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Accounting for incomplete detection: What are we estimating and how might it affect long-term passerine monitoring programs?

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ABSTRACT

A primary objective of ecological monitoring programs typically includes the efficient detection of population trends. Passerines as a group are important ecological indicators and are often included in such programs to provide information on multiple species with a single survey technique. However, commonly used field and analytical approaches may not provide appropriate inference or sensitivity due to assumption violations and differences in the proportion of the population exposed to sampling. Recent methodological developments utilizing repeated point counts and an N-mixture modeling approach for analysis may produce more consistent and interpretable estimates applicable to the superpopulation of individuals using a site during the breeding season. These estimates should be more useful for monitoring because they are not conditioned on presence or availability as are most single-visit approaches. We used repeated count data collected in Denali National Park and Preserve, Alaska (Denali) between 1995 and 2009 from 12 common passerine species to assess variation in presence and availability throughout the season, estimate trends in superpopulation abundance, and provide recommendations for the design of future monitoring programs. We found that variation in detection due to presence and availability was large and differed among species. After accounting for these sources of variation, we estimated abundance of Wilson's warblers (*Wilsonia pusilla*) had declined by approximately 48% and fox sparrow (*Passerella iliaca*) abundance had increased by approximately 250% over 15 years. Combined, our results suggest that if trend estimation is a priority, passerine monitoring programs should formally address all components of the detection process, including the probabilities of presence and availability.

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1. Introduction

While valuable and necessary for conservation, many long-term monitoring programs have suffered from poor planning and study design (Lindenmayer and Likens, 2009, 2010; Reynolds et al., 2011; Thompson et al., 2011). Lack of detailed thought and direction during the design phase of a monitoring program can prevent proper inference for the population or system of interest and limit utility for management (Nichols and Williams, 2006). Similarly, improper or incomplete understanding of the type of inference that can be made based on the field sampling methods and associated analyses can further reduce the utility of monitoring data, potentially leading to erroneous conclusions or delays in appropriate conservation decisions. The development of suitable monitoring schemes for passerine birds, and the problem of incomplete detection have received much attention in the scientific literature in recent years (e.g., Alldredge et al., 2007a; Farnsworth et al., 2002, 2005; Nichols et al., 2009; Rosenstock et al., 2002), but uncertainty in the appropriate direction for long-term passerine monitoring programs remains.

The comparability of estimates of detection probability (p) and abundance based on different field methods is largely dependent on those components of the detection process addressed by each method and the validity of the assumptions made regarding those remaining. A recent methodological review by Nichols et al. (2009) identified 4 primary components of p: (1) the probability that the bird's home range includes at least a portion of the sampling unit, p_s, (2) the probability that the bird is present within the sample unit during the survey period, p_p, (3) the probability that the bird is available for detection during the sampling event, p_a, and (4) the probability that a bird is detected given that it is present and available, p_d. The first, p_s, was identified as a part of all detection methods that is generally dealt with through study design. The remaining three components must be addressed explicitly, or one must assume that the unaddressed components of p do not vary across time and space, otherwise inference will apply to an undefined segment of the population. These assumptions may not be reasonable in many situations and can lead to large differences

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in inference and conclusions. In addition, because each of the most commonly applied field techniques addresses different components of incomplete detection, the definition of the 'population' to which the resulting abundance estimates apply varies. This limits meaningful comparisons of estimates based on different field methods, and leads to further confusion regarding which 'population' is being monitored.

Unadjusted point counts are one of the most commonly used field sampling approaches for long-term monitoring of passerine populations in North America (e.g., Peterjohn, 1994; Ralph et al., 1995; Rosenstock et al., 2002; Sauer et al., 2003) and were generally developed with the broad goal of identifying and assessing changes in the abundance of breeding passerines at large scales (e.g., Hutto, 1998; Peterjohn, 1994). These methods implicitly assume that p_p, p_a, and p_d vary little (or not at all) relative to population trends (Anderson, 2001; Nichols et al., 2009; Ralph et al., 1995; Rosenstock et al., 2002). The raw counts are treated as an index of abundance across space and time (Johnson, 2008) and are used to assess population trajectory (e.g., Ralph et al., 1995). Despite widespread use, these index surveys often violate the assumption of a relatively constant p (Burnham, 1981; Farnsworth et al., 2002; Thompson, 2002; Wilson and Bart, 1985), and a reliance on standardization to meet the assumptions of constant p is unreasonable in most circumstances. Unexplained variation in p can produce biased estimates of abundance and trends (Kéry et al., 2005; Pollock et al., 2002) and can reduce efficiency in estimating population change (Sauer et al., 2003). The inclusion of covariates related to systematic changes in detection components through the use of Bayesian hierarchical models has been shown to reduce bias for large-scale passerine monitoring programs based on simple point count data (Link and Sauer, 1997, 1998, 2002). However, this approach cannot account for covariates such as succession or arrival timing that may also be associated with trends in abundance (Nichols et al., 2009). This approach may likewise be less efficient than methods directly addressing components of p, particularly for programs at local-scales. This emphasizes the need for appropriate data collection and statistical model use to avoid unnecessary and unsupportable assumptions about perfect or homogeneous detection (Conroy et al., 2011).

Distance-sampling and associated analytical tools (Burnham et al., 1980, Buckland et al., 2001) have commonly been applied to passerine bird monitoring programs in an effort to solve problems related to incomplete detection (Buckland, 2006; Marques et al., 2007; Rosenstock et al., 2002), by directly addressing p_d and thereby improving estimates of abundance. However, distance sampling surveys based primarily on auditory cues often violate the basic assumptions of the approach and produce unreliable estimates of abundance (Alldredge et al., 2007b; Bachler and Liechti, 2007; Efford and Dawson, 2009; Simons et al., 2009). Double observer methods (Alldredge et al., 2008; Nichols et al., 2000) also address p_d with fewer unmet assumptions, but if only conducted once per season at each site, either method confounds variation in p_p and p_a with variation in abundance. Time of detection methods (Alldredge et al., 2007a, 2007c; Farnsworth et al., 2002) estimate both p_d and p_a, but do not address p_p. Each of these approaches, while providing a defensible estimate of some components of p, must make tenuous assumptions regarding the remaining elements. It is highly likely that p_p and p_a change temporally (e.g., hourly, daily, annually), suggesting that estimates of abundance based on a sampling approach that does not directly address these detection components will be biased by an unknown amount. The risk of bias has obvious implications for long-term monitoring programs, although recent developments in field and analytical methods suggest a potential solution.

Kéry et al. (2005) recently demonstrated that temporally repeated counts could be useful as an alternative field sampling technique for passerines that included the estimation of p_p as part of the overall p. Counts were repeated over multiple days during a relatively short portion of the breeding season, and the series of counts was then analyzed using hierarchical N-mixture models (Kéry, 2008; Royle, 2004). This approach is a direct extension of the methods developed for occupancy estimation (MacKenzie et al., 2006; Royle and Nichols, 2003), and the use of zero-inflated Poisson (ZIP) mixtures can improve fit when individuals are not detected at a large proportion of sampling points (Joseph et al., 2009; Martin et al., 2005; Wenger and Freeman, 2008). One of the primary advantages of these methods is that p_d, p_a, and p_p are all included in the composite estimate of p when sampling is conducted over multiple days throughout the breeding season. The resulting abundance estimates are analogous to "use" in an occupancy framework (MacKenzie et al., 2006; Mordecai et al., 2011) and represent the "superpopulation" of territories used during the season that intersect the sampled space at each sampling location. However, because the area sampled is undefined, superpopulation abundance cannot generally be expressed as density. This is very similar to the definition of the superpopulation used in the capture–recapture literature (Kendall et al., 1997; Nichols et al., 2009; Schwarz and Arnason, 1996; Williams et al., 2002).

The primary advantage to using the superpopulation for inference is that it represents the total breeding population using a site during the season and is not conditioned on presence or availability across time and space for appropriate inference. Patterns in migratory arrival differ among species, and both p_p and p_a are likely to increase to a peak and then decline in differing patterns among species throughout the breeding period. The breadth of this peak may also vary among species with some having high p_p and p_a for a longer periods. Similarly, the timing of peak vocalization likely varies among species. Some species sing primarily early in the morning and become nearly silent later in the day, while others may be more likely to vocalize mid-morning or even sing at a rather consistent rate throughout the day. This suggests that the date and time of any given survey is unlikely to be optimal for all species, and without addressing p_p and p_a directly, it becomes difficult to identify to which population or portion of the population the abundance estimates apply. Monitoring programs are often intended to continue for decades, and the likelihood of p_p and p_a remaining relatively constant through time is low. In addition, if trends in peak arrival or breeding periods were to occur, trends in abundance based on single visit surveys would likely be highly dependent on untestable assumptions about annual variation in survey timing, conditions, and migratory arrival patterns. The subsequent reduction in power would result in longer time periods necessary to detect population trends, increased potential for detecting false trends, and decreased efficacy of passerine conservation programs in general.

Efforts to estimate abundance and identify trends in a suite of passerine birds in Denali National Park and Preserve (Denali) have been underway since 1992 as part of the National Park Service's (NPS) long-term ecological monitoring program. More recently, the passerine monitoring work in Denali was included in the Central Alaska Monitoring Network's program (MacCluskie et al., 2005) as part of the national NPS Inventory and Monitoring effort (Fancy et al., 2009). Past passerine monitoring efforts in Denali consisted of unadjusted point counts and distance sampling surveys but were determined to be unlikely to meet objectives due to identified assumption violations (see Alldredge et al., 2007b; Hoekman and Lindberg, 2012). We used repeated count data collected in Denali between 1995 and 2009 to demonstrate the potential inferential and logistical advantages of repeated point count methods for long-term passerine monitoring programs. Our primary objectives were to: (1) assess the magnitude of temporal variation in p for the most common species in Denali, (2) assess trends

in superpopulation abundance for the most common species, and (3) provide recommendations for the design and implementation of future multi-species passerine monitoring programs.

2. Methods

We conducted repeated roadside surveys along the first 118 km of the 144-km Denali park road in the northern foothills of the Alaska Range in the northeastern portion of Denali (63°35.8′N, 149°38.2′W). This narrow, two-lane road is paved for the first 24 km and is the only road located within the park. The road bisects many of the main habitat types found in the northeastern portion of Denali. Surveys generally followed North American Breeding Bird Survey (BBS) methodology (Peterjohn, 1994) and included 3 roadside routes of 50 points each at 0.8 km spacing. Standard 3-min point counts were conducted at each point multiple times annually. During each count all birds seen or heard within ~400 m were recorded (Peterjohn, 1994), although only records of singing males were used for analysis. We standardized surveys by generally starting each survey 0.5 h before sunrise, finishing each survey within ~6 h, and surveying only one route/day/observer. Surveys were conducted from late-April to early-July by trained observers, and each route was surveyed at least twice in each year it was included in the analyses. Up to three observers conducted surveys each year, but the same routes were not always surveyed by the same individual. Surveys were conducted on days with good visibility, little or no precipitation, and when wind speed was <13 kph. Repeated counts were conducted during six years (1995, 1996, 1997, 1998, 2006, and 2009), and the number of repeated counts on each route varied (Table 1). During a year when a route was sampled, revisits to each route were separated by 2–21 d. We assigned one dominant habitat type to each point including needle-leaf forest, mixed forest, tall scrub, low scrub, and bare ground based on Viereck's vegetation classification scheme for Alaska (Viereck et al., 1992).

2.1. Model assumptions

For data collected using repeated counts and analyzed using ZIP mixture models, there are several assumptions that must be met or addressed to assure proper inference, including: (1) population closure, (2) constant probability of detecting an individual over survey occasions, (3) detection probabilities are the same among individuals of the same species, and (4) individuals are not double counted during a survey. If population closure is not maintained, estimates of abundance will be biased high, although covariates such as survey date may be included to relax this assumption (Weir et al., 2005). The assumption of constant detection among occasions may also be relaxed through the use of appropriate covariates (e.g., time of day, observer). The third assumption applies to all commonly used survey methods and may be relaxed using mixture distributions (Williams et al., 2002; Nichols et al., 2009; Pledger et al., 2010). The final assumption can usually be met by conducting counts over a short duration to minimize movement of individuals and potential errors. Violation of these assumptions can result in biased estimates of detection probability, presence, and abundance; therefore, we included random effects and several covariates expected to account for a majority of the expected variation in detection, presence, and abundance for each species and addressing the first three assumptions. We used a short (3 min) count period to reduce the chances of double counting individuals, thereby meeting the fourth assumption.

Table 1
Number of repeated surveys for each Breeding Bird Survey-style route and dates of first and last count periods for the six survey years in Denali National Park and Preserve, Alaska between 1995 and 2009. Routes are 39.2 km in length and contain 50 points at 0.8 km intervals.

Year	Route 1	Route 2	Route 3	First Count	Last Count	Observers
1995	18	15	2	April 30	July 4	1, 3, 6
1996	18	12	2	April 18	July 13	1, 7, 8
1997	2	2	2	June 3	June 28	7
1998	2	0	0	June 4	June 11	7
2006	10	8	0	May 3	July 6	4
2009	6	6	3	May 7	June 28	2, 5

2.2. Statistical analyses

We restricted our analysis to singing males to prevent overestimation of the superpopulation that could be caused by detections of migrants or non-territorial individuals. We estimated the overall p (the product of p_a, p_p, and p_d), probability of occupancy (probability a site contained a territory), abundance (number of used territories overlapping the sampling space at a given point), and trends in abundance for 12 species of breeding passerines using hierarchical zero-inflated Poisson (ZIP) mixture models similar to those developed by Joseph et al. (2009) and Wenger and Freeman (2008). Our formulation followed the description of zero-inflated mixture models by Joseph et al. (2009) where the abundance distribution is not truncated at zero (i.e., zeros can arise from either the Bernoulli or Poisson processes). The Wenger and Freeman (2008) formulation attributes all zeros to stochastic processes (i.e., all zeros are attributed to the Bernoulli process and the Poisson is restricted to be >0), but this scenario is only likely to be true when abundance is moderate to high so that zeros are unlikely to be generated from the Poisson process. The general form of the model we used can be written as:

$$n_{ijt} \sim \text{binomial}(K_{it}, OccP_{ijt})$$

$$OccP_{ijt} = \text{occ}_{it} \times p_{ijt}$$

$$occ_{it} \sim \text{Bernoulli}(\psi_{it})$$

$$K_{it} \sim \text{Poisson}(\lambda_{it})$$

$$\text{logit}\ (p_{ijt}) = \alpha_0 + \sum_k \alpha_k x_{ijt} + e_{ijt}$$

$$\text{logit}\ (\psi_{it}) = \beta_0 + \sum_k \beta_k x_{it} + e_{it}$$

$$\log\ (\lambda_{it}) = \gamma_0 + \sum_k \gamma_k x_{it} + e_{it}$$

where n_{ijt} represents the observed counts at each point $i = 1,2,\ldots,I$ points, during each repeated count $j = 1,2,\ldots,J$ counts, in each year $t = 1,2,\ldots,T$ years. These counts are viewed as realizations of a binomial process with abundance K_{it} and probability of occupancy and detection, $OccP_{ijt}$. Detection (p_{ijt}), occupancy (ψ_{it}), and mean abundance (λ_{it}) can all be modeled as functions of covariates (x), and random effects (e). Note that fixed and random effects were not allowed to vary among repeated counts (j) for occupancy or abundance because the occupancy and abundance of territories were assumed to be fixed throughout the season. Using this basic framework, we created a model structure that included fixed and random effects that addressed suspected sources of variation in detection, occupancy, and abundance. This model was then applied to each species individually. We added two covariates to address variation in p_p of males within territories and p_a due to singing behavior. First, we added a quadratic effect of survey timing relative to sunrise to the detection portion of the model expecting that singing rates for each species (i.e., p_a) would change throughout the day,

Table 2
Annual number of detections of singing males for each of 12 species of breeding passerine birds in Denali National Park and Preserve, Alaska between 1995 and 2009. Counts are summed across all sample periods and routes for each year.

Species	1995	1996	1997	1998	2006	2009
Ruby-crowned kinglet (*Regulus calendula*)	125	185	16	15	97	58
Arctic warbler (*Phylloscopus borealis*)	258	284	61	0	92	131
Swainson's thrush (*Catharus ustulatus*)	212	175	41	62	159	89
American robin (*Turdus migratorius*)	510	374	44	36	283	137
Varied thrush (*Ixoreus naevius*)	345	252	19	16	241	162
Orange-crowned warbler (*Vermivora celata*)	1019	606	157	84	369	371
Wilson's warbler (*Wilsonia pusilla*)	1144	934	264	130	513	372
American tree sparrow (*Spizella arborea*)	2979	2137	480	203	1278	819
Savannah sparrow (*Passerculus sandwichensis*)	775	501	219	32	204	293
Fox sparrow (*Passerella iliaca*)	572	420	138	47	605	718
White-crowned sparrow (*Zonotrichia leucophrys*)	3379	2963	769	210	1591	1061
Dark-eyed junco (*Junco hyemalis*)	669	466	85	58	397	311

possibly in a nonlinear manner. We expected that some species would be most detectable early in the morning, while others may peak later in the morning or even maintain a relatively constant singing rate throughout the day. Second, the addition of a quadratic effect of survey date allowed the probability of presence (i.e., p_p) to approach zero during the beginning of the season before the arrival of migrant species, increase as migrants arrived, and then decline as breeding was completed. We also included a random observer effect, assuming that observer abilities might affect detection (e.g. Link and Sauer, 2002). Occupancy was modeled as a function of habitat type, assuming that some species may occur in particular habitats more often than others. Abundance was assumed to vary among habitat types, and we included a linear trend term on the log scale to investigate the possibility that abundance in all habitats might be changing through time. Finally, year was also included as a random effect on abundance to account for remaining annual variation. Overall, this provided a flexible model that simultaneously accounted for much of the variation we expected in detection between surveys and years, while providing estimates of occupancy and superpopulation abundance corrected for incomplete detection.We selected 12 of the most common breeding passerine species detected during the surveys for analysis (Table 2) and fit the above model to the data for each. We used program R 2.9.0 (R Development Core Team, 2009) for data preparation, WinBUGS 1.4.3 (Spiegelhalter et al., 2004) for model fitting, and the package R2WinBUGS (Sturtz et al., 2005) as an interface between the two. We used diffuse normal priors on parameters with all $\alpha_k \sim N(0,100)$, $\beta_k \sim N(0,100)$, and $\gamma_k \sim N(0,100)$. The priors for the standard deviation of the random effects were $\sigma \sim \mathrm{UNIF}(0,100)$. We ran 2 independent Markov chains for 100,000 iterations after a 100,000-iteration burn-in, thinned these values by five to reduce storage requirements, and retained the remaining values for inference. We assessed convergence using the Gelman–Rubin diagnostic (Brooks and Gelman, 1998) and scaled continuous covariates (mean = 0, SD = 1) to improve convergence properties. The hierarchical modeling approach allowed us to account for unbalanced samples (e.g., different numbers of revisits at each point) in the analysis because missing values are estimated along with the other parameters in the model during the updating process (Gelman et al., 2004). The formal inclusion of both missing values and random terms also provided proper estimates of precision for all parameters, and all derived estimates were generated during the updating process directly. All estimates are presented as means and 95% Bayesian credible intervals (analogous to frequentist confidence intervals [CI]).

3. Results

We found substantial variation in p throughout the season, as well as within the recommended 10–30 June survey period for interior Alaska (Handel and Cady, 2004). Total detections varied dramatically among species (Table 2), detection probability was strongly affected by both survey date and time after sunrise (Table 3), and the shape, magnitude, and pattern of these effects varied substantially among species (Figs. 1 and 2). No range of survey dates or times was optimal for detecting all species (Figs. 1 and 2), and differences among observers were large, with some observers detecting more than five times as many individuals of some species on average after controlling for survey date and time (Table 4). During the recommended survey period for interior Alaska, these sources of variation combined (see Figs. 1 and 2 and Table 4) could have resulted in a nearly 10-fold difference between observed counts and estimated abundance for some species during a single visit, depending on which observer conducted the survey and the

Table 3
Parameter estimates and 95% credible intervals of the effects of hours since sunrise (hour) and survey date (date) on detection probability, and estimated annual percent change in abundance (trend) for each of 12 species of breeding passerine birds in Denali National Park and Preserve, Alaska between 1995 and 2009. Estimates for hour and date are presented on the logit-scale and covariates have been standardized to have a mean = 0 and SD = 1. Estimates of trends were converted to real scale and are interpreted as percent change in abundance/year. Bold numbers indicate estimates with 95% credible intervals that do not include 0.

Species	Hour	Hour^2	Date	Date^2	Trend (%)
Ruby-crowned kinglet	**−0.21** (−0.38, −0.04)	0.04 (−0.11, 0.18)	**−0.91** (−1.08, −0.75)	**−0.46** (−0.58, −0.34)	−0.9 (−9.7, 8.8)
Arctic warbler	0.02 (−0.17, 0.22)	0.10 (−0.02, 0.22)	**4.92** (4.72, 5.00)	**−2.35** (−2.51, −2.17)	1.6 (−13.0, 26.7)
Swainson's thrush	**−0.96** (−1.18, −0.76)	**0.20** (0.03, 0.36)	**1.91** (1.64, 2.19)	**−1.42** (−1.66, −1.18)	−1.8 (−13.3, 22.3)
American robin	**−0.70** (−0.82, −0.59)	**0.15** (0.05, 0.25)	**−0.31** (−0.40, −0.23)	**−0.36** (−0.44, −0.29)	−0.6 (−9.5, 9.6)
Varied thrush	**−0.62** (−0.85, −0.40)	**−0.35** (−0.54, −0.17)	**−0.39** (−0.49, −0.30)	**−0.26** (−0.34, −0.19)	1.0 (−5.6, 8.3)
Orange-crowned warbler	**−0.11** (−0.18, −0.04)	**0.07** (0.01, 0.12)	**1.02** (0.92, 1.12)	**−0.98** (−1.08, −0.88)	−1.1 (−8.4, 6.0)
Wilson's warbler	**0.30** (0.22, 0.38)	**−0.21** (−0.27, −0.15)	**0.95** (0.86, 1.05)	**−1.33** (−1.43, −1.22)	**−4.3** (−8.5, −0.2)
American tree sparrow	**−0.12** (−0.18, −0.07)	**−0.12** (−0.16, −0.08)	0.01 (−0.03, 0.04)	**−0.27** (−0.30, −0.23)	−2.6 (−7.5, 3.9)
Savannah sparrow	**−0.19** (−0.29, −0.10)	0.02 (−0.05, 0.09)	**0.56** (0.47, 0.65)	**−0.83** (−0.93, −0.73)	−1.4 (−7.4, 4.9)
Fox sparrow	**0.13** (0.05, 0.21)	−0.03 (−0.10, 0.03)	−0.03 (−0.09, 0.03)	**−0.33** (−0.39, −0.26)	**6.4** (3.3, 9.7)
White-crowned sparrow	**−0.29** (−0.34, −0.24)	0 (−0.04, 0.04)	**0.53** (0.49, 0.57)	**−0.47** (−0.51, −0.44)	−2.1 (−6.6, 2.0)
Dark-eyed junco	**−0.40** (−0.51, −0.29)	0.05 (−0.04, 0.14)	**0.20** (0.14, 0.26)	−0.05 (−0.11, 0)	−0.3 (−8.3, 6.2)

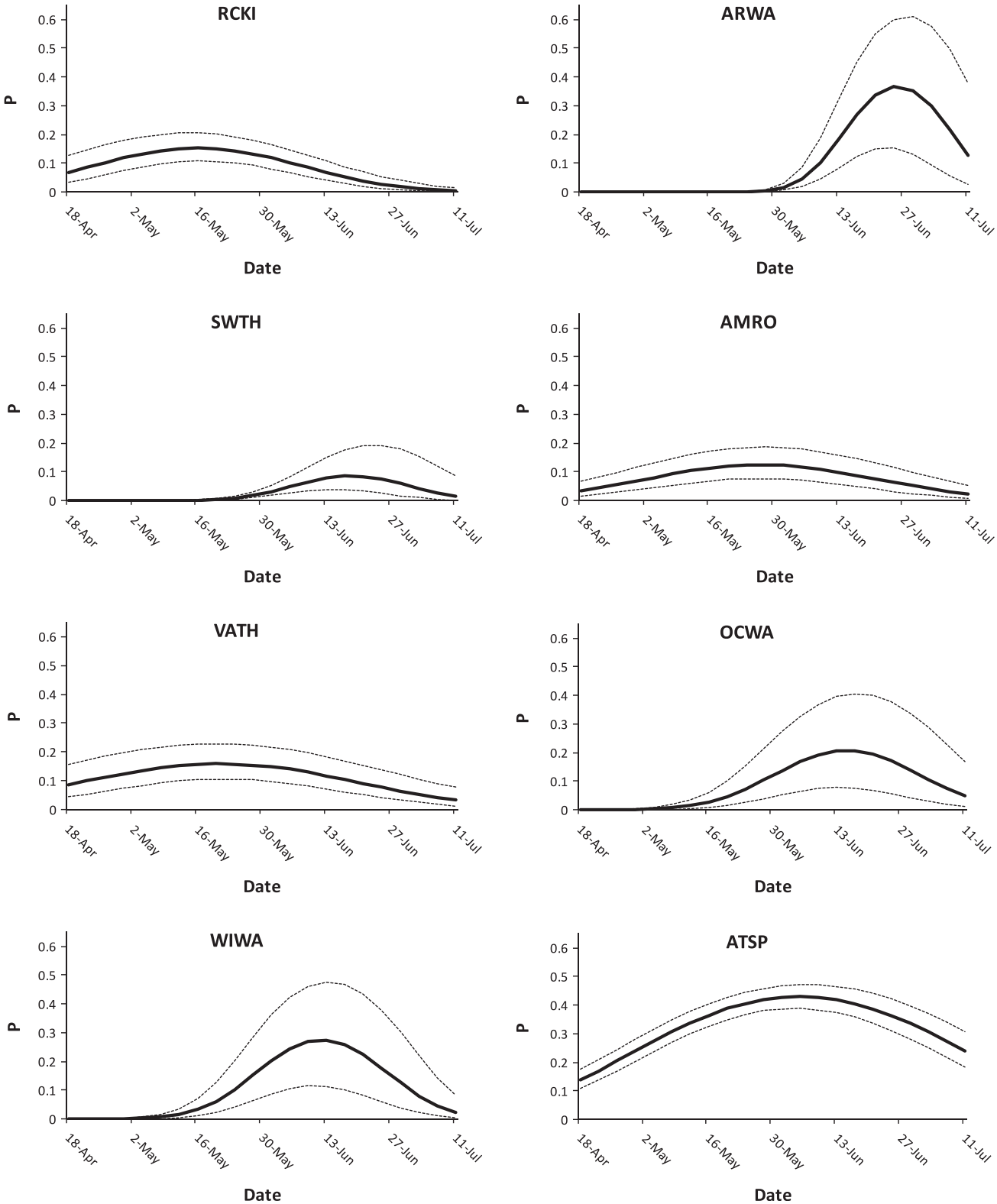

Fig. 1. Detection probability (*P*) of territories relative to survey date (date) for ruby-crowned kinglet (RCKI), arctic warbler (ARWA), Swainson's thrush (SWTH), American robin (AMRO), varied thrush (VATH), orange-crowned warbler (OCWA), Wilson's warbler (WIWA), American tree sparrow (ATSP), Savannah sparrow (SAVS), fox sparrow (FOSP), white-crowned sparrow (WCSP), and dark-eyed junco (DEJU) in Denali National Park and Preserve, Alaska between 1995 and 2009. Estimates assume mean species-specific observer effect, mean number of hours since sunrise, and approach 0 during periods when a species is unavailable for sampling due to migration patterns. Dashed lines indicate 95% credible intervals.

date and time it was completed. Much of this variation was related to covariates representing changes in p_p and p_a and confirmed that presence and availability were not constant under most circumstances for most species.

After accounting for these sources of variation in *p*, we estimated that fox sparrow (*Passerella iliaca*) abundance increased at a rate of 6.4% (95% CI: 3.3–9.7%) annually over the 15 years of our study while Wilson's warblers (*Wilsonia pusilla*) decreased at

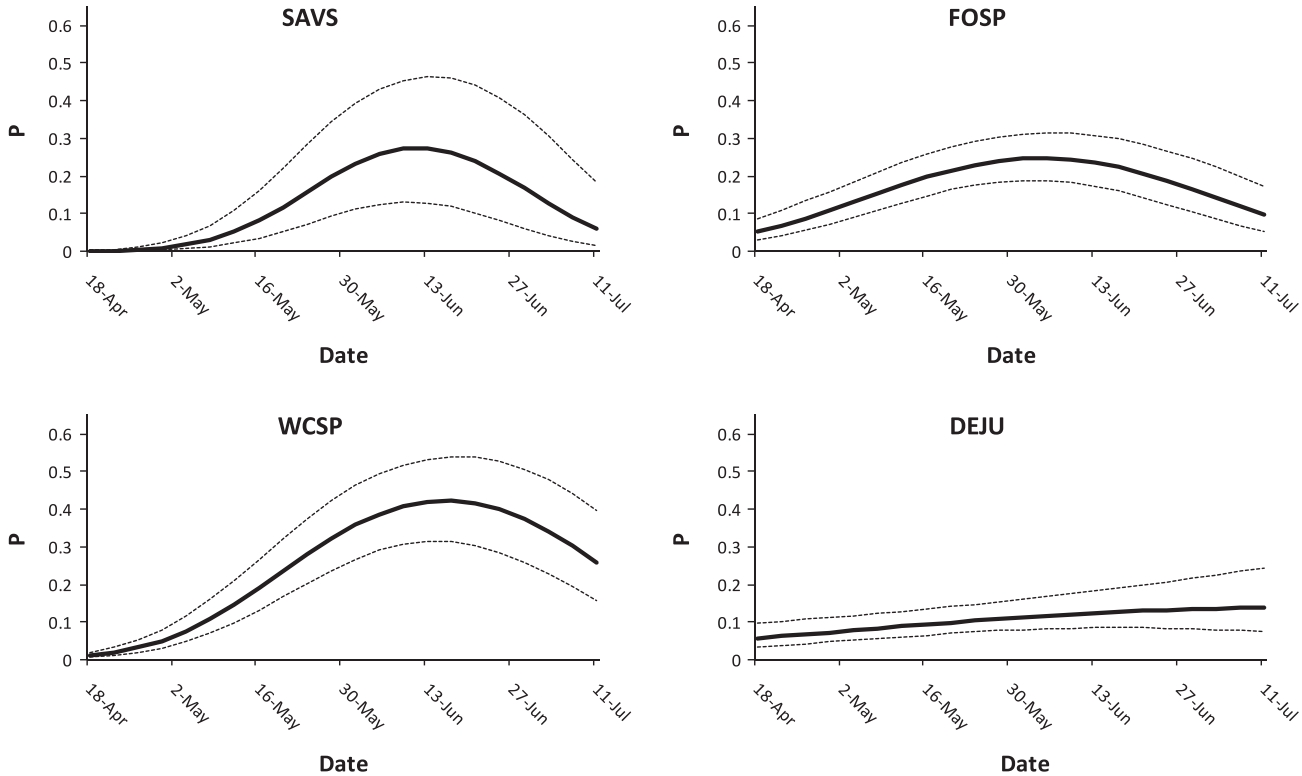

Fig. 1. (*continued*)

a rate of −4.3% (95% CI: −8.5% to −0.2%) annually. This translates to an approximately 250% increase in fox sparrow abundance and a 48% decline in Wilson's warbler abundance along the Denali park road between 1995 and 2009. Credible intervals around the trend estimates for the remaining species overlapped zero providing limited evidence of population changes (Table 3). Estimates of occupancy and abundance indicated that both species were less common in mixed forest and most common in scrub habitats (Table 5), assuming the effective sampling area is similar between habitats and species.

4. Discussion

The primary goal of many long-term monitoring programs is to identify population trends quickly, efficiently, and accurately to inform timely conservation decisions. Unfortunately, many commonly employed field approaches inadequately address incomplete detection, potentially limiting their sensitivity and utility for the conservation of passerine populations. Our results demonstrated that none of the components of p were likely to be constant during the breeding season for the species we considered, and the magnitude of the variation we observed suggested that abundance and trend estimates would be at substantial risk for bias and reduced precision if the detection process was not completely addressed. Estimates of superpopulation abundance are readily interpretable as the number of territories overlapping the sample space that are used during the breeding season and are not dependent on untenable assumptions about the probabilities of presence and availability across space and time. Single-visit approaches typically confound abundance with p_p, (and often p_a), suggesting that repeated count methods generating estimates of superpopulation abundance may be more suitable than many other techniques for long-term passerine monitoring.

Our results agree with extensive past work identifying survey date (Bibby et al., 2007; Skirvin, 1981), time of day (Robbins, 1981), and observer (Link and Sauer, 2002; Norvell et al., 2003; Sauer et al., 1994) as important sources of variation in p. Changes in p relative to survey date likely reflected the timing of migratory arrival for each species, and a comparison among species revealed that peak detection periods did not overlap in many cases. The probability of detecting early migrants (e.g., ruby-crowned kinglet) declined to near 0 by the time later migrants arrived on the study area (e.g., Swainson's thrush, arctic warbler), revealing the importance of understanding and addressing p_p and p_a during the sampling period for each species. Similarly, changes in p related to time of day demonstrated that patterns in singing rates varied by species throughout the morning hours. For example, detection probabilities for Swainson's thrush and American robin were highest 0.5 h prior to sunrise and declined to near 0 within 6 h, while the probability of detecting a Wilson's warbler was highest approximately 4–5 h after sunrise. In addition, although all observers were given extensive standardized training, some observers were >5 times as likely to detect individuals of some species (e.g., orange-crowned sparrow, Savannah sparrow), while detection probabilities were fairly constant among all observers for other species (e.g., ruby-crowned kinglet, American tree sparrow). This suggests that some observers do poorly with certain species, while some species are consistently detected by all observers. Combined, these results provide strong evidence that survey standardization is an unsatisfactory solution to the problem of incomplete detection for most species. Our results also quantified this variation and revealed that variation in p could be very large (i.e., 10-fold) for a given species depending on time, date, and observer, even when conducted during the standardized survey period for Alaska (i.e., 10–30 June within approximately 6 h of sunrise).

Because the assumptions of relatively constant p_p and p_a are difficult to meet, abundance estimates generated from data collected using alternative field methods are often quite variable between years and projects. Therefore, direct comparisons among surveys employing different field methods are generally not appropriate

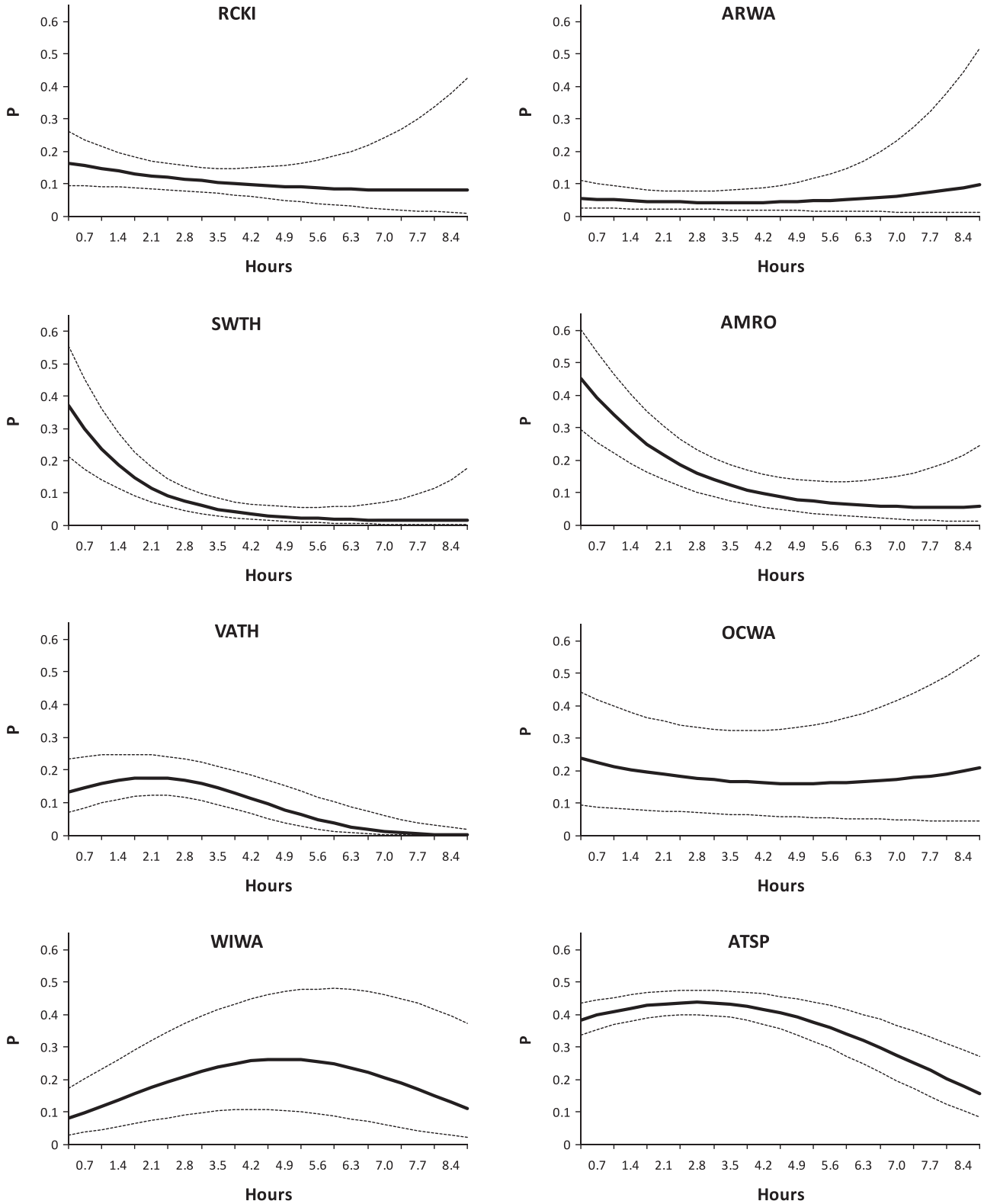

Fig. 2. Detection probability (*P*) of territories relative to the number of hours since sunrise (hours) for ruby-crowned kinglet (RCKI), arctic warbler (ARWA), Swainson's thrush (SWTH), American robin (AMRO), varied thrush (VATH), orange-crowned warbler (OCWA), Wilson's warbler (WIWA), American tree sparrow (ATSP), Savannah sparrow (SAVS), fox sparrow (FOSP), white-crowned sparrow (WCSP), and dark-eyed junco (DEJU) in Denali National Park and Preserve, Alaska between 1995 and 2009. Estimates assume the mean species-specific observer effect and mean survey date. Dashed lines indicate 95% credible intervals.

(e.g., Reidy et al., 2011; Thompson and La Sorte, 2008). When variation in p_p and p_a are not formally addressed, the estimates of abundance do not necessarily apply to the same population between years but instead represent the population that is present and available for sampling during a given year's survey. This has implications for trend estimation because in order to efficiently

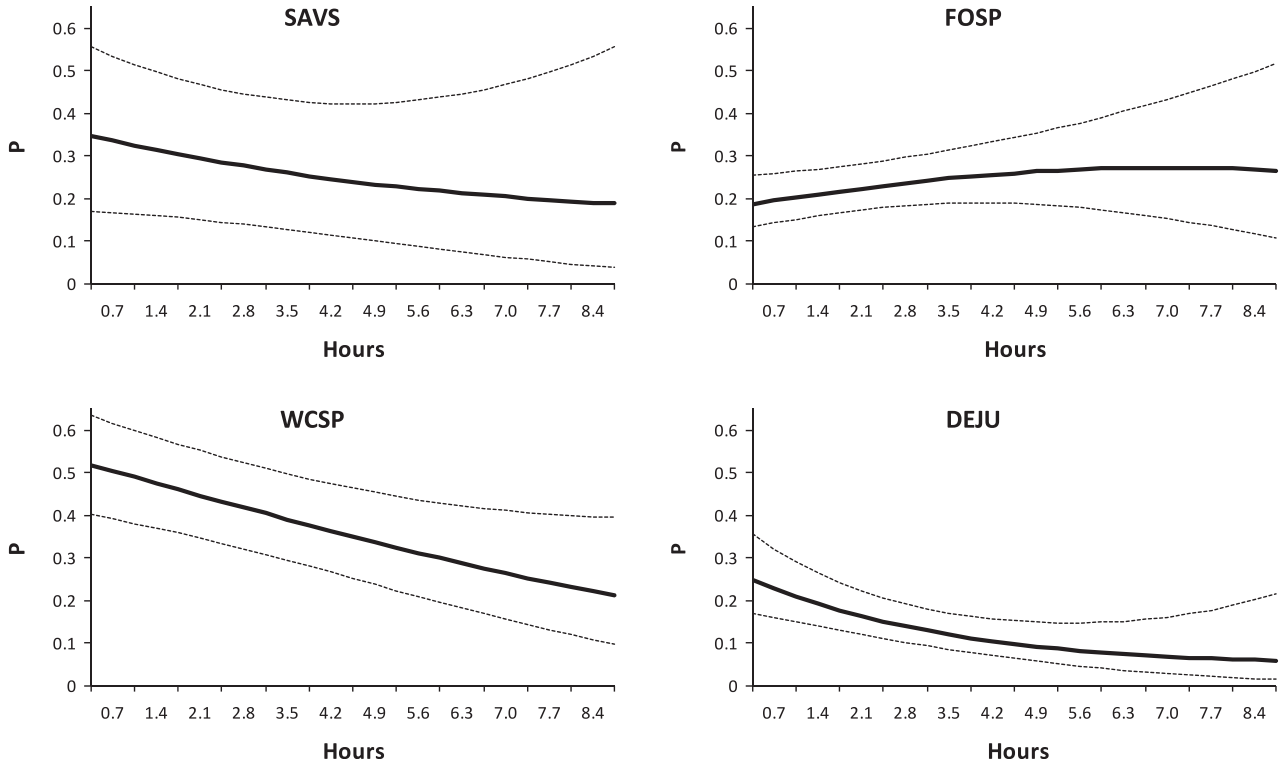

Fig. 2. (*continued*)

Table 4
Observer-specific estimates of detection probability for 12 species of breeding Passerine birds in Denali National Park and Preserve, Alaska (1995–2009) for mean time of day and survey date. Estimates are individual levels of the observer random effect on detection probability. Integers one through eight represent observer identification and σ^p is the standard deviation of the observer random effect on detection probability. The three species with the most variation in detection probability are shown in bold.

Species	1	2	3	4	5	6	7	8	σ^p
Ruby-crowned kinglet	0.11	0.09	0.09	0.13	0.12	0.10	0.11	0.11	0.27
Arctic warbler	0.02	0.04	0.09	0.05	0.06	0.05	0.03	0.05	0.75
Swainson's thrush	0.04	0.08	0.05	0.05	0.05	0.05	0.04	0.06	0.44
American robin	0.11	0.17	0.14	0.12	0.13	0.12	0.16	0.05	0.56
Varied thrush	0.16	0.24	0.12	0.18	0.11	0.14	0.12	0.11	0.48
Orange-crowned warbler	**0.17**	**0.24**	**0.25**	**0.14**	**0.04**	**0.25**	**0.15**	**0.34**	**1.14**
Wilson's warbler	**0.19**	**0.40**	**0.23**	**0.36**	**0.07**	**0.25**	**0.34**	**0.34**	**1.06**
American tree sparrow	0.42	0.45	0.45	0.41	0.42	0.46	0.41	0.41	0.14
Savannah sparrow	**0.19**	**0.38**	**0.39**	**0.22**	**0.07**	**0.34**	**0.35**	**0.32**	**0.99**
Fox sparrow	0.23	0.35	0.18	0.27	0.24	0.27	0.28	0.20	0.37
White-crowned sparrow	0.37	0.37	0.33	0.36	0.58	0.48	0.38	0.25	0.55
Dark-eyed junco	0.09	0.17	0.09	0.11	0.16	0.15	0.10	0.10	0.41

assess trends, one should sample the same population over time (Westcott et al., 2012). Variation in survey timing alone could result in inference to different portions of the overall population from year to year, and standardization has been shown to be an inadequate solution to this problem (Burnham, 1981; Farnsworth et al., 2002; Rosenstock et al., 2002; Thompson, 2002). Increased variation in abundance estimates due to unmeasured variation in *p* has been shown to decrease the sensitivity of monitoring programs where trend estimation is likely a primary objective (Kéry et al., 2005; Pollock et al., 2002), however, implementation of a field protocol that provides inference to the superpopulation may be a reasonable alternative.

We expect that the superpopulation may actually be the population of interest for many monitoring programs due to its inference to the breeding population using a site. In addition, estimates of superpopulation abundance are not conditioned on components of the detection process, are less dependent on untestable assumptions, and trends can be directly interpreted as unconditional changes in the number of breeding individuals using the study area. Unsurprisingly, superpopulation abundance estimates have been found to be higher than abundance estimates based on other methods (e.g., Hunt et al., 2012) because estimates include individuals that are not present or available in the study site during a single survey. Discrepancies in abundance estimates due to underlying assumptions associated with each field method can lead to confusion due to a lack of a clear definition of the 'abundance' being measured using each approach (Nichols et al., 2009). We suspect this lack of clarity in inference may be partially responsible for the extensive discussions in the recent literature concerning the pros and cons of various field and analytical protocols, and the sometimes conflicting results based on them (e.g., Hunt et al., 2012, Johnson, 2008; Thompson and La Sorte, 2008). While we agree that further development of methods addressing all components of *p* are crucial for effective monitoring, we suspect that a lack of clarity regarding inference is also a major problem that could be compounded if trends in detectability were to occur.

Table 5
Estimates and 95% credible intervals of occupancy and abundance for 4 habitats and 2 species, fox sparrows and Wilson's warblers, in Denali National Park and Preserve, Alaska for the average level (0) of the random year effect.

Habitat type	$\hat{\psi}_{\text{fox sparrow}}$ †	$\hat{\psi}_{\text{Wilson's warbler}}$	$\hat{N}_{\text{fox sparrow}}$	$\hat{N}_{\text{Wilson's warbler}}$
Coniferous	0.97 (0.76, 1)	0.98 (0.86, 1)	0.42 (0.27, 0.63)	2.04 (1.33, 3.10)
Mixed forest	0.35 (0.18, 0.65)	0.67 (0.46, 0.99)	1.00 (0.42, 1.82)	3.08 (1.69, 4.93)
Tall scrub	0.93 (0.85, 1)	0.99 (0.95, 1)	1.84 (1.35, 2.46)	5.88 (4.05, 8.64)
Low scrub	0.90 (0.84, 0.96)	0.97 (0.92, 1)	1.86 (1.38, 2.44)	5.32 (3.67, 7.84)
σ_{yr} ††			0.12 (0.004, 0.41)	0.22 (0.04, 0.62)

† $\hat{\Psi}$ = occupancy, $\hat{N}$ = predicted mean abundance given occupancy.
†† σ_{yr} = the standard deviation of the year random effect on abundance.

Research has shown that migratory arrival timing has changed for many avian species (Cotton, 2003; Parmesan, 2007; Root et al., 2003), suggesting that p_p on any given date will likely change through time for some species. If this occurs, the ability to separate trends in abundance from trends in timing of arrival will be critical for effective monitoring and conservation. The approach we describe provides a formal approach to modeling changes in migratory timing by including appropriate temporal and environmental covariates in the detection model. Variation in p due to timing can then be directly separated from variation in abundance, reducing bias and increasing precision in trend estimates (Kéry et al., 2005; Royle and Dorazio, 2006, 2008; Royle et al., 2007). While it has been suggested that simple unadjusted counts may be useful in some limited situations (Johnson, 2008), we would argue that most passerine monitoring programs would benefit from more robust protocols based on the methods we describe. Recognition of large declines (e.g., $\geqslant$3.5%/year) may be possible using unadjusted counts (Bart et al., 2004; Thogmartin et al., 2007), but one of the most important functions of long-term monitoring programs is to provide timely information on more subtle trends before dramatic changes in populations occur (Westcott et al., 2012). Without a sensitive monitoring tool, it is likely only the most dramatic population trends will be evident after large declines in abundance have occurred.

Despite the short duration and sporadic nature of sampling (i.e., 6 years out of 15), we detected population trends in, and basic habitat associations for, 2 of the 12 species we considered. Although we did not address the power of the approach we used, our results show that a repeated count approach can provide trend information about passerine populations with relatively few sampling periods. This suggests that the number of years necessary to detect trends may be reduced because much of the variation in detection can be formally addressed. We found large amounts of temporal variation in p, indicating that ignoring variation in p_p and p_a would decrease the precision of estimates, thereby increasing the number of survey years necessary to detect trends and decreasing the effectiveness of long-term monitoring for conservation of passerine populations. Recent work has suggested that increased precision of abundance estimates for monitoring programs was a major contributor to the identification of population trends (Seavy and Reynolds, 2007; Westcott et al., 2012). Despite the ability of less complex methods to identify large population declines over long time horizons in some situations (e.g., Bart et al., 2004; Johnson, 2008), we argue that monitoring programs should strive to increase estimator precision and stability using the best techniques available. Improvements in precision and inference would facilitate appropriate conservation actions prior to dramatic changes in population size.

5. Conclusions

Overall, our results suggest that the sensitivity and effectiveness of many passerine monitoring programs, particularly those currently in the design phase, could be improved by a more theoretically sound approach combining repeated count surveys for data collection and mixture models for analysis. When possible, repeated visits should cover the expected range in temporal variation (e.g., time of day, season date) to improve the estimation of these covariates. We contend that inference to the superpopulation may be of the most utility for conservation due to its direct and intuitive definition and a reduced dependence on assumptions about the detection process as compared to more commonly used methods. Using these more sensitive methods, we found that despite discontinuous sampling (6 years) over a relatively short study period (15 years) we were able to identify trends in 2 of the 12 species investigated. If the identification of population trends is a primary goal, we suggest that methods correcting for all sources of incomplete detection are necessary. Repeated count methods may also be particularly useful if changes in migratory arrival timing are expected.

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