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RESEARCH ARTICLE

A hierarchical model combining distance sampling and time removal to estimate detection probability during avian point counts

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ABSTRACT

Imperfect detection during animal surveys biases estimates of abundance and can lead to improper conclusions regarding distribution and population trends. Farnsworth et al. (2005) developed a combined distance-sampling and time-removal model for point-transect surveys that addresses both availability (the probability that an animal is available for detection; e.g., that a bird sings) and perceptibility (the probability that an observer detects an animal, given that it is available for detection). We developed a hierarchical extension of the combined model that provides an integrated analysis framework for a collection of survey points at which both distance from the observer and time of initial detection are recorded. Implemented in a Bayesian framework, this extension facilitates evaluating covariates on abundance and detection probability, incorporating excess zero counts (i.e. zero-inflation), accounting for spatial autocorrelation, and estimating population density. Species-specific characteristics, such as behavioral displays and territorial dispersion, may lead to different patterns of availability and perceptibility, which may, in turn, influence the performance of such hierarchical models. Therefore, we first test our proposed model using simulated data under different scenarios of availability and perceptibility. We then illustrate its performance with empirical point-transect data for a songbird that consistently produces loud, frequent, primarily auditory signals, the Golden-crowned Sparrow (*Zonotrichia atricapilla*); and for 2 ptarmigan species (*Lagopus* spp.) that produce more intermittent, subtle, and primarily visual cues. Data were collected by multiple observers along point transects across a broad landscape in southwest Alaska, so we evaluated point-level covariates on perceptibility (observer and habitat), availability (date within season and time of day), and abundance (habitat, elevation, and slope), and included a nested point-within-transect and park-level effect. Our results suggest that this model can provide insight into the detection process during avian surveys and reduce bias in estimates of relative abundance but is best applied to surveys of species with greater availability (e.g., breeding songbirds).

Keywords: Alaska, Bayesian analysis, density, detection probability, distance sampling, *Lagopus*, point transect, time removal, WinBUGS, *Zonotrichia atricapilla*

Modelo jerárquico combinando muestreo por distancia y eliminación de tiempo para estimar la probabilidad de detección de aves durante conteos en puntos

RESUMEN

La detección imperfecta durante los muestreos de animales sesga las estimaciones de abundancia y puede llevar a conclusiones inadecuadas sobre distribución y tendencias poblacionales. Farnsworth et al. (2005) desarrollaron un modelo combinado de muestreo por distancia y eliminación de tiempo para muestreos de puntos y transectas que contempla tanto la disponibilidad, la probabilidad de que un animal esté disponible para ser detectado (e.g., que un ave cante), como la perceptibilidad, la probabilidad de que un observador detecte un animal dado que está disponible para detección. Desarrollamos una extensión jerárquica del modelo combinado que brinda un marco de análisis integral para un grupo de puntos de muestreo en el cual se registran tanto la distancia desde el observador como el tiempo de la detección inicial. Con la implementación de un marco de trabajo bayesiano, esta extensión facilita la evaluación de covariables sobre la abundancia y la probabilidad de detección, incorporando conteos con cero exceso (i.e. inflación cero), considerando la autocorrelación espacial y estimando la densidad poblacional. Las características específicas de las especies, como los despliegues comportamentales y la dispersión territorial, pueden llevar a diferentes patrones de disponibilidad y perceptibilidad, lo cual puede a su vez influenciar el desempeño de estos modelos jerárquicos. Por lo tanto, primero evaluamos nuestro modelo propuesto usando datos simulados bajo diferentes escenarios de disponibilidad y perceptibilidad. Luego ilustramos su desempeño con datos empíricos de puntos y transectas para un ave canora que produce consistentemente señales principalmente auditivas fuertes y frecuentes (*Zonotrichia atricapilla*) y para dos especies de *Lagopus* sp., que producen señales principalmente visuales

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más intermitentes y sutiles. Los datos fueron colectados por múltiples observadores en puntos y transectas a lo largo de un amplio paisaje en el sudoeste de Alaska, por lo que evaluamos covariables a nivel de punto sobre perceptibilidad (observador, hábitat), disponibilidad (fecha dentro de la estación, tiempo del día) y abundancia (hábitat, elevación, pendiente), e incluimos un efecto anidado de punto dentro de la transecta y a nivel de parque. Nuestros resultados sugieren que este modelo puede ayudar a entender el proceso de detección de las aves durante los muestreos y reducir el sesgo en las estimaciones de abundancia relativa, pero se aplica mejor a los muestreos de especies con mayor disponibilidad (e.g., aves canoras reproductivas).

Palabras clave: Alaska, análisis bayesianos, densidad, eliminación de tiempo, *Lagopus*, muestreo por distancia, probabilidad de detección, transecta de puntos, WinBUGS, *Zonotrichia atricapilla*

INTRODUCTION

Monitoring a species of interest to determine its population size, trend, or distribution requires robust, unbiased estimators of abundance or, at a minimum, a parameter directly proportional to abundance. Incomplete detection of animals during surveys can bias population estimates and lead to incorrect assessments of conservation status or of the effectiveness of management actions (Burnham 1981, Rosenstock et al. 2002, Thompson 2002, Norvell et al. 2003, Kéry and Schmid 2004). Numerous methods exist to adjust counts of animals for incomplete detection, including distance sampling (Buckland et al. 2001, Johnson et al. 2010), time removal (Farnsworth et al. 2002, Etterson et al. 2009), repeated counts (Royle and Nichols 2003, Royle 2004), double observer (Cook and Jacobson 1979, Nichols et al. 2000), mark–recapture (Laake et al. 2011), double sampling (Bart and Earnst 2002), and some combinations thereof (e.g., Farnsworth et al. 2005, Sólymos et al. 2013). The applicability of these methods varies widely with respect to the parameter of interest, behavior of the species, characteristics of the survey area, timing of the survey, and logistical, time, and resource constraints. For example, multiple-observer methods require additional manpower; repeated surveys within a season are expensive, logistically challenging, and affected by closure assumptions; and mark–recapture methods are not always possible or practical to implement.

Addressing imperfect detection is complicated by multiple causal mechanisms. Nichols et al. (2009) identified 2 parts of the detection process during bird surveys: coverage probability and detection probability. Coverage probability is the probability that the location of the bird is within a sampling unit at the time of the survey and is the product of the probability that (1) a bird has a home range that overlaps the sampling unit (p_s) and (2) is present in the study area at the time of the survey (p_p) (Nichols et al. 2009). These probabilities are a function of the timing and spatial coverage of a survey, and their computation is often based on knowledge of the study design. Detection probability also consists of 2 components: availability (p_a), which is the probability that an animal is present in the survey area and signaling its presence to the observer (e.g., a bird is vocalizing or is in view); and perceptibility (p_d), which is the probability that an animal available for detection (e.g., a bird sings) is detected by the observer (Marsh and Sinclair 1989). Availability and perceptibility are often strongly influenced by the animal's cue-production rate, the distance between the animal and the observer, and the observer's sensory abilities; these factors, in turn, may vary significantly with other influences such as time of season, time of day, habitat, and weather conditions (e.g., Farnsworth et al. 2002, Alldredge et al. 2007c, Nichols et al. 2009). Several methods or combinations of methods can estimate both components of detection probability; however, most require either multiple observers or repeat surveys at a point within a short period to avoid violating the assumption of population closure (e.g., time-of-detection, robust design, or multiple-observer capture–recapture; Bailey et al. 2004, Alldredge et al. 2007a, Nichols et al. 2009).

Distance sampling and time removal are methods that require only a single survey and observer. For distance sampling, an observer measures the distance to each detected animal. This method is used extensively in line-transect and point sampling because of its relative efficiency in terms of cost and time (Buckland et al. 2001, Rosenstock et al. 2002, Norvell et al. 2003, Sillett et al. 2012). Conventional distance sampling will, however, produce negatively biased estimates of density if the critical assumption of perfect detection at zero distance is violated (Buckland et al. 2001). Such conditions may arise if an animal that is present at the survey point does not give a cue during the survey period (availability bias) or if the observer does not detect a cue that was given (perception bias) (Laake and Borchers 2004).

To account for availability in avian point-count surveys, Farnsworth et al. (2002) described a time-removal model (also called "time-to-detection model") that treats subsets of the survey period as independent replicates ("occasions") in which birds are "captured" (i.e. counted) and mentally removed from the population (i.e. not counted again) during later subperiods. As animals within a closed population are counted and removed from further consideration, the number of individuals available for detection will decrease through time. Hence, following the logic of a removal model to estimate population size (Zippin 1958), Farnsworth et al.'s (2002) model estimates

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the proportion of the population never detected during a survey and, by subtraction, the proportion of the population available for detection (p_a).

Together, distance-sampling and time-removal methods can quantify both important components of detection. Farnsworth et al.'s (2002) method relies on birds perceived within a time interval to estimate availability and, thus, estimates the product of p_a and p_d (Marsh and Sinclair 1989, Nichols et al. 2009); including distance sampling allows separation of each detection component. Additionally, combining these methods allows explicit modeling of heterogeneity in detection probability. Some heterogeneity arises from individual variation in the frequency, intensity, or duration of signals to the observer, which for songbirds is often strongly related to distance from the observer, date within season, and time of day. Such heterogeneity is often ignored when modeling detection probability (Farnsworth et al. 2002, 2005), but ignoring it can positively bias estimates of detection probability (and negatively bias density estimates) because the group of detected individuals contains a greater proportion of the population that is consistently easy to detect during repeated surveys (e.g., birds closer to the observer or singing more frequently) than is included in the group of undetected individuals.

Conventional distance sampling is robust to some individual heterogeneity in p_d as long as other modeling assumptions are met (Buckland et al. 2001). Perhaps the greatest benefit of combining distance sampling with a method to address availability, such as Farnsworth et al.'s (2002) time-removal model, is that it allows one to relax the assumption that detection probability on the line or at the point is perfect (i.e. $p(0) = 1$; Buckland et al. 2001:30). Pollock and Kendall (1987) recommended mark–recapture methods to estimate detection probability as an alternative to distance sampling because of this bias. However, heterogeneity tends to increase at greater distances from the observer (Laake et al. 2011) and may render capture–recapture-based multiple-observer methods of all but the smallest fixed-radius areas subject to such bias unless detection probability is also modeled as a function of distance.

Combining distance-sampling with time-removal methods can address this issue, along with heterogeneity, using less survey effort than multiple observers or repeated surveys. An observer need only record the time interval and estimated distance to each animal when it is first detected during a single survey. Such efficient survey methodology is particularly attractive for large-scale wildlife surveys, especially in areas where temporally repeated sampling is logistically difficult and expensive.

Farnsworth et al. (2005) first described a combined distance-sampling and time-removal model for auditory point-count surveys that assumes the following: (1) A bird that is present during a survey may be detected only if it vocalizes; and (2) detection probability, given availability, declines as a function of distance from the observer. Thus, overall detection probability p is the product of each component of detection, $p = p_a \times p_d$ (Farnsworth et al. 2005). They implemented the model in Program SURVIV (White 1992), but their model did not include ways to incorporate covariates on either component of detection or an integrated way to estimate abundance. Availability and perceptibility can be highly influenced by weather, observer ability, habitat, species, seasonal date, and time of day, among other factors (Alldredge et al. 2007c, Fitzpatrick et al. 2009). Although estimates of density across broad regions and survey periods may be robust to unmodeled sources of heterogeneity in detection (i.e. "pooling robust"; Buckland et al. 2001), not incorporating sources of variability at the survey-point level may lead to biased estimates of detection probability and density at more refined spatial and temporal scales (Thompson 2002). Wildlife are not distributed evenly across the landscape, and habitat and environmental factors may strongly influence the abundance of a species at a given survey point. Elucidating patterns and factors that influence detection and abundance is often of primary interest to ecologists and can provide important information to inform monitoring and management efforts, beyond how many animals are present in an area.

Royle et al. (2004) developed a hierarchical distance-sampling model for spatially replicated counts with a distance-sampling protocol to estimate and model abundance adjusted for p_d (also see Hedley and Buckland 2004, Johnson et al. 2010, Sillett et al. 2012, Oedekoven et al. 2013, Schmidt and Rattenbury 2013). Etterson et al. (2009) created a similar hierarchical N-mixture model using Farnsworth et al.'s (2002) time-removal method to estimate abundance adjusted for p_a. In these models, covariate effects on both abundance and detection can be modeled directly as a generalized linear model. Especially when implemented in a Bayesian framework, straightforward extensions include fixed and random effects, spatial autocorrelation, excess zeros, and replicated counts through time (Thogmartin et al. 2004, Martin et al. 2005, Etterson et al. 2009, Sauer and Link 2011, Kéry and Schaub 2012). However, because models of both Royle et al. (2004) and Etterson et al. (2009) incorporate only 1 component of detection probability (i.e. p_d or p_a, respectively), the modeled detection probability is really a conflated estimate of $p_a \times p_d$ and the resulting abundance estimates are subject to unmeasured amounts of negative bias.

Here, we extend and integrate Farnsworth et al.'s (2005) combined time-removal and distance-sampling model for point-count surveys and Royle et al.'s (2004) hierarchical distance-sampling model into a Bayesian hierarchical N-mixture framework with separate processes for abundance (i.e. the total number of birds present in the surveyed area

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TABLE 1. Summary of the capabilities that we incorporated into our distance-sampling and time-removal *N*-mixture model compared with those of similar existing models.

	Explicit abundance model allowing					
	Individual-level formulation	Heterogeneity in availability	Heterogeneity in perceptibility	Spatial covariates on abundance	Time removal + distance sampling	Bayesian implementation
This model	X	X	X	X	X	X
Royle et al. (2004)			X	X		
Farnsworth et al. (2005)		X	X		X	
Etterson et al. (2009)			X	X		
Oedekoven et al. (2013)	X		X	X		
Sólymos et al. (2013)		X	X	X	X	

during the survey period, *N*), perceptibility (p_{d}), and availability (p_{a}). Our new model (1) accommodates covariates on all processes, (2) allows estimates of detection-adjusted population density, (3) allows modeling of spatial autocorrelation, and (4) accounts for extra dispersion in the form of zero inflation (Table 1). To illustrate our model, we use simulated data and field examples from avian point-transect data collected across a broad landscape in Alaska. Furthermore, we implement the model in a Bayesian framework using the accessible JAGS program (Plummer 2003), allowing flexible model development by nonspecialists.

METHODS

Model Description

We created this model to accommodate single-visit point-transect data replicated at $k = 1, 2, \ldots, K$ points in an area of interest. At each survey point during a prescribed period (e.g., 5 min), a single observer records distance from the central observation point to each bird detected and the survey time elapsed to its initial detection (i.e. time-to-detection), at which time the bird is "removed" from further counting. For each bird detected *i*, radial distance is recorded into discrete classes $b = 1, 2, \ldots, B$ out to a maximum distance ($\max_{\mathrm{d}}$) and time-to-detection is assigned to a time interval $j = 1, 2, \ldots, J$. The observed data, then, are the counts of individuals at each point (y_k) and the period (j_i) and distance class (b_i) for individuals $i = 1, 2, \ldots, y$, where y is the total number of birds detected across all spatial sample units. Although the model is formulated using discrete time and distance intervals for ease of computation, truly continuous observations can be accommodated to greater levels of precision simply by using a large number of fine intervals.

The model requires the following primary assumptions: (1) Points are placed randomly with respect to bird distribution; (2) birds are detected at their initial location prior to any movement; (3) birds are identified without error (e.g., with respect to species and without double counting at a point); (4) distances are measured accurately or observations are recorded in the appropriate distance classes; (5) p_{a} and p_{d} are independent; (6) the population is closed during surveys to births, deaths, immigration, and emigration; and (7) the entire population is present during surveys (i.e. probability of presence, $p_{\mathrm{p}} = 1$; Nichols et al. 2009).

This model uses Royle's (2004) *N*-mixture model with a novel observation-level formulation of Farnsworth et al.'s (2005) joint distance-sampling and time-removal model to estimate detection probability (Farnsworth et al. 2002). The observation-level formulation is convenient to implement in popular Bayesian analysis software (e.g., JAGS; Plummer 2003) and also allows for some flexibility to incorporate other effects at the individual level. The model is expressed in terms of the "conditional likelihood," in which the observation model is expressed as conditional on the observed count of individuals at each sample point (y_k). Then a second model component is described for y_k, conditional on the population size at each sample point (N_k), which is assumed to be a random variable itself so that one can model variation among sample points in the population. Analyzing the joint likelihood (e.g., Royle et al. 2004) cannot be done in JAGS easily because the multinomial parameter N_k cannot be an unobserved random variable. However, it is straightforward to implement the model on the basis of factorization of the joint model into 3 hierarchical levels: individual-level data (i.e. observations conditional on y_k), point-specific counts (i.e. y_k conditional on N_k), and population size (i.e. N_k).

Level 1: Individual-level Data

We assumed independence of time-of-removal and distance so that the overall probability of detection can be expressed as the product of the probabilities of availability (p_{a}), derived from detections during *J* time intervals, and perceptibility (p_{d}), derived from detections within *B* distance classes. Cell probabilities π can be expressed as a categorical distribution for individual observations such that dclass_i is the distance class and $\mathrm{tinterval}_i$ is the time interval of detection of individual *i*. Thus, the observation model, specified conditional ($^{\mathrm{c}}$) on

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y_k, has the following 2 components:

$$\text{tinterval}_i \sim \text{Categorical}(\pi^{\text{c}}_{\text{a}})$$

$$\text{dclass}_i \sim \text{Categorical}(\pi^{\text{c}}_{\text{d}})$$

for $i = 1, 2, \ldots, y_k$.

For p_{a}, we generally followed Farnsworth et al. (2002) in constructing a time-removal model to estimate availability based on initial detections of birds within each of 3 equal time intervals, but we added a covariate model to address individual heterogeneity. We expected point-level covariates (e.g., date within season and time of day each point was surveyed) to provide useful information on the detection process for all individuals in the population. Specifically, individuals are detected with probability a during each time interval and the conditional cell probabilities $\pi^{\text{c}}_{\text{a}}$ are defined by

$$\pi^{\text{c}}_{\text{a}_{jk}} = \frac{\pi_{\text{a}_{jk}}}{p_{\text{a}_k}}$$

where $\pi_{\text{a}_{jk}}$ is the probability of availability in time interval j at point k and p_{a_k} is the probability of an individual being available during at least 1 time interval at point k. The time-interval-specific probability of availability is calculated as $\pi_{\text{a}_{jk}} = a_k(1 - a_k)^{j-1}$, where a_k is an individual's probability of detection during 1 time interval at point k. We accounted for heterogeneity by modeling point-level covariates x affecting the probability of availability as a logistic regression $\text{logit}(a_k) = \alpha + \beta_x x_k$. We derived point-specific p_{a_k} by summing the time-interval-specific probability of availability $\pi_{a_{jk}}$ across j ($j = 1$ to J), where

$$p_{\text{a}_k} = \sum_{j=1}^{J} \pi_{\text{a}_{jk}}$$

We also explored 2 alternative models to account for heterogeneity in availability: a simple 2-point mixture model and a combined mixture–covariate model. (1) In the simple mixture model, we considered the case (general model M_{c} described in Farnsworth et al. 2002) in which the population as a whole is modeled simply as a combination of 2 groups, the first of which comprises birds that are readily available for detection (e.g., dominant males that sing often or for longer duration), all of which are assumed to be detected during the first time interval (i.e. $p_{\text{a}} = 1$). Individuals in the second group, comprising an expected proportion c of the population, are less available (e.g., submissive males that sing less frequently) and are detected with probability a during each time interval (where $a = 1 - q$; cf. Farnsworth et al. 2002). Multinomial probabilities are specified as in our covariate model above, except that they incorporate c and are not indexed by point k: for $j = 1$, $\pi_{\text{a}_1} = 1 - c(1 - a)$ and for $j = 2$ to J, $\pi_{\text{a}_j} = ca(1 - a)^{j-1}$. (2) In the combined model, we modeled the population as a combination of 2 groups as in the preceding simple mixture model, but then further modeled availability a_k of the second (less available) group as a logistic regression function of point-level covariates, as in our covariate model. We found that both of these approaches were inferior to our covariate model during simulations and analysis of field data. In the simple mixture model, estimates of p_{a} were similar to those from the covariate model but much less precise, with concomitant effects on precision of density estimates. In the combined model, we found problems of nonidentifiability in attempting to estimate both c and a_k, and resulting estimates of p_{a} and density were again highly imprecise. In both the simple mixture and combined models, estimates of c and a rely on the detections of individuals in group 2, thereby leading to poor estimability if p_{a} is high or c is low, or both. Furthermore, heterogeneity in detection probabilities has been demonstrated to be problematic in analysis of capture–recapture data if there is uncertainty in the underlying distributions (e.g., beta vs. logit normal distribution), even when sample sizes are large (Link 2004). We therefore recommend and present results for p_{a} using only our covariate model approach, which uses all detections to inform p_{a} and includes only biologically meaningful covariates.

For modeling probability of perception, we followed a similar approach. The conditional multinomial cell probabilities for distance are constructed as

$$\pi^{\text{c}}_{\text{d}_{bk}} = \frac{\pi_{\text{d}_{bk}}}{(p_{\text{d}_k})}$$

where $\pi_{\text{d}_{bk}}$ is the probability of detection in distance class b at point k and p_{d_k} is the probability of being detected in any distance class within the truncation radius at point k. We defined the multinomial cell probability π in distance class b using a rectangular rule of approximating the integral where the probability that distance r is within the bounds of b with width δ is

$$\pi_{r_b} = \Pr\left(r_b - \frac{\delta}{2} \le r \le r_b + \frac{\delta}{2}\right) \sim g(r)_{bk} f(r)_b$$

and the half-normal distance function is

$$g(r)_{bk} = \exp\left(-\frac{r_b^2}{2\sigma_k^2}\right)$$

where r_b is the midpoint radial distance in distance class b and

$$f(r)_b = \frac{2 r_b \delta_b}{\max_{\text{d}}^2}$$

is the probability density function of radial distance from the observation point for each distance class out to the

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maximum truncation distance $\max_d$ (Buckland et al. 2001). The scale parameter σ_k represents the rate of decay of $g(r)_{bk}$ as a function of distance for each point. Point-level covariates x on p_d can be modeled as a log-linear function of σ_k where $\log(\sigma_k) = \log(\sigma_0) + \beta_x x_k$. We derived point-specific p_{d_k} by summing the multinomial cell probability $\pi_{d_{bk}}$, the probability that an individual was detected at point k in distance bin b, across b ($b = 1$ to B), where

$$p_{d_k} = \sum_{b=1}^{B} \pi_{d_{bk}}.$$

Level 2: Point-specific Counts

Because we wanted to examine goodness-of-fit of the availability component of the model independently from that of the perceptibility part of the model, we expressed the model for the point-level counts y_k as the product of 2 components. First, we estimated the number of individuals in the local population that were available for sampling (navail_k) as a random variable with sample size N_k and probability of availability p_{a_k} where $\text{navail}_k \sim \text{Binomial}(N_k, p_{a_k})$. Then, the observed (i.e. detected) number of individuals per point y_k is a binomial random variable with sample size navail_k and probability of detection p_{d_k}: $y_k \sim \text{Binomial}(\text{navail}_k, p_{d_k})$.

Level 3: Population Size

Because abundance may vary among points in relation to measurable attributes, we modeled the population size for each point N_k as a Poisson distribution with mean expected value λ, $N_k \sim \text{Poisson}(\lambda_k)$ (Royle et al. 2004). Point-level covariates x affecting abundance can be incorporated into the expected value where $\log(\lambda_k) = \alpha + \beta_x x_k$. Density D_k is then N_k-adjusted for the area surveyed A. For example, birds detected within a 300-m radius of the observer would have

$$A = \frac{\pi \times 300^2}{10,000} = 28.27\,\text{ha}$$

and

$$D_k = \frac{N_k}{28.27\,\text{ha}}$$

Simulated Dataset

We investigated model performance by simulating data to evaluate model assumptions and examined the range of parameter values under which our model provides acceptable estimates. We simulated overdispersed point-transect data with $p_d < 1$ and $p_a < 1$, both of which were influenced by several covariates, and with spatial autocorrelation among points within a transect. Ignoring spatial autocorrelation can lead to underestimating standard errors and overfitting models (Legendre 1993). Thus, we included transect-specific intercepts α_t as a random effect on the expected count to account for non-independence among points within a transect where $\log(\lambda_k) = \alpha_t + \beta_x x_k$.

We modeled a population of a simulated grassland bird species as a function of moderately correlated ($r_{\max} = 0.5$) covariates (i.e. habitat). Abundance was positively or negatively associated with the proportion of grass (Grass, $\beta_{\text{Grass}} = 1.0$), agriculture (Ag, $\beta_{\text{Ag}} = -0.5$), forest (Trees, $\beta_{\text{Trees}} = -0.05$), and wetland (Wet, $\beta_{\text{Wet}} = 0.5$; Wet^2, $\beta_{\text{Wet2}} = -0.5$) at the survey point. Furthermore, p_d declined with the proportion of trees at a point ($\beta.\text{d}_{\text{Trees}} = -0.3$) and p_a declined with date within season (Date, $\beta.\text{a}_{\text{Date}} = -0.3$). We simulated data at 100 points surveyed along 10 transects of 10 points each using baseline values of 5 distance classes, 3 equal time intervals, maximum truncation distance $\max_d = 300$ m, $p_a = 0.9$, $p_d = 0.4$, and $\lambda \sim 9$. We further examined model performance when availability and perceptibility were low ($p_a = 0.4$, $p_d = 0.4$, and $\lambda \sim 20$). We created 500 dataset realizations for each scenario to assess bias and coverage of the 95% credible intervals (CIs) for each parameter of interest. We estimated scaled relative bias as the deviation of each realized parameter estimate minus the true value scaled as a proportion of the true value, where

$$\text{relative bias} = \frac{\text{estimate} - \text{truth}}{\text{truth}}$$

We defined "coverage" as the percentage of realizations with 95% CIs that included the true value for each parameter. R code to simulate the dataset and create the JAGS model used in this example are provided in Supplemental Material Appendices A and B.

Field Study

We further evaluated the model using empirical survey data collected in southwest Alaska. From mid-May to mid-June, 2004–2008, 5 observers conducted unlimited-radius point counts of birds primarily in upland habitats (>100 m elevation) at 1,021 points along 169 transects in 63 randomly selected sample plots within 3 national parks: Aniakchak National Monument and Preserve, Katmai National Park and Preserve, and Lake Clark National Park and Preserve (Ruthrauff et al. 2007, Ruthrauff and Tibbitts 2009). Points were spaced ~500 m apart along transects with a random start and oriented across habitat and elevational gradients. Habitats in the parks are largely unfragmented except by natural disturbance (e.g., volcanic eruptions and wildfires). Observers recorded exact radial distance (with laser rangefinder) and exact time to initial detection for each bird during 5-min

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point-transect surveys and recorded data on habitat and physiographic features at each point. Observers detected >100 species of landbirds and shorebirds, but we illustrate the model with 2 examples: Golden-crowned Sparrow (*Zonotrichia atricapilla*) and 2 ptarmigan species, Willow Ptarmigan (*Lagopus lagopus*) and Rock Ptarmigan (*L. muta*). Because the numbers of observations were low and the detections were primarily visual for both species of ptarmigan, we estimated both availability and perceptibility jointly, but examined species-specific habitat associations for abundance.

After an exploratory analysis of the raw distance data (Buckland et al. 2001), we truncated ~10% of the farthest observations, which were those beyond 280 m for Golden-crowned Sparrows and beyond 450 m for ptarmigan. We then created 4 unequal distance bins that had approximately equal numbers of observations and adequately fit a half-normal density function. We divided the survey into 3 equal (100-s) periods for estimating availability. We used an analysis of variance of mean detection distance by time interval to examine the assumption of independence between distance and time intervals within the selected truncation radius. After finding evidence of increasing mean detection distance in later time intervals only for Golden-crowned Sparrow, we reran the models with data truncated at a smaller radius (200 m) within which the independence assumption was satisfied. We compared resulting density estimates to assess the effect of violating this assumption for this species.

We modeled 8 coarse-scale habitat categories, elevation, and slope as covariates on abundance. We derived elevation and slope from the National Elevation Dataset (Gesch 2007) and summarized mean values within a 150-m radius of each point. We examined elevation effects for Aniakchak National Monument and Preserve separately from the other 2 parks combined because the broad array of habitats sampled across Lake Clark and Katmai (approximately 100–1,600 m) were found to be very compressed elevationally (to ~600 m) in Aniakchak, most likely because of the more severe weather conditions (wind, snow, and cold) typical of the Aniakchak area (Ruthrauff and Tibbitts 2009). Phenology of vegetation was relatively delayed the year Aniakchak was sampled, and the highest-elevation points were extensively snow covered (Ruthrauff and Tibbitts 2009). Across all parks, habitat categories included the following: shrub <20 cm tall and mesic herbaceous cover (Dshrubherb); shrub >20 cm tall (Shrub); bare ground and perennial ice and snow (Baresnow); open water (Water); wetlands and wet sedge (Wetland); coniferous forest consisting of white spruce (*Picea glauca*), Sitka spruce (*P. sitchensis*), or black spruce (*P. mariana*) (Spruce); mixed deciduous–coniferous forest (Mixed); and deciduous forest (Dec). Habitat was characterized to a 150-m radius at most points ($n = 779$), except those in closed forest or tall shrub habitat with limited visibility, where habitat was characterized within 50 m ($n = 242$). We assumed that habitat composition recorded by observers applied to larger spatial scales because habitat composition was strongly correlated at multiple scales; correlation between habitat composition at 150 m and 800 m was 0.81.

We modeled p_{d} as a function of the following covariates: wind speed (mph), 2 observer groups (i.e. multiple observers were grouped by hearing ability), and the proportion of dense habitat cover (i.e. closed tall shrub and forest cover) within either a 50- or 150-m radius of the point. We modeled p_{a} as a function of Julian date within season and time of day. For Golden-crowned Sparrow, we restricted analysis to detections of singing males; but for ptarmigan, we analyzed all visual and auditory detections of adults, including males, females, and those of unknown sex. Thus, to estimate total breeding density of Golden-crowned Sparrows, we assumed a 50:50 sex ratio and multiplied estimated density of males by 2. We fit transect-specific intercepts as described in the simulated data example. We assumed that either (1) abundances at higher levels of spatial nesting (e.g., transects within plots and plots within parks) were independent because of the large distances between transects, plots, and parks; or (2) the spatial autocorrelation at larger scales was related to features of the landscape, which could be alleviated with the inclusion of relevant spatially structured environmental covariates like the ones we included in our analysis (Wintle and Bardos 2006).

We accounted for an overabundance of zero counts during surveys, which can bias model fit when birds are not observed at a large proportion of survey points (Martin et al. 2005, Joseph et al. 2009). To do so, we included a zero-inflation term z multiplied by the Poisson mean λ_k. The population size per point is then a Poisson distribution with mean λ', where λ' is the product of the expected count λ and a Bernoulli draw z of the zero-inflation parameter ψ: $z \sim \text{Bernoulli}(\psi)$.

Model Implementation and Goodness-of-Fit

For simulated and field data, we conducted a Bayesian analysis in JAGS version 3.2.0 (Plummer 2003), in which we called JAGS remotely from R version 2.15.2 (R Core Team 2012). We standardized (i.e. $\bar{x} = 0$, SD $= 1$) all covariates to facilitate convergence. We assigned random effects including nested point-within-transect intercepts and observer groups on perceptibility as normal distributions with mean μ and precision τ (i.e. $\tau = 1/\text{variance}$). For fixed effects, including the hyperparameter μ, we specified vague normal prior distributions with mean 0 and variance 100 for coefficients; for variances, we chose uniform priors ranging from 0 to 1,000 at the σ scale (Rota et al. 2011, Kéry and Schaub 2012). We conducted 100,000–250,000

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TABLE 2. Results from 500 realized datasets with 95% Bayesian credible intervals (CIs) in relation to the true value of covariate coefficients and model parameters and the proportion of simulations with 95% CIs that included the true value (coverage). We simulated data at 100 points located in 10 transects with 10 points each, using baseline values of 5 distance classes and 3 time intervals. We created 2 scenarios: high availability, where $p_a \sim 0.9$, $p_d \sim 0.4$, $\lambda \sim 9$, and $y \sim 300$ (95% CI: 254–333); and low availability, where $p_a \sim 0.4$, $p_d \sim 0.4$, $\lambda \sim 20$, and $y \sim 300$ (95% CI: 250–333). Model fit for each component of detection probability was assessed with Bayesian *P* values. See text for description of covariates.

	High availability ($p_a \sim 0.9$)			Low availability ($p_a \sim 0.4$)		
	Mean true value	Simulated mean (95% CI)	Coverage	Mean true value	Simulated mean (95% CI)	Coverage
Perceptibility						
Tree	−0.3	−0.31 (−0.49 to −0.18)	0.96	−0.3	−0.29 (−0.42 to −0.19)	0.95
Availability						
Season date	−0.3	−0.17 (−0.48 to 0.12)	0.87	−0.3	−0.13 (−0.32 to 0.09)	0.82
Abundance						
Tree	−0.05	−0.07 (−0.38 to 0.18)	0.94	−0.05	−0.10 (−0.33 to 0.11)	0.95
Ag	−0.5	−0.50 (−0.67 to −0.33)	0.96	−0.5	−0.49 (−0.64 to −0.37)	0.99
Wet	0.5	0.52 (0.32 to 0.75)	0.96	0.5	0.49 (0.29 to 0.65)	0.97
Wet^2	−0.5	−0.53 (−0.81 to −0.37)	0.94	−0.5	−0.50 (−0.68 to −0.36)	0.99
Grass	1.0	1.00 (0.86 to 1.16)	0.94	1.0	1.01 (0.87 to 1.13)	0.96
Derived parameters						
p_d	0.40	0.42 (0.35 to 0.51)	0.93	0.40	0.42 (0.36 to 0.49)	0.92
p_a	0.90	0.88 (0.81 to 0.94)	0.94	0.41	0.38 (0.24 to 0.58)	0.96
N	855	854 (682 to 1048)	0.96	1913	2,478 (1,250 to 4,272)	0.98
Model fit						
Bayesian *P* value (p_d)	–	0.52 (0.44 to 0.58)	–		0.49 (0.36 to 0.58)	–
Bayesian *P* value (p_a)	–	0.52 (0.44 to 0.58)	–		0.49 (0.36 to 0.58)	–

iterations from 3 Markov chains, thinned by 1 in 50, and discarded the first 50,000–100,000 draws as burn-in. We assessed model convergence using the Gelman-Rubin potential scale reduction parameter, $\hat{R}$, where $\hat{R} = 1$ at convergence (Gelman and Rubin 1992). We accepted coefficient estimates with $\hat{R}$ between 1.0 and 1.1. Finally, for the availability and perceptibility components of the models, we used Bayesian *P* values generated from the posterior predictive distributions to assess goodness-of-fit (Gelman et al. 1996), where a *P* value close to 0.5 indicates a fitting model but a value close to 0 or 1 suggests doubtful fit (Kéry 2010:108). For each model parameter, we present the point estimate with 95% CIs.

RESULTS

Simulated Dataset

Point estimates of model parameters based on posterior summaries resembled true parameter values for all model components, and coverage ranged from 0.87 to 0.98 for the default model in which availability was high ($p_a \sim 0.9$) and perceptibility was low ($p_d \sim 0.4$) and from 0.82 to 0.98 when both availability and perceptibility were low (~0.4). Both scenarios had similar numbers of simulated detections (~300; Table 2). Although coverage was similar for the 2 simulated datasets, the precision of the abundance estimate was lower when availability was reduced, despite similar numbers of observations (Table 2 and Figure 1). To compare results from binned ($B = 5$) versus essentially unbinned distance data, we analyzed the same simulated dataset (high availability) with 300 one-meter distance classes. Exploratory analysis of unbinned data resulted in similar posterior distributions of mean p_d per points but was computationally less efficient, with ~50× greater run times needed to reach convergence (i.e. ~7 days vs. ~3.5 hr on a computer with a 3.4-GHz processor and 16 GB memory). Similarly, when we divided the data into 10 vs. 3 periods, the resulting mean p_a was similar to the baseline values but needed ~10× greater run time to reach convergence.

Field Results

For this analysis we included 536 male Golden-crowned Sparrows detected within a maximum truncation distance of 280 m and 162 ptarmigan ($n_{\text{willow}} = 92$, $n_{\text{rock}} = 70$) during 1,021 point-transect surveys in southwest Alaska. After detections were binned into 4 distance classes, detection functions appeared to be generally appropriate, with little clustering or spikes at intermediate distances. Markov chains in models reached convergence ($R_{\max} < 1.1$), and Bayesian *P* values ranged from 0.33 for ptarmigan availability to 0.67 for sparrow perceptibility, which suggests that the model adequately fit the data. Mean availability for detection during the 5-min surveys (p_a) was 0.95 (95% CI: 0.93–0.97) for sparrows and 0.64 (95% CI: 0.42–0.85) for ptarmigan. Cumulative perceptibility (p_d, i.e.

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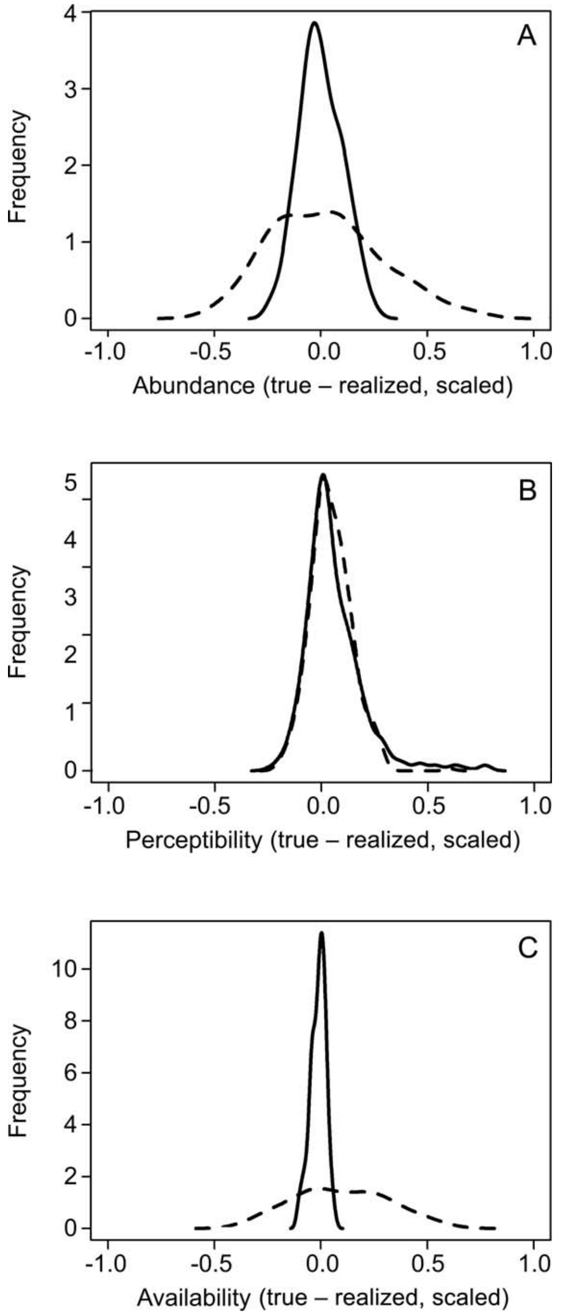

FIGURE 1. Smoothed frequency distributions of parameter estimates for (**A**) abundance, (**B**) perceptibility, and (**C**) availability under 2 scenarios of mean availability of individuals for detection during point-transect surveys: high ($p_a \sim 0.9$, solid lines) and low ($p_a \sim 0.4$, dashed lines). Parameter estimates from 500 realized datasets were centered by subtracting estimates from true simulated values (truth — realized) and scaled by dividing by the mean true value of each simulation. Scaling the estimates provides the relative uncertainty around each parameter estimate in relation to true values. For example, a value of 0.2 is equivalent to stating that the estimated value was ~20% greater than the true value. We evaluated the following 2 scenarios at 100 points, adjusting abundance to obtain similar numbers of detections under the 2 levels of availability: high availability ($\lambda \sim 5$, $y \sim 300$, $p_a \sim 0.9$, $p_d \sim 0.4$, $N \sim 900$) and low availability ($\lambda \sim 20$, $y \sim 300$, $p_a \sim 0.4$, $p_d \sim 0.4$, $N \sim 1900$) , where λ = expected abundance per point, y = number of individuals detected, p_a = availability, p_d = perceptibility, and N = total population size.

the probability of detecting an individual within the maximum truncation distance, given that it was available to be detected) was 0.39 (95% CI: 0.33–0.46) for sparrows within 280 m and 0.33 (95% CI: 0.24–0.41) for ptarmigan within 450 m; p_d within 100 m of the observer was 0.87 for sparrows and 0.93 for ptarmigan. Perceptibility was negatively influenced for sparrows by the amount of dense cover at the survey point (Figure 2B), but there was no evidence of cover effects for ptarmigan, and no suggestion of wind-speed effect or substantial difference between the 2 observer groups for either ptarmigan species (Figures 2A and 3A; Table 3). Cumulative perceptibility at mean values for wind speed and dense cover were slightly greater for observer group 1 than for group 2 for both sparrows (group 1 $p_d = 0.40$, 95% CI: 0.35–0.47; group 2 $p_d = 0.36$, 95% CI: 0.31–0.41) and ptarmigan (group 1 $p_d = 0.34$, 95% CI: 0.26–0.45; group 2 $p_d = 0.31$, 95% CI: 0.24–0.39), but CIs overlapped broadly (Table 3). Availability (p_a) of sparrows for detection decreased as the season progressed (Figure 2C), and availability of ptarmigan decreased with time of day (Figure 3B and Table 3).

For Golden-crowned Sparrows, abundance was positively associated with shrub habitat >20 cm tall and with deciduous forest and showed a quadratic relationship with elevation in Katmai and Lake Clark (Figure 2D–2F and Table 3). Abundance of both species of ptarmigan was negatively associated with mixed and coniferous forest types (Figure 4A–4D and Table 3). Both ptarmigan species showed a quadratic relationship with elevation in Katmai and Lake Clark, but this relationship held only for Rock Ptarmigan in Aniakchak. Predicted abundance peaked at lower elevations in both regions for Willow Ptarmigan than for Rock Ptarmigan (Figure 4E–4H and Table 3). The estimated zero-inflation factor z was 1.00 (95% CI: 0.99–1.00) for sparrows and 0.99 (95% CI: 0.81–1.00) for ptarmigan, which indicated that there was not an excess of true zero counts (Martin et al. 2005). Mean predicted density of individuals (ha^{-1}) across points from 2004 to 2008 was 0.117 (95% CI: 0.042–0.306) for Golden-crowned Sparrow, 0.007 (95% CI: 0.001–0.031) for Rock Ptarmigan, and 0.006 (95% CI: 0.001–0.026) for Willow Ptarmigan. For Golden-crowned Sparrows detected within $\max_d = 280$ m, mean detection distance increased by ~40 m from the first to the third period ($F = 4.50$, df = 2 and 534, $P < 0.001$), violating the assumption of independence between p_d and p_a. When we reran the models with $\max_d = 200$ m, within which detection distance was independent of time

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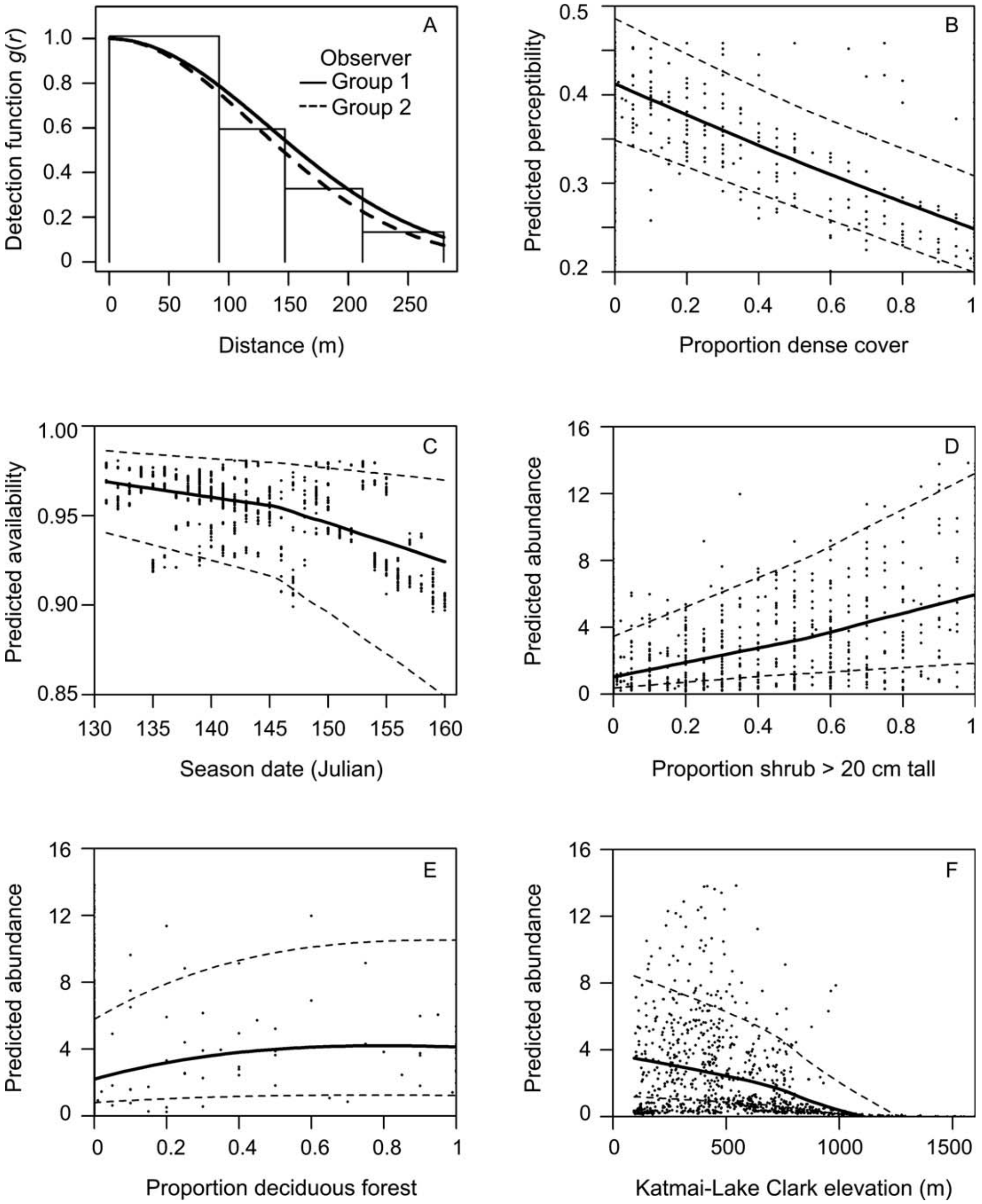

FIGURE 2. Modeled relationships between covariates and (**A–C**) components of detection probability and (**D–E**) predicted abundance per point for Golden-crowned Sparrows observed during 1,021 point-transect surveys in 3 national parks in southwest Alaska. (**A**) Fitted detection functions for observer group 1 (solid line) and observer group 2 (dashed line) in relation to frequencies of observations in each distance bin scaled by detection distance. (**B**) Perceptibility, given availability for detection (p_d), declined with proportion of dense habitat cover (closed tall shrub and forest) at a point and averaged 0.39 (95% credible interval [CI]: 0.33–0.46) within a 280-m radius of the observer. (**C**) Availability for detection, given presence at a point, (p_a), averaged 0.95 (95% CI: 0.93–0.97) during the 5-min surveys and declined with season date (Julian date within year; $\bar{x} = 144$; May 14). Predicted abundance per point within a 280-m radius ($\sim$25 ha) averaged 2.9 adults (95% CI: 1.0–7.5) and (**D**) increased with the proportion of shrub $>$ 20 cm tall and (**E**) deciduous forest within a 50-m or 150-m buffer around each point and (**F**) decreased with elevation in Katmai and Lake Clark. We provide predicted values per point (points) and loess-smoothed trends (solid lines) with 95% CIs (dashed lines).

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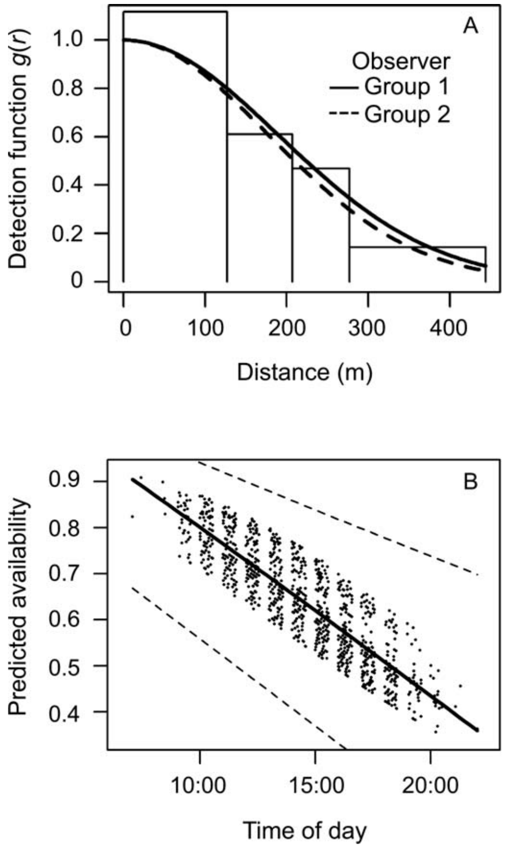

FIGURE 3. Modeled relationships between covariates and components of detection probability for Willow and Rock ptarmigan (combined) observed during 1,021 point-transect surveys in 3 national parks in southwest Alaska. (**A**) Fitted detection functions for observer group 1 (solid line) and observer group 2 (dashed line) in relation to frequencies of observations in each distance bin scaled by detection distance. (**B**) Availability of ptarmigan for detection, given presence at a point, (p_a), averaged 0.64 (95% credible interval [CI]: 0.43–0.85) during the 5-min surveys and declined with time of day of the survey ($\bar{x} = 11{:}15$ Alaska Daylight Time). Mean perceptibility of ptarmigan, given availability for detection, (p_d), was 0.34 (95% CI: 0.24–0.39) within a 450-m radius of the observer; CIs of all modeled covariates for perceptibility contained zero.

($F = 1.06$, df $= 2$ and 443, $P = 0.29$), we obtained a similar but less precise estimate of density (mean $= 0.121$, 95% CI: 0.023–0.324).

DISCUSSION

Imperfect detection of birds during surveys, whether due to birds' failure to give cues during the allotted time or to observers' failure to perceive them, has long hampered count-based efforts aimed at estimating population size and distribution. Here, we have combined a time-removal protocol with distance sampling in a highly flexible hierarchical model for inference about abundance that simultaneously accounts for both components of detection probability—availability and perceptibility—for point-transect surveys. Importantly, our model can be used to predict abundance in nonsurveyed areas within a sampling frame, based on the relationship between count data and spatially indexed environmental covariates, to produce distribution maps and estimates of regional or total population size (cf. Barker et al. 2014).

Our model builds on the seminal work of others but has several characteristics not found in earlier models (Table 1). Farnsworth et al.'s (2005) combined distance-sampling and time-removal model allowed for the estimation of both availability and perceptibility components of detection probability during a single point count. Our model extends that framework to (1) allow for inclusion of covariates on detection probability, (2) explicitly incorporate spatial replication of counts (i.e. providing point-specific estimates of p_d), and (3) link estimates of detection probability to abundance. Burnham et al. (2004) outlined a full-likelihood approach that combined the time-removal model with distance sampling, but our model provides point-specific estimates of detection probability. Royle et al.'s (2004) model extended the hierarchical *N*-mixture model of Royle (2004) by incorporating spatially replicated observation and process components for data collected using distance sampling to estimate perceptibility. Sillett et al. (2012) further expanded functionality to include covariates on perceptibility. Our model extends both frameworks even further to model point-transect data and incorporate a method to address availability. Etterson et al. (2009) incorporated time-removal protocols into a hierarchical *N*-mixture model to account for availability bias, but the model was unable to separate availability from perceptibility, which is typically the larger source of detection bias in avian point counts (Nichols et al. 2009). Most recently, Sólymos et al. (2013) developed a combined time-removal and distance-sampling model to estimate singing rate and perceptibility. Our approach is similar but integrates density estimation into the likelihood, whereas Sólymos et al. (2013) relied on an offset approach to estimate density.

Bayesian analysis using Markov chain Monte Carlo has advantages over maximum-likelihood approaches used in previous models that include random effects and overdispersion parameters (Fiske and Chandler 2011). A Bayesian framework lends substantially increased flexibility to the modeling capabilities, for instance, to estimate spatially explicit density while accommodating extra-Poisson dispersion, include covariates for all levels of the model, and incorporate a nested data structure to account for points being clustered along transects. Furthermore, a Bayesian framework facilitates extensions to accommodate counts repeated through time to estimate population trends (Etterson et al. 2009, Sauer and Link 2011) or

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TABLE 3. Mean coefficients and derived parameters with 95% credible intervals (CIs) from posterior distributions of Bayesian hierarchical models that estimated breeding densities of Golden-crowned Sparrows and Rock and Willow ptarmigan in 3 national parks in southwest Alaska. Observers counted birds during 1,021 point-transect surveys from 2004 to 2008. We divided observers into 2 groups (Obs1 and Obs2) by ability and provide scale parameters on detection (σ) for each group. We report perceptibility (p_{d}) and availability (p_{a}) of birds detected as well as a zero-inflation parameter (z), and Bayesian P values for the 2 components of detection probability (i.e. measure of goodness-of-fit). Bold denotes covariates with 95% CIs that do not contain zero (i.e. a measure of significance). See text for description of covariates.

	Golden-crowned Sparrow	Ptarmigan species combined	
Perceptibility			
Obs1 σ	**133.49 (121.58 to 148.13)**	**190.02 (163.46 to 230.07)**	
Obs2 σ	**122.87 (112.42 to 134.89)**	**178.06 (155.54 to 206.56)**	
Wind speed	−0.04 (−0.10 to 0.02)	−0.07 (−0.17 to 0.02)	
Dense cover	**−0.11 (−0.16 to −0.07)**	−0.06 (−0.17 to 0.07)	
Availability			
Intercept	**0.66 (0.41 to 0.89)**	**−0.88 (−1.54 to −0.30)**	
Season date	**−0.23 (−0.43 to −0.03)**	0.21 (−0.34 to 0.73)	
Time of day	−0.01 (−0.26 to 0.22)	**−0.36 (−0.66 to −0.06)**	
Abundance		Willow Ptarmigan	Rock Ptarmigan
Transect	0.09 (−0.17 to 0.33)	**−5.46 (−10.18 to −3.07)**	**−6.15 (−8.55 to −3.84)**
Shrub	**0.65 (0.31 to 1.03)**	−0.05 (−0.77 to 0.81)	0.16 (−0.58 to 1.00)
Dshrubherb	0.20 (−0.14 to 0.57)	−0.08 (−0.76 to 0.73)	0.09 (−0.52 to 0.82)
Dec	**0.23 (0.04 to 0.43)**	−0.68 (−1.77 to 0.14)	−5.61 (−11.59 to 0.05)
Mixed	−0.16 (−0.46 to 0.15)	**−6.60 (−15.49 to −1.62)**	**−4.07 (−12.31 to −0.10)**
Spruce	−0.07 (−0.38 to 0.25)	**−7.28 (−15.88 to −0.93)**	**−4.96 (−11.43 to −0.03)**
Baresnow	0.08 (−0.29 to 0.47)	−0.39 (−1.17 to 0.48)	0.12 (−0.58 to 0.94)
Wetland	−0.01 (−0.20 to 0.18)	0.03 (−0.32 to 0.39)	−0.92 (−2.59 to 0.31)
Water	0.03 (−0.09 to 0.15)	−0.51 (−1.44 to 0.08)	−0.23 (−0.92 to 0.21)
Slope	0.02 (−0.10 to 0.13)	0.07 (−0.19 to 0.33)	−0.10 (−0.42 to 0.19)
Elevation (Aniakchak)	1.50 (−0.19 to 3.24)	−1.22 (−5.11 to 2.47)	**−5.75 (−10.43 to −1.40)**
Elevation (Katmai and Lake Clark)	−0.25 (−0.49 to 0.01)	0.14 (−0.66 to 0.95)	**2.37 (1.10 to 3.83)**
Elevation^2 (Aniakchak)	0.79 (−0.40 to 2.00)	−0.85 (−3.57 to 1.68)	**−5.42 (−9.97 to −1.73)**
Elevation^2 (Katmai and Lake Clark)	**−0.45 (−0.69 to −0.23)**	**−1.64 (−2.76 to −0.72)**	**−1.41 (−2.30 to −0.63)**
Derived parameters		Combined	
p_{d}	0.39 (0.33 to 0.46)	0.33 (0.24 to 0.39)	
p_{a}	0.95 (0.91 to 0.98)	0.64 (0.42 to 0.85)	
		Willow Ptarmigan	Rock Ptarmigan
z	1.00 (0.99 to 1.00)	1.00 (0.81 to 1.00)	1.00 (0.93 to 1.00)
Model fit		Willow Ptarmigan	Rock Ptarmigan
Bayesian P value (p_{d})	0.67	0.37	0.40
Bayesian P value (p_{a})	0.41	0.29	0.33

population dynamics (e.g., recruitment; Dail and Madsen 2011); alternative mixture distributions for abundance (e.g., negative binomial); line-transect surveys (e.g., Hedley and Buckland 2004); dependence between availability and perceptibility (Alldredge et al. 2007c); covariates on the zero-inflation parameter (Joseph et al. 2009); and community modeling (Mattsson et al. 2013).

Heterogeneity in Detection Probability

Importantly, our analytical approach allows one to model heterogeneity in both components of detection probability. Latent heterogeneity in capture probability has long been recognized as an important factor to consider when estimating the size of a closed population so as to minimize bias (e.g., Burnham and Overton 1978, Norris and Pollock 1996). For breeding songbirds, models that incorporate heterogeneity in availability for detection have been invariably supported over those that do not (Farnsworth et al. 2002, Alldredge et al. 2007a, Reidy et al. 2011). Our empirical example confirmed these findings, in that we found significant support for a declining detection probability as the season progressed (most likely due to less frequent singing). The ability to model point-level covariates directly, such as date and time of day of the survey, facilitates less biased estimates of abundance at the point level.

Our simulations and ptarmigan examples suggest that although density estimates are likely unbiased, precision is greatly reduced when mean availability for detection is low ($p_{\mathrm{a}} \sim 0.4$) compared to high ($p_{\mathrm{a}} \sim 0.9$), primarily because of the greater uncertainty in estimating the lower p_{a} even with similar numbers of detections. Low availability resulted in imprecise estimates, even with a robust sample size in the simulated dataset (i.e. $n \sim 300$). Thus, we

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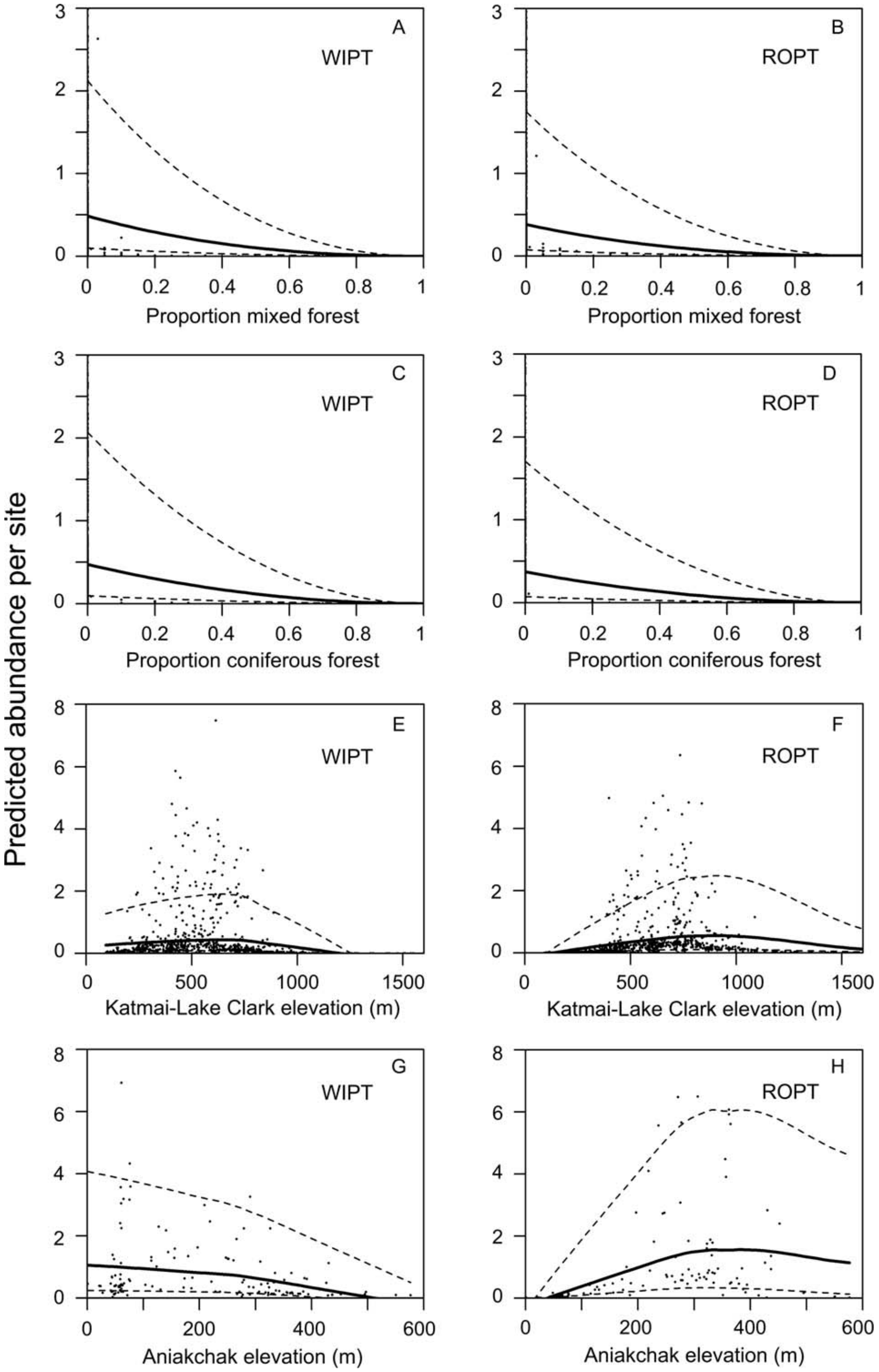

FIGURE 4. Modeled relationships between covariates and predicted abundance per point for Willow Ptarmigan (WIPT) and Rock Ptarmigan (ROPT) observed during 1,021 point-transect surveys in 3 national parks in southwest Alaska. Mean abundance per 64-ha point (450-m radius) was 0.35 adults (95% credible interval [CI]: 0.07–1.58) for Willow Ptarmigan and 0.44 adults (95% CI: 0.09–1.92) for Rock Ptarmigan. Across all parks, abundance of both species declined with the proportion of (**A–B**) mixed forest and (**C–D**) coniferous forest within a 50-m or 150-m buffer around each point. Abundance of the 2 species differed in relation to elevation in (**E–F**) Katmai and Lake Clark versus (**G–H**) Aniakchak, but in both areas Rock Ptarmigan occurred at higher elevations than Willow Ptarmigan. We provide predicted values per point (points) and loess-smoothed trends (solid lines) with 95% CIs (dashed lines).

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caution against designing studies to sample during periods when detection rates are expected to be low (e.g., low rates of singing for auditory surveys). For multispecies surveys for songbirds, for example, one should focus efforts during morning periods and examine pilot data to determine the tradeoffs for different species from sampling during different seasonal periods. Furthermore, simulation studies similar to ours could be used to determine the sampling effort needed (e.g., spatial replicates or total observations) to obtain desired precision for species with inherently low availability (e.g., those detected primarily through visual observations).

Farnsworth et al. (2005) stressed that an estimate of area sampled during a point count is necessary for accurate estimates of density or abundance. Unless either perceptibility or the effective area sampled is known to be constant, a measure of the area sampled (or perceptibility within the survey area) is necessary for unbiased inferences about relative abundance of different species within an area, of a species across habitats, or of a species across time (Buckland et al. 2001:299). Our model accounts for heterogeneity in perceptibility by estimating distance to each observation—arguably the largest source of individual heterogeneity in perceptibility (Burnham et al. 2004, Simons et al. 2009)—and modeling the rate at which perceptibility declines explicitly as a function of distance. Our estimates of perceptibility for the Golden-crowned Sparrow, which gives a loud, clearly whistled song (Norment et al. 1998), indicate that densities in our study area would have been underestimated by 55% within a radius of 280 m and 13% within 100 m if we had not corrected estimates for distance from the observer.

For typical songbird point counts, ignoring distance-related heterogeneity or accounting for it only as a covariate in time-removal or capture–recapture (multiple-observer) models will generally result in estimates of density with a large negative bias, even if counts are restricted to a small (e.g., 50-m) radius (Kissling and Garton 2006, Efford and Dawson 2009, Sólymos et al. 2013). Such bias arises because unmodeled heterogeneity increases with distance, because only the more detectable birds are detected as distance increases, which inflates estimates of detection probability associated with the perception process (Laake et al. 2011). Furthermore, an implicit assumption of multiple-observer methods is that the same group of birds is available for detection by all observers, which will not hold true if one observer can detect birds at greater distances than other observers (Nichols et al. 2000). Restricting counts to a smaller fixed radius may satisfy this assumption (Nichols et al. 2000) but will sacrifice observations, result in a loss of precision in estimates, and still not resolve the problem of variation in effective area sampled due to spatial heterogeneity in perceptibility.

Model Assumptions

Although incorporating the time-removal component in our model allowed us to relax the assumption in conventional distance sampling that the probability of detection at the point is perfect, care should be taken to meet the other primary assumptions: (1) Points are placed randomly with respect to bird distribution; (2) birds are detected at their initial location prior to any movement; (3) birds are identified without error (e.g., with respect to species and without double counting at a point); (4) distances are measured accurately or observations are recorded in the appropriate distance classes; (5) p_a and p_d are independent; (6) the population is closed during surveys to births, deaths, immigration, and emigration; and (7) the entire breeding population is present at the study areas. Assumption 1 can be met through proper study design, such as the stratified random design of our field example, which will ensure that birds are distributed independently of the point locations. Assumptions 2–3 can be problematic if count duration is too long, such that undetected movement occurs (Rosenstock et al. 2002). Simons et al. (2009) suggested that among trained observers, double counting may be a more significant source of bias than misidentification of some species. Point-transect sampling is considered a "snapshot" method in which the observer estimates the number of birds present at a single instant, and even random movement can cause a positive bias in density estimates (Buckland 2006). Duration of the count should thus be long enough to estimate availability but short enough to minimize undetected movement. Thus, surveys should be timed to coincide with periods of optimal cue production (e.g., diurnally and seasonally). Additionally, movement toward or away from observers is likely more prevalent at the beginning of surveys, and Ralph et al. (1995) recommended an acclimation period before beginning point counts. Surveys in open habitats, such as in our study area, are less likely to violate the assumption of undetected movement than those in closed habitats. If the observer is being swamped during multispecies surveys by large numbers of individuals, species can be subdivided into groups and recorded in a series of consecutive surveys to ensure accurate counts (Buckland 2006).

Meeting assumption 4 of accurate estimation of distances is less problematic in open habitats, including our field example, than in forested habitats, where distances to auditory detections can be difficult to determine correctly (e.g., Alldredge et al. 2007b, Simons et al. 2009). In open habitats, observers can use laser rangefinders and visual cues, such as location of shrub clusters, to determine the accurate locations of singing but visually hidden passerines. Experimental studies of broadcast vocalizations in forested habitat with dense understory revealed that errors in distance estimation were particu-

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larly pronounced at distances of ~75 m and when songs were played away from instead of toward observers; training in distance estimation reduced but did not eliminate errors (Alldredge et al. 2007b). When analyzing songbird point-transect counts from a variety of habitats in interior Alaska, Hoekman and Lindberg (2012) found problematic deficits or surpluses of detections near the observer and peaks in detections at intermediate distances (30–60 m), particularly for thrushes (Turdidae); the authors attributed these patterns as most likely due to errors in distance estimation, undetected movement, or both. Pooling observations into broad distance classes, especially near the observer, reduced poor fit of observations to the detection function for some species but resulted in high uncertainty in density estimates (Hoekman and Lindberg 2012).

In our field example, we selected cutoff points to reduce heaping within distance bins, minimize bias near the observer, and facilitate smooth detection functions (Buckland et al. 2001), and we recommend that studies implementing our model also take similar steps to maximize fit of the data to the detection function. We further stress the importance of minimizing errors in distance estimation by using laser rangefinders and training programs for the array of species and habitats encountered within each study area (Rosenstock et al. 2002). Although we did not measure such errors in our field study, we recognize the importance of doing so (Alldredge et al. 2007b, Simons et al. 2009), particularly if detections are almost exclusively auditory, with no assistance from visual cues. Maximum-likelihood methods have been developed to use such auxiliary data (paired true and estimated distances) to correct for bias in density estimates that may result from additive or multiplicative errors in distance estimation (Borchers et al. 2010); we suggest that our model can be usefully extended to do so in a Bayesian framework.

Assumption 5, which requires that the 2 components of detection probability be independent, could be violated if both were influenced by the same factor or if both were functions of distance from the observer or time from the start of the survey period. For example, adverse weather may reduce not only the birds' singing rates but also the perceptibility of their songs to the observer. Concentrating initial efforts on detecting individuals nearest to the observer in an attempt to ensure that $p(0) \sim 1$ may result in distant birds being more likely to be detected during the later time intervals. Similarly, availability and perceptibility may differ within a species depending on the type of cue (visual or auditory) given, which may induce heterogeneity in detection probability that is difficult to model jointly (cf. Marques et al. 2007). For example, for more visible species that provide infrequent auditory cues, individuals close to the observer may be more likely to be detected during initial periods, whereas those farther away, obscured by vegetation, may be more likely than observed individuals to be detected during later periods. For secretive species, individuals close to the observer may alter their singing rate, thereby affecting availability in relation to distance. Other studies of multiple species across broad regions (Handel et al. 2009, Matsuoka et al. 2012, Sólymos et al. 2013) have found that confounding of estimates of p_a and p_d from removal models and distance sampling, respectively, was minimal and that marginal estimation of these parameters was therefore justified. Results from our field example corroborate these findings, in that density estimates for Golden-crowned Sparrow did not differ when data were restricted to a significantly smaller radius within which distance and time intervals were independent. This assumption should be tested for each species and, if necessary, observations should be truncated to an appropriate radius, detection probability should be modeled by type of cue (Marques et al. 2007), surveys should be short in duration and include an acclimation period to minimize effects on availability of individuals close to the observer (Ralph et al. 1995), or the 2 components should be estimated jointly (Burnham et al. 2004).

Single surveys of short duration, such as those employed in our field study, will satisfy the sixth assumption of population closure. Models that employ repeated visits to points across a season for estimating abundance (e.g., Kéry et al. 2005, Royle et al. 2007, Schmidt et al. 2013) will generally violate this assumption because temporary immigration or emigration can occur between visits. Thus, the closure assumption will apply to the territory rather than the bird, and such models will estimate the "superpopulation" of home ranges that overlap the sampling area, rather than the breeding densities estimated by our model. The superpopulation of home ranges exposed to sampling will depend on how mobile the birds are and may vary with density, such that comparisons of estimates should be evaluated carefully (Nichols et al. 2009). Furthermore, if floaters (i.e. nonbreeding individuals) occur in the population, they may move longer distances and be present at multiple survey points across repeated surveys, which could lead to overestimating population size from double counting individuals and underestimating detection probability (Oppel et al. 2014). For most breeding migratory songbirds, the proportion of the population present in an area increases in the spring as birds begin establishing territories on the breeding grounds, approaches an asymptote of 1 during incubation and brood rearing, and then decreases as failed and successful breeders depart for wintering grounds. If surveys are not conducted during peak breeding, our seventh and final assumption that the entire population is present in an area during surveys could be violated, thus biasing relative abundance estimates low. Multispecies

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surveys are vulnerable to violating this assumption because timing of breeding varies among species of sympatrically nesting birds. Birds breeding at higher latitudes and elevations typically have a more abbreviated nesting season (e.g., Slagsvold 1977, Spottiswoode and Møller 2004, Bears et al. 2009), which generally results in greater breeding synchrony both within and among species (Best 1981). Although breeding seasons of many species within a community may overlap considerably, those of others may be almost mutually exclusive (Slagsvold 1977, Best 1981). If the entire population of a given species is not present at the time of a multispecies survey, we suggest limiting inference from this model to those that are fully engaged in breeding activities during the time of the survey or exploring alternative models that allow explicit estimation of p_{p} (e.g., repeat surveys; Nichols et al. 2009).

Practical Application

Methods to adjust raw counts for incomplete detection of individuals rely on assumptions and, thus, still result in indices of population size, though the adjusted estimates should approximate the true population size of interest better than the raw counts would alone (Johnson 2008). Such methods to estimate detection probability may increase costs of monitoring programs (e.g., by requiring repeated surveys or multiple observers) or have unrealistic assumptions, and complex models such as the one presented here may be prohibitive for managers to implement without consultation with a statistician or quantitative ecologist. The benefit, then, of using our model may depend on study objectives and available funding.

Studies focused on examining geographic or temporal variation in population size, mapping species distributions, or exploring mechanisms that underlie imperfect detection of animals will benefit from modeling detection probability using spatially or temporally varying covariates. For example, our model for Golden-crowned Sparrows in southwest Alaska indicated that abundance was positively associated with tall shrubs and deciduous forest at relatively low elevations in upland areas, which is consistent with their predominant distribution at or above tree line in forest–tundra ecotones elsewhere in the state (Kessel and Gibson 1978, Kessel 1989, Petersen et al. 1991). If we had not accounted for either component of detection probability, our model suggests that densities would have been underestimated by an average of 63% and that predicted distributions would have been biased in relation to habitat type because perceptibility decreased with increasing dense cover, with implications for species-specific habitat management. Similarly, not accounting for significant temporal effects on singing rates would have resulted in spatially biased estimates of density because sampling order was not random with respect to time (i.e. survey order was geographically clustered for efficiency in time and cost). Furthermore, the model presented here can provide unbiased, reasonable estimates of model components for observation (i.e. detection probability) and process (i.e. abundance) using data collected by a single observer during a single survey, thus reducing survey cost and effort and better approximating a "snapshot" of abundance in space and time. The combined time-of-detection, distance-sampling method also shares these characteristics but requires tracking individual birds throughout the survey period (Alldredge et al. 2007a), which may not be feasible in areas with high bird densities or for multispecies surveys.

Studies focused on uncommon species or that violate model assumptions may not be appropriate for use with our model. Among some other species in our study, models that had a marginal number of detections (i.e. <75; Buckland et al. 2001) converged and produced reasonable estimates of detection probability and density but, upon closer examination, revealed potential problems such as non-normal posterior distributions and possibly spurious covariate relationships. Additionally, like all model-based estimates, unbiased inference is dependent on adherence to model assumptions, which may be violated under some sampling designs or for certain species. In these cases, unadjusted indices of abundance may produce similar conclusions and management decisions if objectives require only estimates pooled across space and time and population trends are strong (Thompson and La Sorte 2008), or if variance in detection probability is substantially smaller than the variance in population size to be detected and detection probability and population size are independent (Johnson 2008).

Our model can improve understanding of avian populations by (1) reducing bias associated with imperfect detection probability and spatial variability that may lead to inaccurate inferences regarding population size or distribution and (2) increasing our understanding of the processes associated with abundance and detection probability through examination of relevant covariates. If assumptions can be met and sampling design is appropriate, our model can be used to produce predictive landscape-level maps of distribution and abundance that can be useful for both management and conservation. Thus, broad-scale programs to model abundance of birds should not only use rigorous study design and implementation to minimize bias in population-level estimates, but also include methods to estimate survey-specific detection probabilities if objectives include point- or time-specific inferences.

In sum, we propose a novel extension to 2 existing models to estimate detection probability and abundance from spatially replicated surveys. Minimal additional effort by an observer during a single survey can provide a wealth

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of additional information regarding the detection process and mechanisms underlying species abundance. Our model can assist land managers, hindered by logistical and financial constraints on research and monitoring, in obtaining unbiased estimates of population density while minimizing costs. Furthermore, implementation of our model in a Bayesian framework greatly increases flexibility over maximum-likelihood methods (e.g., by allowing random effects at multiple hierarchical levels) while accounting for important but often overlooked sources of heterogeneity in detection probability.

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