater than accounted for by a Poisson with the added covariates. The best model for fall 2008 contained quadratic chaparral and linear elevation terms on mean abundance; the logarithm of the detection function scale parameter contained an effect of chaparral (Table 2). The top model accounted for 98% of the AIC weight. The spring 2009 model set was similar (Table 2), with AIC giving the most weight (74%) to the model that included an additional term (quadratic in elevation) in the abundance model and replaced chaparral with forest cover in the detection model. Estimated model parameters for both models are given in Table 3. Taken together, these models indicate that *A. insularis* was most abundant at upper and middle-elevation areas with continuous oak chaparral, with lower densities in sparser chaparral and in mixed chaparral–bishop-pine woodlands. Jays were more abundant in fall 2008 compared to spring 2009. The magnitude of the abundance and detection effects from both fall and spring are shown in Fig. 4. The bootstrap P value for the best-fitting, fall 2008 model based on the Freeman-Tukey statistic was $P = 0.12$, and $P = 0.17$ under the best-fitting model for spring 2009, suggesting that the negative binomial models provided adequate fits to the data.

Total population size estimates

Based on the best-AIC abundance models, the habitat covariate values for each of the 2787 9-ha grid cells yielded similar estimates of population size from our fall and spring surveys, and a lower estimated population size in 1985, prior to the eradication of sheep from Santa Cruz Island. Abundance estimates per plot or predictions for any arbitrary region can be obtained from the hierarchical, distance-sampling model using the R command *predict* applied to the output object from *gdistsamp* for the desired model (see Appendix for the calculations carried out here). The total population size estimates, based on the 2005 vegetation classification, were 2267 (95% bootstrap CI, 1613–3007) and 1705 (1212–2369) during fall 2008 and spring 2009, respectively. Using on the 1985 vegetation classification, we estimated a mid-1980s population size of 1532 jays (bootstrap SE, 276; 95% CI, [1070, 2148]) from the best-fit fall model and 1408 jays (bootstrap SE, 186; 95% CI, [1160; 1799]) from the best-fit spring model. Extrapolated maps of rangewide *A. insularis* density are given in Fig. 2b for fall 2008 and in Fig. 3b for fall 1985. Our data therefore indicate that the population size of *A. insularis* was 70–80% of the current level at the time that sheep were eliminated from much of Santa Cruz Island. This habitat is concentrated in the large, central valley of Santa Cruz Island, particularly on north-facing slopes (Fig. 2).

DISCUSSION

We obtained the first robust estimates of habitat-specific abundance and total population size of one of North America's most range-restricted bird species. By combin-

TABLE 3. Parameter estimates (with asymptotic standard errors in parentheses) from the models with the lowest AIC values.

Submodel and coefficient	Fall 2008	Spring 2009
Abundance, $\ln(\lambda)$		
Intercept	0.83 (0.198)	1.10 (0.204)
Chaparral	1.43 (0.229)	0.67 (0.667)
Chaparral^2	−0.38 (0.115)	−0.29 (−0.291)
Elev	−0.23 (0.146)	−0.11 (−0.107)
Elev^2		−0.34 (0.148)
Dispersion, α	0.36 (0.0777)	0.78 (0.239)
Detection, $\ln(\sigma)$		
Intercept	4.68 (0.0658)	4.63 (0.540)
Chaparral	−0.20 (0.060)	
Forest		−0.09 (0.043)

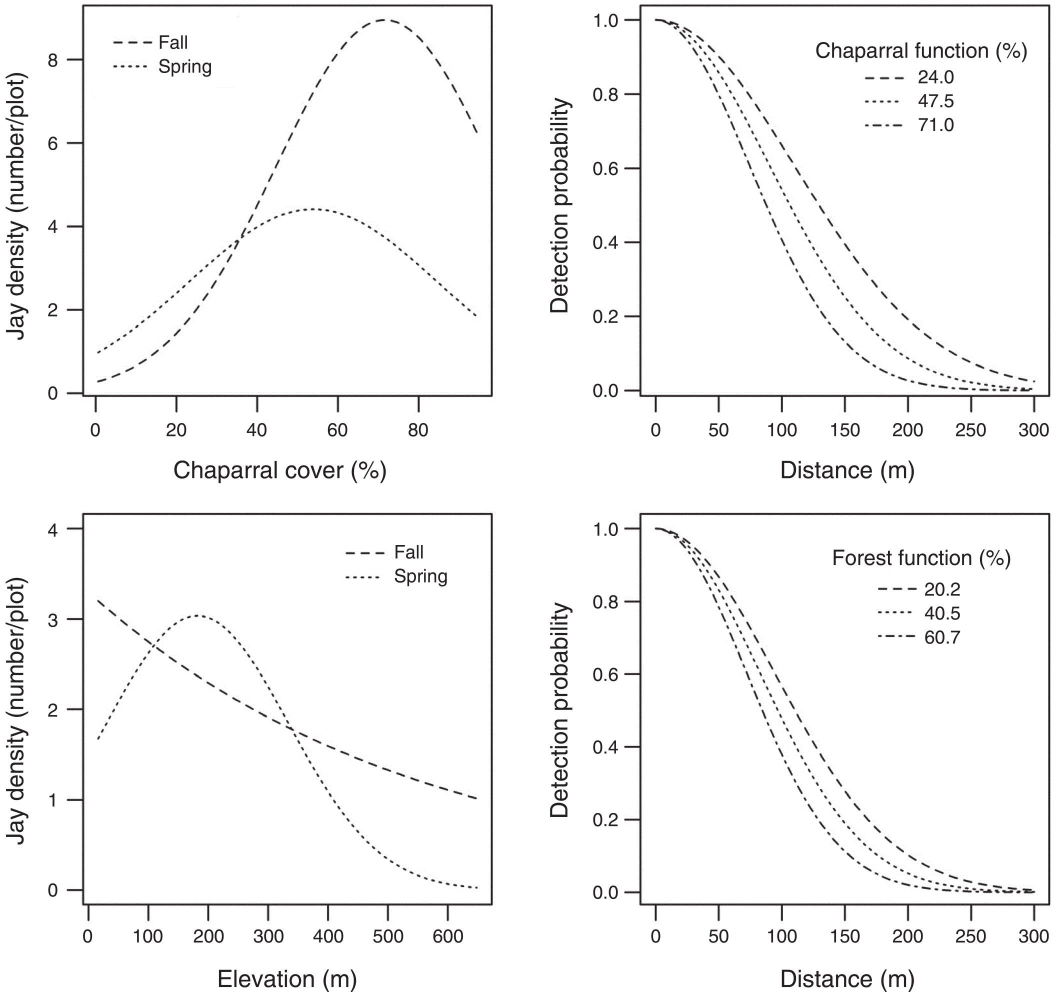

FIG. 4. Expected abundance and detection probabilities as a function of covariates from the best AIC models for fall and spring. Detection functions are shown for the 0.25, 0.50, and 0.75 quartiles of the covariates; chaparral cover (chap) applies to the fall model, whereas forest cover applies to the spring model.

ing random sampling and hierarchical distance-sampling models, we were able to address both of the issues discussed by Yoccoz et al. (2001) as being a challenge for ecological field studies or monitoring schemes, namely spatial sampling and observation error. Below, we discuss methodological and ecological aspects of our study.

Methodological considerations

Our modeling framework improves on conventional distance sampling by specifying a hierarchical model for spatially replicated counts and provides spatially explicit estimates of density as a function of environmental covariates. As such, we can evaluate how changes in such covariates could affect population density, habitat-specific abundance, and detection probability. Moreover, spatially explicit models can provide estimates that adjust, implicitly, for sampling bias, e.g., if sample points tended to favor low elevation sites and density depends on elevation.

Recently, several statisticians have proposed inhomogeneous point-process models for distance-sampling data in order to assess the influence of spatial covariates on animal density (Hedley and Buckland 2004, Johnson et al. 2010, Niemi and Fernández 2010). These models are appealing because spatial variation is modeled as a continuous surface. Our models assumed that density varied among plots but was uniform within plots. Theoretically, high variation in density within plots could bias our estimator. We do not believe this was likely, given the relatively low jay density within survey plots. Furthermore, the potential advantage of modeling density as a continuous surface is limited by the difficulties associated with fitting point-process models to distance-sampling data. For example, convergence problems led Hedley and Buckland (2004) to restrict their model by assuming that density was constant perpendicular to the transect. Even with this restriction, they encountered convergence problems that motivated them to explore two-stage approaches of estimating the detection and abundance parameters separately. Johnson et al. (2010) had more success in fitting inhomogeneous Poisson point-process models, but were not able to directly model overdispersion, which we found to be important in our study. Niemi and Fernández (2010) built upon these efforts to allow for spatial dependence in the residuals, but the complexity of their model caused them to assume that detection probability was known a priori.

An additional practical issue with these inhomogeneous point-process models is that they require data on the exact locations of individuals in space, not just their distances from a point or transect. This may be difficult to measure accurately under many field conditions. Furthermore, covariate modeling in a continuous space framework appears conceptually difficult: in most cases, environmental covariates must represent some average over an area rather than the value of the covariate at an exact point location. This would seem to seriously reduce the benefits of continuous-space frameworks of distance sampling. Thus, although inhomogeneous point-process models allow for modeling density as a continuous surface, several practical issues limit their application to existing data sets and data sets with typical sample sizes. One of the appealing features of the Royle et al. (2004) model framework that we used is the ease with which it can be applied and its accessibility via user-friendly functions in the R package *unmarked* (Fiske and Chandler 2011).

The structure of our model is flexible and could be extended to address a range of ecological questions. Where temporal replicate samples are available for some or all points, the temporal dynamics of the population may be described as well. The simplest description, over short time periods, might be one of temporary emigration from a common super-population (Chandler et al. 2011). Alternatively, and especially over longer time periods, it should be possible to combine our distance-sampling observation model with the dynamic state model developed by (Dail and Madsen 2011), which allows inference about population dynamics parameters of recruitment and local survival.

The need for explicit modeling of the observation process in animal counts is sometimes questioned (e.g., Johnson 2008). Covariate modeling has been conducted as an alternative (e.g., Link and Sauer 2002), where covariates thought to be related to detection probability are modeled in the expectation of a count, thereby correcting for them. The latter approach may be unreasonable if a covariate affects both abundance and detection at the same time. Our study provides just such an example, where in the fall 2008, both jay abundance and jay detection were related to the proportion of a point count area covered by chaparral. We believe that such examples provide a strong motivation for explicit modeling of the observation process in studies of animal abundance.

Biological considerations

Our results highlight the rarity of the Island Scrub-Jay, which has a global population size similar to or less than that of other bird taxa currently listed as threatened or endangered in the United States (e.g., Kirtland's Warbler *Dendroica kirtlandii* [Donner et al. 2008], Red-cockaded Woodpecker *Picoides borealis* [Costa and Daniels 2004]). The Island Scrub-Jay is considered "vulnerable" by the International Union for the Conservation of Nature (Bird Life International 2012) but is not listed by any U.S. federal agency or by the State of California (Shuford and Gardali 2008). We do not believe this species faces an imminent risk of extinction. The entire range of *A. insularis* is protected in Channel Islands National Park, and our results suggest that its abundance has increased due to habitat recovery on Santa Cruz Island. Nevertheless, our population estimates, coupled with the species' restricted range and low allelic diversity (Delaney and Wayne 2005), underscore the vulnerability of *A. insularis* to natural disasters and to diseases such as West Nile virus (Boyce et al. 2011). In addition, the climate in southern California is predicted to become warmer and drier over the coming century (Cayan et al. 2008). Novel, synergistic, and cascading ecological effects will likely develop as climate changes on the California Channel Islands: predator, competitor, and pathogen assemblages could be altered, and vegetation composition could change, as might island fire frequency and severity. Proactive management of the threats to Island Scrub-Jay viability thus seems prudent (Morrison et al. 2011).

The only other empirical study of *A. insularis* abundance (Kelsey and Collins 2000) estimated a total population size of 12 500 jays in 1996–1997. Although we cannot fully assess if total jay abundance declined between the late 1990s and 2008, Kelsey and Collins' (2000) results are problematic. Their estimate was produced by extrapolating the area of 23 jay territories in two, nonrandomly chosen plots to the area of presumed jay habitat across the island, and did not involve systematic, standardized counts of birds. Moreover, the territory sizes (range: 0.59–2.24 ha, mean ± 1 SE = 1.35 ± 0.52 ha, $n = 23$) used by Kelsey and Collins (2000) were substantially smaller than those documented in a later, more extensive, three-year study (range = 0.61–8.85 ha, mean = 3.44 ± 0.15 ha, $n = 137$ [Caldwell 2010]). C. T. Collins and K. A. Corey (*unpublished data*) did observe a decrease in the number of territory holders on a long-term plot that encompasses the University of California's field station (see Fig. 1) between the mid-1990s and 2006. Continued and expanded monitoring on that and other plots since 2007, however, has not suggested a declining population (T. S. Sillett and S. A. Morrison, *unpublished data*), and has revealed that Island Scrub-Jay territory locations can be more dynamic between years than previously thought (Caldwell 2010).

The seasonal patterns in the habitat-specific density, detectability, and abundance of *A. insularis* reflect differences in jay biology between spring and fall. During the breeding season, jays hold and defend territories;

itinerant individuals appear to be uncommon. Size of jay territories is correlated with oak canopy cover, with the smallest and presumably best sites on lower hill and canyon slopes characterized by relatively tall and continuous cover of oaks and other chaparral plant species (Caldwell 2010). Habitats dominated by bishop pine are exceptionally dense and difficult to work during the breeding season, which likely explains why detectability is a function of percent cover of forest habitat (Fig. 4). Breeding individuals can be inconspicuous in early–mid April, before most nests have hatched and parents begin feeding young. In fall, *A. insularis* focus on gathering and caching acorns in oak chaparral (Curry and Delaney 2002). Territory boundaries relax, although pairs still defend against intruders. The principal demographic difference in fall is the presence of non-territorial, hatch-year individuals, which can form small flocks and interact with territorial jay pairs. In general, *A. insularis* are more detectable in fall because frequency of jay vocalizations and interactions increase. Total population size in fall is larger because of hatch-year birds, which have a lower survival probability in their first year compared to adults (Atwood et al. 1990, Collins and Corey 1994).

The oak chaparral habitat favored by Island Scrub-Jays has been concentrated in north-facing slopes of Santa Cruz Island's central valley for the past three decades (Figs. 2a and 3a; see also Van Vuren and Coblentz 1987), and likely longer. This dense vegetation withstood livestock grazing pressure for over a century, which allowed *A. insularis* to persist on Santa Cruz Island through the ranching era. Sheep were eradicated from 90% of the island in the 1980s (Schuyler 1993) and the remainder of the island in the late 1990s (Faulkner and Kessler 2011). The subsequent vegetation recovery (Klinger et al. 1994, Peart et al. 1994) may have also allowed for a 20–30% increase in the jay population (Figs. 2b and 3b). In turn, the scatter-hoarding behavior of *A. insularis* (e.g., DeGange et al. 1989, Johnson et al. 2003) likely has assisted with vegetation recovery (Figs. 2a and 3a). We predict that, barring a natural disaster or disease outbreak, the Island Scrub-Jay population will continue to grow on Santa Cruz Island in the coming decades. Further research is needed to determine how the carrying capacity for *A. insularis* on the island will change with vegetation succession. Management policies that facilitate the regeneration of oak chaparral and woodland on Santa Cruz Island will benefit the Island Scrub-Jay.

In summary, we have demonstrated an accessible hierarchical modeling framework for obtaining unbiased estimates of both population size and habitat-specific abundance over large spatial scales. This framework, in combination with a rigorous spatial sampling design, allowed us to evaluate the conservation status of *A. insularis*, and is generalizable to other study systems. Although fitting hierarchical models to count data can be complex, the free program R and the *unmarked* package make these methods feasible for researchers with limited access to statistical expertise or financial resources.

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SUPPLEMENTAL MATERIAL

Supplement

R code, data, and grid covariates used in the analyses (*Ecological Archives* A022-107-S1).