Articles

Occupancy Modeling of Woodpeckers: Maximizing Detections for Multiple Species with Multiple Spatial Scales

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Abstract

Numerous forest birds benefit from woodpecker presence or have similar habitat requirements. Monitoring populations of forest woodpeckers can be useful for management decisions regarding these and other forest species. Usefulness of monitoring efforts depends on methods employed and the quality of resulting parameter estimates. Estimating the proportion of area occupied by a species can be an attractive and affordable alternative to abundance or survival estimates. The purpose of this study was to assess the distribution and area of occupancy for pileated woodpeckers (*Drycopus pileatus*) and American three-toed woodpeckers (*Picoides dorsalis*) in north-central Idaho, and to compare occupancy estimates using silent point counts, playback surveys, and playback surveys that incorporated estimates of detection probability (*p*). We used a hierarchical multi-scale framework that allowed estimation of occupancy at two spatial scales and applied a removal design such that repeat visits to sampling stations was not necessary to estimate *p*. The initial naïve estimate of occupancy (using presence-absence data) for pileated woodpecker was 0.39, which increased to 0.59 using playback surveys. The corrected estimate of occupancy at the 1-km^2 unit scale was 0.70. The naïve estimate of occupancy for American three-toed woodpeckers using silent point counts and playback surveys were 0.14 and 0.34, respectively. The unbiased estimate of occupancy at the 1-km^2 unit scale was 0.71. Detection probabilities are known to vary spatially and temporally for numerous reasons. Thus, comparisons of naïve estimates of occupancy to monitor forest woodpeckers would be imprudent and could lead to poor management decisions. We recommend incorporating detection probability for monitoring wildlife species and show how this can be done within a single sampling framework for species that utilize the landscape at disparate scales.

Keywords: woodpeckers, occupancy, Management Indicator Species

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Short title: Woodpecker occupancy

Introduction

The role of cavity excavators in forest landscapes has cascading effects involving numerous species of birds, mammals, insects, and fungi (Bull and Jackson 2011). As a result, woodpeckers are often considered keystone species (Martin and Eadie 1999; Aubry and Raley 2002). Many forest woodpeckers are associated with habitats that include large trees and dead wood for foraging and nesting (Mikusiński et al. 2001; Drever et al. 2008), and their sensitivity to timber harvest is well recognized (Imbeau et al. 1999; Roberge and Angelstam 2006; Bull et al. 2007). Because many forest birds have similar habitat requirements, managing for woodpecker diversity should also benefit general forest bird diversity (Martin and Eadie 1999; Dreaver and Martin 2010). Indeed, Mikusiński et al. (2001) and Roberge and Angelstam (2006) have shown a correlation between woodpecker richness and other forest bird richness at the landscape scale.

The pileated woodpecker (*Drycopus pileatus*) is generally associated with mature or old growth forest types (Bull and Jackson 2011) and excavates cavities that are much larger than most other woodpecker species and provide roosting, nesting, and food caching opportunities for various secondary cavity users such as flammulated owl (*Otus flammeolus*), American kestrel (*Falco sparverius*), common goldeneye (*Bucephala clangula*), American marten (*Martes americana*), fisher (*Martes pennant*), and numerous species of bats (Bonar 2000; Aubry and Raley 2002; Martin et al. 2004; Bull and Jackson 2011). Excavated cavities additionally facilitate ecological processes by encouraging decomposition directly as well as indirectly by exposing wood for insect and fungal attack (Aubry and Raley 2002). Besides being an ecological engineer, pileated woodpeckers may depress insect outbreaks that negatively impact the commercial value of forest stands (Aubry and Raley 2002; Edworthy et al. 2011).

The American three-toed woodpecker (*Picoides dorsalis*) is also generally associated with mature or old growth forest types (Imbeau et al. 1999; Leonard 2001; Hoyt and Hannon 2002). American three-toed woodpeckers prefer large snags in moderately burned stands, which may restrict distributions in some areas to recently burned forests (Hutto 1995; Kotliar et al. 2008). Because of their association with natural disturbances, American three-toed woodpeckers are considered susceptible to habitat loss due to fire suppression and salvage logging practices (Imbeau et al. 1999; Leonard 2001; Hoyt and Hannon 2002). In Idaho, it is considered a sensitive species for which population viability is a concern due to predicted downward trends in habitat suitability that would reduce the existing distribution (IDFG 2005). Monitoring of American three-toed woodpeckers is difficult because although they are generally sedentary, they can have irruptive movements that track with insect outbreaks (Yunick 1985). Similar to the American three-toed woodpecker, the Eurasian three-toed woodpecker (*P. tridactylus*) is considered to be a valuable indicator of species richness in European coniferous forests (Roberge and Anglestam 2006).

Monitoring populations of forest woodpeckers can be useful for informing management decisions regarding these and other forest species (Aubry and Raley 2002; Drever and Martin 2010). Usefulness of monitoring efforts, however, relies on the metrics estimated and methods used. Quantitative estimates of abundance, survival, and fecundity are generally considered ideal metrics for monitoring wildlife populations (Anderson and Gutzwiller 2005; Lancia et al. 2005). However, it can be difficult to obtain estimates of abundance or demographic rates for many populations and the cost of such studies cannot be justified in many cases, particularly over large spatial scales and for multiple species. Estimating the proportion of area occupied by the species is an attractive alternative that has been utilized for monitoring numerous species, including birds (Collier et al. 2010; Bruggeman et al. 2011; Hansen et al. 2011), terrestrial mammals (Moritz et al. 2008; Ahumada et al. 2011), primates (Karanth et al. 2010), bats (Weller and Baldwin 2012), amphibians (Jackson et al. 2006; Gould et al. 2012), and reptiles (Zylstra et al. 2010; Sewell et al. 2012). This method is based on detection- nondetection data and can be used over relatively large spatial scales to monitor trends in occupancy simultaneously for multiple species (Schultz et al. 2012). Additionally, with the use of multiple observation occasions, it is possible to estimate the probability of detecting a species, which can greatly improve accuracy of occupancy estimates (Pollock et al. 2002; MacKenzie et al. 2003; MacKenzie et al. 2006).

Forest birds are commonly surveyed using the point count method where an observer remains stationary and records all birds seen or heard over a defined period of time within a defined distance of the observer (Hutto et al. 1986; Lancia et al. 2005). Woodpeckers are generally thought to be conspicuous, owing to their distinctive calls, drumming patterns, and bold colors (Blackburn et al. 1998). Numerous studies have used point count methods for surveying woodpeckers, particularly during concurrent surveys for other bird species (Hutto 1995; Imbeau et al. 1999; Kotliar et al. 2008; Krementz et al. 2012). However, woodpeckers typically have larger territories and vocalize less frequently than most song birds (Blackburn et al. 1998; Farnsworth et al. 2002), suggesting that a substantial proportion of individuals may not be detected using standard point count methods. Johnson et al. (1981) suggested broadcasting recorded calls to survey avian species with these characteristics more efficiently. Shackelford and Conner(1997) noted that vocally mimicking a barred owl (*Strix varia*) often induced woodpeckers to respond by vocalizing or moving closer to the source of the sound; the authors reported a 71% increase in woodpeckers detected after vocally mimicking a barred owl call compared with using silent point counts in Texas. Similarly, Kumar and Singh (2010) detected more than twice as many individuals and a greater number of woodpecker species using playback of recorded calls in tropical forests.

In this study, our primary goal was to assess the distribution and area of occupancy of pileated and American three-toed woodpeckers within the Selway-Middle Fork Clearwater Collaborative Forest Landscape Restoration Program (CFLRP) project area in the Nez Perce-Clearwater National Forest using a single sampling scheme with a rigorous ability to collect data from multiple species with disparate spatial scales. The CFLRP is a federally sponsored program with the purpose of encouraging collaborative, science-based ecosystem restoration of priority forest landscapes. In this CFLRP landscape, the pileated and American three-toed woodpeckers are considered a management indicator species (species whose populations are thought to reflect the effects of management activities on various habitats) and a “species of greatest conservation concern” (IDFG 2005), respectively. Secondarily, we were interested in comparing results from an occupancy analysis using silent point counts and playback surveys that incorporated estimates of detection probability for these two woodpecker species.

Methods

Study area

We conducted our study in the Clearwater Mountains of north-central Idaho, USA (46.097^{o} N, -115.690^{o} W), on the Nez Perce-Clearwater National Forest. The topography is mountainous with areas of steep, rugged terrain and few open valleys and meadows. Elevation ranges from 440 to 2075 m, and annual precipitation ranges from 106 to 174 cm (Natural Resource

Conservation Service 2010). The climate is Pacific maritime with cold, snowy winters and short, warm summers. The habitat is primarily mixed coniferous forest on the mountain slopes with narrow or no riparian areas along streams. At low to mid-elevations, the forest is comprised primarily of Douglas fir (*Pseutotsuga menziesii*), western larch (*Larix occidentalis*), grand fir (*Abies grandis*), and western red cedar (*Thuja plicata*); at higher elevations the forest transitions to subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), mountain hemlock (*Tsuga mertensiana*), and lodgepole pine (*Pinus contorta*) with an increasing incidence of mixed shrub fields (*Alnus* spp., *Salix* spp, *Ceanothus* spp., *Phyocarpus* spp., *Sorbus* spp.) and mountain meadows. The National Forests have been managed under multiple-use and roadless/wilderness frameworks which has resulted in a mixed pattern of stand structures and canopy covers, ranging from open clear-cuts, shrub fields, and regenerating forest to mature forest and old growth stands (Multiple-use and Sustained Yield Act 1960).

Survey methods

During a typical point count survey many woodpeckers that are present may remain undetected for numerous reasons (e.g., conspicuousness, study design, observer experience). Using presence-absence data as an estimate of occupancy is termed a "naïve estimate" and when detection probability (the probability of detecting a species when it is present, hereafter, *p*) is less than one, naïve estimates of occupancy are biased low (MacKenzie et al. 2006). We incorporated estimates of *p* to correct naïve estimates, resulting in unbiased estimates of occupancy.

We used a spatially balanced sampling design to select 44 1-km^2 sampling units from the western portion of the Middle Fork CFLRP Project (Stevens and Olsen 2004). We used a hierarchical multi-scale sampling strategy where each sampling unit was composed of four survey stations to facilitate simultaneous sampling of other species at appropriate scales (Pavlacky et al. 2012). The hierarchical design permits simultaneous estimates of large-scale occupancy (ψ) at the sampling unit level and small-scale occupancy (θ) at the survey station level (Pavlacky et al. 2012). The latter can be interpreted as availability and is defined as the probability of the species occupying a survey station, given it is present within the sampling unit. Stations were positioned 250 m from the edge of the sampling unit such that there was 500 m between the four points, which is consistent with other woodpecker research (Raley and Aubry 1993; Hartwig et al. 2002; Wrightman and Saab 2005). We used the harvest history from the Nez Perce-Clearwater National Forest to stratify our sample grids between actively managed landscapes (i.e., those areas with some form of timber harvest) and unmanaged landscapes (i.e., those without a history of any timber harvest). We allocated our sampling effort to 70% actively managed landscapes and 30% unmanaged landscapes.

We used playback surveys to detect presence of both woodpecker species (Johnson et al. 1981). Surveys were conducted between 0600 and 1100 hours and all four stations within a sample unit were surveyed on the same morning. The survey protocol consisted of a 6-minute period of silent listening, a 6-minute playback survey for American three-toed woodpeckers, and a 6-minute playback survey for pileated woodpeckers, always in that order. If a dominance structure exists among woodpecker species, broadcasting calls from species of greater dominance may reduce detections of subordinate species. Though information on the dominance structure between these species is lacking, we choose to play the American three-toed woodpecker calls first due to its significantly smaller size, believing it would most likely be the subordinate species. Playback surveys consisted of alternating 30 seconds of calls and drumming from the species of interest, and 30 seconds of silent listening. If a species was detected during the silent listening phase, the phase was continued for potential detections of other species and the call playback phase was still conducted for that species. However, as a logistical time saving measure, once we detected a species during its call playback phase (e.g., two minutes into the pileated call playback phase a pileated was detected) we discontinued the survey. We did not survey stations in close proximity to running water such that audibly detecting woodpeckers was inhibited. We used a Foxpro NX3 digital game caller (FOXPRO Inc., Lewistown, PA, USA) to broadcast calls and rotated direction of the caller 120 degrees after each 1-minute call cycle, completing two rotations during each 6-minute playback survey. We used a volume level such that field technicians could not hear the recording at >250m away; however, the ability of woodpeckers to hear the recording at greater distances was not known. We detected woodpeckers visually or by call, and recorded which of the six 1-minute intervals of the survey the detection was made.

Habitat covariates

Before each survey began, we measured habitat variables within 50 m of the survey station. This allowed birds to settle after initial disturbance from entering the site prior to beginning each survey. The habitat variables included number of snags >23 cm in diameter at breast height (DBH) and > 3 m high (Wightman and Saab 2008), height of the base of the canopy measured with clinometers and a rangefinder, and percent ground covered with dead and downed trees with >23 cm diameter (course woody debris, hereafter CWD). All habitat variables were estimated visually from the sampling point to reduce movement that might affect woodpecker activity. We calculated naïve occupancy as the proportion of sampling units a species was detected separately for detections during the silent period and the playback period.

Studies on habitat use have indicated that pileated woodpeckers use old-growth forests with ≥ 60% canopy closure and use is related to density of snags and downed trees and absence of logging (Bull and Holthausen 1993). Three-toed woodpeckers appear to select habitat with mature and old-growth forests for foraging and roosting (Goggans et al. 1989) and forage in areas with trees of greater DBH compared to that available (Kotliar et al. 2008). We drew from these key findings and general landscape ecology concepts, and developed unique hypotheses to build a suite of *a priori* conceptual models. We identified landscape metrics that best captured the conceptual models and used program FRAGSTATS 3.3 (McGarigal et al. 2002) to calculate the metrics around each of our sample stations and sample units. We buffered sampling stations by 250 m radius and the centroids of sample units by 1,250 m, resulting in an area roughly the size of a breeding pair of pileated woodpeckers' home range (490ha; Mellen et al. 1992; Bull and Holthausen 1993).

For habitat classes, we used layers from the LANDFIRE dataset (2006) including canopy cover and canopy height. We updated these layers with data from recent forest harvests using a tassel-cap soil transformation (Healey et al. 2005) of paired LANDSAT Thematic Mapper images in the DeltaCue add-on to ERDAS Imagine (Intergraph Inc. Norcross, GA, USA). We used the Spatial Analyst extension in ArcGIS (ESRI Inc. Redlands, CA USA) to resample habitat layers and apply a minimum mapping unit of 1 ha. We collapsed the number of categories in the LANDFIRE data due to sparse data. The resulting categories were % landscape with 0-9.9%, 10-39.9%, 40-69.9%, and 70-100% canopy cover and % landscape with < 5 m, 5-9.9 m, 10-24.9 m, and 25-50 m canopy height. We limited the potential large-scale occupancy covariates in our *a priori* models to 40-69.9% and 70-100% canopy cover, and 25-50 m canopy height as we felt these metrics would be most useful for describing mature and old-growth forest structure.

Additionally, we included the station-scale covariates of number of snags, CWD, and Canopy Height, as potential small-scale occupancy covariates.

Statistical framework

We divided the 6-minute playback survey into equal periods to create occasions and used stations within a unit as our replicates (Pavlacky et al. 2012). One of the assumptions of occupancy estimation is that detections at a station are independent of each other; that is, detections of an individual species are not more or less likely, subsequent to first detection (MacKenzie et al. 2006). As this was not likely to be true given our method of playback surveys, we used a removal design and only considered detection histories up to first detection at each station for a given species (Farnsworth et al. 2002). This design is unable to estimate unique detection probabilities for each occasion and requires a constraint, such as constant *p* among occasions (MacKenzie et al. 2006). We examined our data by minute of survey for a constant decline in detections, as would be expected under the assumption of a constant *p* (Pavlackey et al. 2012). If this were true, we used the first three minutes for occasion one and the second three minutes for occasion two for each survey station. If equal *p* could not be assumed, we divided the 6-minute playback period into the fewest number of occasions of equal length such that the last two periods showed a steady decline in detections and a constant *p* could be assumed over these periods. Due to the limitations of the removal model and the limited number of observation occasions, we did not consider any covariates to describe *p*.

Models were fit and parameters estimated for pileated woodpecker and American three-toed woodpecker separately using program MARK (MARK Version 6.1, www.phidot.org, accessed 27 September 2011). We used Akaike's Information Criterion corrected for small sample sizes (AIC_c) to compare models and considered any models with $\Delta AIC_c < 2$ of the best fit model to be equally parsimonious (Burnham and Anderson 2002).

Results

We surveyed 167 stations in 44 units for detection – nondetection of pileated and American three-toed woodpeckers from 12 April to 17 June 2012. We were unable to conduct counts at nine sample stations within sample units either due to time constraints or noise interference.

Pileated woodpecker

Pileated woodpeckers were detected at 22 stations in 17 units during the silent listening period, resulting in a naïve estimate of occupancy at the unit scale (ψ) of 0.39 (Table 1). During the playback surveys, we detected pileated woodpeckers at 44 stations in 26 units, increasing the naïve estimate of ψ to 0.59. Frequency of calls decreased from the first three minutes to the second three minutes, so we used a two sampling occasion model and assumed a constant p for the 6-minute playback survey. The top supported model describing occupancy for the pileated woodpecker was the null model (i.e., a single time- and habitat-invariant estimate for each parameter ψ, θ, and p; Table 2). The p for each 3-minute period of the playback survey was 0.31, resulting in 0.52 probability of detecting pileated woodpeckers during the 6-minute playback survey. Accordingly, accounting for imperfect detection, our corrected estimate of ψ was 0.70. Furthermore, given that pileated woodpeckers were present at the sample unit scale, the probability of occupancy for any single sampling station (i.e., availability, θ) was estimated to be 0.73.

The three models that included habitat covariates and their possible influence on ψ had $\Delta AIC_c < 2$ (Table 2). Considering the greater number of parameters in these models and the only minor improvement in deviance estimates, there was very little support for any model with habitat covariates (Burnham and Anderson 2002; Arnold 2010).

American three-toed woodpecker

American three-toed woodpeckers were detected at seven stations in six units during the silent listening period, for a naïve estimate of $\psi = 0.14$ (Table 1). During the playback surveys, American three-toed woodpeckers were detected at 19 stations in 15 units, increasing the naïve estimate of $\psi = 0.34$. Detections of individuals were low during the first two minutes of the playback survey, peaked during minute 3, and decreased over the remaining three minutes. Accordingly, we fitted models using three 2-minute occasions, allowing *p* in the first occasion to differ from a constant *p* in the remaining two occasions. Thus, from the null model, estimates of *p* were 0.13 during the first two minutes of the playback survey and 0.33 for minutes 3-4 and 5-6. The probability of detecting American three-toed woodpeckers during the entire 6-minute playback survey was 0.61. The unbiased estimate of ψ for American three-toed woodpeckers was 0.71. However, given that American three-toed woodpeckers were present at the sample unit scale, the estimated probability of occupying any sampling station (θ) was only 0.26.

There were three apparently equally parsimonious models describing occupancy for the American three-toed woodpecker; the null model and two models with covariates describing ψ (Table 3). Because there was little improvement in estimated deviance with additional covariates, there was little support for models more complex than the null model (Burnham and Anderson 2002; Arnold 2010).

Discussion

We estimated occupancy of pileated and American three-toed woodpeckers at two spatial scales while accounting for the probability of detecting each species. Our method of dividing a single observation into multiple occasions and using a removal framework allowed estimation of *p* without the typical requirement of performing surveys during repeat visits to each station. By using the hierarchical multi-scale framework in our analysis, we were able to tease apart small scale availability from detection probability, resulting in a more informative analysis of occupancy for both species.

Our estimates of occupancy suggest both pileated woodpeckers and American three-toed woodpeckers were widely distributed throughout the Selway-Middle Fork CFLRP area. For both species, the probability of occupation at any randomly selected 1-km^2 survey unit was about 70%. Detection probabilities over the 6-minute playback survey were similar; 0.52 and 0.61 for pileated and American three-toed woodpeckers, respectively. When corrected for detection probability, our estimate of occupancy increased from 0.59 to 0.70 for pileated woodpeckers and more than doubled from 0.34 to 0.71 for American three-toed woodpeckers. Failing to correct for imperfect detection would have resulted in significantly different conclusions regarding the distribution and area of occupancy of these species in our study area. However, simultaneously sampling for multiple species is not without some tradeoffs. We standardized our surveys by always playing American three-toed woodpecker calls before those of pileated woodpeckers. How this might influence the probability of detection of a pileated woodpecker is unknown; if pileated woodpeckers are attracted to or avoid the calls of American three-toed woodpeckers, there maybe be some consistent bias in our detection probability estimate.

While both woodpecker species showed similar patterns in large scale occupancy (i.e., at the sample unit scale), estimates of small scale occupancy were rather disparate between the two species. Within survey units where pileated woodpeckers were present, our models predicted the species would occupy areas covering three of the four survey stations. American three-toed woodpeckers were estimated to occupy areas covering only one of the four survey stations within units occupied. These estimates are reflected in the species' respective home range estimates. Mellen et al. (1992) estimated the average summer home range for 11 individual pileated woodpeckers in coastal Oregon of 478 ha and noted home ranges for pairs were even larger after chicks had fledged. Bull and Holthausen (1993) reported home ranges for seven breeding pairs from June to March between 321 and 630 ha with an average of 407 ha in northeastern Oregon. Territory size of American three-toed woodpeckers has not been widely documented; however, Goggans et al. (1989) estimated home ranges for three individuals after the breeding season at 53, 147, and 304 ha. In a study of Eurasian three-toed woodpeckers in Germany, average nesting season home ranges for 10 pairs was estimated to be 86 ha (Pechacek 2004). Our results suggest that while the two species appear to occupy the same proportion of 1-km^2 units in our study area, American three-toed woodpeckers appear locally rare and are less likely to be detected because of their lower availability, indicating available habitat is not saturated with birds.

One of the benefits of the occupancy framework that we applied is the ability to model occupancy as a function of environmental covariates (MacKenzie et al. 2006). As pileated woodpeckers are often considered a management indicator species of mature forest characteristics (Bull and Jackson 2011) and as American three-toed woodpeckers are generally associated with mature or old growth forest types (Imbeau et al. 1999; Leonard 2001; Hoyt and Hannon 2002), we hypothesized that the percentage of a landscape composed of large trees or heavy canopy cover would influence the occupancy of pileated or American three-toed woodpeckers. However, we did not find strong evidence that any of our environmental covariates helped explain variation in occupancy at either scale for either species better than a simple "null" model. This result was unexpected and warrants further investigation. It is possible that our covariates are not representative of the pattern we were attempting to detect, imprecisely estimated, measured at an inappropriate scale, or that our sample size was insufficient. However, based on our results, we suggest that the assumption of the general association of these woodpecker species with mature forests to be continually challenged with the best analytic methods such that the specifics of habitat requirements for each species become better understood. Such information would allow managers to decide the appropriateness of using pileated woodpeckers as a management indicator species for mature forest characteristics. Furthermore, we feel that if future work across Idaho on American three-toed woodpeckers shows corrected occupancy estimates consistent with ours, their designation as a "species of greatest conservation need" in the state maybe unwarranted due to their wider than originally expected occurrence.

Our use of playbacks greatly increased the number of detections, resulting in approximately a two-fold increase in naïve estimates of occupancy over silent surveys. This method, however, violates an assumption of independence in detections among the six 1-minute intervals and requires the use of a removal model for calculating unbiased estimates of occupancy. The removal model uses only first detections at a survey station for estimating p and generally results in reduced precision compared with a non-removal model unless number of sampling occasions is increased (MacKenzie and Royle 2005; MacKenzie et al. 2006). Precision of our estimates were poor, particularly p for American three-toed woodpeckers. Poor precision in our estimates of p may also have been the result of variation in detection probability through the season due to breeding behavior. Birds are typically less vocal during incubation than breeding and pileated woodpeckers response to playback call is known to vary with nesting chronology (Raley and Aubry 1993). The timing of our field work (mid-April to mid-June) spanned three phases of breeding: courtship, incubation, and hatching (Leonard 2001; Bull and Jackson 2011); and thus our detection probability represents detectability across these phases. Recognizing factors such as these and incorporating them into the modeling framework generally improves parameter estimates. Our use of the removal design, coupled with few observation occasions hindered our ability to incorporate these types of covariates into estimates of p. Repeat visits over time could improve nesting chronology specific estimates of p and have the additional advantage of improved precision of occupancy estimates (MacKenzie et al. 2002). However, this would come at the cost of a relatively large increase in effort and expense. We feel that the removal design we employed balanced the need to correct naïve occupancy estimates for detection probabilities with the practical logistical constraints of limited budgets and personnel.

Natural resource managers need to ensure that the metrics they collect regarding wildlife populations are accurate, yet often they have limited budgets to work with that preclude techniques that provide abundance or demographic rates. Estimating the proportion of area occupied by a species is an attractive alternative. But when detections are imperfect (< 1.0), naïve occupancy estimates are biased low and using such data as the basis for management decisions would be imprudent. Furthermore, with ever shrinking budgets, wildlife managers are increasingly interested in multiple species sampling frameworks that are robust to disparate population scales. Our application of a hierarchical, multi-scale occupation framework allowed us to use the same sampling stations for species with dissimilar territory sizes, yet tease apart availability from detection probability, resulting in greatly improved parameter estimates.

Supplemental Material

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Table S1. Data table containing detection histories of pileated woodpeckers (*Drycopus pileatus*) and American three-toed woodpeckers (*Picoides dorsalis*) in the Clearwater Mountains of north-central Idaho, USA, 2012. Unit_ID = unique unit number. Each unit contained four sampling points (A, B, C, D). 1-3 indicates the first 3-minute occasion that pileated woodpeckers were surveyed, 4-6 indicates the second 3-minute occasion. 1-2 indicates the first 2-minute occasion that American three-toed woodpeckers were surveyed, 3-4 indicates the second 2-minute occasion, and 5-6 indicates the third 2-minute occasion. The number 1 indicates a woodpecker was detected during that occasion, a 0 indicates the woodpecker was not detected, and a dot (.) indicates the survey was not conducted for the occasion, either due to the species being detected in an earlier occasion, or due to time constraints or noise interference. Management indicates whether the unit was in a managed stand (Ma) or unmanaged stand (Un). PLAND CanCov = percent of the unit with 40-69.9% canopy cover, or 70-100% canopy cover. PLAND CanHeight = percent of the unit with canopy height of 25-50m. NSnags = number of snags >23 cm in diameter at breast height (DBH) and > 3 m high within 50m of each survey station (A-D). Height = height of the base of the canopy at each survey station (A-D). CWD = percent ground covered with dead and downed trees with >23 cm diameter within 50m of each survey point (A-D).

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Table 1. Estimates of large-scale occupancy ($\hat{\psi}$), small-scale occupancy ($\hat{\theta}$), and occasion specific detection probability ($\hat{p}$) for pileated woodpeckers (*Drycopus pileatus*) and American three-toed woodpeckers (*Picoides dorsalis*) in the Clearwater Mountains of north-central Idaho, USA, 2012. Naïve estimates of $\hat{\psi}$ were calculated as proportion of sample units where the respective woodpeckers were detected during the 6-minute silent listening period (Silent), and 6-minute playback period (Playback). Observation occasions were three minutes long for pileated woodpeckers and two minutes long for American three-toed woodpeckers. Numbers in parentheses are standard errors for respective estimates.

	Parameter				
	$\hat{\psi}$			$\hat{\theta}$	$\hat{p}$
	Naïve		**Unbiased**		
Species	**Silent**	**Playback**			
Pileated woodpecker	0.39	0.59	0.70 (0.10)	0.73 (0.43)	0.31 (0.21)
American three-toed woodpecker	0.14	0.34	0.71 (0.28)	0.26 (0.22)	0.13 (0.11), 0.33 (0.35)*

* *p* was not assumed to be constant for the American three-toed woodpecker; first number is for minutes 1-2, second number is for both subsequent 2-minute periods of the 6-minute playback survey.

Table 2. Top supported models describing pileated woodpecker (*Drycopus pileatus*) occupancy in the Clearwater Mountains of north-central Idaho, USA, 2012. Psi (ψ) is the estimate of occupancy at the 1-km^2 sample unit scale, theta (θ) is the probability of occupancy at the survey station scale given the unit is occupied; *p* is the detection probability given the species is present at the survey station, and *K* is the number of model parameters. Covariates are: % landscape with 25-50 m canopy height (25-50m), % landscape with 40-69.9% canopy closure (40-70%), and % landscape with 69.9-100% canopy closure (70-100%). Models were selected using Akaike Information Criteria (AIC) and only models with $\Delta AIC_c < 2$ are provided.

Model	*K*	Δ AIC$_c$	Deviance
ψ (.) θ (.) *p*(.)	3	0.00	246.00
ψ (25-50m) θ (.) *p*(.)	4	0.55	244.12
ψ (25-50m + 70-100%) θ (.) *p*(.)	5	1.35	242.36
ψ (25-50m + 40-70%) θ (.) *p*(.)	5	1.36	242.38

Table 3. Top supported models describing American three-toed woodpecker (*Picoides dorsalis*) occupancy in the Clearwater Mountains of north-central Idaho, USA, 2012. Psi (ψ) is the estimate of occupancy at the 1-km^2 sample unit scale, theta (θ) is the probability of occupancy at the survey station scale given the unit is occupied; *p* is the detection probability when the species is present at the survey station, and *K* is the number of model parameters. Probability of detection for the first 2-minute period of the playback survey were allowed to differ from the two subsequent 2-minute periods, denoted by ($t_{1, 2\text{-}3}$). Covariates are: % landscape with 25-50 m canopy height (25-50m) and % landscape with 40-69.9% canopy closure (40-70%). Models were selected using Akaike Information Criteria (AIC) and only models with $\Delta AIC_c < 2$ are provided.

Model	*K*	Δ AIC$_c$	Deviance
ψ (25-50m + 40-70%) θ (.) *p* ($t_{1, 2\text{-}3}$)	6	0.00	151.65
ψ (.) θ (.) *p* ($t_{1, 2\text{-}3}$)	4	0.54	157.44
ψ (40-70%) θ (.) *p* ($t_{1, 2\text{-}3}$)	5	1.48	155.82