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Simultaneous-count models to estimate abundance from counts of unmarked individuals with imperfect detection

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Modelos de Conteo Simultáneo para Estimar la Abundancia a partir de Conteos de Individuos No Marcados con Detección Imperfecta

Ryan et al.

18-516

Palabras clave: bayesiano, buitre, detectable, dinámica de poblaciones, *Gyps*, modelo jerárquico, modelo de mezcla N, monitoreo, *Sarcogyps*

Resumen. Desarrollamos un método para estimar la abundancia poblacional a partir de conteos simultáneos de individuos sin marcaje en múltiples sitios. Consideramos que en cada ocasión de muestreo los individuos de una población podrían ser detectados en uno de los sitios de censos o podrían permanecer sin ser detectados y usamos modelos de conteo simultáneo multinomial o binomial para estimar la abundancia, con el binomial como equivalente a un modelo de mezcla N con un solo sitio. Probamos el desempeño del modelo con simulaciones en un rango de probabilidades de detección, tamaños poblacionales, tasas de crecimiento, número de años, ocasiones de muestreo, y sitios. Después aplicamos nuestro método a tres especies de buitre que se encuentran en peligro crítico en Camboya para demostrar cuán aplicable es el modelo en el mundo real y para proporcionar las primeras estimaciones de abundancia para estas especies en Camboya. Nuestra nueva estrategia trabaja de mejor manera cuando se espera que los modelos existentes tengan un desempeño pobre (es decir, pocos sitios y una gran variación en la abundancia entre sitios) y si los individuos podrían moverse de un sitio a otro entre cada ocasión de muestreo. La estrategia tuvo un mejor desempeñó cuando hubo >8 ocasiones de muestreo y la probabilidad neta de detección fue alta (>0.5). Creemos que nuestra estrategia será especialmente útil para censos simultáneos en sitios de agregación, como los nidos. El método complementa las estrategias existentes para estimar la abundancia de individuos sin marcaje y es el primer método diseñado específicamente para conteos simultáneos.

Simultaneous-count models to estimate abundance from counts of unmarked individuals with imperfect detection

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Multinomial and binomial simultaneous-count models estimate abundance of unmarked individuals in multiple sites.

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Abstract

We developed a method to estimate population abundance from simultaneous counts of unmarked individuals over multiple sites. We considered that at each sampling occasion individuals in a population could be detected at 1 of the survey sites or remain undetected and used either multinomial or binomial simultaneous-count models to estimate abundance, the latter being equivalent to an N-mixture model with one site. We tested model performance with simulations over a range of detection probabilities, population sizes, growth rates, number of years, sampling occasions, and sites. We then applied our method to 3 critically endangered vulture species in Cambodia to demonstrate the real-world applicability of the model and to provide the first abundance estimates for these species in Cambodia. Our new approach works best when existing methods are expected to perform poorly (i.e., few sites and large variation in abundance among sites) and if individuals may move among sites between sampling occasions. The approach performed better when there were >8 sampling occasions and net probability of detection was high (>0.5). We believe our approach will be useful in particular for simultaneous surveys at aggregation sites, such as roosts. The method complements existing approaches for estimating abundance of unmarked individuals and is the first method designed specifically for simultaneous counts.

利用未标记个体的不完全检测进行丰度估计的同时计数模型

【摘要】我们开发了一种利用多个位点未标记个体的同时计数来估计种群丰度的方法。**我**们认为**每次抽**样时**种群中的个体要么出**现**在其中一个**调查**位点，要么没有被**发现，**因此可以用多**项**或二**项**同**时计**数模型来估**计**种群丰度，而后者相当于一个位点的**N混合模型。我们对检测概率、种群大小、增长率、年数、抽样情况和位点进行了一系列模拟，测试了模型的性能。接下来我们将这个方法应用于柬埔寨的三种极度濒危的秃鹫，以证明模型实用性，这也是首次对柬埔寨的这些物种进行丰度估计。当现有方法不适用（如只有少量位点或位点间丰度差异很大），或是几次抽样之间动物的位置发生移动的情况下，我们的新方法最为有效。抽样次数大于八次时，我们的模型表现得更好，其净检测概率较高（>0.5）。我们相信这一方法在对聚集位点（如鸟群栖息处）进行同时调查时尤其适用。它是对现有的未标记个体丰度估计方法的补充，也是第一个专为同时计数调查而设计的方法。**【翻译：胡怡思；审校：聂永刚】**

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关键词：N混合模型，监测，层级模型，种群动态，检测力，贝叶斯，秃鹫，兀鹫属（*Gyps*），黑兀鹫属（*Sarcogyps*）

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Introduction

Abundance is a fundamental measure in ecology and environmental management. Detecting all individuals in a population is usually impossible when monitoring (Dice 1941), so estimates of abundance must account for imperfect detection (MacKenzie et al. 2005). Counts of individuals can provide an index of abundance if the probability of detection does not vary in time or space or if variation in detection is accounted for, which allows population dynamics to be inferred by repeating counts in space or time (Link & Sauer 1998). However, if detection varies in unknown ways or if absolute abundance is the parameter of interest, then counts alone will not be informative (Anderson 2001; MacKenzie et al. 2005; Archaux et al. 2012). Knowing a priori whether the probability of detection varies is usually not possible (Guillera-Arroita et al. 2014), but statistical methods can account for imperfect detection when estimating abundance, generally based on the number of individuals seen and other information, such as distance of sighting, double observation, markings, removals, or a combination of these (e.g., Borchers et al. 1998; Nichols et al. 2000; Buckland et al. 2007; Amundson et al. 2014). Getting such additional information in the field, however, can be difficult, expensive, or compromise animal welfare, so methods have flourished for use with counts of sightings from unmarked animals, such as N-mixture models (Royle 2004a) (Fig. 1a), and with extra data, such as mark-resight (McClintock et al. 2009).

Simple counts remain common, despite the inferential limitations when imperfect detection is ignored, and the many methods to estimate abundance (Kellner & Swihart 2014; Stephens et al. 2015). Some surveys aim to census entire populations by simultaneously counting individuals at multiple locations. Examples include breeding-ground counts of geese (Mitchell 2015), cave counts of seals (Martínez-Jauregui et al. 2012), and roost counts of bats (Westcott et al. 2015). Simultaneous counts are sometimes used in monitoring programs to derive minimum population size, prevent double counting of individuals, or reduce nondetections (e.g., Clements et al. 2013). The utility of this monitoring depends on an assumption that either a constant proportion of the population is detect or simultaneous counts act as complete censuses (i.e., all individuals in the population are counted).

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Two methods account for detection when estimating abundance based on simultaneous count data. First, simple binomial models consider the entire population either detected or undetected (Fig. 1a) and model the observation process over all sites together. With repeated surveys, information on variation in the number of individuals detected is used to estimate detection probabilities and abundance. We call this a *binomial simultaneous-count model*. If counts are simultaneous, the overall population is closed to recruitment, mortality, and migration within survey periods, and all individuals in the population could be detected over the course of sampling, then abundance and detection are analytically simple to estimate. Although simple, we know of no studies in which this approach was used, and information on variation in detection and abundance among sites is lost that may be of interest. Second, the more complex binomial N-mixture model accounts for the observation process at each site (i.e., whether individuals at a site are detected or not detected) (Fig. 1b). Although useful for counts of unmarked individuals, it cannot be applied in all circumstances. Binomial N-mixture models allow abundance at each site to vary with some distribution, typically Poisson (Royle 2004a) or negative-binomial (Martin et al. 2005). Accounting for further variation in abundance or variation in detection among sites requires estimation of covariates, and so it may not be possible to account for such variation where covariates are unknown or if there are too few sites to estimate their coefficients. If the area of sites in binomial N-mixture models is poorly defined, it is impossible to accurately extrapolate density at sites to absolute abundance. If individuals are mobile and may occur at a number of sites on different occasions within a sampling period, the assumption of closure is not met, and estimates will be unreliable. Thus, binomial N-mixture models do not make use of the information that counts are simultaneous.

We developed a multinomial simultaneous-count model , similar to the binomial N-mixture model, that applies specifically to simultaneous counts (Fig. 1c & Table 1). We modeled an observation process over the entire population of interest. With the multinomial simultaneous-count model, at each sampling occasion an individual present in the population is either detected at no more than one site or undetected (Fig. 1c). Thus, the multinomial observation process consists of k+1 groups, where k is the number of surveyed sites; each individual occurs in exactly 1 of these groups. Although more complex than the binomial simultaneous-count model, it allows estimation of site-level detection processes and population abundance.

We differentiated the simultaneous-count model and N-mixture model approaches for the following reasons (Table 1). First, intent, binomial N-mixture models are intended to estimate site-specific abundance or density over many sites, whereas simultaneous-count models are

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intended to estimate the abundance of an entire population over those sites. Second, binomial N-mixture models apply the observation process at each site separately, whereas the simultaneous-count model considers observations in a single process over all sites. Third, although the binomial simultaneous-count and binomial N-mixture models are the same if applied to a single site, the binomial simultaneous-count model is not a mixture model because there is no mixing distribution, only a single estimate of *N*. The simultaneous-count model is based on the assumption that the area surveyed represents the entire population of interest, the population is closed during survey periods, and individuals are not double counted, which is certain when surveys are simultaneous. The advantages of the simultaneous-count model over an N-mixture model are that the probability of detection at individual sites can vary without the need for estimable covariates, estimating abundance does not require a well-defined survey area, and it is not assumed that the population at a site is closed within the survey period (Table 1).

We devised multinomial and binomial simultaneous-count models (SCMs), evaluated their performance via simulation, compared the multinomial and binomial models, and applied the multinomial model to counts of 3 critically endangered vulture species in Cambodia. These vulture populations are globally significant and geographically disjunct from other populations of the same species, and so geographically closed. The binomial N-mixture model cannot be applied easily because there are few monitoring sites, populations are dispersed unevenly in the landscape with no known covariates to account for this, and individuals move among sites between sampling occasions (Clements et al. 2013).

Methods

Simultaneous-count models for abundance

Consider a short-duration survey of a closed population: no migration, recruitment, or mortality, and population is bounded in a distinct geographic area. The population is surveyed simultaneously at *k* sites on multiple occasions when the population is closed. At each site *i* on occasion *t* some number of individuals ($y_{i,t}$) is counted, producing a series of counts ($y_{1:k,\,t}$). On each occasion, each individual in the population is either detected at no more than one site or not detected, resulting in k+1 groupings into which each individual may occur (Fig. 1c). The total population abundance of individuals that could be detected (N) is the sum of all the individuals detected at all k sites plus the number of individuals not detected at any site ($y_{k+1,t}$), which is unknown, so $N = \sum_{i=1}^{k+1} y_{i,t}$.

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If the probability that in a given sampling occasion an individual is detected at site i is π_i, for sites 1:k and the probability an individual is not detected at any of the sites is π_{k+1}, then $\sum_{i=1}^{k+1} \pi_i = 1$ because the individual must be somewhere.

Counts of individuals detected and not detected ($y_{1:k+1,t}$) have a multinomial distribution from a population of N and probabilities of π_1 to π_{k+1}:

$$y_{1:k+1,t} \sim \text{multinomial}(N, \pi_{1:k+1}). \quad (1)$$

The likelihood for this is

$$L(N, \pi_1, \pi_2, \ldots, \pi_{k+1} | y_1, y_2, \ldots, y_{k+1}) = N! \prod_1^{k+1} \frac{{\pi_i}^{y_i}}{y_i!}. \quad (2)$$

When one separates the elements corresponding to the undetected population, this likelihood equals

$$L(N, \pi_1, \pi_2, \ldots, \pi_{k+1} | y_1, y_2, \ldots, y_{k+1}) = \frac{N!\left(1-\sum_1^k \pi_i\right)^{\left(N-\sum_1^k y_i\right)}}{\left(N-\sum_1^k y_i\right)!} \prod_1^k \frac{{\pi_i}^{y_i}}{y_i!} . \quad (3)$$

If one considers the binomial equivalent of this, where observations from all surveyed sites are treated as a single site,

$$\sum_1^k y_i \sim \text{binomial}\left(N, \sum_1^k \pi_i\right), \quad (4)$$

then the likelihood is

$$L\left(N, \sum_1^k \pi_i, \pi_{k+1} | \sum_1^k y_i, y_{k+1}\right) = \frac{N!\left(1-\sum_1^k \pi_i\right)^{\left(N-\sum_1^k y_i\right)}}{\left(N-\sum_1^k y_i\right)!} \times \frac{\left(\sum_1^k \pi_i\right)^{\left(\sum_1^k y_i\right)}}{\left(\sum_1^k y_i\right)!} . \quad (5)$$

Although Eqs. 3 and 5 are not equivalent, the elements of the likelihood including N are identical, so the likelihoods with respect to N are exactly proportional to each other. Therefore, both binomial and multinomial formulations of the model should generate the same estimates of N.

The π_i probability is not the probability that an individual occurs at site i. Individuals present at a site but not detected are incorporated into probability π_{k+1}. So π_i could be considered the product of the probability that an individual occurs at site i on a given occasion and the probability that the individual is detected given that it occurs there.

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The simultaneous-count model is based on the assumption that individuals are not double counted and that the population is closed during sampling. Closure can be relaxed to estimate an open (changing) population if, for example, there is a mix of periods of population closure and repeated surveys interspersed with periods when the population is open, when N may vary.

Figure 1 contrasts the simultaneous-count models and the binomial N-mixture model, and Table 1 contrasts these and multinomial N-mixture models. The SCM detection process and abundance estimates operate at the population level, whereas in N-mixture models, the detection process and abundance estimates operate at a single site level. The multinomial process in multinomial N-mixture models results from additional information, such as removals of individuals, double-observer counts, or encounter histories (e.g., Royle 2004b; Kéry & Royle 2010, 2016).

Simulations

We conducted simulation experiments to test how well the simultaneous-count models estimated known values. In each simulation set, we varied the parameter of interest and repeated simulations over orthogonal combinations of detection probability, number of sampling occasions, and sites for both multinomial and binomial simultaneous-count models (Table 2). We simulated an initial population (N_0) of 1000 individuals sampled on 2-64 occasions and with a net probability of detection (p') of 0.1, 0.5, or 0.9 (Table 2). The p' variable is the sum of the probabilities that an individual is detected at each site, $p' = \sum_1^k \pi_i = 1 - \pi_{k+1}$, and equals p in the binomial models. We split p' evenly among sites such that $\pi_1 = \pi_2 = \cdots = \pi_k = \frac{p'}{k}$. For example if $p' = 0.5$ and there were 2 sites, the probability an individual would be detected at 1 of those sites was $\pi_1 = \pi_2 = \frac{0.5}{2} = 0.25$. We conducted 5 sets of simulations (binomial models, number of sites, growth rate, population size, and spread of population) . The full combination of parameters are listed in Table 2. For binomial models, we sought to establish that the model we specified was consistent with sampling at a single site (i.e., when both models should be identical). For number of sites, we compared how the simultaneous-count models performed with differing numbers of sites (1, 2, 3, 5, 7, and 9). For growth rate, we examined how simultaneous count models estimated changes in abundance when surveying an open population under a robust design. We specified an exponential population growth rate (R): $R = N_{t+1}/N_t$ and $N_t = N_0 \times R^t$. We simulated surveying populations at 1, 3, or 7 sites over 2, 4, or 8 years with 2, 4, or 8 sampling occasions per year and R of 0.9, 0.98, 1, 1.02, and 1.1. For population size, we examined performance of the models with populations of 10, 100, 1000, or 10 000 individuals in 1, 3, or 7 sites and did not truncate λ, the hyperprior for N (see Analyses below). For spread of observed population, we

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compared outcomes when the probability of detection was even among sites, as for our other simulations, with when the probability of detection differed among sites. Where probabilities of detection differed, half of the net probability of detection was assigned to a single site and the remainder was spread evenly among the remaining sites so that $\pi_1 = \frac{p\prime}{2}$, and $\pi_2 = \cdots = \pi_k = \frac{p\prime}{2(k-1)}$.

Analyses

We specified the models in a Bayesian framework with JAGS (Plummer 2003) version 4.3.0. Priors for $\pi_{1:k+1}$ were drawn from a Dirichlet distribution, and priors for N were drawn from a Poisson distribution: $\pi_{1:k+1} \sim$ Dirichlet$(\alpha_{1:k+1})$, $N \sim$ Poisson(λ), and $y_{1:k+1,t} \sim$ multinomial$(N, \pi_{1:k+1})$ or $y_{1:k,t} \sim$ binomial(N, p) in the multinomial and binomial models respectively. A Poisson distribution was the prior for a discrete N, although other prior distributions are possible. We set weak priors for λ (10^{-6}, 10^{-6}), and to improve model convergence, we truncated our prior distribution for λ at 5,000 (except set 4, see above). Priors for α were such that each $\alpha_{1:k} = \frac{1}{k}$, and $\alpha_{k+1} = 1$. Thus, equal prior weight was given to the probability of detection and nondetection and was equivalent in both multinomial and binomial models with the same data. New data were randomly generated for each simulation, and we ran 100 simulations for each combination of parameters.

The standard distributions in WinBUGS, OpenBUGS, and JAGS do not allow multinomial likelihoods with missing values—in this case the number of individuals not detected. Conceptually, the detection process could be modeled in the multinomial SCM as a binomial for detection and nondetection, with a multinomial process for occurrence at each site, but this was not possible because the number of individuals detected each occasion varied. Hence, we specified the multinomial model with the "ones trick" (Spiegelhalter et al. 2003). The ones trick allows the estimation of a likelihood from a distribution not specified within the software, where the likelihood is written in full.

Models were fit in JAGS with 3 chains, 100,000 iterations, 50,000 burn-in, and up to 3 updates if not converged initially. Convergence was confirmed post hoc with Gelman-Rubin statistics (Gelman & Rubin 1992; Brooks & Gelman 1998), where all $\hat{R}$ values were <1.1, or those simulation fits were discarded. All analyses were conducted in R version 3 (R Core Team 2017). Code to replicate the entire analysis and results summary files are available (see Supporting Information).

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Cambodian vulture populations

We developed the SCM to estimate the abundance of the Cambodian populations of 3 critically endangered vultures: Red-headed Vulture (*Sarcogyps calvus*), Slender-billed Vulture (*Gyps tenuirostris*), and White-rumped Vulture (*Gyps bengalensis*). In northeastern Cambodia, animal carcasses are provided to vultures to prevent poisoning and to supplement food because wild ungulate populations are small (Loveridge et al.2018). Carcass-provision sites are surveyed simultaneously on 2 occasions/year 2 weeks apart in June, which is outside of the breeding season. These counts provide a lower limit on the population estimate (Clements et al. 2013; Loveridge et al. 2018). We used count data from 2006–2014 from these simultaneous surveys at 6 sites for which data were available for all years: Chhaep Wildlife Sanctuary, Prey Siem Pang Kang Lech Wildlife Sanctuary, Phnom Prich Wildlife Sanctuary, Lomphat Wildlife Sanctuary, Srepok Wildlife Sanctuary, and at the Sesan River (Loveridge et al. 2018; Clements et al. 2013). Several other sites were included in a few years (Loveridge et al. 2018), but because most occasions yielded few to no birds, we excluded them to simplify analyses. This is not likely to substantially affect the results. Birds present at these excluded sites are estimated in the unobserved population, and we assumed detection rate is not affected by birds being attracted to excluded sites. Individuals stay within the study area and move among sites (Clements et al. 2013), suggesting our key assumptions were met (see Simultaneous Count Models for Abundance) and a binomial N-mixture model may not be appropriate.

We used the multinomial SCM to model two possible population trajectories: constant abundance or exponential growth (fit as in our simulations). We also considered changes in probability of detection. Birds may stay near a carcass after feeding (personal observation) and the time between sampling occasions is short, so we expected more vultures may appear at the second occasion each year. Therefore, we modeled either constant probability of detection or varied detection between the 2 occasions within each year but held constant detection over years. Detection was varied by the same coefficient over all sites (ν) such that if the probability of detection at any site i on occasion t in year y is $\pi_{i,t,y}$, then $\pi_{i,t+1,y} = \nu \times \pi_{i,t,y}$. The probability an individual is not detected varied by coefficient μ, such that where there are k sites, then

$$\nu = \frac{1-\mu\times\pi_{k+1,t,y}}{1-\pi_{k+1,t,y}} \quad . \qquad (6)$$

Full specifications for these models are in Supporting Information. We expected that abundance would change over time and that detection would be higher in the second sampling occasion than the first. We compared model fits with deviance information criterion (DIC), although alternative model comparison methods are available and may better suit other applications (Tenan et al. 2014).

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Results

Simulations

For a single-site population, binomial and multinomial simultaneous-count models were equally accurate in estimating population size and probability of detection (fig. 2a, b). Both models also performed similarly in capturing the true population value within the 95% CI (Fig. 2c). A large number of sampling occasions were necessary to achieve accurate estimates for both models, probably stemming from the model prior that detection and nondetection were equally likely.

With larger numbers of sites, again both models performed similarly in estimating abundance and detection rates, regardless of the number of sites (Fig. 3a,b). In some areas with the multinomial SCM, many 95% CIs did not contain the true value. This overconfidence was more likely in simulations with more sites, low probability of detection, and more sampling occasions (Fig. 3c.), which suggests the model may perform poorly when there is little information.

In an open population, estimates of growth rate were accurate and unbiased (Supporting Information), although estimates of abundance and probability of detection when abundance changed over time were similarly accurate when abundance was constant. Results were similar with different population sizes, except for the largest population (10,000) (Supporting Information). Estimates when population was 10,000 did not appear to get closer to the true abundance with increasing effort, and many estimates failed to capture the true value. We expect this was caused by an inappropriate prior, which was the same regardless of the true population size, rather than an inherent failing of the model. This pattern occurred for both the multinomial and binomial models.

Whether the observed population was spread evenly or unevenly among sites did not affect performance (Supporting Information). Results for uneven splits were equally accurate to even.

Vulture population estimates

The top model for Red-headed Vulture was an exponentially changing population with constant probabilities of detection, whereas the top model for Slender-billed and White-rumped Vultures was the exponential population trend and detection varied with sampling occasion. We report here only the top supported models. For Slender-billed and White-rumped Vultures, the top models were clearly best supported, whereas for Red-headed

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Vulture, the top model with constant detection was only slightly better supported than the model where detection varied between sampling occasions. In the top model for Red-headed Vulture, the estimate of change in probability of detection was close to 1 and had credible intervals bounding 1, suggesting little support for variation in probability of detection.

Red-headed Vultures were estimated to be declining (growth rate 0.93 [95% CI 0.90–0.96], population 81 [42–153] in 2014 [Fig. 4], net probability of detection 0.33 [0.13–0.49]). Slender-billed Vultures were estimated to be increasing (growth rate 1.08 [1.05–1.12], population 104 [71–176] in 2014 [Fig. 4], net probability of detection 0.59 [0.51–0.88], change in probability of detection 1.22 [1.1–1.35]). White-rumped Vultures were estimated close to stable over the survey period (growth rate 0.99 [0.97-1], population 583 [363–1028] in 2014 [Fig. 4], probability of detection 0.26 [0.14–0.39], and change in probability of detection 1.12 [1.04–1.15]).

Discussion

We developed a method to estimate abundance from simultaneous count data. The approach applied well to cases with few sites and large differences in counts among them that could not be accounted for by known covariates with a standard binomial N-mixture model. Because of similarities in their likelihood functions, estimates of abundance were equivalent for the multinomial and binomial versions of the simultaneous-count models (Figs. 2-3 & Supporting Information); however, the more complex multinomial model allowed us to estimate the probability an individual is detected at each site (Table 1 & Fig. 1).

Most models performed poorly with little information, and the simulation results were in line with simulation studies for binomial N-mixture models, which suggest that with low sample sizes, low densities, and low probabilities of detection, estimates can be biased; reliable estimates require large sample sizes (Yamaura 2013; Gomez et al. 2017). Similarly, in our simulations with low probability of detection and large numbers of sites, the estimates of the multinomial simultaneous-count model were overconfident and biased toward priors. When the probability of detection was high, reliable estimates still required many sampling occasions (Fig. 3), which may be challenging for simple or short-term monitoring programmes to achieve. Both the binomial and multinomial SCMs appeared to estimate growth rate very well, even with few observations, few sites, and low net probability of detection (Supporting Information). This ability to estimate growth rate could be very useful for monitoring programmes where knowing the trend of a population may be key; however, the utility of the SCM approach over simpler generalized linear models (GLM) is reduced if accurate estimates of abundance are not available.

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Monitoring programmes are often interested in abundance, but estimating abundance can be difficult if programmes lack the wherewithal to collect data more sophisticated than simple counts, or if established robust methods cannot be applied (Banks-Leite et al. 2014). Where only an index of abundance is necessary, a GLM approach may be suitable (Banks-Leite et al. 2014; Barker et al. 2018). Generalized linear models can perform poorly compared with binomial N-mixture models when the probability of detection is low (Yamaura 2013), and detection cannot be known a priori. Neither can GLMs estimate absolute abundance. However, this is also a concern with identifiability of detection and abundance parameters in N-mixture model approaches (Barker et al. 2018), and these may apply to SCMs. However, with the simultaneous-count model approach, abundance can be estimated from counts over multiple sites based on the assumptions that individuals can be detected once at most on each sampling occasion and that all individuals may be detected on some occasion without some of the restrictions of binomial N-mixture models (Table 1).

The SCM approach complements existing methods in circumstances where they are hard to apply. Although the simultaneous-count model is related to models in the N-mixture family, it is distinct from other approaches (Table 1). Binomial N-mixture models work best with large spatial replication and little variation in abundance and probability of detection or with estimation of covariates that affect abundance and probability of detection (e.g., Royle 2004b; Kéry 2008; Kéry et al. 2009). Although the SCMs estimate abundance of a focal population, N-mixture models primarily estimate density of a population of unknown size. In the SCM approach and the N-mixture models the observation process is modeled differently; the former observation process occurs over all sites jointly, whereas the latter process occurs at each site individually. Although the area where the population is estimated need not be known with an SCM, binomial N-mixture models assume defined, closed sites and can produce unreliable estimates of abundance if this assumption is not met (Barker et al. 2018). So binomial N-mixture models are well suited to large-scale monitoring programmes, such as national species surveys (Royle 2004a; Kéry et al. 2005, 2009), and the SCM approach would not apply well to them because the assumption of no double counting may not be met, they may ignore useful site covariates that may improve estimates, and the multinomial model does not perform well with large numbers of sites (Fig. 3c).

Spatially explicit methods for estimating density of unmarked individuals work best with dense sampling sites (Chandler & Royle 2013). But for small programs; rare or highly clustered species, such as discrete roost sites; sparse sampling arrays; and populations distributed unevenly in the landscape, data with sufficient replication to account for observed variability may not be available. In these circumstances the simultaneous-count model approach performs well. For instance, the high probability of detection of Mediterranean monk seals (*Monachus monachus*) observed in 2 breeding caves in West Africa suggests the SCM approach may be well suited for similar studies (Martínez-Jauregui et al. 2012). In

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simultaneous counts of roosting bats, the SCM approach may be suitable for some species , such as the spectacled flying-fox (*Pteropus conspicillatus*), which occurs at few roosts, but not others, such as the grey-headed flying fox (*Pteropus poliocephalus*), which occurs at many locations (Westcott et al. 2015; CSIRO 2017). Furthermore, to provide finer-grained information about detection probability at each site, one may choose between the simpler binomial simultaneous-count model and the multinomial simultaneous-count model.

Ours is the first attempt to estimate the total abundance and trend of vulture populations in Cambodia. Although detection probabilities were low, so these examples are at the lower edge of the reliability of the multinomial simultaneous-count model. Existing methods to estimate abundance were unsuitable for these populations given the few sites and uneven distribution of vultures, so monitoring had relied on interpreting minimum number alive or use of GLMs to estimate trends in counts over time (Loveridge et al. 2018; Clements et al. 2013). These existing methods do not account for imperfect detection and so can be misleading (Guillera-Arroita et al. 2014), but the simultaneous-count approach allowed abundance to be estimated. The results suggest the status of the species is mixed: Red-headed Vulture appeared to be declining, White-rumped Vulture appeared to be declining slightly or close to stable, and Slender-billed Vulture appeared to be increasing up to 2014. We suggest caution when interpreting our estimates for White-rumped and Red-headed Vulture, given the number of sites (6) and estimates of net detection (0.26 and 0.33, respectively) were similar to simulations that were overconfident in their estimates of abundance (fig. 3c). We assumed individuals can be detected at any site, and satellite tracking suggests this is true for Slender-billed and White-rumped Vultures (Clements et al. 2013), but for Red-headed Vultures this is unknown; they are territorial and may not move over multiple sites (del Hoyo et al. 1994). Alternative specifications of the SCM, such as other growth-rate forms or changes in probability of detection, may provide better estimates of abundance and growth rate.

For many species and circumstances, existing methods to estimate wildlife population dynamics are unsuitable. Ongoing pressure to better manage wildlife and international initiatives such as the Aichi Targets (COP10 2010) demand better wildlife monitoring tools. Monitoring needs cost-effective frameworks that are repeatable, scaleable, and avoid conflicting or ambiguous interpretations (Hayward et al. 2015). Our approach fills a particular gap in estimating abundance from simultaneous counts of unmarked individuals. Our simulations indicated circumstances in which the models performed well — few sites and relatively high probability of detection — and poorly, which allows consideration of these circumstances when planning studies and interpreting results. An SCM may best be avoided where probability of detection is low, sampling occasions are few, sites are many, or supplementary information, such as markings, is available. Future work could account for covariation in abundance and detection, examine the implications of failures to meet

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assumptions, such as strictly simultaneous counts or no double counted individuals, and make use of alternative parameterizations (Lindén & Mäntyniemi 2011). The method can be used in real-world monitoring, as exemplified by our case study. The simultaneous-count model approach provides a useful complementary approach to other methods for monitoring biodiversity and will be the best approach for estimating the abundance of discrete populations of unmarked individuals at a small number of sites (<6), where the net probability of detection is high (>0.5), and when simultaneous counts can be achieved on a relatively high number of sampling occasions (>8).

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Supporting information

Model specifications for vulture case study (Appendix S1) and additional figures for results of simulations on population growth rate, population abundance, and population spread (Appendix S2) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author. Code to replicate the entire analysis and results summary files are available from https://zenodo.org/record/1473876#.W_QbtuSWyUk.

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under varying circumstances of visits, sampling sites, detectability, and abundance, in small-sample situations. Ornithological Science **12**:73–88.

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Table 1. Comparison of features of simultaneous-count model and N-mixture model approaches used to estimate abundance.

	Simultaneous count		N-mixture	
Detection model	binomial	multinomial	binomial	multinomial
Modeling of observation-process level	all sites (summed together)	all sites	single site	single site
Data	simultaneous counts	simultaneous counts	counts	counts and other data (e.g., encounter history)
Estimates	total population size	total population size	abundance or density at site	abundance or density at site
Detection probability estimated at each site	no	yes	yes, unique with covariates	yes, unique with covariates
Scale of closure required	population	population	site	site
Accommodation of variation in detection or abundance among sites	yes	yes	with inclusion of covariates	with inclusion of covariates
Robust to poorly defined site area	yes	yes	no	no

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Table 2. Experimental design for simulation studies of performance of simultaneous count models to estimate abundance.

Simulation set	Binomial models	Sites	Growth rate	Population size	Spread of observed population
Open or closed population	closed	closed	open	closed	closed
Sampling occasions per year	2, 4, 8, 16, 32, 64	2, 4, 8, 16, 32, 64	2, 4, 8	2, 4, 8, 16, 32, 64	2, 4, 8, 16, 32, 64
Net probability of detection (p')	0.1, 0.5, 0.9	0.1, 0.5, 0.9	0.1, 0.5, 0.9	0.1, 0.5, 0.9	0.1, 0.5, 0.9; split evenly and unevenly among sites
Population size (N_0)	1,000	1,000	1,000	10, 100, 1,000, 10,000	1,000
Number of sites	1	1, 2, 3, 5, 7, 9	1, 3, 7	1, 3, 7	3, 7
Population growth rate (R)	–	–	0.9, 0.98, 1, 1.02, 1.1	–	–
Years	1	1	2, 4, 8	1	1

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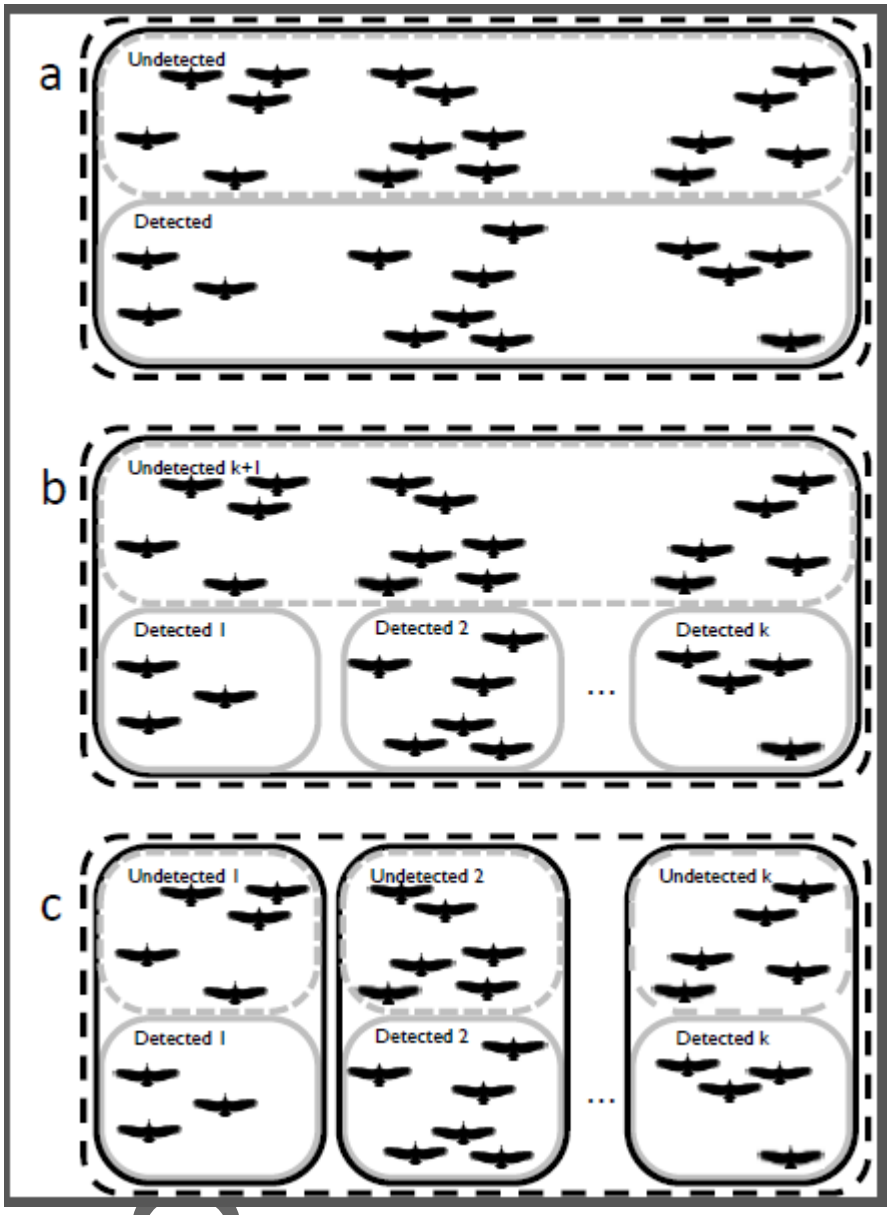

Figure 1. The processes over *k* sites for a (a) binomial simultaneous-count model in which individuals in the population are either detected or not detected, (b) binomial N-mixture model in which individuals at each site are either detected or not detected, and (c) multinomial simultaneous-count model in which individuals in the population are either detected in 1 of the *k* sites or undetected (dashed black line, population of interest; black line, observation process; grey line, detected individuals; dashed gray line, undetected individuals).

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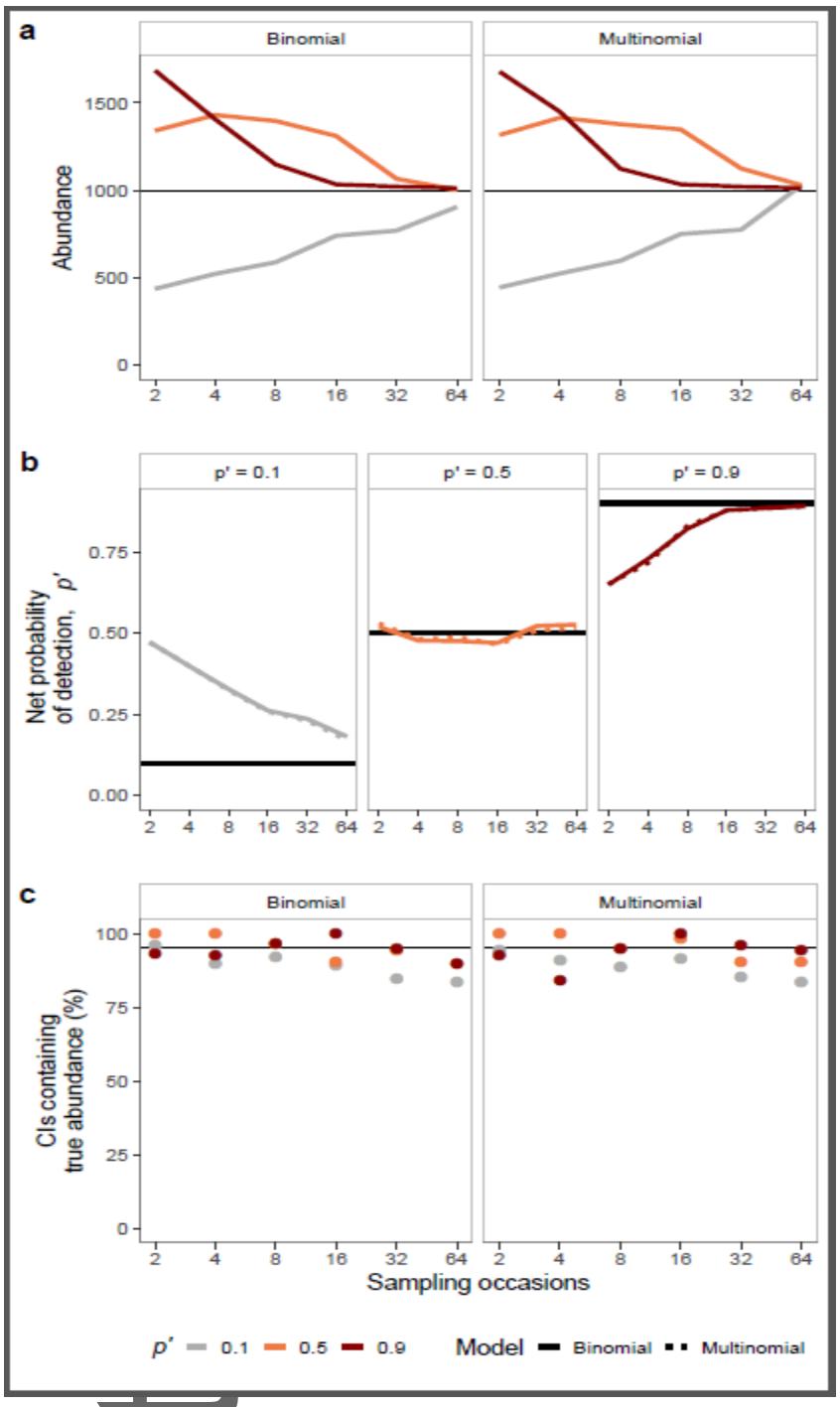

Figure 2. For binomial and multinomial simultaneous-count models, mean estimates at a single site of (a) abundance and (b) probability of detection relative to number of sampling occasions and probability of detection (p') (horizontal lines, true values). (c) Percentage of 95% CIs for estimates of abundance that include the true value (horizontal line, 95%).

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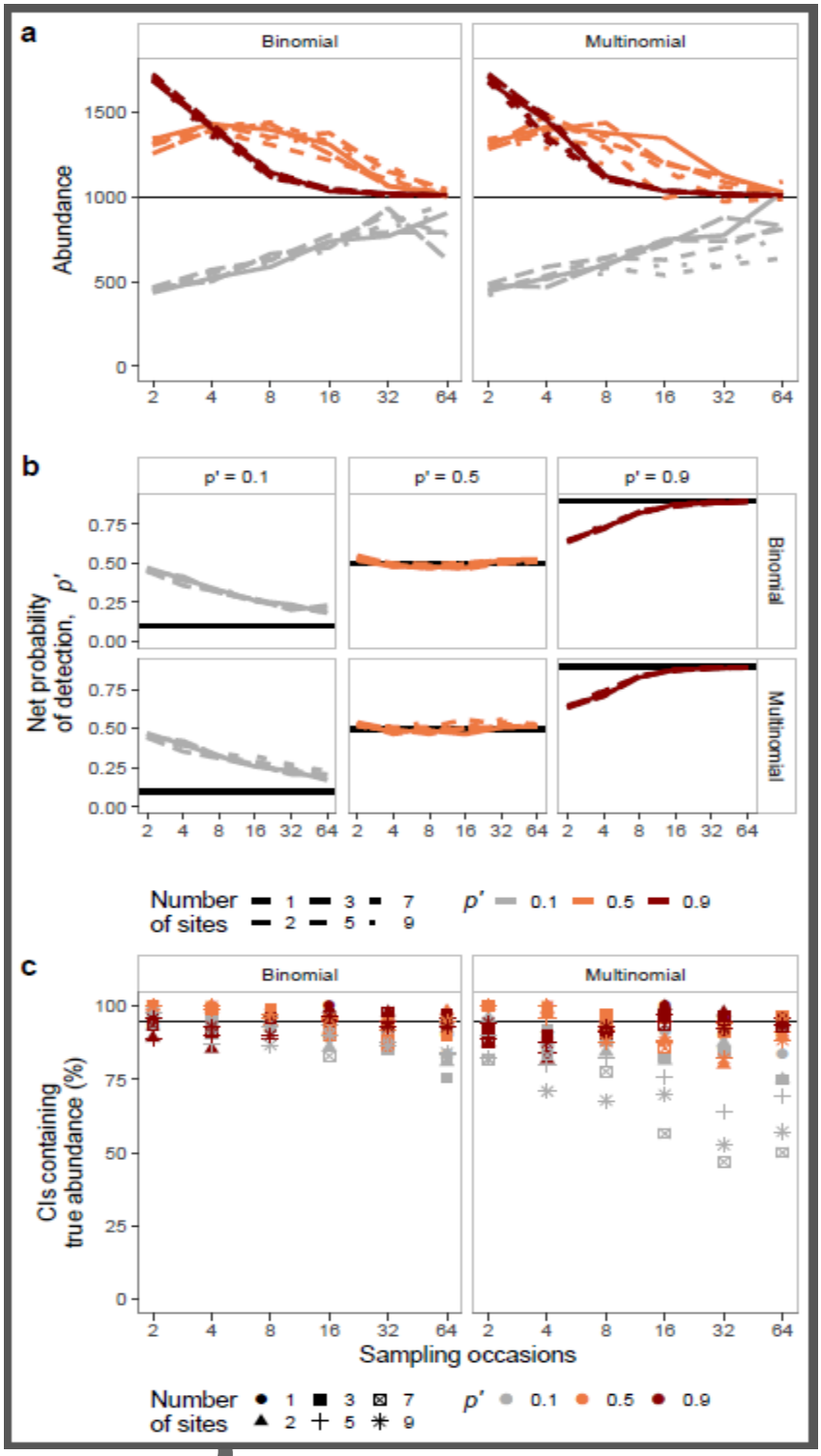

Figure 3. For binomial and multinomial simultaneous-count models, mean estimates of (a) abundance (horizontal line, true value of abundance) and (b) probability of detection (p') relative to number of sampling sites and sampling occasions (horizontal lines, true value of p'). (c) Percentage of 95% CIs for estimate of abundance that include the true value (horizontal line, 95%).

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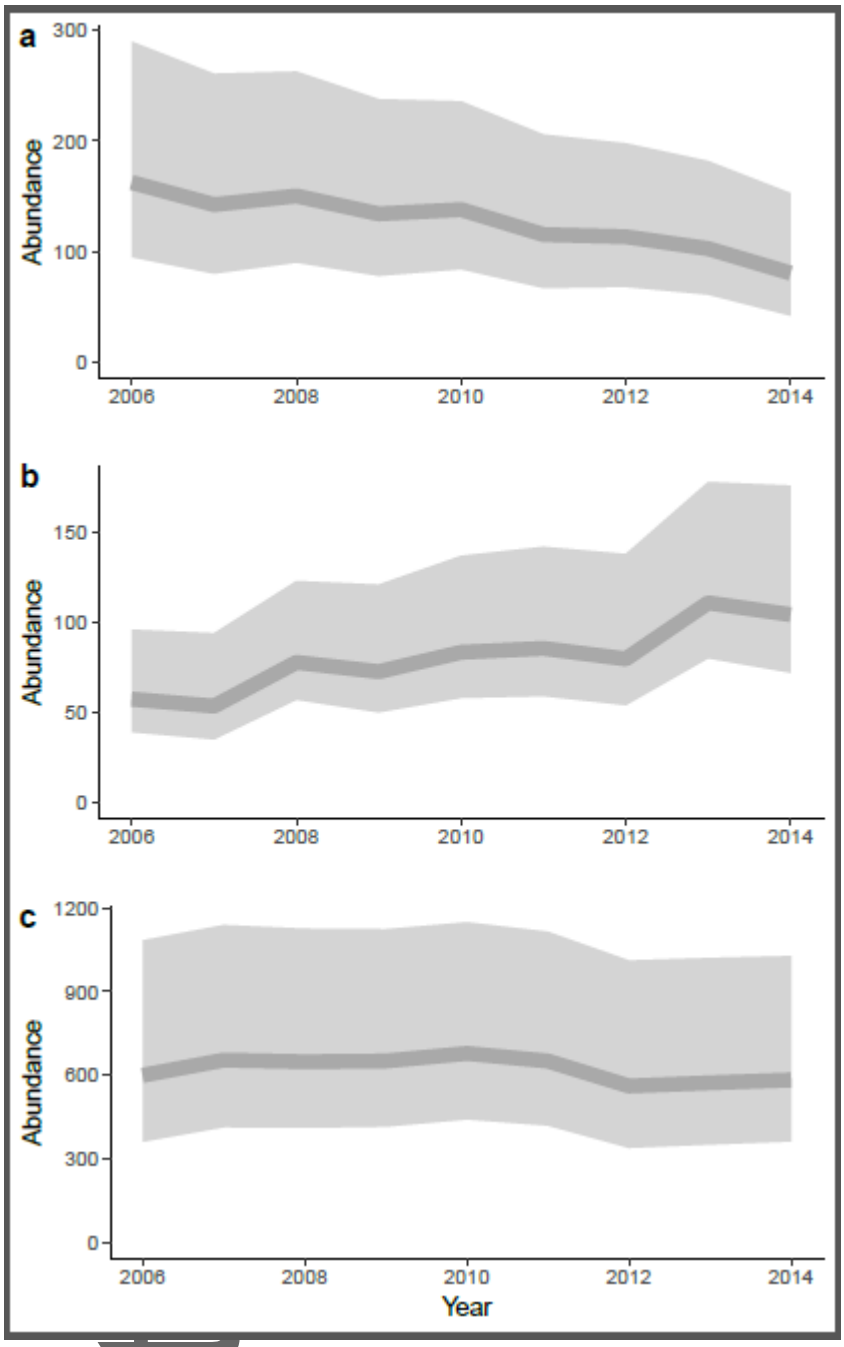

Figure 4. Abundance estimates (shading 95% CI) for Cambodian populations of (a) Red-headed Vulture, (b) Slender-billed Vulture, and (c) White-rumped Vulture, 2006–2014.

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