Special Section: The Value and Utility of Presence–Absence Data to Wildlife Monitoring and Research

ESTIMATING SITE OCCUPANCY AND ABUNDANCE USING INDIRECT DETECTION INDICES

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Abstract: Knowledge of factors influencing animal distribution and abundance is essential in many areas of ecological research, management, and policy-making. Because common methods for modeling and estimating abundance (e.g., capture–recapture, distance sampling) are sometimes not practical for large areas or elusive species, indices are sometimes used as surrogate measures of abundance. We present an extension of the Royle and Nichols (2003) generalization of the MacKenzie et al. (2002) site-occupancy model that incorporates length of the sampling interval into the model for detection probability. As a result, we obtain a modeling framework that shows how useful information can be extracted from a class of index methods we call indirect detection indices (IDIs). Examples of IDIs include scent station, tracking tube, snow track, tracking plate, and hair snare surveys. Our model is maximum likelihood, and it can be used to estimate site occupancy and model factors influencing patterns of occupancy and abundance in space. Under certain circumstances, it can also be used to estimate abundance. We evaluated model properties using Monte Carlo simulations and illustrate the method with tracking tube and scent station data. We believe this model will be a useful tool for determining factors that influence animal distribution and abundance.

JOURNAL OF WILDLIFE MANAGEMENT 69(3):874–883; 2005

Key words: occupancy models, indirect detection indices, population estimation.

Knowledge of animal abundance and the factors influencing abundance is essential in many areas of ecological research (e.g., demography, habitat or treatment effects), management (e.g., pest control, harvest quotas), and policy-making (e.g., species listings). Because it is seldom possible to census populations of interest, abundance is usually estimated by laying forth a set of assumptions and then constructing a statistical model linking data and parameters, so an estimator can be derived. Indeed, the importance of abundance estimators in ecological research and management is affected by the vast array of methods and models available for estimating population size (e.g., Seber 1982, Williams et al. 2002). Most approaches for estimating abundance are based on counts (C) of animals, the expectation (E) of which can be related to population size (N) through the detection probability (p), such that $E[C] = pN$ (Williams et al. 2002). Because C is observable and N is the quantity to be estimated, the problem of estimating animal abundance comes down to estimating p, so we can compute the population size estimate using the natural estimator $\hat{N} = C/\hat{p}$. Numerous models exist for estimating p, the most common of which are based on capture–recapture sampling using marked individuals (Seber 1982, Pollock et al. 1990, Williams et al. 2002) and distance sampling (Buckland et al. 2001). Such models are likelihood-based, allow abundance and other parameters to be modeled as functions covariates (e.g., habitat), and software for estimating parameters is readily available (White and Burnham 1999, Thomas et al. 2002).

Common criticisms of capture–recapture and distance sampling methods are that they are time-consuming, expensive, and difficult to implement. Therefore, they are sometimes not practical when large areas or many populations need to be sampled or when species are elusive or difficult to mark. Consequently, indices that do not require capturing or marking individuals and that can be easily implemented over large areas are often used as surrogate measures of population size (in spite of the loss of strong inference). Indices can be classified as direct, where the index is based on counts of individuals that are present, or indirect, where the index is based on evidence left by an animal (e.g., tracks, hair). For both classes of indices, the underlying premise is that the index (I) is proportional to abundance (N), such that $I = \beta(N)N$. In this expression, $\beta(N)$ may represent a detection probability (p) or per capita rate of cue production, and it might vary as a function of N. In particular, $\beta(N)$ may be monotonic or nonmonotonic, or linear or nonlinear—

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each of which has certain implications for how the index should be interpreted (Williams et al. 2002). Because valid interpretation of indices requires that $\beta(N)$ be known and unchanging, and because this is almost never true in practice, indices are generally of only limited value. In many applications of indices where $\beta(N)$ is unknown, it is tacitly assumed $\beta(N)$ is constant for all N (i.e., $\beta(N) = \beta$) and that it is homogenous such that $\beta_i = \beta_j$ $(i \neq j)$, where the subscript denotes points in time or space (or some arbitrary category). Given these assumptions are true, indices can be used to estimate relative abundance among points: $E[I_1/I_2] \approx E[I_1]/E[I_2] = \beta_1 N_1/\beta_2 N_2 = \beta N_1/\beta N_2 = N_1/N_2$ (Williams et al. 2002). However, without validation of these assumptions, or if there is error in the indices, estimated relative abundance likely will be biased (Barker and Sauer 1992), and conclusions based on the estimate will be unfounded.

Indirect indices are often implemented by establishing detection stations that record visits by the target species over some sampling interval. During the sampling interval, stations may be visited by multiple individuals multiple times, and detection stations do not remove individuals from the population. At the end of the sampling interval the investigator records visits to stations and resets the stations so they can detect visits over the next sampling interval. By reset we mean all evidence of visitation by the target species is removed, erased, flagged, or otherwise labeled by the investigator, so the evidence is not counted as a visit during subsequent checks of the station. Hereafter, we refer to indirect indices that use detection stations that can be reset as IDIs. Examples of IDIs abound in the literature and include scent-station surveys, where the detection station is an attractant-supplemented stake centered in a circle of fine material used as a tracking substrate (Linhart and Knowlton 1975, Conner et al. 1983, Diefenbach et al. 1994); tracking plate surveys, where the detection station is a sooted aluminum plate that records tracks (Barrett 1983, Orloff et al. 1993, Olson and Werner 1999); tracking tube surveys, where the detection station is a tunnel (e.g., PVC pipe) that records tracks on a paper strip lying between marking sources at the tunnel entrances (Glennon et al. 2002, Nams and Gillis 2003); hair snare surveys, where the detection station consists of a snare device (e.g., tape, barbed wire) that collects hair from individuals visiting the station (Mowat and Strobeck 2000, Belant 2003); and snow track surveys, where a snow-covered transect represents the detection station, and visits are recorded by sets of tracks intersecting the transect (the station is reset by new snow or marking existing tracks; Stanley and Bart 1991, Hayward et al. 2002). Indirect indices like scat surveys (Clevenger and Purroy 1996, Harrison et al. 2004, Webbon et al. 2004) or pellet-group surveys (Freddy and Bowden 1983, Mooty et al. 1984, Haerkoenen and Heikkilae 1999), where the detection station is a transect, strip, or plot of land, are normally not considered IDIs because it is usually not possible to locate all of the scat or every pellet group when the station is checked (i.e., detectability is <1; Bulinski and McArthur 2000). Thus, for these indices the detection stations can not be completely reset before the next sampling interval.

Typically, data gathered from IDIs are collapsed into a binary variable (i.e., station was visited/not visited over the sampling interval) and are summarized as the proportion of stations visited. Sometimes these proportions are standardized by the length of the sampling interval (e.g., Nams and Gillis 2003) and are used directly as an abundance index (I) for N, or these proportions are used to compute relative abundance in time or space. In either case, the implicit assumption is that $\beta(N)$ is constant and homogenous. As noted above, however, unless this assumption is verified or $\beta(N)$ is known, the relationship between I and N will be unknown, and the validity of the index will be in question. We present a modeling framework that shows how useful information can be extracted from IDIs when the detection station data are binary. Specifically, we show how IDIs can be used to (1) estimate site occupancy when detectability of individuals is <1, (2) model patterns of abundance in space to identify factors influencing occupancy and abundance, and (3) estimate animal abundance under certain restrictive assumptions.

DATA AND MODEL

We consider a sampling situation where an investigator uses an IDI to gather information about a population of interest and where it is reasonable to assume the population is demographically and geographically closed over the period that sampling occurs. Data collection proceeds by establishing R detection stations laid out in a grid, transect, or some other pattern, that record visits by the species over some sampling interval. At the end of a sampling interval, the investigator checks each station and records the length of the sampling interval and whether it was visited by the target species, and the investigator resets the

station for the next sampling interval (hereafter we assume stations are reset when they are checked). More formally, let i index detection stations ($i = 1,\ldots, R$) and j index sampling occasions (i.e., checks of stations at the end of a sampling interval; $j = 1,\ldots,J_i$; the index on J allows the number of occasions to vary among stations), then the data recorded are w_{ij}, where $w_{ij} = 1$ if the ith station was visited between sampling occasions j and $j - 1$ ($w_{ij} = 0$ otherwise), and t_{ij}, where t_{ij} = the time (e.g., days) elapsing between sampling occasions j and $j - 1$ (we define $j = 0$ to be the occasion on which stations are established). We assume visits recorded at a station during a sampling interval do not vanish before the investigator checks the station (e.g., under windy conditions, snow tracks at a station may disappear before the station is checked). If this assumption is violated, the value recorded for t_{ij} will be incorrect, and this will bias estimated detection probabilities.

Data from IDIs have much in common with data from site-occupancy studies, where a population of sites are surveyed, and presence–absence of the species of interest at each site is determined. In most site-occupancy studies, interest is in the proportion of sites that are occupied, and it is often implicitly assumed that presence-absence can be determined without error. For this to be true, however, it is necessary that the conditional-on-occupancy detection probability equal 1. Recognizing that this is often not the case and that some sites will appear to be unoccupied because animals that were present went undetected, MacKenzie et al. (2002) developed a model for estimating conditional-on-occupancy detection probabilities (p) and occupancy probabilities (ψ) using data from multiple visits to sites. This model was later generalized by Royle and Nichols (2003) to allow abundance at sites to be modeled and estimated using suitable covariates (e.g., habitat). They accomplished this by considering the likelihood to be a mixture of site-specific unconditional detection probabilities that depend on only the number of animals available for detection. Specifically, they modeled the site-specific unconditional detection probability p_i as $1 - (1 - r)^{N_i}$, where r is the detection probability of an individual and N_i is the number of animals available for detection at site i. Royle and Nichols (2003) assumed closure of the site-specific populations (i.e., N_i was constant for each site) and, while not stated explicitly, they also assumed that members of N_i were not members of N_j ($i \neq j$). That is, sites need to be far enough apart so that distinct individuals can not be detected at >1 site (i.e., the site-specific populations sampled are disjoint sets). Under this assumption $N = \Sigma N_i$.

If we consider detection stations in IDI studies to be sites where presence-absence is determined on multiple occasions, and if we assume site-specific populations sampled by IDIs are closed and disjoint, then it is clear IDIs are nearly identical in structure to the occupancy studies considered by Royle and Nichols (2003) and we would expect their model could be applied to IDI data. However, the sampling situation for IDIs differs from that of Royle and Nichols in an important way. Royle and Nichols considered the sampling interval during which presence–absence was determined to be extremely short and constant among sites (in their example the interval was only 5 minutes), whereas sampling intervals for IDIs are usually long (on the order of days) and may vary among sites. Consequently, for IDIs we expect that the unconditional detection probability at a station will depend on the number of animals available for detection at that station (i.e., N_i) and on the length of the sampling interval (i.e., t_{ij}). That is, assuming $N_i > 0$ and remains constant over the sampling interval, then we expect the detection probability at site i to be near 0 if the interval is too short, and if it is too long we expect it to be near 1. Thus, for IDIs we modify the Royle and Nichols (2003) expression for the unconditional detection probability in the following way. Let p_{ij} be the unconditional detection probability for the ith detection station on the jth sampling occasion, and let r be the detection probability of an individual over a unit time interval (conditional on presence); then $p_{ij} = 1 - (1 - r)^{t_{ij}N_i}$. From this expression, which now incorporates the length of the sampling interval (t_{ij}), we see that if $N_i = 0$ then $p_{ij} = 0$, no matter how long the sampling interval is, and if $N_i > 0$ then p_{ij} is in the interval (0, 1) for $t_{ij} > 0$ and increases toward 1 as t_{ij} grows large.

In IDI studies, w_{ij} is the outcome of a Bernoulli trial with parameter p_{ij}, where $p_{ij} = \Pr(w_{ij} = 1 \mid N_i, r) = 1 - (1 - r)^{t_{ij}N_i}$. Thus, if we let $\mathbf{w}_i = (w_{i1}, w_{i2}, \ldots, w_{iJ_i})$, then the likelihood ($L$) for the ith site is:

$$L(r \mid \mathbf{w}_i, N_i) = \prod_{j=1}^{J_i} p_{ij}^{w_{ij}} (1 - p_{ij})^{1-w_{ij}}.$$

Under this model, r is not identifiable because N_i is unknown. Nevertheless, it is possible to estimate r by following the reasoning and steps in

Royle and Nichols (2003). Briefly, we suppose site-specific abundances N_i are realizations of a random variable having discrete probability distribution $f(N \mid \boldsymbol{\lambda})$, where $\boldsymbol{\lambda}$ is a parameter vector and $\Pr(N = k) = f(N = k) = f_k$ $(k = 0, 1, \ldots)$. Under this assumption, we can remove the unobserved N_i from the likelihood by averaging the conditional (on N_i) likelihood over the possible values of N_i. The resulting integrated likelihood is:

$$L(r, \boldsymbol{\lambda} \mid \mathbf{w}_i) = \sum_{k=0}^{K} \left\{ \prod_{j=1}^{J_i} p_{ij}^{\,w_{ij}} (1 - p_{ij})^{1-w_{ij}} \right\} f_k \ ,$$

where here, $p_{ij} = 1 - (1 - r)^{t_{ij}k}$ and K is the number of support points (sensu Royle and Nichols 2003). Then, assuming independence of data from the R detection stations and letting $\mathbf{W} = \{w_{ij}\}$, we take the product over R to yield the full likelihood:

$$L(r, \boldsymbol{\lambda} \mid \mathbf{W}) = \prod_{i=1}^{R} \left[\sum_{k=0}^{K} \left\{ \prod_{j=1}^{J_i} p_{ij}^{\,w_{ij}} (1 - p_{ij})^{1-w_{ij}} \right\} f_k \right] .$$

As was done in Royle and Nichols (2003), we specify a parametric form for f_k (e.g., a Poisson or negative binomial distribution). The Poisson model is appealing because it can be motivated by supposing individuals (i.e., home range centers) are distributed randomly in space according to a homogeneous Poisson point process. Under a Poisson model the parameter, λ, is the expected abundance at the ith site (i.e., $E[N_i] = \lambda$). Thus, we can estimate the probability a species is present at a site (i.e., the occupancy probability of a detection station) as $1 - f(0 \mid \hat{\lambda}) = 1 - \exp(-\hat{\lambda})$, which is qualitatively equivalent to the parameter ψ in MacKenzie et al. (2002). Likewise, as in Royle and Nichols (2003), $\hat{\lambda}$ is an estimate of the average abundance at a site, so when populations are closed and disjoint, overall abundance ($\hat{N}$) can be estimated as $R\hat{\lambda}$.

In many studies, we would expect N_i to exhibit excess variation (i.e., overdispersion) relative to the Poisson model. One approach for dealing with overdispersion is to use a negative-binomial distribution for f_k instead of a Poisson (e.g., Royle and Nichols 2003). We evaluate this approach in the next section. A second approach for accommodating overdispersion is to incorporate covariates thought to influence abundance. For example, habitat measurements are collected as part of many studies, and a common goal is to evaluate the relationship between abundance and these covariates. Covariates can be easily incorporated into a Poisson abundance model using the standard log-linear model relating abundance to covariates. For example, if at station i covariates $x_{i1}, \ldots, x_{ik}$ exist, then the model for λ_i, which is the expected abundance at site i (i.e., $\lambda_i = E[N_i]$), is $\log(\lambda_i) = \alpha_0 + \alpha_1 x_{i1} + \cdots + \alpha_k x_{ik}$. Such models were successfully used by Royle et al. (2004) for modeling the relationship between bird density and habitat covariates under conventional point-counting protocols. In a similar manner, covariates that are thought to affect detection probability can be modeled. For detection covariates, we consider standard linear-logistic models of the form: $\text{logit}(r) = \beta_0 + \beta_1 u_{ij1} + \cdots + \beta_k u_{ijk}$, where $u_{ij1}, \ldots, u_{ijk}$ are the values of k detection covariates measured at site i during visit j. We give 2 examples using covariates for r in the next section.

SIMULATIONS AND EXAMPLES

We evaluated the performance (i.e., bias and precision) of our model with respect to the parameters λ and ψ under 2 simulation scenarios. Our goal was to provide insight into how well the model would be expected to perform under realistic sample sizes, as well as its robustness to assumption violation. Under the first scenario we let the distribution $f(N)$ be Poisson, and we assumed a Poisson model for f_k for our analysis. For these simulations $R = 100$ detection stations, $J_i = 6$ sampling occasions (stations were established on the 0th occasion), and the sampling interval (days) between sampling occasions was $\{t_{ij}\} = (2, 4, 6, 8, 10, 12)$. We investigated 3 other cases for $\{t_{ij}\}$ (i.e., [7, 7, 7, 7, 7, 7], [6, 7, 8, 6, 7, 8], and [1, 1, 1, 13, 13, 13]), but because they yielded similar results we did not report on them here. The levels investigated for r, the detection probability of an individual over a unit time interval, and λ_i, the expected abundance of individuals at site i, were $r \in \{0.05, 0.10, 0.20\}$ and $\lambda_i = \lambda \in \{1.5, 3.0\}$. We averaged results over 1,000 repetitions (Table 1). Under the second scenario, we investi-

Table 1. Performance of our model using simulated data, with $R = 100$, $J_i = 6$, and $\{t_{ij}\} = (2, 4, 6, 8, 10, 12)$ for all i. In these simulations the probability distribution $f(N)$ was Poisson, and for our analysis we modeled f_k as a Poisson. Results are presented for $\psi \in \{0.78, 0.95\}$, and all combinations of $r \in \{0.05, 0.10, 0.20\}$ and $E[N_i] = \lambda \in \{1.5, 3.0\}$, and are averages over 1,000 repetitions.

	$\lambda = 1.5$, $\psi = 0.78$,				$\lambda = 3.0$, $\psi = 0.95$			
r	$\hat{\lambda}$	SE	$\hat{\psi}$	SE	$\hat{\lambda}$	SE	$\hat{\psi}$	SE
0.05	1.53	0.245	0.78	0.050	3.19	0.720	0.95	0.026
0.10	1.52	0.200	0.78	0.043	3.14	0.567	0.95	0.022
0.20	1.51	0.184	0.78	0.040	3.12	0.814	0.95	0.021

Table 2. Performance of our model using simulated data, with $J_i = 6$ and $\{t_{ij}\} = \{2, 4, 6, 8, 10, 12\}$ for all i. In these simulations the probability distribution $f(N)$ was negative binomial with $E[N_i] = \lambda \in \{1.5, 3.0\}$ and CV = 2.0, and for our analysis we modeled f_k as a Poisson or a negative binomial. Results are presented for $\psi \in \{0.65, 0.88\}$ and $r \in \{0.05, 0.10, 0.20\}$ and, except for $\hat{\lambda}_{med}$ (where *med* denotes median), columns are averages over 1,000 repetitions.

		Poisson model for f_k					Negative binomial model for f_k				
R	r	$\hat{\lambda}$	SE	$\hat{\lambda}_{med}$	$\hat{\psi}$	SE	$\hat{\lambda}$	SE	$\hat{\lambda}_{med}$	$\hat{\psi}$	SE
$\lambda = 1.5$, $\psi = 0.65$											
100	0.05	1.04	0.483	1.03	0.64	0.052	1.97	3.078	1.44	0.65	0.062
	0.10	1.09	0.437	1.08	0.66	0.048	1.58	0.506	1.48	0.65	0.047
	0.20	1.08	0.440	1.07	0.66	0.049	1.62	0.604	1.50	0.65	0.047
200	0.05	1.03	0.477	1.03	0.64	0.036	1.67	1.708	1.48	0.65	0.042
	0.10	1.08	0.431	1.08	0.66	0.035	1.54	0.328	1.49	0.65	0.033
	0.20	1.08	0.431	1.08	0.66	0.036	1.53	0.358	1.48	0.65	0.034
$\lambda = 3.0$, $\psi = 0.88$											
100	0.05	2.04	0.999	2.01	0.87	0.038	5.09	10.861	2.84	0.88	0.046
	0.10	2.16	0.881	2.14	0.88	0.031	3.20	1.168	2.94	0.87	0.034
	0.20	2.20	0.851	2.17	0.89	0.032	3.21	1.205	2.88	0.88	0.033
200	0.05	2.03	0.993	2.02	0.87	0.026	3.62	3.880	2.94	0.88	0.031
	0.10	2.15	0.872	2.14	0.88	0.022	3.08	0.788	2.95	0.88	0.024
	0.20	2.17	0.852	2.16	0.88	0.024	3.10	0.811	2.97	0.87	0.024

gated the effect of overdispersion on the performance of our model. We did this by assuming $f(N)$ was negative binomial with $E[N_i] = \lambda \in \{1.5, 3.0\}$ and CV = 2.0, and for our analysis we modeled f_k as a Poisson or a negative binomial. As was true under the first scenario, $J_i = 6$ and $\{t_{ij}\} = \{2, 4, 6, 8, 10, 12\}$. We present results for $R \in \{100, 200\}$, $\psi \in \{0.65, 0.88\}$, and $r \in \{0.05, 0.10, 0.20\}$ as averages over 1,000 repetitions (Table 2).

Under the first scenario, we found that $\hat{\lambda}$ had a small but positive bias (Table 1), which was consistent with the simulation results obtained by Royle and Nichols (2003). Coefficients of variation for $\hat{\lambda}$ ranged from 13% to 22%. With respect to $\hat{\psi}$, our model performed very well, and estimates were essentially unbiased. Coefficients of variation for $\hat{\psi}$ ranged from 2% to 6%. Under the second scenario, we found that when the $\{N_i\}$ exhibited excess variation but were analyzed under a Poisson, which did not account for overdispersion, $\hat{\lambda}$ was strongly negatively biased (for our simulations relative bias was approximately −30%). However, in these same simulations $\hat{\psi}$ was essentially unbiased and was robust to the presence of excess variation in the $\{N_i\}$, even though a less-than-optimal model was used for f_k. When we analyzed the data under a model that accounted for overdispersion, specifically the negative binomial, our estimates of λ improved substantially, except at the lowest values of r. For $r = 0.05$, $\hat{\lambda}$ was positively biased, whereas the median value for $\hat{\lambda}$ was centered near the true value of λ (Table 2). This, in combination with the large standard errors, suggested the sampling distribution for $\hat{\lambda}$ was strongly skewed (heavy right tail). Instability of estimates, like that we observed for $\hat{\lambda}$, is common when certain model parameters are near a boundary (in this case r was near 0). We suggest that when fitting real data, investigators examine the condition number of the Hessian matrix for their parameters to see if it is large. If it is, then it is likely the matrix is ill-conditioned (Schneider 1987:427) and the optimization routine will yield a poor estimate of λ. For $r = 0.10$ and $r = 0.20$ the sampling distributions for $\hat{\lambda}$ also appeared to be skewed, but only slightly, and in these cases we got reasonably good estimates, especially for $R = 200$. Under the negative binomial model for f_k, $\hat{\psi}$ was unbiased in nearly every case we investigated.

Example 1 – Tracking Tubes For Small Mammals

Nams and Gillis (2003) described a study wherein tracking tubes were used to index small mammals in a boreal forest region of northern Nova Scotia, Canada. One of their goals was to determine whether small mammals change in their tendency to enter tracking tubes with the cumulative length of time a tube had been in place (i.e., a time effect). In terms of our notation, they were interested in whether r was constant (i.e., a no-time-effect model) or whether r increased or decreased with cumulative length of time (i.e., a time-effect model). Nams and Gillis (2003) recorded the number of sets of tracks entering a tube over a sampling occasion, the length of sampling occasions (days), and species if it could be determined. Dr. Vilis O. Nams (Nova Scotia Agricultural College, Nova Scotia, Canada) provided us with his data for 12 lines of tracking tubes having 80 tubes per line (thus $R = 960$), each of which were rechecked 5, 6, or 8 times (i.e., $J_i \in \{5, 6, 8\}$) over a 4-week period. We collapsed the Nams and Gillis (2003) data for individual tubes into a binary variable, where 1

Table 3. Analytical results for the Nams and Gillis (2003) tracking tube data under a Poisson model for f_k, and a negative binomial model for f_k. The covariate model includes a time-effect representing the cumulative length of time tubes had been in place. For *Peromyscus maniculatus* a solution could not be obtained for the negative binomial model. Akaike Information Criterion (AIC) values with boldface type indicate the models best supported by the data.

	No-covariate model					Covariate model						
Species	$\hat{\beta}_0$	SE	$\hat{\lambda}$	SE	AIC	$\hat{\beta}_0$	SE	$\hat{\beta}_1$	SE	$\hat{\lambda}$	SE	AIC
Poisson model for f_k												
Clethrionomys gapperi	−3.7	0.11	0.37	0.039	1,809.3	−3.8	0.11	0.10	0.049	0.37	0.036	1,809.5
Peromyscus maniculatus	−4.6	0.20	0.76	0.170	1,706.1	−4.6	0.15	0.29	0.054	0.58	0.073	**1,698.8**
Sorex spp.	−3.3	0.06	0.75	0.045	3,779.5	−3.3	0.06	0.21	0.035	0.67	0.034	3,769.5
Negative binomial model for f_k												
Clethrionomys gapperi	−4.2	0.749	0.59	0.442	1,811.0	−4.2	0.75	0.14	0.306	0.59	0.439	**1,802.2**
Peromyscus maniculatus	–	–	–	–	–	–	–	–	–	–	–	–
Sorex spp.	−3.5	0.271	0.96	0.260	3,780.9	−3.6	0.28	0.15	0.018	0.99	0.276	**3,748.1**

denoted the tube was used at least once over the sampling occasion (0 otherwise), and we analyzed these data under a no-time-effect model for r and a time-effect model for r. Specifically, for the no-time-effect model $\text{logit}(r) = \beta_0$, whereas for the time-effect model $\text{logit}(r) = \beta_0 + \beta_1 u_{ij}$, where u_{ij} was the cumulative length of time the tracking tube had been in place on the jth occasion. A result with $\beta_1 < 0$ would indicate tracking tube use decreased with cumulative length of time, whereas a result with $\beta_1 > 0$ would indicate tracking tube use increased with cumulative length of time.

We analyzed the Nams and Gillis (2003) data for 2 species and 1 genus, under both Poisson and negative binomial models for f_k (Table 3). Using the Akaike Information Criterion (AIC) to identify the model best supported by the data (Akaike 1973, Burnham and Anderson 2002), we found that a positive time-effect model was selected for all species. Thus our analysis agreed with that of Nams and Gillis (2003); tracking tube use increased with the length of time the tubes had been in place. For both *Clethrionomys gapperi* and *Sorex* spp., AIC selected the negative binomial model for f_k over the Poisson, indicating there may have been some overdispersion in the data. Using the following form of the negative binomial (e.g., Lawless 1987):

$$\Pr(N_i = k) = \frac{\Gamma(k+\theta)}{k!\Gamma(\theta)}\left(\frac{(1/\theta)\lambda}{1+(1/\theta)\lambda}\right)^k\left(\frac{1}{1+(1/\theta)\lambda}\right)^\theta,$$

where λ and θ are the parameters, $E[N_i] = \lambda$, and $\text{Var}[N_i] = \lambda + \lambda^2/\theta$, we get $\psi = 1 - \Pr(N_i = 0) = 1 - [1 + (1/\theta)\lambda]^{-\theta}$. For *C. gapperi*, $\hat{\lambda} = 0.59$ and $\hat{\theta} = 0.795$, thus $\hat{\psi} = 0.36$ and $\hat{N} = R\hat{\lambda} = 566$. Likewise, for *Sorex*, $\hat{\lambda} = 0.99$ and $\hat{\theta} = 2.15$, thus $\hat{\psi} = 0.56$ and $\hat{N} = R\hat{\lambda} = 950$. For *Peromyscus maniculatus*, no solution could be found for the negative binomial model, so we used the Poisson to estimate ψ and N. Here, $\hat{\lambda} = 0.58$, so $\hat{\psi} = 1 - \exp(-\hat{\lambda}) = 0.44$ and $\hat{N} = R\hat{\lambda} = 557$.

Example 2 – Scent Stations

Scent stations have a long history of use for monitoring coyote (*Canis latrans*) and other mammal populations over large areas. Hein and Andelt (1994) described a study at the Rocky Mountain Arsenal, Colorado, where 60 scent stations, separated by an average distance of 1.1 km, were used to index deer, rodent, lagomorph, and coyote numbers. Scent stations were monitored daily for 2 weeks, with half the stations receiving a supplemental deer carcass the first week and the other half receiving a supplemental deer carcass the second week. Hein and Andelt concluded that coyotes visited sites with carcasses more than sites without carcasses but that the presence of deer carcasses did not influence visitation by deer, rodents, or lagomorphs. Dr. William F. Andelt (Colorado State University, Fort Collins, Colorado) provided us with the raw data from Hein and Andelt (1994), which we reanalyzed under our model. We evaluated 2 models; the first was a no-carcass-covariate model where $\text{logit}(r) = \beta_0$, and the second was a carcass-covariate model, where $\text{logit}(r) = \beta_0 + \beta_1 u_{ij}$ and u_{ij} was an indicator variable equal to 1 if a carcass was present at the ith station on the jth occasion (0 otherwise). We evaluated the Poisson and negative binomial models for f_k. However, we only pre-

Table 4. Analytical results for the Hein and Andelt (1994) scent station data under a Poisson model for f_k (a solution could not be obtained under the negative binomial model for any of the species). The covariate model includes a carcass effect (see text). Akaike Information Criterion (AIC) values with boldface type indicate the models best supported by the data.

	No-covariate model					Covariate model						
Species	$\hat{\beta}_0$	SE	$\hat{\lambda}$	SE	AIC	$\hat{\beta}_0$	SE	$\hat{\beta}_1$	SE	$\hat{\lambda}$	SE	AIC
Lagomorph	0.24	0.031	0.80	0.121	**341.0**	0.25	0.039	0.23	0.039	0.81	0.122	342.9
Rodent	0.28	0.039	3.17	0.480	**536.2**	0.28	0.043	0.28	0.042	3.18	0.481	538.2
Deer	0.09	0.029	2.16	0.711	**383.1**	0.07	0.027	0.10	0.033	2.22	0.753	384.3
Coyote	0.08	0.031	5.11	1.973	537.9	0.04	0.026	0.06	0.044	8.47	5.970	**532.5**

sent results for the Poisson model (Table 4) because for all species the likelihood was maximized at the boundary when we used the negative binomial.

Our results are in agreement with those of Hein and Andelt (1994); coyotes used scent stations with a supplemental deer carcass more often than stations without a supplemental deer carcass, whereas deer, rodent, and lagomorphs did not. Under the Poisson model occupancy was estimated as $\hat{\psi} = 1 - \exp(-\hat{\lambda})$, which for lagomorphs, rodents, deer, and coyotes yielded 0.55, 0.96, 0.88, and 1.00, respectively. Likewise, for $\hat{N}$ (where $R = 60$) we got 48, 190, 130, and 508, respectively (see DISCUSSION for the probable cause of the rather large numbers for deer and coyotes).

DISCUSSION

The model of Royle and Nichols (2003) was motivated, in part, as a means of developing estimators of site-occupancy (sensu MacKenzie et al. 2002) that accommodate heterogeneity in the probability a species will be detected at a site due to variation in abundance. Our model extends the Royle and Nichols (2003) model by explicitly incorporating the length of the sampling interval into this probability. As a consequence, we obtain a model that allows useful information to be extracted from IDIs when the detection station data are binary. Specifically, our model shows how data from IDIs can be used to estimate site occupancy, model factors influencing patterns of occupancy and abundance in space, and estimate abundance under certain circumstances.

Our simulations (Tables 1, 2) showed site-occupancy estimates under our model were robust to the parametric form chosen for f_k. When we simulated abundance data at detection stations under a Poisson and analyzed them under a Poisson, estimates were unbiased, as we expected. Moreover, when we simulated abundance data at detection stations in a manner incorporating overdispersion relative to the Poisson (i.e., using a negative binomial), site-occupancy estimates were unbiased under a negative binomial model but were also unbiased under a Poisson model. Thus, $\hat{\psi}$ appeared insensitive to model choice for the cases we examined and, with respect to occupancy estimation, suggested our model would perform well in practice.

In contrast to $\hat{\psi}$, our abundance estimate $\hat{\lambda}$ was sensitive to the parametric form chosen for f_k. When abundance at detection stations was simulated under a negative binomial to produce overdispersion relative to the Poisson, estimates under a negative binomial model were relatively good, though there was some positive bias when detectability was low (i.e., $r = 0.05$). However, when we analyzed those same data under a Poisson model for f_k, estimates of λ were strongly negatively biased (Table 2). It therefore seems preferable to accommodate overdispersion in the data by using biologically relevant covariates and an appropriate link function, because in real-world datasets it is common to find excess variation of some form in the $\{N_i\}$ and because we typically will not know the form this excess variation will take, so we will not know the appropriate model to use. Whereas we did not evaluate the use of covariates for λ, the approach was used successfully in other studies (Royle et al. 2004), and we believe it merits further investigation for our model. The covariate approach has the added advantage that it can provide information on habitat or other factors that might influence patterns of occupancy or abundance.

The tracking tube and scent station examples we provided illustrate some of the strengths and weaknesses of our model. A strength is that we now have a model linking data from IDI studies with parameters of interest, namely site occupancy and abundance. We are no longer forced to treat data from IDIs as indices having an unknown relationship with the parameter(s) of interest. Another strength is that the model offers a flexible framework for evaluating covariates. By using a covariate in the tracking tube example, we learned tubes were used more fre-

quently the longer they were in place, and by using a covariate in the scent station example, we learned carcasses increased coyote visitation but had no effect on the other species monitored. This information should prove useful in the design of future studies using these methods.

A weakness of our model is that results from our model could be misleading if model assumptions are ignored. Our estimate of population size ($\hat{N}$) exploits the fact that if $\hat{\lambda}_i$ is an estimate of the station-specific population at risk of detection (analogous to the population at risk of capture in a capture–recapture context), then the sum of $\hat{\lambda}_i$ over the R detection stations is an estimate of the population at risk of detection. However, the veracity of this estimate is predicated on the assumption that detection stations are far enough apart that station-specific populations at risk of detection do not overlap (i.e., they are disjoint sets). Even though $\hat{\lambda}_i$ is an asymptotically unbiased estimate of the population at risk of detection for the ith station, if some individuals at this station are also at risk of detection at the jth station ($i \neq j$), then summing these estimates will create a positive bias in $\hat{N}$ because some individuals are double counted. We believe this explains the high values we observed for deer and coyotes in our scent station example above. Both deer and coyotes are wide-ranging animals (e.g., coyotes can travel 4 km a night; Nowak 1991), yet the spacing of the scent stations averaged only 1.1 km. Thus, it seems certain that some individuals were detected at multiple stations, and that our estimate of 508 for coyotes was positively biased. Indeed, Hein and Andelt (1995) sampled the same area less than a year later, and using mark-resight methods, they estimated the population of coyotes to be only 73 individuals.

The problem of double counting in IDIs and the need to have adequate spacing between stations has been recognized by others. For example, Diefenbach et al. (1994) recommended that scent stations be far enough apart that bobcats (*Lynx rufus*) could not visit >1 station, and Zielinski and Stauffer (1996) spaced track plates for fisher (*Martes pennanti*) and marten (*M. americana*) a distance of twice the diameter of the mean male home range to ensure independence of stations. Our scent station example underscores the importance of spacing stations far enough apart that station-specific populations at risk of detection are disjoint sets, and this should serve as a warning to investigators using this method to estimate abundance. Moreover, it suggests that whenever possible the focus of IDI studies should be on modeling factors influencing λ_i, rather than estimating N. In ecological research this will often be possible because we are typically more interested in comparing occupancy or abundance in time or space to evaluate treatment or habitat effects—and these effects can be built into the model explicitly using the log link—than in determining absolute abundance.

An issue related to that of detection station spacing is the effective area of detection of a station. For some territorial species near carrying capacity, we might expect home range sizes to increase as species density decreases or to decrease as species density increases. In such cases, the effective area sampled by a detection station may change as a function of density; at low species density we might expect the effective area sampled to be larger than at high species density. One consequence of this effect is that abundance estimates for 2 areas could be identical, in spite of the fact that densities differ. The severity and pervasiveness of this problem is currently unknown, and it merits further research, as it is relevant to any method where abundance, rather than density, is being estimated. For species that are not territorial, or species that are territorial but are well below carrying capacity, we would not expect this situation to occur.

Several extensions of the model we presented will be important for increasing its applicability. One that we are currently investigating is to generalize the model to accommodate data other than binary detection data. Many IDI sampling methods yield data that are more informative than simple presence/absence data, in the form of counts of visits to each station. This extra information can be exploited in the model we described previously. Under the special case where the number of visits recorded are of unique individuals, the model proposed by Royle (2004) is directly applicable. More commonly, it is not possible to determine the number of distinct individuals visiting a station, just the total number of visits, say T_i. In this case, one plausible model is to assume that each of the N_i individuals visit station i m_j times (for individuals $j = 1, 2, \ldots, N_i$) and that m_j has a Poisson distribution with parameter θ, the visitation intensity of individuals in the local population. When the stations are visited multiple times, subject to closure of the population, this additional parameter can be estimated using a mixture model analogous to that proposed by Royle (2004). Indeed, simple moment estimators of θ and λ are available under this Poisson-Pois-

son mixture model, and it can be shown that $\hat{\theta} = [\mathrm{Var}(T_i)/\mathrm{Mean}(T_i)] - 1$ and that $\hat{\lambda} = \mathrm{Mean}(T_i)/\hat{\theta}$. More detailed evaluation of such models is necessary, and this is an area of ongoing research for us.

MANAGEMENT IMPLICATIONS

In management settings, a common goal is to determine the distribution and abundance of a species over some area or region of interest and to identify factors influencing distribution and abundance. Our model is a tool that can be used to accomplish that goal, at small and large scales, for species that typically can be detected only indirectly (e.g., by tracks or hair). When setting up an IDI study that will be analyzed under our model, it is crucial that there be an adequate number of stations (usually in excess of 100), that stations can be completely reset each time they are checked, that stations are checked multiple times (e.g., >5), and that stations are far enough apart that a member of the target species can not visit >1 station over the duration of the study. This latter requirement can often be met by determining the average length of the major axis of home range size (e.g., from literature), then spacing stations a distance greater than mean length plus 2 standard deviations. In the case of snow track surveys, where detection stations are not points as they are for many other IDI methods, we might for example specify a straight-line route where we record presence or absence of tracks intersecting a 1.6-km segment of road (i.e., the detection station), then travel a distance of 8 km (more or less depending on the home range size of the target species) before recording presence or absence of tracks intersecting the next 1.6-km segment of road.

Our simulation results suggested that site-occupancy estimates under our model are robust but that abundance estimates are sensitive to model assumptions. We therefore caution the reader to closely examine assumptions if abundance estimates are the goal. In some cases, it may even be beneficial to verify estimates under our model using a double sampling approach, where more intensive methods are used to estimate abundance for a randomly selected subset of the detection stations.

ACKNOWLEDGMENTS

We express our sincere thanks to W. F. Andelt and V. O. Nams for providing us with the data used in our examples. W. Andelt, R. Barker, P. Cryan, A. Ellingson, C. Vojta, and an anonymous referee provided helpful comments on an earlier draft of this manuscript. This work was funded by the U.S. Geological Survey, Fort Collins Science Center, and the U.S. Geological Survey, Patuxent Wildlife Research Center.

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Associate Editor: Vojta.