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Population Ecology

Hierarchical Multi-Scale Occupancy Estimation for Monitoring Wildlife Populations

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ABSTRACT Occupancy estimation is an effective analytic framework, but requires repeated surveys of a sample unit to estimate the probability of detection. Detection rates can be estimated from spatially replicated rather than temporally replicated surveys, but this may violate the closure assumption and result in biased estimates of occupancy. We present a new application of a multi-scale occupancy model that permits the simultaneous use of presence–absence data collected at 2 spatial scales and uses a removal design to estimate the probability of detection. Occupancy at the small scale corresponds to local territory occupancy, whereas occupancy at the large scale corresponds to regional occupancy of the sample units. Small-scale occupancy also corresponds to a spatial availability or coverage parameter where a species may be unavailable for sampling at a fraction of the survey stations. We applied the multi-scale occupancy model to a hierarchical sample design for 2 bird species in the Black Hills National Forest: brown creeper (*Certhia americana*) and lark sparrow (*Chondestes grammacus*). Our application of the multi-scale occupancy model is particularly well suited for hierarchical sample designs, such as spatially replicated survey stations within sample units that are typical of avian monitoring programs. The model appropriately accounts for the non-independence of the spatially replicated survey stations, addresses the closure assumption for the spatially replicated survey stations, and is useful for decomposing the observation process into detection and availability parameters. This analytic approach is likely to be useful for monitoring at local and regional scales, modeling multi-scale habitat relationships, and estimating population state variables for rare species of conservation concern.

KEY WORDS availability probability, closure assumption, detection probability, hierarchical model, monitoring, multi-scale, occupancy estimation, point count, Pollock's robust design, removal design.

Estimating the proportion of sites occupied by a species is important for answering a wide variety of questions in ecology and conservation biology (MacKenzie et al. 2006). Occupancy models accounting for the incomplete detection of species represent a significant methodological advancement (MacKenzie et al. 2002, Tyre et al. 2003) and are gaining wide use in applied ecology. In studies of metapopulation biology, occupancy rates are necessary for estimating extinction and colonization probabilities (Hanski 1998, Moilanen 2002, MacKenzie et al. 2003). Occupancy estimation is also a useful framework for studying disease ecology (McClintock et al. 2010), habitat relationships (Gu and Swihart 2004), and resource selection (MacKenzie 2006). Finally, the proportion of sites occupied is a useful state variable for the adaptive management of wildlife populations (Yoccoz et al. 2001, Martin et al. 2009) and large-scale population monitoring for detecting a change or trend in the population state over time (Thompson et al. 1998, Manley et al. 2005). In both cases, valid inference of a population state in any given year requires a probabilistic sample design and the estimation of detection probabilities (Yoccoz et al. 2001, Pollock et al. 2002, Rosenstock et al. 2002, Kéry and Schmidt 2008).

Occupancy estimation is particularly well suited for monitoring populations of rare species relative to other state variables and estimation methods (MacKenzie et al. 2005, Joseph et al. 2006). However, rare species present formidable challenges for both spatial sampling and estimating detection probabilities (MacKenzie et al. 2005). Rare species by definition occupy small fractions of the landscape, but it may be informative to distinguish between species that that are locally common and those that are locally rare. In addition to low detection probabilities (MacKenzie et al. 2005), the low availability of rare species in large sample units may lead

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to less than desired coverage probabilities (Nichols et al. 2009).

Sample designs for occupancy estimation require repeated surveys of a sample unit to estimate the probability of detection (MacKenzie et al. 2006). The repeated surveys may be represented by temporal replication at discrete time occasions, spatial replication at separate locations, or by the replication of different observers (MacKenzie et al. 2006). Estimating detection from spatially replicated surveys on a single visit may be advantageous to large-scale monitoring programs when budget or logistical constraints preclude multiple repeat visits in time. However, under certain sampling situations, estimating detection from spatially replicated surveys can violate the closure assumption and result in biased estimates of occupancy (Kendall and White 2009, Hines et al. 2010). The closure assumption for estimating the probability of detection is conditional on the presence of the species and implies that the sample unit is either occupied or unoccupied for all surveys (MacKenzie et al. 2006, Rota et al. 2009). When the sample unit is occupied and a fraction of the spatially replicated surveys have negligible probabilities of detecting the species, the estimate of detection is biased low and the estimate of occupancy is biased high (Kendall and White 2009). This lack of closure creates a dependency between the spatially replicated surveys that is manifested by the incomplete availability of the species at the survey locations (Kendall and White 2009). The lack of closure associated with the spatial replication of surveys can be addressed through design- or model-based methodology. For example, the bias can be removed by sampling spatially replicated subunits with replacement (MacKenzie et al. 2006, Kendall and White 2009). Alternately, bias can be removed by using the robust design parameterization that allows replicated surveys to be open to changes in occupancy (Rota et al. 2009), and by decomposing the observation processes into detection and availability probabilities (Hines et al. 2010). The spatial replication of survey stations within sample units is a feature of many sample designs for avian monitoring (Robbins et al. 1986, Carlson and Schmiegelow 2002, Manley et al. 2005, Buckland 2006, Ferland et al. 2006); therefore, robust methods for estimating occupancy from such designs are needed.

We apply the multi-scale occupancy model developed by Nichols et al. (2008) to a hierarchical sample design for avian monitoring. The model permits the simultaneous use of presence–absence data at 2 spatial scales, accounts for non-independence of detections between scales, addresses the closure assumption for spatially replicated survey stations, and estimates occupancy at both small and large scales. The estimate of small-scale occupancy is incorporated as an availability parameter to account for situations where the species is present at the sample unit, but unexposed to sampling at some of the survey stations (Nichols et al. 2008). We introduce a new parameterization of the model, present example applications for brown creepers (*Certhia americana*) and lark sparrows (*Chondestes grammacus*) in the Black Hills National Forest, and discuss potential uses and extensions of the model.

STUDY AREA

We collected bird abundance and occurrence data between 23 May and 14 July 2009 throughout the South Dakota and Wyoming portions of the Black Hills National Forest, as part of an ongoing avian monitoring program (White et al. 2010). The Black Hills National Forest covered an area of 5,390 km^2 in South Dakota and 819 km^2 in Wyoming, and both areas were dominated by Ponderosa pine (*Pinus ponderosa*) forest.

METHODS

Consider a sample design where N sample units are subsampled by R spatially replicated survey stations to determine the presence or absence of a species. Although the sample units may be naturally occurring features such as ponds or vegetation patches, the units may be better represented by quadrats selected from a predefined area using a probabilistic sample design. The occupancy state of the spatially replicated survey stations may vary by location, but it may be reasonable to assume the occupancy state of each individual survey station does not change during the course of the study. Each sample unit consists of R primary survey stations, for which the occupancy state may be open to vary spatially. At each primary survey station, investigators use appropriate methodology to detect the species at K repeated surveys of the station. This can be considered a within-season (Nichols et al. 2008) robust design (Pollock 1982, MacKenzie et al. 2003), where the K surveys are the secondary occasions nested within each of the R primary survey stations. The occupancy framework presented here differs from that of MacKenzie et al. (2003) in that we do not make inference about extinction or colonization, but instead estimate occupancy at 2 spatial scales (Nichols et al. 2008). For example, consider a study with $R = 4$ survey stations, $K = 3$ survey occasions, and an encounter history $H_i = 010\ 101\ 000\ 001$ (where $0 =$ non-detection and $1 =$ detection during 3 survey occasions at 4 stations). In this example, the target species was detected at survey station 1 on occasion 2, at station 2 on occasions 1 and 3, was not detected at station 3, and was detected at survey station 4 on occasion 3. When the survey occasions are sampled without replacement, the robust design can be combined with a removal design (MacKenzie 2006, Rota et al. 2009). Under this design, surveys for the species stop after the first detection and the survey stations are removed from the set that are actively being surveyed (MacKenzie et al. 2006). The survey occasions following the first detection can be considered a form of missing data (MacKenzie et al. 2006), and accordingly the above encounter history can be written as $H_i = 01.\ 1..\ 000\ 001$.

The multi-scale occupancy model applied in this study was originally developed for use with multiple remote sampling devices (Nichols et al. 2008). Our application of the model differs from that of Nichols et al. (2008) in that we estimate small-scale occupancy using spatial rather than temporal replicates. The parameters of the model are as follows: p_t is the probability of detection at occasion t given the sample unit and survey station is occupied; θ_r is the probability of occupancy for survey station r given the sample unit is occupied; and ψ_i is the probability of occupancy for sample unit i. The assumptions of the multi-scale occupancy model are 1) no un-modeled heterogeneity in the probabilities of detection and occupancy, 2) each survey station is closed to changes in occupancy over the sampling period, 3) the detection of species at each survey station are independent, and 4) the target species are never falsely detected (MacKenzie et al. 2006). Because the removal design requires a constrained parameterization where detection is held constant across survey occasions, an additional assumption for the removal design is a constant per minute probability of detection in each interval (MacKenzie et al. 2006).

Heterogeneity in detection probability can result in negatively biased occupancy estimates (MacKenzie et al. 2006). When detection rates vary over the course of the sampling season and the spatially replicated surveys for each sample unit are conducted on a single day, a form of heterogeneity in detection probability may be induced (MacKenzie et al. 2006). An additional form of heterogeneity may occur when detection varies over the course of the day and the spatially replicated surveys are conducted at different times of day (MacKenzie et al. 2006). Therefore, when spatial replicates are sampled on a single day or at different times of day, studies should be designed to ensure sampling occurs over time periods when detection probabilities are not expected to vary. For example, sampling designs for landbirds are often restricted to pre-fledgling periods and early morning hours when singing males are actively courting and defending territories. Alternately, when the mechanisms that drive changes in detection are well understood, heterogeneity in detection probabilities can be accommodated and modeled as a function of environmental covariates (MacKenzie et al. 2006). The removal design is well suited for situations where the survey occasions are not independent, and where species are more or less likely to be detected in subsequent survey occasions (MacKenzie et al. 2006). The assumption of a constant per minute probability of detection in the intervals can be verified by a decline in the frequency of detections through time after setting all subsequent sample intervals following the first detection to missing data.

The occupancy parameters ψ and θ allow the estimation of occupancy at 2 spatial scales (Nichols et al. 2008). The parameter ψ represents species occurrence at the larger scale, and can be interpreted as the proportion of sample units occupied. The parameter for the smaller scale, θ, corresponds to species occurrence at the survey stations conditional on species presence at the sample unit, and can be interpreted as the proportion of survey stations occupied when the sample unit is occupied. The parameter θ accounts for circumstances in which member(s) of the species may be present at some survey stations, but not at others. The product $\psi\theta$ corresponds to the probability of small-scale occupancy, which indicates the extent to which members of the species are present at the survey stations and exposed to sampling (Nichols et al. 2008). The product $\psi(1 - \theta)$ represents large-scale, but not small-scale occupancy (Nichols et al. 2008). Although θ in the original application accounts for situations when a species is temporarily unavailable due to movement (Nichols et al. 2008), in the present application θ corresponds to a spatial availability parameter where species may be unavailable for sampling at a fraction of the survey stations. Availability in this context corresponds to a coverage probability or the extent that an animal(s) home range or territory at least partially overlaps a sample unit (Nichols et al. 2009). The estimates of θ could be influenced by a number of factors including territory size, local population density, and habitat heterogeneity.

We used the multi-scale model to decompose the observation process into availability and detection probabilities (Nichols et al. 2009, Hines et al. 2010, Riddle et al. 2010). The value $(1 - \theta)$ represents the probability of no availability given presence, $\theta(1 - p)$ corresponds to the probability of no detection given presence and availability, and θp reflects the probability of detection given presence and availability. This parameterization relaxes the closure assumption for the spatially replicated survey stations and allows some survey stations to have negligible probabilities of detection.

We defined the sampling frame by superimposing a 1 km $\times$ 1 km grid over the Black Hills National Forest. We used a stratified random design and selected 46 sample units in South Dakota and 10 sample units in Wyoming using generalized random-tessellation stratification (Stevens and Olsen 2004) and R software (SPSURVEY package, R Version 2.13.1, www.R-project.org, accessed 6 Mar 2011). Each 1–km^2 sample unit contained 16 survey stations ($R = 16$) separated by 250 m. The sample units were surveyed on a single day during the avian breeding season from 23 May through 14 July 2009. We sampled avian occurrence using 5-min point counts (Reynolds et al. 1980) between one-half hour before sunrise and 1100 hr at each accessible survey station, and measured the distance to each bird detection using a laser rangefinder. The repeated sample occasions K at each survey station were represented by the 1-min intervals comprising the point count duration. Using the 5 1-min intervals recorded during sampling, we binned minutes 1 and 2, and minutes 3 and 4, resulting in 3 sample occasions of different interval length ($K = 3$). We binned the minute intervals to maintain a constant detection rate in each interval and ensure a monotonic decline in the detection frequency histogram through time. Binning the intervals improved irregularities in the detection frequency histogram due to time lags between detecting and recording species when sampling diverse bird communities (Celis-Murillo et al. 2009). We used a removal design (MacKenzie et al. 2006, Rota et al. 2009) and surveyed avian occurrence until the first detection, after which we set all subsequent sample intervals to missing data. We truncated the data and used only detections within 125 m of the sample points (half of the distance between survey stations). The frequency of song detections declined over the 3 time intervals for both species, but the frequency histogram for the brown creeper exhibited a fatter tail in the later intervals than that of the lark sparrow.

We fitted a single model with 2 groups to estimate brown creeper or lark sparrow occupancy in the South Dakota and

Wyoming portions of the Black Hills National Forest. We modeled detection probability (p) as constant over time and strata. The removal design prevented the estimation of time specific detection rates (MacKenzie et al. 2006). Because we detected brown creepers on only 4 and lark sparrows on only 3 survey stations in the Wyoming stratum, we considered the data too sparse for estimating stratum specific detection probabilities. As in the previous analysis example, we held small-scale occupancy (θ) constant across the 16 survey stations because differences between the numbered survey stations had no biological relevance. As with the detection parameter, we considered the data too sparse to estimate stratum specific θ. We fitted the model, accounted for unequal interval length and obtained maximum likelihood estimates of the parameters using SAS software (PROC NLMIXED; SAS/STAT Version 9.2; SAS Institute, Inc., Cary, NC; Appendix). The unequal time intervals were accommodated by raising the probability of not being detected $(1 - p)$ to the power of the length of the time interval, and the resulting detection probability was 1 minus the probability of not being detected $[1 - (1 - p)^2$ for a species detected in an interval length of 2 min] (Appendix). Overall large-scale occupancy (ψ) in the Black Hills National Forest was estimated by $\hat{\psi} = f_{SD} \times \hat{\psi}_{SD} + f_{WY} \times \hat{\psi}_{WY}$, where f_{SD} and f_{WY} were the relative proportions of sample units in the South Dakota and Wyoming strata, and $\hat{\psi}_{SD}$ and $\hat{\psi}_{WY}$ were the occupancy estimates for the South Dakota and Wyoming strata, respectively. We approximated the sampling variance and standard error of the overall large-scale occupancy estimate using the delta method (Powell 2007) and SAS software (PROC IML, SAS/IML Version 9.2).

RESULTS

We detected brown creepers at 16 survey stations, at 8 sample units in South Dakota and 2 sample units in Wyoming. The estimated detection probability using the removal design was $\hat{p} = 0.28$, which approached the moderate range where unbiased estimates of occupancy are expected (MacKenzie et al. 2002). Brown creepers occupied 11% of the survey stations when present at the sample units ($\hat{\theta}$) and 27% of the sample units ($\hat{\psi}$) in the Black Hills National Forest (Table 1), indicating that small-scale occupancy was considerably lower than large-scale occupancy. This means that brown creepers were locally rare, but occupied a relatively larger fraction of the landscape. The naïve estimate of large scale occupancy of brown creepers was 0.18 and therefore the adjusted occupancy estimate accounting for incomplete detection and availability ($\hat{\psi} = 0.27$) was 50% greater than the naïve estimate. The relatively large false absence rate was primarily due to the low availability of brown creepers at the survey stations. This suggests brown creepers have a high probability of being overlooked at the sample unit because they occupied only a small proportion of survey stations when present at the sample unit.

We detected lark sparrows at 30 survey stations, at 9 sample units in the South Dakota stratum and at 2 sample units in the Wyoming stratum. The removal estimate of detection for the lark sparrow was $\hat{p} = 0.37$. Lark sparrows occupied 32% of the survey stations when present at the sample units ($\hat{\theta}$) and 20% of the sample units ($\hat{\psi}$) in the Black Hills National Forest (Table 1). This means that lark sparrows were relatively common at the local scale, but occupied a smaller fraction of the landscape. The naïve estimate of large scale occupancy for lark sparrows was 0.196. Therefore, the adjusted occupancy estimate accounting for incomplete detection and availability ($\hat{\psi} = 0.200$) was 2% greater than the naïve estimate. The low false absence rate was primarily due to the relatively high availability of lark sparrows at the sample stations. In other words, lark sparrows were unlikely to be overlooked at the sample units because they occupied a relatively large proportion of sample stations when present at the sample unit.

Table 1. Parameter estimates, standard errors (SE), coefficients of variation (CV), and lower (LCL) and upper (UCL) 95% confidence limits for brown creeper and lark sparrow occupancy, 23 May to 14 July 2009 in the Black Hills National Forest, South Dakota and Wyoming, USA. Psi ($\hat{\psi}$) is the estimate of large-scale occupancy for 1-km^2 sample units in the Black Hills National Forest estimated using the delta method. The parameters $\hat{\psi}_{SD}$ and $\hat{\psi}_{WY}$ are the estimates of large-scale occupancy for the South Dakota and Wyoming portions of the Black Hills National Forest. Theta ($\hat{\theta}$) is the forest-wide estimate of small-scale occupancy for 4.9-ha plots surrounding the point count locations. The parameter $\hat{p}$ is the removal estimate of detection probability estimated from the binned minute intervals.

Parameter	Estimate	SE	CV	LCL	UCL
Brown creeper					
$\hat{\psi}$	0.27	0.09	0.34	0.08	0.45
$\hat{\psi}_{SD}$	0.26	0.10	0.37	0.11	0.50
$\hat{\psi}_{WY}$	0.30	0.20	0.66	0.06	0.74
$\hat{\theta}$	0.11	0.05	0.42	0.04	0.25
$\hat{p}$	0.28	0.15	0.51	0.08	0.63
Lark sparrow					
$\hat{\psi}$	0.20	0.05	0.27	0.09	0.31
$\hat{\psi}_{SD}$	0.20	0.06	0.30	0.10	0.35
$\hat{\psi}_{WY}$	0.21	0.13	0.63	0.05	0.58
$\hat{\theta}$	0.32	0.06	0.19	0.21	0.45
$\hat{p}$	0.37	0.10	0.27	0.19	0.58

DISCUSSION

Our application of the multi-scale occupancy model was useful for decomposing the observation process into availability and detection components as well as addressing the closure assumption for spatially replicated survey stations. Accounting for incomplete detection is an important consideration for wildlife monitoring programs (Thompson et al. 1998, Yoccoz et al. 2001, Pollock et al. 2002, Kéry and Schmidt 2008). The detection process may be decomposed into several components (Nichols et al. 2009, Hines et al. 2010, Riddle et al. 2010), including spatial availability (species may not be exposed to sampling at all surveys stations) and detection (exposed species may go undetected). Certain species, such as the brown creeper in the present study, occur infrequently at the spatially replicated survey stations and are therefore more likely to be missed during sampling. The multi-scale occupancy model developed by Nichols et al. (2008) effectively adjusts the estimate of large scale occupancy upward to account for the incomplete availability of species within the sample units. The availability parameter in this context corresponds to a coverage probability or the extent that an animal(s) home range or territory at least partially overlaps a sampling unit (Nichols et al. 2009). We suggest the robust design parameterization relaxes the closure assumption for the spatially replicated survey stations and allows some survey stations to have negligible probabilities of detection (Kendall and White 2009). This parameterization accounts for incomplete availability at the survey stations and adjusts the estimate of θ for incomplete detection (Nichols et al. 2008), which may reduce the negative bias in p and positive bias in ψ that results from applying the standard occupancy model to spatially replicated subunits (Kendall and White 2009). The theory underlying the model addresses the lack of closure associated with the spatial replication of subunits (Nichols et al. 2008), but simulations to evaluate the performance of the model is an area of further research. In tandem with the removal design, the model allows the estimation of detection and occupancy parameters from a single field visit to the sample unit. In the case of equal minute intervals, the multi-scale occupancy model can easily be fit in programs MARK (MARK Version 6.1, www.phidot.org, accessed 14 Jun 2010) and PRESENCE (PRESENCE Version 3.1, www.mbr-pwrc.usgs.gov, accessed 11 Apr 2011).

In the analysis examples, we used multi-scale occupancy estimation to make inference about site occupancy at 2 spatial scales. Each survey station covered an area of 4.9 ha and the occurrence of bird species at the small scale was considered to be territory occupancy. When the sample units are approximately the size of a territory, occupancy can be interpreted as abundance or the number of territories (MacKenzie et al. 2006). The published accounts of territory size ranged from 0.01 ha to 6.4 ha for the brown creeper (Hejl et al. 2002) and 0.01 to 6.0 ha for the lark sparrow (Martin and Parrish 2000). Because the area sampled by the survey stations approached the maximum territory size for the 2 species, we considered small scale occupancy an estimate of the minimum number of occupied territories within the sample unit. We interpreted large scale occupancy of the 1-km^2 sample units as regional occupancy or the fraction of the landscape occupied by a species. In the analysis examples, the estimates of large-scale occupancy for brown creepers and lark sparrows were similar, but the estimates of small-scale occupancy for these species were considerably different (Table 1). The brown creeper demonstrated low small-scale occupancy when present at the sample units ($\hat{\theta} = 0.11$, 1.8 territories), whereas the lark sparrow showed higher small-scale occupancy ($\hat{\theta} = 0.32$, 5.1 territories; Table 1). Although the least abundant species also tend to be the least widespread (Gaston and Lawton 1990), the correlation between local abundance and regional occupancy may be an artifact associated with sampling rare species (Wright 1991). As mentioned above, the multi-scale occupancy model is particularly useful for accounting for incomplete detection and availability that arise when sampling rare species. Species inhabiting discontinuous habitats, such as lark sparrows in patchy grasslands of the Black Hills National Forest, are expected to show high local abundance and low regional occupancy (Gaston and Lawton 1990) Alternately, species with low local abundance and low regional occupancy, such as the brown creeper, face double jeopardy and are vulnerable to habitat alteration at local and regional scales (Lawton 1993). In particular, low local abundance may identify species at risk of future declines in regional occupancy (Zuckerberg et al. 2009).

The multi-scale occupancy model developed by Nichols et al. (2008) is particularly well suited for hierarchical sample designs, such as spatially replicated survey stations within sample units that are typical of avian monitoring programs (Robbins et al. 1986, Carlson and Schmiegelow 2002, Manley et al. 2005, Buckland 2006, Ferland et al. 2006). The estimation of occupancy at multiple scales and sampling variance at each level of the hierarchy requires careful consideration of the independence of the spatially replicated survey stations. In our application of Nichols et al. (2008) multi-scale occupancy model, small-scale occupancy is estimated assuming the conditional independence of the spatially replicated survey stations. That is, the spatially replicated survey stations are independent conditional on the occupancy state of the sample unit. The multi-scale occupancy model allows the simultaneous use of presence–absence data at 2 spatial scales and appropriately accounts for the non-independence of the spatially replicated survey stations.

MANAGEMENT IMPLICATIONS

We anticipate the multi-scale occupancy model will be useful for monitoring wildlife populations at local and regional scales, modeling multi-scale habitat relationships, and estimating population state variables for rare species of conservation concern. Large-scale monitoring programs have been criticized for the inability to provide information on the status of wildlife populations at local scales most relevant to land management agencies (Downes et al. 2005, Sauer and Knutson 2008). Monitoring occupancy at small and large scales offers the potential to evaluate changes in the population state in terms of local territory occupancy and regional occupancy. Estimating the proportion of sites occupied at 2 spatial scales may be useful for linking population responses to habitat conditions at local and landscape scales. Because population responses to habitat conditions are scale dependent, the management of wildlife habitats must be implemented at multiple spatial scales (Block et al. 2001, George and Zack 2001). Evaluating the effects of management activities and habitat modification on species occurrence at multiple scales may prove useful for prioritizing conservation efforts at local management unit and ecoregional scales. Rare species present formidable challenges for sampling, monitoring, and ultimately the conservation of populations. These are species for which strong inference on population parameters are most needed and are species for which such information is most difficult to obtain (MacKenzie et al. 2005). By distinguishing between species that are locally rare and those that are locally common, multi-scale occupancy estimation may provide a more comprehensive understanding of patterns of occurrence for rare species. The ability to use occurrence data at the level of the survey station allows larger sample sizes for estimating detection than can be realized at the level of the sample unit. At the local scale, the application examples for the Black Hills National Forest provided estimates of territory occupancy for low density, species of conservation concern. The brown creeper is a U.S. Forest Service Management Indicator Species and both birds are Wyoming Partners in Flight species of conservation concern (Priority II). At the ecoregional scale, the multi-scale occupancy model has recently been used to estimate population state variables for 11 rare species of conservation concern throughout the Badlands and Prairies Bird Conservation Region (White et al. 2010).

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Appendix. SAS code for estimating the parameters of the multi-scale occupancy model (PROC NLMIXED; SAS/STAT Version 9.2; SAS Institute, Inc., Cary, NC).

```
%let NumPoints=16;       * Number of points surveyed within a block (1 km^2);
%let NumIntervals=3;     * Number of intervals surveyed at a point;
%let NumPsiGroups=2;     * Number of groups (psi estimates);
%let IntLen1=2;          * Number of minutes in first interval;
%let IntLen2=2;          * Number of minutes in second interval;
%let IntLen3=1;          * Number of minutes in third interval;
%let IntLen4=1;          * Number of minutes in fourth interval;
%let IntLen5=1;          * Number of minutes in fifth interval;
%let EncHistLen=%eval(&NumPoints*&NumIntervals+1);
title 'Multi-scale Occupancy Model';
data EncHist;
      array Groups{&NumPsiGroups} Freq1-Freq&NumPsiGroups;
      length HISTRY $ &EncHistLen; *length should be 1 more than the number
of characters in the encounter history;
* Have to edit this statement to read the psi groups;
      input ID $ 1-17 HISTRY $ 20-68 Freq1 69-69 Freq2 71-71;
      freq=max(Freq1,Freq2);
/*
         1         2         3         4         5         6         7
8         9         0         1
1234567890123456789012345678901234567890123456789012345678901234567
8901234567890123456789012345678901234567890 */
      cards;             * Brown creeper data;
/*SD-BCR17-BH11*/  1..000......00000000000000000000000001.000000000 1 0
/*SD-BCR17-BH12*/  000000000000000000000000...000000000...000000000 1 0
/*SD-BCR17-BH13*/  ...000000000...000000......000000000...000000000 1 0
/*SD-BCR17-BH14*/  000000......000000.............................. 1 0
/*SD-BCR17-BH15*/  000000......000.........000.........000000...... 1 0
/*SD-BCR17-BH16*/  000000000...000...000...000000000...000000000... 1 0
/*SD-BCR17-BH17*/  ............000000000000000000000000...000000... 1 0
/*SD-BCR17-BH18*/  000000000...000000000000000000...000000000000000 1 0
/*SD-BCR17-BH19*/  000000000000000......000000......000000000000000 1 0
/*SD-BCR17-BH02*/  000000000000000000000000000000000000000000000000 1 0
/*SD-BCR17-BH20*/  ...1..000000000......000000......0001..00001.000 1 0
/*SD-BCR17-BH22*/  .........000.........000......000000......000000 1 0
/*SD-BCR17-BH23*/  000.........000000000000000000...000...000000000 1 0
/*SD-BCR17-BH24*/  000...000000000...0001..000...000000...000000000 1 0
/*SD-BCR17-BH25*/  .....................000......000000...000...... 1 0
```

```
/*SD-BCR17-BH26*/  000000000000000000...000000000000000000000000000 1 0
/*SD-BCR17-BH27*/  000000000000000000000000000000000000000000000000 1 0
/*SD-BCR17-BH28*/  000000000000000......000000......000000000...... 1 0
/*SD-BCR17-BH29*/  01.0000000000000000000000000000000000001..000000 1 0
/*SD-BCR17-BH03*/  ......000000......000000......000000......000000 1 0
/*SD-BCR17-BH30*/  000000......000000......000000......000000...... 1 0
/*SD-BCR17-BH31*/  ...000000000...000000000...000000000...000000000 1 0
/*SD-BCR17-BH32*/  000000000...000000000...000000000000000000000000 1 0
/*SD-BCR17-BH33*/  000000000000000000000000000000000000000000000000 1 0
/*SD-BCR17-BH34*/  0000000000001..000000000000000000000000000000000 1 0
/*SD-BCR17-BH36*/  ......000000.........000.........000......000000 1 0
/*SD-BCR17-BH37*/  000000000000000000000000000......000000000000000 1 0
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/*SD-BCR17-BH39*/  1..000000000000000000000........................ 1 0
/*SD-BCR17-BH04*/  000.........000000...000000000000000.........000 1 0
/*SD-BCR17-BH40*/  000000000000000000000000000000000000000000000000 1 0
/*SD-BCR17-BH41*/  000000000...000000000...000000000...000000000000 1 0
/*SD-BCR17-BH42*/  0000000000000000000001..000000000000000000000000 1 0
/*SD-BCR17-BH44*/  000000000000000000000000000000000000000000000000 1 0
/*SD-BCR17-BH45*/  000000000000000000000000000000000000......000000 1 0
/*SD-BCR17-BH47*/  000000000000000000000...000000.................. 1 0
/*SD-BCR17-BH48*/  .................................000000000000000 1 0
/*SD-BCR17-BH49*/  000000000000000000000000000000000000000000000000 1 0
/*SD-BCR17-BH05*/  000000.........000000........................... 1 0
/*SD-BCR17-BH50*/  000000000000000000000000000000000000000000000000 1 0
/*SD-BCR17-BH51*/  000000000000000000000000000000000000000000000000 1 0
/*SD-BCR17-BH52*/  000000000000000000000000000000000000000000000000 1 0
/*SD-BCR17-BH55*/  000000000000000000000000000000000000............ 1 0
/*SD-BCR17-BH56*/  000000000000000000000000000...000000......000000 1 0
/*SD-BCR17-BH57*/  001.........000.........000000000000000000000000 1 0
/*SD-BCR17-BH60*/  000000000000000000000000000000000000000000000000 1 0
/*SD-BCR17-BH08*/  000000000000000000000...000000.................. 1 0
/*WY-BCR17-BH01*/  000000...000000000......000000......000000...... 0 1
/*WY-BCR17-BH10*/  000000000......0000000000000000000001..1..00001. 0 1
/*WY-BCR17-BH02*/  000000000000000000000000000000000000000000000000 0 1
/*WY-BCR17-BH03*/  000000000000000......000000.........000......... 0 1
/*WY-BCR17-BH04*/  .........000.........000.........000.........001 0 1
/*WY-BCR17-BH05*/  000000000000000000000000000000000000000000000000 0 1
/*WY-BCR17-BH06*/  000000000000000000000000000000000000000000000000 0 1
/*WY-BCR17-BH07*/  000000000000000000000000........................ 0 1
/*WY-BCR17-BH08*/  000000000000000000000000000000000000000000000000 0 1
/*WY-BCR17-BH09*/  000000000.....................000000...000000000 0 1
 ;
 proc contents;
 proc print;
 run;
proc nlmixed ecov;
* Multi-scale Occupancy Estimation Nichols et al. (2008) J. Applied Ecology;
      parms logitdelta=-0.1 logitp1min=-0.1 logitpsi1=-0.1  logitpsi2=-0.1;
      array CAP{&NumPoints} _temporary_;
```

```
       array CUM1{&NumPoints} _temporary_;
       array CUM2{&NumPoints} _temporary_;
       array IntLen{5} _temporary_;
       IntLen[1]=&IntLen1; IntLen[2]=&IntLen2; IntLen[3]=&IntLen3;
IntLen[4]=&IntLen4; IntLen[5]=&IntLen5;
*   CUM1 = Delta*product of p;
*   CUM2 = (1 - Delta);
*   CAP set to 1 for subsites with detection, zero otherwise;
       do j=1 to &NumPoints; CAP[j]=-1; CUM1[j]=0; CUM2[j]=0; end;
       if Freq1=1 then Psi=1/(1+exp(-logitpsi1));
       else Psi=1/(1+exp(-logitpsi2));
       Delta=1/(1+exp(-logitdelta));
       p1min=1/(1+exp(-logitp1min));
       IOCCAS=0;
       CELPRB=Psi;
       SOMEINFO=0;
       do j=1 to &NumPoints;
             CUM1[j]=Delta;
             do i=1 to &NumIntervals;
                   IOCCAS=IOCCAS+1;
                   if substr(HISTRY,IOCCAS,1)^='.' then do;
                         CAP[j]=MAX(0,CAP[j]);
                         if substr(HISTRY,IOCCAS,1)='1' then do;
                               CAP[j]=1;
                               CUM1[j]=CUM1[j]*(1-(1-p1min)**IntLen[i]);
                               SOMEINFO=1;
                         end;
                         else do;
                               CUM1[j]=CUM1[j]*(1-(1-(1-p1min)**IntLen[i]));
                         end;
                   end;
             end;
             if CAP[j]=-1 then do;   * No data for this visit/subsite;
                   CUM1[j]=1;
                   CUM2[j]=0;
             end;
             else do;
                   if CAP[j]=1 then do;
                         CUM2[j]=0;
                               end;
                               else do;
                                     CUM2[j]=1-Delta;
                               end;
                         end;
                         CELPRB=CELPRB*(CUM1[j]+CUM2[j]);
                   end;
                   if SOMEINFO=0 then do;
                         CELPRB=CELPRB+(1-Psi);
                   end;
                   model freq ~ general(log(CELPRB));
                   estimate 'Psi1' 1/(1+exp(-logitpsi1));
                   estimate 'Psi2' 1/(1+exp(-logitpsi2));
                   estimate 'Delta' Delta;
                   estimate 'p1min' p1min;
                   run;
```