Journal of Applied Ecology

Journal of Applied Ecology 2008, **45**, 1321–1329 doi: 10.1111/j.1365-2664.2008.01509.x

Multi-scale occupancy estimation and modelling using multiple detection methods

James D. Nichols[1]*, Larissa L. Bailey[1], Allan F. O'Connell Jr.[2], Neil W. Talancy[3], Evan H. Campbell Grant[1], Andrew T. Gilbert[4], Elizabeth M. Annand[5], Thomas P. Husband[3] and James E. Hines[1]

[1]USGS Patuxent Wildlife Research Centre, 12100 Beech Forest Road, Laurel, MD 20708, USA; [2]USGS Patuxent Wildlife Research Centre, 10300 Baltimore Avenue, Beltsville, MD 20705, USA; [3]University of Rhode Island, Department of Natural Resources Science, 1 Greenhouse Road, Kingston, RI 02881, USA; [4]USGS Patuxent Wildlife Research Centre, 196 Whitten Road, Augusta, ME 04330, USA; [5]IAP Worldwide Services, Inc., 7315 North Atlantic Avenue, Cape Canaveral, FL 32920, USA

Summary

1. Occupancy estimation and modelling based on detection–nondetection data provide an effective way of exploring change in a species' distribution across time and space in cases where the species is not always detected with certainty. Today, many monitoring programmes target multiple species, or life stages within a species, requiring the use of multiple detection methods. When multiple methods or devices are used at the same sample sites, animals can be detected by more than one method.

2. We develop occupancy models for multiple detection methods that permit simultaneous use of data from all methods for inference about method-specific detection probabilities. Moreover, the approach permits estimation of occupancy at two spatial scales: the larger scale corresponds to species' use of a sample unit, whereas the smaller scale corresponds to presence of the species at the local sample station or site.

3. We apply the models to data collected on two different vertebrate species: striped skunks *Mephitis mephitis* and red salamanders *Pseudotriton ruber*. For striped skunks, large-scale occupancy estimates were consistent between two sampling seasons. Small-scale occupancy probabilities were slightly lower in the late winter/spring when skunks tend to conserve energy, and movements are limited to males in search of females for breeding. There was strong evidence of method-specific detection probabilities for skunks. As anticipated, large- and small-scale occupancy areas completely overlapped for red salamanders. The analyses provided weak evidence of method-specific detection probabilities for this species.

4. *Synthesis and applications.* Increasingly, many studies are utilizing multiple detection methods at sampling locations. The modelling approach presented here makes efficient use of detections from multiple methods to estimate occupancy probabilities at two spatial scales and to compare detection probabilities associated with different detection methods. The models can be viewed as another variation of Pollock's robust design and may be applicable to a wide variety of scenarios where species occur in an area but are not always near the sampled locations. The estimation approach is likely to be especially useful in multispecies conservation programmes by providing efficient estimates using multiple detection devices and by providing device-specific detection probability estimates for use in survey design.

Key-words: detection probability, model, occupancy, Pollock's robust design, red salamander, sampling, striped skunk

---

*Correspondence author. E-mail: jnichols@usgs.gov

Introduction

Recent attention in conservation biology has focused on the concept of multiple-species conservation in the context of protecting endangered species and assessing biodiversity within entire communities (Barrows *et al.* 2005; Buckland *et al.* 2005). To meet this challenge, monitoring programmes are being developed where multiple detection methods are deployed within a sample unit to detect multiple species of a given taxon (Sorensen, Coddington & Scharff 2002; Manley *et al.* 2004, 2005; O'Connell *et al.* 2006), or individuals of various sizes or life-history phases for a given species (Smith *et al.* 2006; Mattfeldt & Grant 2007). Under such designs, data from these detection methods may simply be combined to indicate whether or not the taxon or group of interest was detected by at least one method. Data from multiple-method designs are sometimes used to test the effectiveness of the different detection methods (Bailey *et al.* 2004; O'Connell *et al.* 2006, Mattfeldt & Grant 2007). Studies directed at such tests might use separate analyses for each detection method and then compare resulting estimates of detection and occupancy probabilities (Bailey *et al.* 2004), or each method may be designated as a unique sampling occasion in a robust design analysis (O'Connell *et al.* 2006; Mattfeldt & Grant 2007). This latter approach ignores the lack of independence among detections from multiple methods induced by the possibility of individual animals being detected by more than one method within a sampling occasion. Use of multiple, single-method analyses is inefficient, as it ignores information from all but the focal detection method.

In this study, we develop models for multiple detection methods that permit simultaneous use of data from all methods for inference about method-specific detection probabilities. The approach not only deals with the lack of independence of detections within a sampling occasion, but also exploits this dependence to permit inference about scale-specific occupancy. Specifically, we estimate parameters associated with both large- and small-scale occupancy (defined below). We first describe the model and then present two example applications. Finally, we discuss uses and extensions of the approach.

Model

The model was initially developed for use with remote sampling devices, and this description reflects that motivation, although the approach applies to any situation in which multiple detection methods are used in the same locations. Consider a sampling design in which L different detection or sampling devices are deployed at each of S sample stations for K occasions. Each station samples a sample unit, which may be larger in area than the station itself. We consider single-season models (e.g., MacKenzie *et al.* 2002, 2006) and thus assume closure over the K occasions. Thus, a sample unit is either occupied for all occasions or not occupied, and there are no changes in occupancy status over the course of the study. In the situation where the sample unit naturally includes all movements of the animals belonging to the target species (e.g. fish in a pond, carnivores on a barrier island), closure refers to species presence or absence at every sampling occasion. In the more general situation, occupancy refers to member(s) of the target species having some non-negligible probability of being present in the sample unit at every sampling occasion, and the definition of closure is based on whether this is true or not for the species. The design can be viewed as a robust design (Pollock 1982; Mackenzie *et al.* 2003). However, the modelling differs from that of MacKenzie *et al.* (2003) in that we do not model seasonal colonizations and extinctions, but simply presence or absence at the sample unit. The detection history data summary reflects the robust design perspective. For example, consider a study with $L = 3$ detection devices, $K = 2$ sampling occasions and a detection history of $H_i = 011\ 010$. The species of interest was detected by devices 2 and 3 at sampling occasion 1 and only by device 2 at sample occasion 2.

Define the following parameters:

p_t^s = Pr (detection at occasion t by device s | sample unit occupied and species present at immediate sample station site); ψ = Pr (sample unit occupied); θ_t = Pr (species present at immediate sample site at occasion t | sample unit occupied).

The two occupancy parameters, ψ and θ_t permit the modelling of occupancy at two different spatial scales. The basic occupancy parameter, ψ, corresponds to species occurrence at the larger scale, as described above, where member(s) of the species have some non-negligible probability of being present at the sample unit and hence exposed to the detection devices. The occupancy parameters for the smaller scale, θ_t, refer to the presence of member(s) of the target species at the sample station site where the detection methods are collocated, conditional on species presence in the sample unit. This probability accounts for situations in which member(s) of the species may be present at the immediate sample site at some times and sample occasions, t, but not at others. Because of the closure assumption, the large-scale occupancy probability, ψ, applies to all of the sample occasions. In addition to this larger scale occupancy, the product $\psi\theta_t$ represents the probability of small-scale occupancy, indicating presence of individual(s) of the species at the local site exposed to detection devices at sampling occasion t. The product $\psi(1 - \theta_t)$ indicates occupancy at the large scale, but not at the small scale, for sampling occasion t. Stated differently, the species may be temporarily unavailable for detection because members are not in the immediate vicinity of the detection devices.

In order to illustrate the modelling, consider the following detection history: 010 000. This history indicates a study with $L = 3$ detection devices and $K = 2$ sample occasions. The target species was detected by device 2 at occasion 1 and went undetected by all devices at occasion 2. The probability of this history can be written as:

$$\Pr(010\ 000) =$$

$$\psi\left[\theta_1(1 - p_1^1)p_1^2(1 - p_1^3)[(1 - \theta_2) + \theta_2\prod_{s=1}^{L}(1 - p_2^s)\right].$$

The sample unit is known to be occupied (associated probability ψ) because the species was detected at some time during the sampling. Similarly, the species was known to have been present at the immediate sample site at occasion 1 (associated probability θ_1), because it was detected by one of the devices then. The product $(1-p_1^1)p_1^2(1-p_1^3)$ indicates detection by device 2, but not by devices 1 and 3 at occasion 1. The sum within the interior brackets specifies the two possible ways of obtaining no detections (000) during occasion 2. The first term, $(1-\theta_2)$, is the probability that the species was not locally present at the immediate sample site at occasion 2. The second term, $\theta_2\Pi_{s=1}^{3}(1-p_2^s)$, denotes the probability that member(s) of the species were present at the immediate sample site at occasion 2 but simply not detected by any of the devices.

Now consider the detection history for a site with no detections by any device at either sample occasion, 000 000. The probability associated with this history can be written as:

$$\Pr(000\,000) = (1-\psi) + \psi(1-\theta_1)(1-\theta_2) + \psi\theta_1(1-\theta_2)\prod_{s=1}^{3}(1-p_1^s) + \psi(1-\theta_1)\theta_2\prod_{s=1}^{3}(1-p_2^s) + \psi\theta_1\theta_2\prod_{s=1}^{3}(1-p_1^s)(1-p_2^s).$$

The first of these five additive terms reflects the probability that the sampled unit was not occupied (no occupancy at the larger scale). Hence, there are no multiplicative terms for small-scale occupancy or detection probabilities. The second additive term is the probability that the sample unit was occupied, but that members of the species were not present at the immediate sample site during either occasion 1 or 2. The third additive term denotes the probability that the species was present at the immediate sample site at occasion 1, but simply not detected then, and not present at occasion 2. The fourth additive term denotes presence at the immediate sample site at occasion 2, but no detection then, and no presence at occasion 1. The final term is the probability that members of the species were present at the immediate sample site at both occasions 1 and 2, but went undetected by all devices at both occasions.

As in other occupancy modelling, the likelihood is proportional to the product of probabilities corresponding to the detection histories for the set of sample units surveyed in the study:

$$L(\underline{\psi}, \underline{\theta}, \underline{p} \mid \underline{H}) \propto \prod_{i=1}^{S}\Pr(H_i),$$

where underlines denote vectors and matrices of parameters and detection data. All parameters can be modelled as functions of site-specific covariates. Probabilities of detection and presence at the immediate sample site can also be modelled as functions of covariates associated with sampling occasions, t. The efficacy of different models can be assessed via likelihood ratio tests or model selection (MacKenzie *et al.* 2006). For example, inference about the utility of different detection devices might be based on one model with method-specific detection probabilities (p_t^s) and another with detection probabilities constant for all methods (p_t), with formal evaluation via model selection or a likelihood ratio test.

We note that the above distinction between occupancy at two scales will usually imply some minimal time interval between sampling occasions. The occasions must be sufficiently far apart (e.g. a period of at least 1 day) that it is reasonable for members of a species to be present at the immediate sample location during one occasion and not during another. This consideration brings up another point. Although our focus in this study is on multiple sampling methods applied simultaneously, we note that application of a single method at two different time-scales (essentially a within-season robust design, see Pollock 1982) may also yield data that can be modelled similarly. For example, if birds were sampled by point counts for nine consecutive minutes divided into three 3-min samples ($L = 3$) for each of K different days in a season, then a similar modelling approach could be used, producing inferences at two spatial scales. Clearly, the appropriate time-scales will depend on the sampling methods and, most importantly, on the species and biological question(s) of interest.

We note that this new parameterization is not required in order to obtain unbiased estimates of large-scale occupancy, $\hat{\psi}$. In the above example, it is possible to simply collapse the detection data from the three devices at each sampling occasion to reflect detection by at least one device or non-detection by all devices. The example detection history used above, 010 000, would simply be rewritten as: 1 0. The first three device-specific detection entries are collapsed to yield 1 for the first occasion, whereas the second three entries are collapsed to yield 0 for the second occasion. Analysis of data collapsed in this manner provides unbiased estimates of ψ and p_t, with the caveat that detection probability for occasion t is now redefined as the product of the probabilities of presence in the immediate sample location and detection conditional on presence in the immediate sample location, $\theta_t[1-\Pi_{s=1}^{L}(1-p_t^s)]$. The utility of the modelling approach described here is to provide efficient inference about θ_t and device-specific detection.

Example analysis 1: striped skunks *Mephitis mephitis*

SAMPLING DESIGN AND DATA

We apply the above model to data for striped skunks collected via surveys for carnivores conducted in 2004 at eight national parks in the northeastern USA (see Fig. S1, Supplementary Material). Details on the study design and sampling protocols are described in Talancy (2005). Briefly, the parks range in size from 24 to 1378 ha and are located in the Temperate Broadleaf and Mixed Forest biomes (Olson *et al.* 2001). Sample units were chosen using a stratified (based on vegetation categories), systematic sampling design with two levels of randomization: (i) a random start within a 100 × 100 m (1 ha) grid overlaid onto a map of each park and (ii) random selection of a 'site'

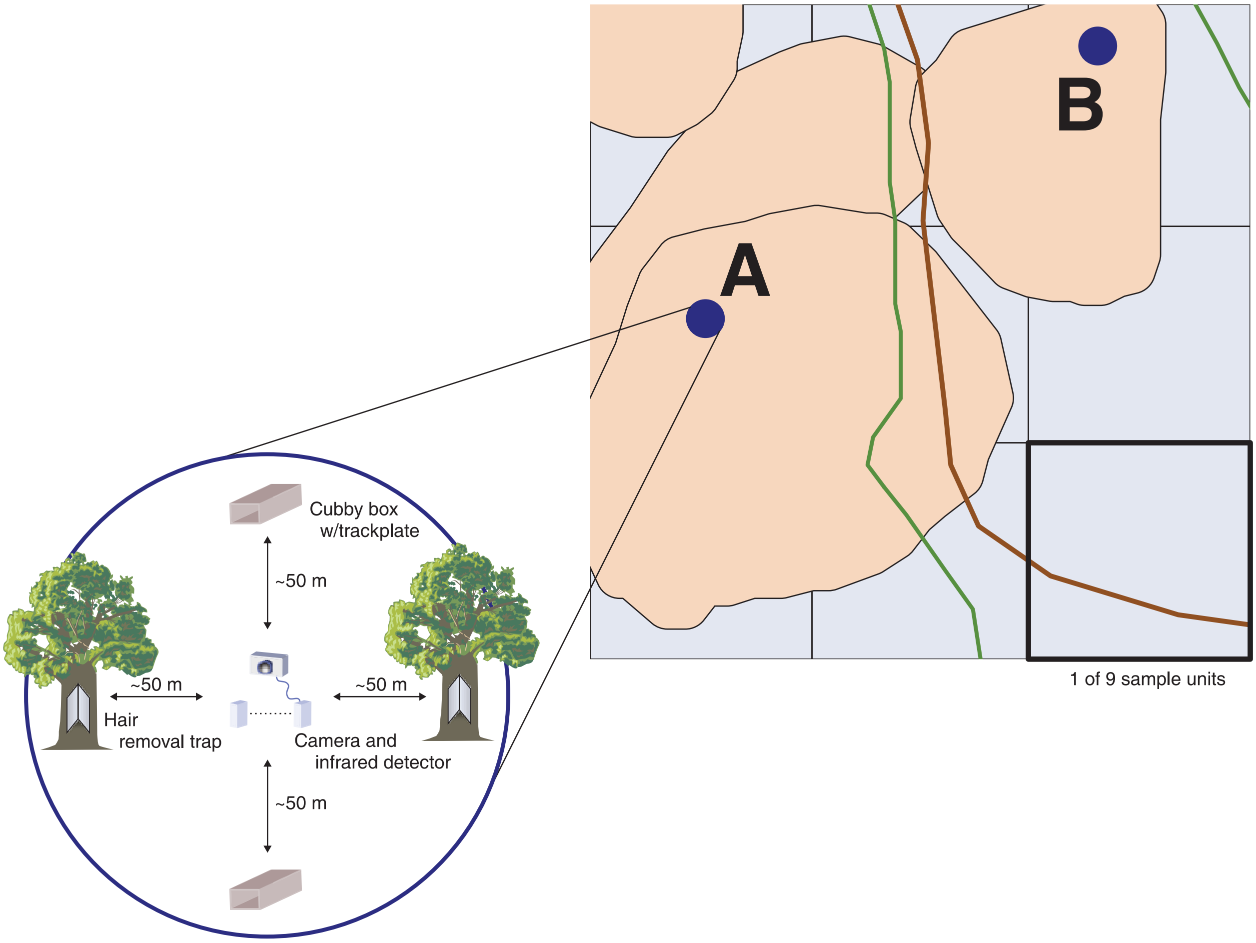

Fig. 1. Diagram representing hypothetical ranges for 4 skunks distributed among 9 sample units (each grid cell is a sample unit). Two of the sample units (a and b) were randomly selected for sampling, and a detection array (sample station site) was randomly placed within each of these units. Each detection array consisted of a single camera at the centre and 2 track plates and 2 hair removal traps placed equidistant (~50 m) from the camera in the four cardinal directions.

location for the sampling station within each selected grid cell (Gilbert *et al.* 2008). Three methods were used to detect mammals at each site: remote cameras with infrared sensors (Trailmaster®), hair removal traps (Mowatt & Paetkau 2002), and enclosed track plates (i.e. cubby boxes, Barrett 1983; Zielinski & Kucera 1995). The detection devices were arranged in a circular array (Fig. 1) with a single camera at the centre and two track plates and two hair removal traps placed equidistant (~50 m) from the camera in the four cardinal directions. A small amount of bait and a generic scent lure (Cronks Outdoor Supplies, Wiscasset, ME, USA) were applied at each site. Detections from the two track plates were combined, as were detections from the two hair traps at each site ($L = 3$ detection methods).

Each site was sampled continuously for ~2 weeks in the winter/spring and ~2 weeks in summer/autumn. Sites were visited every 3 days (on average) during each 2-week period, then following the 2-week period, cameras were rotated to another set of sites. For any given site, the two sampling seasons were separated by 4–5 months, with all sampling occurring between January–November 2004. Overall, the sampling design consisted of 47 sample units, each with detection arrays that were sampled in two seasons, with five sampling occasions per season. Striped skunks were detected at six units in the winter/spring and at seven units in the summer/autumn.

MODELS AND ESTIMATION

First, we explored possible changes in large-scale occupancy state (i.e. occupancy dynamics) between the winter/spring and summer/autumn sampling seasons by condensing detections from each array and fitting both single-season and multi-season models to the striped skunk data. A likelihood ratio test between a single-season model which implies a static occupancy state for sites across both seasons (closed occupancy with no changes between winter/spring and summer/autumn) vs. a multi-season model (MacKenzie *et al.* 2003) where vital rate probabilities (colonization and extinction) were > 0 between seasons (closed to changes in occupancy within each season), provided evidence to reject the simpler null model ($P < 0{\cdot}02$). This result implies that the occupancy state at the large-scale was dynamic between seasons; therefore, we applied

Table 1. Summary of model selection statistics for the top 5 models for striped skunk data *Mephitis mephitis* from winter/spring and summer/autumn seasons 2004. K represents the number of parameters in the model and $-2\text{Log}(L)$ is twice the negative log-likelihood value. Small sample Akaike Information Criteria (AIC) were calculated for each model, conservatively using the number of detection arrays (sample station sites) as the effective sample size ($S = 47$). Relative AIC_c values and Akaike weight, w, are reported for each model (ΔAIC_c represents the difference in AIC_c value relative to the top model, Burnham & Anderson 2002). Detection probabilities may vary among method (s) or sampling occasion (t); occupancy may be modelled as a function of percentage of overstorey cover (over) associated with each sample unit

Winter/Spring					Summer/Autumn				
Model	K	$-2\text{Log}(L)$	ΔAIC_c	w	Model	K	$-2\text{Log}(L)$	ΔAIC_c	w
ψ, θ, p^s	5	94·93	0·00	0·67	ψ, θ, p^s	5	123·63	0·00	0·44
ψ (over), θ, p^s	6	94·92	2·63	0·18	ψ (over), θ, p^s	6	121·69	0·71	0·31
ψ, θ, p_{s+t}	9	88·46	4·92	0·06	ψ, θ, p	3	131·09	2·56	0·12
ψ, θ_t, p^s	9	89·04	5·50	0·04*	ψ (over), θ, p	4	129·15	3·01	0·10
ψ, θ, p	3	106·74	6·90	0·02	ψ, θ_t, p^s	9	120·05	7·82	0·01*

*When reporting model averaged estimates of θ, the median of the $\hat{\theta}_t$ estimates were used ($t = 5$ sampling occasions).

our multi-method model separately to winter/spring and summer/autumn detection data.

We considered 16 a priori models to describe the processes that gave rise to the detection data. For simplicity, we considered a single unit-specific covariate, per cent overstorey cover, and investigated its influence on large-scale occupancy probability (ψ) only (see Talancy 2005 for details). Striped skunks are considered habitat generalists (Rosatte & Larivière 2003), but they have been found to prefer habitat complexity, especially edges (Bixler & Gittleman 2000; Hwang, Larivière & Messier 2007); thus, we expected large-scale occupancy probabilities to be either constant across units or negatively associated with forest overstorey cover. We modelled detection probability as constant over time and detection methods, p, as time-independent but different among methods, p^s, as time-dependent but constant among methods, p_t, or with method as an additive effect with time p_{s+t}. Models with multiplicative effects of method and time are possible, but were hypothesized to be unnecessary for these data. We modelled small-scale occupancy, θ, as either time-independent θ, or time-dependent θ_t. Estimates of θ could reflect a number of influences including range size and movement distances, seasonal and daily activity patterns, or local densities. Striped skunks are fairly sedentary animals during winter in northern latitudes, but their movements also vary by season and sex (Rosatte & Larivière 2003; Bixler & Gittleman 2000). Male striped skunks at northern latitudes become active during the breeding season (late winter and early spring) as they move in search of females (Rosatte 1987). On the other hand, female skunks restrict their movements during warmer months when they are pregnant or lactating (Verts 1967). In general, skunks are more easily detected or captured during the colder months when food is scarce (Bailey 1971; Hackett *et al.* 2007). Thus, we predicted that θ might be lower in the winter/spring than in the summer/autumn but relatively constant within seasons. Models were fit and maximum-likelihood estimates were obtained using the program PRESENCE (Hines & MacKenzie 2004). In cases where there was no clear 'best' model, we computed model-averaged estimates (Buckland, Burnham & Augustin 1997) for parameters of interest.

RESULTS

Estimated large-scale probabilities of occupancy, ψ, were low and consistent between the two seasons, $\hat{\psi} \approx 0{\cdot}16$, despite the evidence for unit-specific changes in occupancy status provided in our multi-season analysis, suggesting that striped skunks may shift their habitat use between seasons. Thus, although the sample units being used may have changed between seasons, the manner in which these different units were being used appeared to be similar across the two seasons. Model selection statistics (Table 1) provided only limited evidence that occupancy probabilities were influenced by per cent overstorey cover during winter/spring [summed weights for ψ (Over) models = 0·18], but somewhat more evidence in the summer/autumn (combined model weight = 0·41). As predicted, models that did contain the overstorey covariate suggested a negative relationship with striped skunk occupancy. Point estimates of conditional (on large-scale occupancy) small-scale occupancy, θ_t, were consistent within seasons (little evidence of time variation) and higher in the summer/autumn [model averaged θ = 0·67, SE(θ) = 0·31] than winter/spring [model averaged θ = 0·52, SE(θ) = 0·20], consistent with our a priori expectations of greater local movement during the winter/spring. However, the standard error estimates are large and do not permit strong inferences about seasonal variation in θ. In both seasons, there was strong evidence of detection probability differences among the three detection methods (Tables 1, 2). Hair removal traps were consistently poor at detecting skunks with model-averaged detection probabilities ≤ 0·10 in both seasons (Table 2). Cameras performed better, with slightly higher point estimates in the summer/autumn [model averaged $\hat{p} = 0{\cdot}35$, $\hat{\text{S}}\text{E}(\hat{p}) = 0{\cdot}19$] than the winter/spring [model averaged $\hat{p} = 0{\cdot}25$, $\hat{\text{S}}\text{E}(\hat{p}) = 0{\cdot}14$, Table 2]. Somewhat surprisingly, cubby boxes were 3·5 times more likely to detect striped skunks in the winter/spring than in the summer/autumn [model averaged: winter/spring $\hat{p} = 0{\cdot}73$, $\hat{\text{S}}\text{E}(\hat{p}) = 0{\cdot}23$; summer/autumn $\hat{p} = 0{\cdot}20$, $\hat{\text{S}}\text{E}(\hat{p}) = 0{\cdot}10$]. One possible explanation for the seasonal variation in cubby box detection probability is that male striped skunks become active during late winter/spring searching for

Table 2. Striped skunk detection probability estimates $\hat{p}$ and associated standard errors (in parenthesis) are given for the top multi-method models for winter/spring and summer/autumn seasons. The three detection methods include: cameras (cam), hair removal traps (hair) and cubby boxes with track plates (cub). w is the Akaike weight for each model

Winter/Spring					Summer/Autumn				
Model	w	$\hat{p}$ (SE)	$\hat{p}$ (SE)	$\hat{p}$ (SE)	Model	w	$\hat{p}$ (SE)	$\hat{p}$ (SE)	$\hat{p}$ (SE)
ψ, θ, p^s	0·67	0·24 (0·14)	0·08 (0·08)	0·73 (0·23)	ψ, θ, p^s	0·44	0·39 (0·18)	0·08 (0·06)	0·20 (0·11)
ψ (Over), θ, p^s	0·18	0·24 (0·14)	0·08 (0·08)	0·73 (0·23)	ψ (Over), θ, p^s	0·31	0·39 (0·18)	0·08 (0·06)	0·20 (0·11)
ψ, θ, p_{s+t}	0·06	0·29* (0·22)	0·10* (0·12)	0·80* (0·23)	ψ, θ, p	0·12	0·19 (0·09)	0·19 (0·09)	0·19 (0·09)
ψ, θ_t, p^s	0·04	0·24 (0·14)	0·08 (0·08)	0·73 (0·23)	ψ (Over), θ, p	0·10	0·19 (0·09)	0·19 (0·09)	0·19 (0·09)
ψ, θ, p	0·02	0·25 (0·11)	0·25 (0·11)	0·25 (0·11)	ψ, θ_t, p^s	0·01	0·44 (0·14)	0·09 (0·06)	0·22 (0·10)

*Parameter estimate reported is the median value among the five detection probability estimates for each device.

females. The higher detection probability during this period can also be attributed to increased capture success as a result of limited food availability. This inference is consistent with the lower estimates for local scale occupancy (θ_t) during the winter/spring.

Example analysis 2: stream salamanders *Pseudotriton ruber*

SAMPLING DESIGN AND DATA

We applied the multi-method model to data for the northern red salamander *Pseudotriton ruber* collected at 25 sites on 12 lower order steams at two national parks in the Washington D.C. area [Chesapeake and Ohio Canal National Historic Park (C&O), Rock Creek National Park (RC)]. Each site or 'stream reach' was 30 m long × 3 m wide: consisting of a 2-m search of the stream bank and 1 m of water (often encompassing the entire width of the stream). Sites on the same stream were spaced 100–200 m apart. Searching natural cover was considered one detection method. Natural cover objects within the stream reach were carefully turned and replaced, and an aquarium net was used to facilitate capturing adult and larval salamanders in the aquatic habitat (Mattfeldt & Grant 2007). Leaf litter bags were placed every 5 m along each stream reach, representing a second detection method (see Mattfeldt & Grant 2007 for details). Sites were surveyed twice from 16 June–29 July 2005. All life-history stages of *P. ruber* (adult, juveniles and larvae) are available for detection during this sample period. At least one individual was detected at two of 11 sites in RC and five of the 14 sites at C&O, yielding naïve occupancy probabilities of 0·18 and 0·38 for each park, respectively. *P. ruber* detections came primarily from leaf litterbags, accounting for detection at five of the seven known occupied sites.

MODELS AND ESTIMATION

Since larval individuals cannot vacate the stream habitat, we would expect θ to approach 1 for this salamander species. We considered a set of eight a priori models to describe potential variation in detection and occupancy probabilities (Table 3). Specifically, we model occupancy probability as different among national parks [ψ (park)] or constant among all sites, ψ. Detection probability was modelled similarly to our striped skunk example: constant among methods and sampling occasions, p, different between the two methods p^s, different between the two sampling occasions p_t, or as an additive model p_{s+t}. *P. ruber* is known to accumulate in leaf litter of streams, but can be found under natural cover (Petranka 1998). Thus, a priori we expected differences in detection probabilities between methods for this species with litterbags having the higher probability of detection.

Table 3. Summary of model selection statistics for eight multi-method models fit to *P. ruber* data from stream reaches in two national parks in the greater Washington D.C. area. K represents the number of parameters in the model and $-2\text{Log}(L)$ is twice the negative log-likelihood value. ΔAIC_c is the difference in AIC_c value relative to the top model where small sample criteria were calculated using the number of stream reaches ($S = 25$) as the effective sample size. w is the Akaike weight (Burnham & Anderson 2002). Detection probabilities may vary among method (s) or sampling occasion (t); occupancy probabilities may differ between the two national parks

Model	K	$-2\text{Log}(L)$	ΔAIC_c	Weight, w
ψ, θ, p	3	59·31	0·00	0·40
ψ, θ, p^s	4	58·09	1·64	0·18
ψ (park), θ, p	4	58·22	1·77	0·17
ψ, θ, p_t	4	59·22	2·77	0·10
ψ (park), θ, p^s	5	57·00	3·71	0·06
ψ, θ, p_{s+t}	5	57·99	4·70	0·04
ψ (park), θ, p_t	5	58·14	4·85	0·04
ψ (park), θ, p_{s+t}	6	56·92	7·13	0·01

RESULTS

Consistent with our expectations, estimates of small-scale occupancy ($\hat{\theta}$) were always 1. Naïve estimates of large-scale occupancy were twice as high in RC compared to C&O. However, after adjusting for non-detection, there was little evidence that large-scale occupancy (ψ) differed between these areas [model-averaged estimates: $\hat{\psi}(\text{RC}) = 0{\cdot}48$, $\widehat{\text{SE}}[\hat{\psi}(\text{RC})] = 0{\cdot}31$ and $\hat{\psi}(\text{C\&O}) = 0{\cdot}60$, $\widehat{\text{SE}}[\hat{\psi}(\text{C\&O})] = 0{\cdot}35$, Tables 3 and 4]. Admittedly, low detection probabilities for both methods (Table 4), coupled with small sample sizes, hinder our ability to detect spatial and temporal differences in parameter

Table 4. Parameter estimates under top three multi-method occupancy models fit to *P. ruber* detection data from 25 stream reaches in two national parks in the Washington D.C. area: Rock Creek National Park (RC) and Chesapeake & Ohio Canal National Historic Park (C&O)

	Model: ψ, θ, p		Model: ψ, θ, p^s		Model: ψ (park), θ, p	
Parameter	Estimate	SE	Estimate	SE	Estimate	SE
$\hat{\psi}$(RC)	0·56	0·312	0·54	0·298	0·36	0·281
$\hat{\psi}$(C&O)	0·56	0·312	0·54	0·298	0·73	0·424
$\hat{p}$(leaf)	0·16	0·099	0·23	0·141	0·16	0·099
$\hat{p}$(cover)	0·16	0·099	0·11	0·084	0·16	0·099

estimates. The total Akaike weight for models that included method as a factor influencing detection probability was 0·29, providing weak evidence for method-specific detection probabilities. Consistent with our a priori expectation, the models that included this variation [e.g. (ψ, θ, p^s)] indicated that detection probability via leaf litterbags was higher than that obtained with area-constrained cover searches (Table 4). Certainly, our results suggest refraining from using natural cover searches as the only detection method for this species. If leaf litterbags were not used in this study, *P. ruber* would have only been detected at two sites. Application of occupancy models to such sparse data is not recommended, and leads to poor estimates of occupancy and detection probability (Mattfeldt & Grant 2007).

Discussion

Historically, few studies have used multiple detection methods in occupancy surveys. Recently, however, mid- to large-scale surveys organized by agencies such as the US Forest Service (Manley *et al.* 2004, 2005) and the National Park Service (Tuberville *et al.* 2005; O'Connell *et al.* 2006) are increasingly based on designs with multiple remote detection methods. The modelling approach presented here deals explicitly with detection probability and should thus be preferred to surveys that simply view nondetections as true absences (e.g. MacKenzie *et al.* 2006). In addition, our approach offers three advantages over use of currently available occupancy models for analysis of data from surveys using multiple methods. First, it deals explicitly with the lack of independence among detections by different methods at the same sampling occasion induced by animal(s) presence at the local sample site. Secondly, the approach makes efficient use of data from the different methods both for estimating occupancy and for comparing detection probabilities associated with the different methods. Thirdly, the approach permits direct estimation and modelling of a parameter associated with animal occurrence at the local sample site, thus permitting inference about occupancy at two spatial scales.

We suspect that the first two advantages listed above will be those of most interest to parties involved with biodiversity conservation and management. Monitoring programmes are most useful to conservation efforts when they are embedded as components of larger management processes (Yoccoz, Nichols & Boulinier 2001; Nichols & Williams 2006). Indeed, multispecies surveys are beginning to be used in evaluating large-scale conservation and management programmes (Donald *et al.* 2007). The use of multiple detection devices should become increasingly commonplace in multispecies surveys, and the ability to make efficient use of data produced by all devices is important. In addition, the ability to estimate device-specific detection probabilities should prove especially useful in the design of multispecies surveys. In particular, such estimates can be used in numerical (e.g. simulation) studies to provide guidance about the consequences to precision of resulting estimates, of eliminating specific detection devices from the detection array. Indeed, information about device-specific detection probabilities and device costs can be used in efforts to optimize study designs for multiple species.

Our first example with striped skunk data provided relatively strong evidence of variation in detection probabilities among the different detection methods. Consistent with our previous studies, hair removal traps were ineffective at detecting striped skunks, despite the use of different trap designs (Talancy 2005; O'Connell *et al.* 2006). Any design of single-species surveys for striped skunks would have to strongly consider the elimination of hair-removal traps from the array of sampling devices. The skunk analysis also provided weak evidence of a predicted difference in local movement probabilities, with lower point estimates of θ (possibly reflecting more movement) in winter/spring than summer/autumn. The stream salamander example was very small from an occupancy perspective, and sample sizes did not permit strong inference. Nevertheless, the analysis provided weak evidence of the predicted difference in detection probabilities associated with the two methods. In addition, the approach provided no evidence of local movement in and out of the sampled streams at the species level, again consistent with predictions.

In the initial description of the model, we noted that a similar approach could be used with a single detection method using replication applied at two time-scales; a short time-scale (e.g. minutes) and a longer temporal scale (e.g. days). Indeed, K. Pollock (personal communication) recommended use of this basic approach with avian point count data for abundance estimation as a means of estimating temporary emigration for individual birds (also see Nichols, Thomas & Conn in press). These considerations emphasize that our approach with multiple detection methods can be viewed simply as another variation on the robust design of Pollock (1982). Similarly, the separate estimation of the small- and large-scale occurrence probabilities is similar in concept to the use of the robust design for estimation of temporary emigration in capture–recapture studies (Kendall, Nichols & Hines 1997). We initially considered implementing the above modelling approach using existing algorithms in software developed for multiple season occupancy studies (e.g. the program PRESENCE, MacKenzie *et al.* 2006; the program MARK, White & Burnham 1999), but additional routines were added to PRESENCE in order to implement the parameterization presented above.

The modelling approach presented above was developed with multiple detection devices and survey methods in mind. However, some occupancy studies are based on investigator surveys for animal sign (e.g. hair, scent or other sign from rub trees; presence of burrows, dens, scat or tracks; Wilson *et al.* 1996). Detections of different types of animal sign can be modelled similarly to data from different detection methods using the model described above.

Our modelling approach assumes that if an individual is detected by one of the detection devices, it or another member of the species is available for detection by the other devices at the immediate sample site. We believe this to be the case for both of our examples. However, if the species of interest is locally rare or solitary, and one of the detection devices is a method that retains (a trap) or repels (a camera's flash) an individual upon detection, then our model could be extended to include device-specific detection probabilities that differ based on whether or not the species was detected by one of the other devices at the immediate sampling site.

Multi-season extensions of this model will prove useful in monitoring programmes and can be developed by combining the approach described above with that of MacKenzie *et al.* (2003). These extensions will permit inference about colonizations and extinctions between seasons, as well as about small-scale occupancy within seasons. These extensions are straightforward, and the main decision involves whether to use the existing multi-season software or to write specific new software that explicitly incorporates our within-season parameterization.

Acknowledgements

Funding for field work was provided by the US National Park Service's Inventory and Monitoring Program and US Geological Survey's Amphibian Research and Monitoring Initiative. We would like to thank Elizabeth Johnson, Steve Fancy, Gregory Shriver, Brian Mitchell, Charles Roman, Shawn Carter, and Sandra Mattfeldt for their support. Kinard Boone adapted Fig. 1 from field notes. The manuscript benefited from constructive comments by Paul Lukacs, Darryl MacKenzie, Howard Stauffer, and Drew Tyre.

References

Bailey, L.L., Simons, T.R. & Pollock, K.H. (2004) Estimating site occupancy and species detection probability parameters for terrestrial salamanders. *Ecological Applications*, **14**, 692–702.

Bailey, T.N. (1971) Biology of striped skunks on a southwestern Lake Erie marsh. *The American Midland Naturalist*, **85**, 196–207.

Barrett, R.H. (1983) Smoked aluminum track plots for determining furbearer distribution and relative abundance. *California Fish and Game*, **69**, 188–190.

Barrows, C.W., Schwartz, M.B., Hodges, W.L., Allen, M.F., Rotenberry, J.T., Bai-Lian, L., Scott, T.A. & Chen, X. (2005) A framework for monitoring multiple-species conservation plans. *Journal of Wildlife Management*, **69**, 1333–1345.

Bixler, A. & Gittleman, J.L. (2000) Variation in home range and use of habitat in the striped skunk (*Mephitis mephitis*). *Journal of Zoology (London)*, **251**, 525–533.

Buckland, S.T., Burnham, K.P. & Augustin, N.H. (1997) Model selection: an integral part of inference. *Biometrics*, **53**, 603–618.

Buckland, S.T., Magurran, A.E., Green, R.E. & Fewster, R.M. (2005) Monitoring change in biodiversity through composite indices. *Philosophical Transactions of the Royal Society, Series B*, **360**, 243–254.

Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-theoretic Approach*, 2nd edn. Springer-Verlag, New York.

Donald, P.F., Sanderson, F.J., Burfield, I.J., Bierman, S.M., Gregory, R.D. & Waliczky, Z. (2007) International conservation policy delivers benefits for birds in Europe. *Science*, **317**, 810–813.

Gilbert, A.T., O'Connell Jr., A.F., Annand, E.M., Talancy, N.W., Sauer, J.R. & Nichols, J.D. (2008) *An Inventory of Terrestrial Mammals at National Parks in the Northeast Temperate Network and Sagamore Hill National Historic Site*. US Geological Survey, Scientific Investigations Report 2007-5245, Laurel, MD, USA.

Hackett, H.M., Lesmeister, D.B., Desanty-Combes, J., Montague, W.G., Millspaugh, J.J. & Gompper, M.E. (2007) Detection rates of eastern spotted Skunks (Spilogale Putorius) in Missouri and Arkansas using live-capture and non-invasive techniques. *The American Midland Naturalist*, **158**, 123–131.

Hines, J.E. & MacKenzie, D.I. (2004) *PRESENCE*, version 2·0. Available at <http://www.mbr-pwrc.usgs.gov/software.html>.

Hwang, Y.T., Larivière, S. & Messier, F. (2007) Local and landscape-level den selection of striped skunks on the Canadian prairies. *Canadian Journal of Zoology*, **85**, 33–39.

Kendall, W.L., Nichols, J.D. & Hines, J.E. (1997) Estimating temporary emigration and breeding proportions using capture–recapture data with Pollock's robust design. *Ecology*, **78**, 563–578.

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L. & Hines J.E. (2006) *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence*. Academic Press, New York.

Mackenzie, D.I., Nichols, J.D., Hines, J.E., Knutson, M.G. & Franklin, A.B. (2003) Estimating site occupancy, colonization and local extinction probabilities when a species is not detected with certainty. *Ecology*, **84**, 2200–2207.

Mackenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A. & Langtimm, C.A. (2002) Estimating site occupancy when detection probabilities are less than one. *Ecology*, **83**, 2248–2255.

Manley, P.N., Schlesinger, M.D., Roth, J.K. & Van Horne, B. (2005) A field-based evaluation of a presence-absence protocol for monitoring ecoregional-scale biodiversity. *Journal of Wildlife Management*, **69**, 950–966.

Manley, P.N., Zielinski, W.J., Schlesinger, M.D. & Mori, S.R. (2004) Evaluation of a multiple-species approach to monitoring species at the ecoregional scale. *Ecological Applications*, **14**, 296–310.

Mattfeldt, S.D. & Grant, E.H.C. (2007) Are two methods better than one?: area constrained transects and leaf litterbags for sampling stream salamanders. *Herpetological Review*, **38**, 43–45.

Mowat, G. & Paetkau, D. (2002) Estimating marten *Martes americana* population size using hair capture and genetic tagging. *Wildlife Biology*, **8**, 201–209.

Nichols, J.D. & Williams, B.K. (2006) Monitoring for conservation. *Trends in Ecology & Evolution*, **21**, 668–673.

Nichols, J.D., Thomas, L. & Conn, P.B. (in press) Inferences about landbird abundance from count data: recent advances and future directions. *Ecological and Environmental Statistics*.

O'Connell, A.F. Jr., Talancy, N.W., Bailey, L.L., Sauer, J.R., Cook, R. & Gilbert, A.T. (2006) Estimating site occupancy and detection probability parameters for mammals in a coastal ecosystem. *Journal of Wildlife Management*, **70**, 1625–1633.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P. & Kassem, K.R. (2001) Terrestrial ecoregions of the world: A new map of life on earth. *Biosciences*, **51**, 933–938.

Petranka, J.W. (1998) *Salamanders of the United States and Canada*. Smithsonian Institution Press, Washington D.C.

Pollock, K.H. (1982) A capture-recapture design robust to unequal probability of capture. *Journal of Wildlife Management*, **46**, 752–757.

Rosatte, R.C. (1987) Striped, spotted, hooded, and hog-nose skunk. *Wild Furbearer Management and Conservation in North America* (eds M. Novak,

J. Baker, M. Obbard & B. Malloch), pp. 519–613. Ontario Trappers Association, Toronto, Canada.

Rosatte, R. & Larivière, S. (2003) Skunks (Genera *Mephitis*, *Spilogale*, and *Conepatus*). *Wild Mammals of North America: Biology, Management, and Conservation. Second Edition*. (eds G.A. Feldhammer, B.C. Thompson & J.A. Chapman), pp. 692–707. Johns Hopkins University, Baltimore, MD, USA.

Smith, L.L., Barichivich, W.J., Staiger, J.S., Smith, K.G. & Dodd Jr., C.K. (2006) Detection probabilities and site occupancy estimates for amphibians at Okefenokee National Wildlife Refuge. *American Midland Naturalist*, **155**, 149–161.

Sorensen, L.L., Coddington, J.A. & Scharff, N. (2002) Inventorying and estimating subcanopy spider diversity using semiquantitative sampling methods in an Afromontane forest. *Environmental Entomology*, **31**, 319–330.

Talancy, N.W. (2005) *Effects of Habitat Fragmentation and Landscape Context on Medium-sized Mammalian Predators in Northeastern National Parks*. Thesis. University of Rhode Island, Kingston, RI, USA.

Tuberville, T.D., Willson, J.D., Dorcas, M.E. & Gibbons, J.W. (2005) Herpetofaunal species richness of southeastern national parks. *Southeastern Naturalist*, **4**, 537–569.

Verts, B.J. (1967) *The Biology of the Striped Skunk*. University of Illinois Press, Urbana, IL, USA.

White, G.C. & Burnham, K.P. (1999) Program MARK: survival rate estimation from both live and dead encounters. *Bird Study*, **46** (Supplement), S120–S139.

Wilson, D.E., Cole, F.R., Nichols, J.D., Rudran, R. & Foster, M.S. (eds) (1996) *Measuring and Monitoring Biological Diversity: Standard Methods for Mammals*. Smithsonian Institute Press, Washington, D.C.

Yoccoz, N.G., Nichols, J.D. & Boulinier, T. (2001). Monitoring of biological diversity in space and time. *Trends in Ecology & Evolution*, **16**, 446–453.

Zielinski, W.J. & Kucera, T.E. (1995). *American Marten, Fisher, Lynx, and Wolverine: Survey Methods for Their Detection*. General Technical Report PSW-GTR-157. Pacific Southwest Research Station, US Forest Service, Albany, CA, USA.

Received 15 December 2007; accepted 14 May 2008
Handling Editor: Paul Lukacs

Supplementary material

The following supplementary material is available for this article:

Fig. S1. Map showing eight national parks in the northeastern United States where striped skunk data were collected.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2664.2008.01509.x
(This link will take you to the article abstract).