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Survey and Analytical Methods for Long-Term Monitoring
of Wildlife Metacommunities in California Montane Forests

By

Brett Jonathan Furnas

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Environmental Science, Policy and Management

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:

Professor Reginald H. Barrett, Chair

Professor Steven R. Beissinger

Professor Rauri C. K. Bowie

Fall 2013

Survey and analytical methods for long-term monitoring of wildlife metacommunities in California montane forests.

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Abstract

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by

Brett Jonathan Furnas

Doctor of Philosophy in Environmental Science, Policy and Management

University of California, Berkeley

Professor Reginald Barrett, Chair

Long-term, large-scale monitoring of wildlife metacommunities is needed to recognize population declines early enough to identify environmental stressors and facilitate adaptive planning. Potential outcomes include information supporting the designation of new species of conservation concern, or better yet, conservation actions that avert the need for conferring critical statuses. By surveying multiple species, declines of individual species need not be considered in isolation, but can be compared to responses of other species in the metacommunity. However, multi-species monitoring presents a variety of new challenges in terms of appropriate survey methods and analytical techniques for drawing valid ecological inferences.

In this study, I investigated several related aspects of multi-species monitoring. One theme was the role of automated survey methods (e.g., audio recorders and camera stations) that leave a permanent record and easily provide for temporal replication of surveys. I applied occupancy models to repeat surveys for addressing detection probability and providing unbiased estimates of species occurrence. Lastly, I evaluated several novel quantitative methods for comparing community properties using monitoring data.

In the first chapter I considered the effectiveness of automated recorders for monitoring common birds in California forests. I applied single-species occupancy models to 46 species using 5 years of monitoring data in which automated recorders were placed at 453 random sites across a 5.4-million-ha northern California study area. The devices were programmed to record sounds during up to 3 surveys each morning on 3 consecutive days during the breeding season when songbirds were singing from territories. Skilled interpreters reviewed these recordings to identify all species heard during each survey. With Monte Carlo simulation and results from occupancy models, I demonstrated 80% power for monitoring declines as small as 2.5% per year over 20 years for 32 species given a sampling effort of 100 new sites per year. I also determined an effective survey area radius of 30 m to 50 m for automated recorders, and showed that the devices provided similar occupancy estimates as traditional point counts despite lower survey-level detection probability.

In the second chapter I applied multi-species occupancy models to the calculation of biodiversity indices describing metacommunity organization. I used the same automated recorder data set for birds from Chapter One. Specifically, I applied simulation and Bayesian hierarchical models to demonstrate how a failure to address detection probability heterogeneity underestimates the evenness of species occupancy distributions. In models of the bird data I found that a number of species traits (migration, foraging guild, territoriality, body size) were informative in explaining detection probability. By pooling information from common species in a multi-species model, I was able to draw stronger inferences about rarer species than by modeling these species individually. Lastly, I illustrated the ecological significance of species-traits modeling and found that warbler and woodpecker occupancies were evenner than for sparrows.

In the third chapter, I proposed a new quantitative method for comparing species abundance distributions. I illustrated this method using avian point count surveys from 4 research forests in California. I applied bootstrap resampling to probabilistically compare the abundances of intermediate ranks among and within species abundance distributions. I found higher abundances of intermediately-common species on 2 of the forests, and ascribed this finding to differences in forest productivity and habitat complexity leading to greater niche partitioning of resources. At the metacommunity-level, I found higher abundances of intermediately-common species for neotropical migrants compared to resident birds.

In the fourth chapter, I considered the use of baited camera stations for monitoring Pacific fisher (*Pekania pennant pacifica*) and other mammals. Cameras were placed at 172 randomly selected forest sites across 2.8 million ha of northwestern California. The duration of each survey was 2 to 4 weeks. I estimated regional occupancy from these data at 2 survey scales (e.g., individual sites [0.465] and pairs of sites 1.6 km apart [0.651]). I also demonstrated 80% power for monitoring declines as small as 2.0% per year over 20 years given a sampling effort of 100 new sites per year. Lastly, I calculated the median latency to first detection for 13 other species of mammals detected at $\geq 5\%$ of sites, showed that latency was ≤ 6 days for 10 of these species, and argued that these results strengthen the case for expanding the use of camera traps to multi-species monitoring.

Para los dos halcones y la estrella de mil colores!

“There are some who can live without wild things and some who cannot.”
— Aldo Leopold

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Most of the data brought to bear in this dissertation are from the Ecoregion Biodiversity Monitoring project. It is a rare example of sustained, long-term, multi-species wildlife monitoring at a large spatial scale. It is part of California's State Wildlife Action Plan, and it has been federally-funded by a series of State Wildlife Grants since the project's inception in 2001. Over the years numerous Department staff have assisted with the often challenging day-to-day, month-to-month, and year-to-year implementation of this project. They include biologists David Smith, David Walker, Steve Burton, Pete Figura, Jennifer Carlson, Scott Hill, Brian Ehler, David Lancaster and Richard Shinn, and a long list of summer field crews. Scientific aides Russ Landers, Heather Barrett and Michael McGrann are singled out for their dedication and substantial contributions to the project.

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Chapter 1

Automated recorders and occupancy models for monitoring common forest birds at the regional scale in California

ABSTRACT

Long-term monitoring of multiple wildlife species at large spatial scales is needed to recognize population declines early enough to identify environmental stressors and facilitate adaptive planning. For this purpose automated recorders are an attractive method for monitoring birds, because they leave a permanent record that can be independently verified and conveniently scheduled to repeatedly survey different locations at the same time of the day. Since 2002, the California Department of Fish and Wildlife has used these devices to survey songbirds across 5.4 million ha of northern California in primarily forested habitats on public and private lands. In this study, I assessed the utility of automated recorders and single-species, single-season occupancy models for monitoring common forest birds. I found that a survey protocol of three 5-minute recordings at different times of the morning repeated over 3 consecutive days led to robust occupancy estimates for species detected at > 5% of survey sites. For 32 species I demonstrated 80% power ($\alpha = 0.1$) for monitoring average annual occupancy declines as small as 2.5% over 20 years given a sampling effort of 100 sites per year. The effective survey radius of automated surveys was 30 m to 50 m, but signal strength was reduced by protective containers used to prevent moisture damage to the recorder microphones. Lastly, a test of concurrent automated recorder and point count surveys yielded similar occupancy estimates despite systematic differences in detection probability. These results suggest that automated recorders, used alone or in conjunction with point counts, can facilitate effective monitoring of avian metacommunities at large spatial scales.

INTRODUCTION

A sustained commitment to effective, long-term, large-scale, biodiversity monitoring is needed for conservation planning efforts in the context of environmental changes affecting wildlife populations (Manley et al. 2005, Haughland et al. 2010, Koch et al 2011, Schultz et al. 2013). In particular, well-designed monitoring can recognize population declines early enough to facilitate adaptive planning. Potential outcomes include information supporting the designation of new species of conservation concern, or better yet, conservation actions that avert the need for conferring critical statuses.

Automated recorders are an increasingly common tool for surveying birds, bats and amphibians (Rempel et al. 2005, Acevedo and Villanueva-Rivera 2006, Brandes 2008, Gorresen et al. 2008, Celis-Murillo et al. 2009, Depraeterea et al. 2012). They provide a permanent record of species identification that can be reviewed by multiple interpreters (Rempel et al. 2005). Since 2002, the California Department of Fish and Wildlife has used automated recorders to survey birds across a large portion of northern California in the USA. Skilled interpreters review these recordings to identify all species heard during each survey. This project, named Ecoregion

Biodiversity Monitoring project (EBM), is intended to track long-term, large-spatial-scale, population trends of numerous species for informing conservation planning.

Occupancy modeling (MacKenzie et al. 2006) has been recommended for monitoring programs, because incidence data is often easier and less expensive to collect than abundance data, especially at large spatial scales (MacKenzie and Nichols 2004). This analytical approach is well-suited for application in multi-species monitoring efforts (DeWan and Zipkin 2010). The data collected from automated recorders are particularly amenable to occupancy modeling (Gorresen et al. 2008), in part because replicate surveys can be synchronized to occur at comparable times of the day and year thereby reducing a temporal source of variability in detection probability. The permanent record provided by automated recorders facilitates review of species occurrence by more than one person, and these data can be used in occupancy models that address both omission and commissions errors (Royle and Link 2006, Miller et al. 2011).

In this study, I considered the use of automated recorder survey data from EBM in single-species, single-season occupancy models for monitoring common forest birds. First, I assessed the relative importance of detection covariates for improving model performance, and constructed a rank occupancy distribution to approximate the relative abundances of common forest birds. Second, I used the results to calibrate a power analysis demonstrating how many species could be monitored well (power > 0.8) for tracking occupancy trends as small as 2.5% per year over 20 years. Third, I evaluated the technical limitations of automated devices to record bird sounds from different distances and for discriminating these signals from background noise. Fourth, I conducted a side-by-side comparison of automated recorders and traditional point counts (Ralph et al. 1995, Bibby et al. 2000) to determine if these methods provided similar occupancy estimates despite systematic differences in survey-level detectability. Lastly, I summarized the overall utility of automated recorders, used by themselves or in conjunction with point counts, for application in regional-scale, multi-species monitoring efforts.

STUDY AREA

The EBM surveys occurred across a 5.4-million-ha area of northern California in the USA (Fig. 1, Miles and Goudey 1997). Conifer-dominated forests covering 64% of this region were primarily Klamath Mixed Conifer, Sierran Mixed Conifer, Douglas Fir (*Pseudotsuga menziesii*), White Fir (*Abies concolor*), Red Fir (*Abies magnifica*), Lodgepole Pine (*Pinus contorta*), Ponderosa Pine (*Pinus ponderosa*), Jeffrey Pine (*Pinus jeffreyi*), Eastside Pine, Montane Hardwood-Conifer, and Juniper (*Juniperus spp.*) forest types (Mayer and Laudenslayer 1988). Elevations range from 60 m to 4,270 m. The geology is a mix of steep mountains and volcanic plateaus, and average annual precipitation varied from 20 to 300 cm (Schoenherr 1992). Forest ownership was a mix of public (64%) and private (36%) lands.

METHODS

Sampling Design

Survey sites were randomly selected without replacement annually from the U.S. Forest Service hexagon grid for the Forest Inventory and Analysis (FIA) program (U.S. Forest Service

Forest Service 2012a) which completely overlaps the study area. The distance between adjacent hexagon centroids was 5.35 km. Permission was granted for surveying public agency and private industrial forestland ownerships. Survey sites were usually located at hexagon centroids, but private property, steep terrain, and other logistical issues often required relocating sites to more accessible, secondary locations within selected hexagons. When this occurred, a supplemental random distance and direction procedure was followed to avoid biased placement of survey sites. In cases where relocation was not feasible the selected hexagon was not sampled. For the reasons listed above the sampling design was best described as quasi-random.

Biophysical conditions (elevation, slope, total basal area of live and dead trees) and land use (ownership, wilderness designation) at EBM sites were compared to reported values from the FIA program for all forestlands in the California North Interior region (i.e., Lassen, Modoc, Shasta, Siskiyou and Trinity counties) that largely matched the EBM study area (U.S. Forest Service 2012a). This allowed me to judge how representative EBM sites were of habitat conditions and the avian metacommunity (Holyoak et al. 2005) hosted across all forestlands within the study area.

Although EBM has been an ongoing effort, data analysis addressed in this study was limited to sites surveyed from 2006 to 2010 when survey methods were most consistent. I adopted a post-stratification procedure to further limit inferences to conifer-dominated habitats. Using land-use land-cover information derived from satellite imagery (U.S. Forest Service 2012b), I calculated the proportion of the 400 m radius area surrounding each survey in conifer forest cover. All sites identified as < 0.5 conifer forest cover were excluded.

Avian Surveys

Bird surveys were conducted using inexpensive digital voice recorders manufactured by Olympus Corporation (www.olympusamerica.com). These devices allowed recordings to be made automatically at preset times daily. The models varied by year (e.g., DS-2, DS-40, DS-61), but recordings were set to the highest quality with a sampling rate of 44.1 KHz. Microphones also varied by year. In the initial years, I used external omni-directional microphones; recently I switched to factory-provided stereo microphones attached to the recording units. For all configurations, the frequency reception of the combined recorder and microphone spanned a range of at least 100 Hz to 14,000 Hz. To protect the devices from moisture and small mammals, each recorder was placed in a lightweight, plastic food container, or the external microphone was placed in a plastic bag (see Fig. S1). The automated recorder in its protective covering was placed on the ground within 5 m of the randomized site location; the field crew had final discretion for micro-site location of the recorder where it would maximize sound reception properties (e.g., away from the side of a large tree or below a shrub canopy).

The devices were programmed to record sounds at up to 3 surveys each morning on 3 consecutive days during the breeding season when songbirds were singing from territories. Surveys occurred from the middle of May through the first week of July. Each survey was 5 minutes in length and began 30 minutes before sunrise, at sunrise, or either 15 or 30 minutes after sunrise. Prior to 2009 there were typically only 2 surveys per day occurring at sunrise and after sunrise. After completion of the field season a biologist reviewed the recordings and listed

all species detected within each 5-minute survey. The interpretation work was accomplished by listening to the recordings while simultaneously viewing the spectrograms using Raven Pro software (Cornell Lab of Ornithology, Ithaca, NY, USA). Explanatory notes were sometimes included with detections, especially in cases of atypical vocalizations or when an interpreter was uncertain about a species identified. Only biologists who scored at least 70% on a test interpreting species from sample recordings worked on this task. Although multiple biologists participated in the interpretation of recordings, each recording was interpreted by a single person.

The costs of avian monitoring under EBM were either documented or estimated by task (e.g., equipment, field technicians, transportation, interpretation of automated recordings). These costs were aggregated to estimate the total cost and average cost per survey site in USD. Planning, management and overhead expenses can vary considerably among organizations and were not reported.

Occupancy Modeling

Occupancy modeling allows simultaneous estimation of detection and occupancy probabilities in relation to covariates (MacKenzie et al. 2006). As surveys occurred at different sites in different years I adopted a single-species, single-season modeling approach (MacKenzie et al. 2006, p. 83; Tingley et al. 2012). To model species individually, I used a zero-inflated-binomial model structure to calculate the likelihood of parameters given the data. For average occupancy across years (ψ) and detection probability (p) that varied by site (j) and temporal survey replicate (k): $\text{logit}(\psi) = \beta_{\text{intercept}}$ and $\text{logit}(p_{jk}) = \mathbf{x}_{\text{covariates}} \beta_{\text{covariates}}$. For a single species the likelihood was given by,

$$L(\beta_{\psi}, \beta_p \mid \mathbf{y}, \mathbf{x}) = \prod_{j,k} x_j \beta_{\psi} (x_{jk} \beta_p)^{y_{jk}} (1 - x_{jk} \beta_p)^{1-y_{jk}} + (1 - x_j \beta_{\psi}) \cdot \mathbb{I}[\Sigma y_k = 0], \text{ where } \mathbf{y} \text{ was}$$

the dichotomous detection history, and \mathbf{x} were covariates.

Models were solved by minimizing negative log likelihoods using the *nlm* function (see Section 3.1.1. in Royle and Dorazio [2008] for an example of this solution method) in the R programming language (Version 2.12, www.r-project.org.). Model averaging (Burnham and Anderson 2002) was implemented for making multi-model inferences about the evidence supporting the role of several covariates potentially explaining detection probability. It was also necessary to include additional variables in all models to address non-independence among observations. These covariates were categorical variables representing the 3 different survey times and the 5 different survey years.

I tested 3 *a priori* hypotheses examining whether detection probability: (1) decreased later in the breeding season as singing activity lessened (Catchpole 1973, Krebs et. al.1981, Logan 1983, Cuthill and Hindmarsh 1985, Lampe and Espmark 1987); (2) varied with forest density (Bibby and Buckland 1987, Schieck 1997) in different ways by different species, in part because bird song evolved for optimizing sound transmission in preferred habitats (Morton 1975, Slabbekoorn et al. 2002, Baker 2006); and (3) increased similarly for most species when latent atmospheric and physiological factors were more amenable for singing (Henwood and Fabrick 1979, Larom et al. 1997, Lengagne and Slater 2002, Brown and Handford 2003). The covariates

representing these respective hypotheses were Julian day of survey, the proportion of conifer forest cover across the 400-m-radius circle surrounding a survey site, and the total number of species detected at a site during a given survey period.

Model-averaged estimates of occupancy and detection probability effects were calculated for all model subsets of the 3 covariates, while always including time of day and year as categorical variables in the null and all other models. All variables were rescaled to smaller values suitable to tractable log likelihood minimizations on the *logit* scale (Bolker 2008). As the ratio between the number of sites and number of parameters was often <40, the small sample size, second-order “AIC_C” information criterion (Hurvich and Tsai 1989, Burnham and Anderson 2002) was used to obtain model weights. I used relative importance values (Burnham and Anderson 2002, p. 167) derived from model weights to judge the evidence supporting the 3 *a priori* hypotheses about detection covariates. To assess the directionality of effects I evaluated the distribution of model-averaged parameter estimates for species for which relative importance was > 0.8. To determine how detection probability varied among species, I calculated survey-level detection probabilities for each species at each site given the site and survey covariate values. Next, I averaged the predicted survey-level detection probabilities across sites for each species for each of the 3 daily survey times. Lastly, I calculated the expected site-level detection probability for each species:

$p^* = 1 - [(1 - p_1)^3(1 - p_2)^3(1 - p_3)^3]$, where p_1, p_2, p_3 were fitted detection probabilities for the 3 daily survey times.

I calculated model-averaged estimates of ψ using weights from the full set of detection covariate models. The models did not address spatial or annual differences in occupancy; rather they provided a baseline description of average occupancy at the study-area-scale during the years 2006 through 2010.

Power to Detect a Trend

For each species, I assessed the statistical power to detect an occupancy trend (Purcell et al. 2005, Nielsen et al. 2009, Meyer et al. 2010). Time series were simulated for each species representing the annual occupancy estimates hypothetically monitored over 20 years. The true starting occupancy values were those estimated from this study. Each species’ trend was first modeled as a steady 2.5% annual decline from the starting occupancy value:

$$\psi_t = [1 - 0.025(t - 1)]\psi_1 \text{ for year } t.$$

The “monitored” occupancy values used for assessing a trend were stochastically generated about the time series of declining true values by assuming a normal sampling distribution, $\psi_{\text{observed}} \sim \text{Norm}(\psi_{\text{true}}, \sigma_{\psi_{\text{true}}}^2)$. I used the standard errors from occupancy models, and adjusted them to reflect a sample size of 100 sites per year by multiplying by $\sqrt{453/100}$. However, standard errors from the occupancy models were estimated using a variable number of survey replicates by year as described in the Methods Section. To provide a conservative assessment of monitoring power, I considered these standard errors to liberally reflect

measurement uncertainty associated with 9 survey replicates. Additionally, I adjusted $\sigma_{\psi_{true}}$ downwards as ψ_{true} decreased by multiplying by $\sqrt{\psi_t(1-\psi_t)} / \sqrt{\psi_1(1-\psi_1)}$.

I ran 10,000 Monte Carlo simulations of each decline scenario for each species and tested for a simple linear trend via ordinary least squares regression. I calculated power as the proportion of simulations where I could reject ($P < 0.1$) the null hypothesis of a zero or positive slope for the trend line. All power analyses assumed a constant annual sampling effort of 100 sites in conifer habitats. Power analyses were repeated for 2 additional scenarios: declines of 2.5 and 5.0% per year over 10 years.

Automated Recorder Signal Reception Degradation with Distance

In September 2013 I conducted a field experiment evaluating how the audibility of bird sounds received by the automated recorders decayed with distance, and how this limited the ability of interpreters to visually distinguish bird sounds from background noise in recording spectrograms. A full-factorial combination (4) of 2 types of recorders (Olympus DS-40 and DM-620 using built-in microphones) both with and without a protective container was set to record manually, and placed on the ground. Playback recordings of 2 bird songs (hermit warbler [*Setophaga occidentals*] and American robin [*Turdus migratorius*]) and a bird call (brown creeper [*Certhia Americana*]) were sequentially broadcast (3 repetitions of each bird sound) from 10 m increments in distance from the recorders out to 100 m. This process was repeated along 2 to 4 directional transects at 8 forested locations in northern California with gentle slopes but otherwise generally representative of sites where EBM survey occurred. A total of 1,044 bird sounds were recorded for each distance increment (10 m to 100 m), and they were imported into Raven Pro software for viewing spectrograms and measuring relative signal power in decibels. I calculated signal power of each bird sound, and then plotted median and interquartile ranges against distance. This was done separately for bird songs versus calls, with and without protective containers.

Comparison with Point Counts

In a second field test, I concurrently compared the effectiveness of automated recorders with point counts (Bibby et al. 2000) surveyed by an experienced birder who estimated distances to birds heard or seen. The surveyor placed the recorder on the ground and manually activated it at the beginning of each 5-minute point count. He surveyed 60 points along 12 transects in northern California montane conifer habitats from early June through the middle of July 2008. The points along each transect were separated by at least 250 m. He surveyed a single transect each morning commencing 30 minutes after sunrise and continuing through mid-morning, and each transect was repeated once on a different day. After completion of all the fieldwork, a separate, experienced birder interpreted which species were detected from the recording accompanying each point count.

I applied incidence data from point counts and interpretation of recordings to simple occupancy models without covariates due to the small sample size (60 sites, 2 survey replicates). Models were run only for those species detected at $\geq 10\%$ of points by both methods. I compared occupancy estimates based on the 2 types of data by averaging ratios of species occupancy

estimates from point counts to those from interpretation of the recordings. A ratio of one represented systematic agreement between occupancy estimates provided by automated recorders and point counts. Monte Carlo sampling of occupancy estimates using the standard errors from the models allowed me to construct a confidence interval about the ratio. In consideration of the small sample size, I relaxed the Type I error rate to 0.2 for this exercise. To provide a sensitivity analysis of the distance beyond which automated recorders were ineffective, I sequentially ran occupancy models on the point count data after truncating detections using the following limiting distances: 20 m, 30 m, 40 m, 50 m, 75 m and 100 m. My expectations were that the ratio would 1) increase with distance, 2) always be less than a ratio derived from naïve, unmodeled occupancies, and 3) most closely coincide with a value of one for the distance representing the effective range of the automated recorders.

RESULTS

Location of Survey Sites

Of the 587 sites surveyed for birds from 2006 through 2010, 453 (78%) were post-stratified as montane conifer for inclusion in occupancy models (Fig. 1). For this stratum, the 5th and 90th percentile elevation values were 546 m and 1,981 m, respectively. Site location offsets from the centroids of randomly-selected sampling grid hexagons occurred at 27% of sites. I did not keep consistent records on how many additional hexagons were abandoned for surveys because an offset was not attempted. However, average elevation and total basal area of live and dead trees at EBM montane conifer sites were similar to values reported for all forestlands throughout the study area. The EBM sites modestly under-represented private ownerships, steeper locations, and wilderness locations away from roads (Table 1).

Bird Surveys

Six biologists participated in the interpretation of recordings. A total of 125 avian species was detected at coniferous sites. These birds spanned 36 families and 13 orders. However, I only modeled data and reported results from the 46 most common avian species detected (Table 2; $\psi_{naïve} > 0.05$), and excluded all detections for which interpreters indicated uncertainty about species identification in their notes. Uncertainty was most frequent for hermit warbler (11.3% of sites), dusky flycatcher (*Empidonax oberholseri*, 7.9%), Hammond's flycatcher (*Empidonax hammondii*, 7.7%), gray flycatcher (*Empidonax wrightii*, 6.8%), white-headed woodpecker (4.0%), purple finch (*Haemorhous purpureus*, 3.8%), and Cassin's Finch (*Haemorhous cassinii*, 2.0%).

The use of protective containers greatly reduced damage to automated recorders. The types of damage included destruction of microphones and corrosion of batteries by moisture, and the gnawing of wires and other electrical components by rodents. However, plastic bags used to protect external microphones were less effective. Besides heightened risk of rodent damage, the bags trapped condensation that damaged microphones even in the absence of precipitation. Ventilation holes mitigated this problem for automated recorders placed in protective containers.

To complete annual surveys I required a minimum of 25 automated recorders costing USD 150 each. Assuming a 2-year average lifespan and the cost of batteries and protective containers, the equipment cost per site was USD 25. Other per site costs were USD 125 to USD 160 for field personnel and USD 40 to USD 50 for vehicles. The cost of interpreting species heard from these recordings was USD 12 to USD 17 per 5-minute survey period. The total cost of data collection (excluding planning, management and overhead expenses) was USD 300 to USD 390 per site. Given these assumptions the total cost of 5 years of avian survey data collection was USD 135,000 to USD 175,000 excluding planning, management and overhead expenses.

Detection Probabilities

A higher number of species heard was positively associated with detection probability for most species (average importance =0.982, 96% ≥ 0.8 , see Fig. S2). In contrast, survey date had a lower importance value of 0.56 averaged across species (33% ≥ 0.8). For species for which survey date was an important (≥ 0.8) predictor, the effect was more often (67%) a decrease in detection probability for later survey dates. Forest cover in the vicinity of survey sites had an importance value of 0.61 averaged across species (39% ≥ 0.8). For species for which this variable was important, the effect was split between increased (56%) and decreased (44%) detection probability.

Detection probability varied considerably among species, especially in terms of time of the morning a survey occurred (see Fig. S3). For example, American robin, black-headed grosbeak (*Pheucticus melanocephalus*), common nighthawk (*Chordeiles minor*), Pacific-slope flycatcher (*Empidonax difficilis*), spotted towhee (*Pipilo maculatus*), and Townsend's solitaire (*Myadestes townsendi*) were substantially more detectable before sunrise than after. Cassin's vireo (*Vireo cassinii*), green-tailed towhee (*Pipilo chlorurus*), hermit warbler, Nashville warbler (*Oreothlypis ruficapilla*), red-breasted nuthatch (*Sitta canadensis*), Steller's jay (*Cyanocitta stelleri*), and warbling vireo (*Vireo gilvus*) followed the opposite pattern. Western tanager (*Piranga ludoviciana*) had the highest survey-level detection probability (>0.6) for all 3 survey times. The per survey detection probability for all species was usually (66% of species-survey time combinations) greater than 0.2. Assuming 9 survey replicates, site-level detection probability (p^*) was above 0.8 for 31 of the 46 species I modeled (see Fig. S4).

Occupancy Estimates

There were 7 species with occupancy estimates > 0.5 which I considered to be super-common species (Fig. 2). These were western tanager, dark-eyed junco (*Junco hyemalis*), red-breasted nuthatch, mountain chickadee (*Poecile gambeli*), Steller's jay, northern flicker (*Colaptes auratus*), and yellow-rumped warbler (*Setophaga coronata*). Corrected occupancies were significantly ($P < 0.1$) higher than naïve values for 65% of all modeled species. The largest corrections were for the 4 species of woodpeckers (northern flicker, white-headed woodpecker [*Picoides albolarvatus*], hairy woodpecker [*Picoides villosus*], and pileated woodpecker [*Dryocopus pileatus*]) and these adjustments were due to low (< 0.5) site-level detection probabilities.

As expected the increased accuracy for estimating occupancy via modeling came at the expense of reduced precision. The median of standard errors on occupancy estimates was 68% higher [IQR: 7-268%] than would be expected under a simple Bernoulli distribution without additional dispersion due to uncertainty in detection probability.

Power to Detect a Trend

My analysis showed that 32 of the 46 species I modeled can be monitored for study area-scale, average annual declines as small as 2.5% over 20 years with statistical power ≥ 0.8 (see Fig. S5). This assessment assumed a yearly sampling effort of 100 sites in conifer habitats. For a 10-year timeframe only 6 species met the 2.5% per year standard. However, 25 species met a relaxed, 5.0% per year standard.

Signal Reception

Data analyses from the playback field experiment revealed that signal power of recorded bird sounds was reduced by approximately 10 decibels at 50 m for recorders and microphones placed in protective containers versus those that were not (Fig. 3). Furthermore, signal power was asymptotic at greater distances for recorders in protective containers. Indeed, I had great difficulty distinguishing bird sounds from background noise in spectrograms for distances of 80 m to 100 m for all recordings associated with protective containers.

Consequently, I used the median power value at 100 m from protective container recordings to represent the background noise level. I estimated the effective distance beyond which accurate species interpretation of recordings was unlikely as the distance at which 25th percentile value was higher than my estimate of background noise. Taking this approach I found an effective distance of 50 m for bird songs (e.g., Fig. 3a, American robin and hermit warbler) and 30 m for bird calls (Fig. 3b, brown creeper [*Certhia Americana*]) for automated recorders placed in protective containers.

Comparison with Point Counts

Survey-level detection probability was higher for point counts (median among species= 0.53) versus automated recorders (median among species= 0.40). The occupancy ratio between point counts and automated recorders was >1 , except for low distance thresholds (e.g., 20 m and 30 m) that excluded many point count detections but not automated recorder detections (Fig. 4). In contrast, ratios were almost always (5 of 6 distance thresholds) closer to one for modeled occupancy estimates. The greatest agreement between occupancy estimates from the 2 survey methods was for point count truncation thresholds of 40 m and 50 m.

DISCUSSION

Survey Design

Although not fully random, EBM surveys were reasonably representative of middle elevation (500 m to 2,000 m) conifer forests across a 5.4-million-ha, northern California study

area, thereby strengthening the case that my use of automated recorders provided accurate species occupancy estimates at the regional scale. However, wilderness areas were underrepresented. This was, in part, because travel to and from survey sites was the most expensive and time-consuming task for conducting the bird surveys. Surveys along transects (Tingley et al. 2012) or trails (McGrann 2012) might improve the efficiency of surveying remote locations, but are also potentially subject to systematic bias (Thompson 2002 – Chapter 12) and reduced inference across the entire study area. I am currently testing a hybrid approach to blend data from the main set of random sites with a subset of surveys along wilderness trail systems. Steep slopes were also underrepresented. This issue will be harder to resolve, because prolonged travel by survey crews across slopes exceeding 80% was restricted due to safety concerns. One approach for addressing these sampling biases would be to include covariates for these characteristics in models, and provide a weighted occupancy estimate that corrects for uneven sampling effort.

Occupancy Modeling

Site-level detection probabilities from the automated recorders were high ($p^* > 0.8$) for most species (67%), which highlights their effectiveness for monitoring a large proportion of the northern California forest songbird metacommunity. The total number of species heard during a survey period was the covariate with the greatest importance for explaining survey-level detection probability across species. This variable likely functioned as a proxy for a number of latent factors, such as weather, background noise, and recording malfunctions that I was unable to easily classify separately. Survey year was also an important detection covariate originally included to ensure independence between observations. This covariate also served to control for differences between interpreters who reviewed surveys from different years and differences in the automated recorders used in different years.

Detection probabilities of woodpeckers were consistently lower than for passerines. This finding is consistent with evolutionary differences between passerines and other taxa that have allowed the former to specialize on song as a means of attracting mates which over time has led to diversification via sexual selection and adaptive radiation (Lovette and Bermingham 1999, Irwin et al. 2008, Campagna et al. 2011). Another explanation for the lower detection probabilities observed for woodpeckers is the difficulty in distinguishing between the drumming sounds of different woodpecker species (Stark et al. 1998). The integration of automated playback into the automated recorder protocol might increase detection probabilities for woodpeckers which respond vocally and by drumming to playbacks of their call.

An advantage of automated recorders is that they leave a permanent record that can be independently reviewed by more than one interpreter, thereby reducing observer bias. This is important because misclassification error can lead to substantial error in occupancy estimates (Royle and Link 2006). In this study, interpreters reported sizeable (> 5% of sites) identification uncertainties for hermit warbler and several species of *Empidonax* flycatchers. As I excluded all instances of uncertain species identification from the models, this issue was likely to have negatively biased occupancy estimates. This is because frequently there was identification uncertainty about all surveys at a site such that occupancy models might not have been able to adjust detection probability based on a reduced number of surveys in which the species was

confidently identified. Much of the uncertainty about hermit warbler was due to geographical variation in its song form (Janes and Riker 2006) that I plan to address by providing interpreters with information on local dialects. I will rectify the problem for other species by updating my models to explicitly include information about interpretation uncertainty and differences between duplicate interpretation results into the model equations. Royle and Link (2006) provided a framework for this approach using a latent class mixture model which could be expanded upon to include actual information about uncertainties and discrepancies (Miller et al. 2011).

For most of the species modeled I believe surveys met the closure assumption (MacKenzie et al. 2006, p. 104) required of occupancy modeling. This is because survey replicates occurred over a short time period (e.g., 3 days) during the breeding season when most songbirds were maintaining territories. Possible exceptions included common raven (*Corvus corax*) and finches (*Fringillidae*). Furthermore, my occupancy estimates were unlikely to have changed much due to immigration over the dates surveyed. This is because surveys began approximately one month after most visitors arrived from migration.

Monitoring Trends

The power analysis demonstrated that, for a modest investment of 100 sites per year, automated recorder surveys should be able to monitor 32 species of birds for declines as small as 2.5% per year over 20 years. This is the same standard recommended for the North American Breeding Bird Survey (Bart et al. 2004). For 10 years one should be able to monitor 26 species for declines as small as 5% per year. For monitoring timeframes of less than a decade, it might be very difficult to distinguish short-term population cycles from long-term trends linked to stressors of conservation concern (e.g. climate change, habitat degradation). This is because transient or random annual events can lead to autoregressive effects resulting in multi-year population cycles (Elias et al. 2006, Ludwig et al. 2006).

Species-level monitoring at large spatial scales is needed for identifying population trends and prioritizing conservation actions before species become endangered (Rich et al. 2004, Manley et al. 2005, Noon et al. 2012, Schultz et al. 2013). In particular, multi-species monitoring utilizing occupancy modeling has been recommended for increased consideration by U.S. state wildlife agencies implementing Wildlife Action Plans using federal funds from State Wildlife Grants (DeWan and Zipkin 2010). Additionally, California Partners in Flight recommended monitoring of 12 focal birds representing “functioning coniferous forest ecosystems” (CalPIF 2002). I demonstrated that 7 of these species met a 20-year monitoring standard using automated recorder surveys. These species were brown creeper (*Certhia americana*), dark-eyed junco, fox sparrow (*Passerella iliaca*), golden-crowned kinglet (*Regulus satrapa*), MacGillivray’s warbler (*Geothlypis tolmiei*), olive-sided flycatcher (*Contopus cooperi*), and western tanager.

By monitoring an entire avian metacommunity (or at least a large fraction of the common passerines with automated recorders), declines of individual species need not be considered in isolation, but can be compared to responses of other species in the metacommunity. For example, it would be important to distinguish whether the decline of a moderately-common

species was related to an environmental stressor affecting it or associated with competitive release of other species sharing the same niche.

In this study, I focused on monitoring common species. One reason for this focus was the value of being able to detect a decline and inform conservation planning before a species becomes rare or endangered. This approach is consistent with the Partners in Flight (Rich et al. 2004) goal of “keeping common birds common.” Furthermore, common birds may disproportionately reflect ecological processes within an avian metacommunity (Lennon et al. 2004, Gaston and Fuller 2008, Koch et al. 2011). Nevertheless, rare species can be addressed using multi-species occupancy models (Dorazio and Royle 2005, Zipkin et al. 2009, Tingley and Beissinger 2013) that can pool data from species with similar traits or conservation issues. Indeed, the EBM data using automated recorders can be applied to either a single- or multi-species modeling framework. One reason I chose to use single-species occupancy models for monitoring common species, however, is that multi-species models tend to pull species-specific estimates towards the metacommunity mean, a phenomenon known as “Bayesian shrinkage” (Zipkin et al. 2009).

Automated Recorders versus Point Counts

Occupancy modeling provides a straightforward method for correcting data from different survey methods associated with different detection probabilities such that the occupancy estimates are comparable. My side-by-side comparison of automated recorders and point counts demonstrated the efficacy of this process. The ratio of occupancies estimated using data from the different survey methods converged on one despite a higher survey-level detection probability for point counts.

A difference in effective survey area was of greater concern than detection probability in my comparison of automated recorders and point counts. This was because occupancy is expected to be higher for a larger survey area (Gaston and He 2011). Therefore, to compare results from automated recorders with those using other methods, it was important to understand the effective survey area of surveys. Findings from 2 field experiments I conducted indicated that the automated recorders in protective containers can detect most species vocalizing within a circular area of radius 30 m to 50 m. This suggests that automated recorders are comparable to point counts, which are often truncated at 50 m because of inaccuracies beyond this distance (Ralph et al. 1995, Scheick 1997). Additionally, a small survey area may be an asset because incidence is expected to most frequently equate to a single territory, thereby strengthening the case for occupancy as a surrogate for abundance. Nevertheless, more investigation is warranted as the effective distance of automated recorders is expected to vary by species, and by recording device.

Automated recorders offer an effective alternative to point counts. One advantage of automated recorders is that they are more amenable to scheduling surveys at comparable times of the day and for cost-effectively allowing multiple repeat surveys for use in occupancy modeling. By surveying at the same times each day diurnal variability in detection probability is likely reduced. Furthermore, the permanent record provided by automated recorders allows more than one interpreter to independently review the data, a decision that need not be made at the time of

surveys. As a practical matter, this feature allows me the flexibility to choose whether to re-analyze all of the EBM surveys back to 2002 for addressing false-positives using an alternative model structure. On the other hand, I also identified a number of issues for using automated recorders. It is important to note, however, that many of these issues apply similarly to point counts (e.g., study design, detection probability, misclassification, closure assumption). Rather than choosing between automated recorders and point counts, I suggest that the combination of both may be the best approach. One option would be to conduct point counts during the deployment and retrieval of automated recorders. Both streams of data could then be used in the same occupancy model for reducing bias and improving precision.

Data Storage

The ability to collect survey recordings presents new challenges in terms of how to properly store and document these data. Indeed, some bioacoustics researchers and curators have identified the need to develop standards for organizing and sharing audio recordings of wildlife (Bradbury et al. 1999, Gaunt et al. 2005). The EBM bird survey recordings have value beyond the ability to confirm the species identifications made by interpreters. They are a random sample of how bird song varies spatially and temporally by species across a large portion of northern California.

MANAGEMENT IMPLICATIONS

I reported on the utility of automated recorders for surveying birds, and demonstrated how occupancy modeling of this type of data can facilitate long-term monitoring of an avian metacommunity at the regional scale. These devices are a good option for monitoring birds, because they leave a permanent record that can be independently verified and conveniently scheduled to repeatedly survey different locations at the same time of the day. They are also advantageous for surveying remote sites representative of a large region, because a surveyor is not required to be present for each automated survey replicate. In this study, I focused on monitoring common species, but multi-species occupancy models can be readily applied for drawing inferences about rarely detected species. Despite providing lower survey-level detection probabilities than point counts, I showed that automated recorders programmed to make 9 survey replicates over 3 days led to high site-level detection probabilities for many common species. Indeed, I demonstrated 80% power for monitoring declines as small as 2.5% per year over 20 years for 32 species.

Multi-species monitoring should constitute an essential function of agencies charged with managing and conserving wildlife. Automated recorders, used by themselves or in conjunction with point counts, are well suited to helping biologists achieve this goal for songbirds. Furthermore, the combination of large assessment and small survey scales is likely to make occupancy modeling of automated recorder data a good proxy for abundance.

Table 1. Summary statistics on land classification and biophysical conditions at Ecoregion Biodiversity Monitoring (EBM) sites where automated recorder bird surveys occurred from 2006 to 2010. Land classification, elevation and slope information was derived from geographic information systems (California Department of Fish and Wildlife, unpublished data). Total live and dead tree basal area measurements were made using a 10-sq.ft-factor angle gauge (Avery and Burkhart 1994). The EBM averages were compared with reported values from the U.S. Forest Service’s Forest and Inventory Analysis (FIA) program for all forestlands in the California North Interior region (i.e., Lassen, Modoc, Shasta, Siskiyou and Trinity counties) that largely matches the EBM study area.

	Private Land	Wilderness	Average Elevation	Average Slope	Average Basal Area
EBM survey sites	27.2%	4.4%	1,334 m	24.7%	22.3 m ² /ha
All forestlands (FIA)	31.9%	10.4 %	1,353 m	29.2 %	23.2 m ² /ha

Table 2. Most common birds detected ($\geq 5\%$ of sites) with automated recorders in northern California forests from 2006 through 2010.

AOU Code ^a	Common Name	Scientific Name	AOU Code ^a	Common Name	Scientific Name
AMRO	American Robin	<i>Turdus migratorius</i>	LAZB	Lazuli Bunting	<i>Passerina amoena</i>
BHCO	Brown-headed Cowbird	<i>Molothrus ater</i>	MGWA	MacGillivray's Warbler	<i>Geothlypis tolmiei</i>
BHGR	Black-headed Grosbeak	<i>Pheucticus melanocephalus</i>	MOCH	Mountain Chickadee	<i>Poecile gambeli</i>
BLUE ^a	Mountain Bluebird (or Western Bluebird)	<i>Sialia currucoides</i> (or <i>Sialia mexicana</i>)	MODO	Mourning Dove	<i>Zenaidura macroura</i>
BRCR	Brown Creeper	<i>Certhia americana</i>	MOUQ	Mountain Quail	<i>Oreortyx pictus</i>
CAFI	Cassin's Finch	<i>Haemorhous cassinii</i>	NAWA	Nashville Warbler	<i>Oreothlypis ruficapilla</i>
CAVI	Cassin's Vireo	<i>Vireo cassinii</i>	NOFL	Northern Flicker	<i>Colaptes auratus</i>
CBCH	Chestnut-backed Chickadee	<i>Poecile rufescens</i>	OSFL	Olive-sided Flycatcher	<i>Contopus cooperi</i>
CHSP	Chipping Sparrow	<i>Spizella passerina</i>	PIWO	Pileated Woodpecker	<i>Dryocopus pileatus</i>
CONI	Common Nighthawk	<i>Chordeiles minor</i>	PSFL	Pacific-slope Flycatcher	<i>Empidonax difficilis</i>
CORA	Common Raven	<i>Corvus corax</i>	PUFI	Purple Finch	<i>Haemorhous purpureus</i>
DEJU	Dark-eyed Junco	<i>Junco hyemalis</i>	RBNU	Red-breasted Nuthatch	<i>Sitta canadensis</i>
DUFL	Dusky Flycatcher	<i>Empidonax oberholseri</i>	RECR	Red Crossbill	<i>Loxia curvirostra</i>
EVGR	Evening Grosbeak	<i>Coccothraustes vespertinus</i>	SPTO	Spotted Towhee	<i>Pipilo maculatus</i>
FOSP	Fox Sparrow	<i>Passerella iliaca</i>	STJA	Steller's Jay	<i>Cyanocitta stelleri</i>
GCKI	Golden-crowned Kinglet	<i>Regulus satrapa</i>	TOSO	Townsend's Solitaire	<i>Myadestes townsendi</i>
GRFL	Gray Flycatcher	<i>Empidonax wrightii</i>	TRES	Tree Swallow	<i>Tachycineta bicolor</i>
GTTO	Green-tailed Towhee	<i>Pipilo chlorurus</i>	WAVI	Warbling Vireo	<i>Vireo gilvus</i>
HAFL	Hammond's Flycatcher	<i>Empidonax hammondii</i>	WBNU	White-breasted Nuthatch	<i>Sitta carolinensis</i>
HAWO	Hairy Woodpecker	<i>Picoides villosus</i>	WETA	Western Tanager	<i>Piranga ludoviciana</i>
HETH	Hermit Thrush	<i>Catharus guttatus</i>	WEWP	Western Wood-Pewee	<i>Contopus sordidulus</i>
HEWA	Hermit Warbler	<i>Setophaga occidentalis</i>	WHWO	Wht.-headed Woodpecker	<i>Picoides albolarvatus</i>
HOWR	House Wren	<i>Troglodytes aedon</i>	YRWA	Yellow-rumped Warbler	<i>Setophaga coronata</i>

^aAmerican Ornithologists’ Union species codes (Banks et al. 2003), except for bluebirds lumped into a genus-level taxon code.

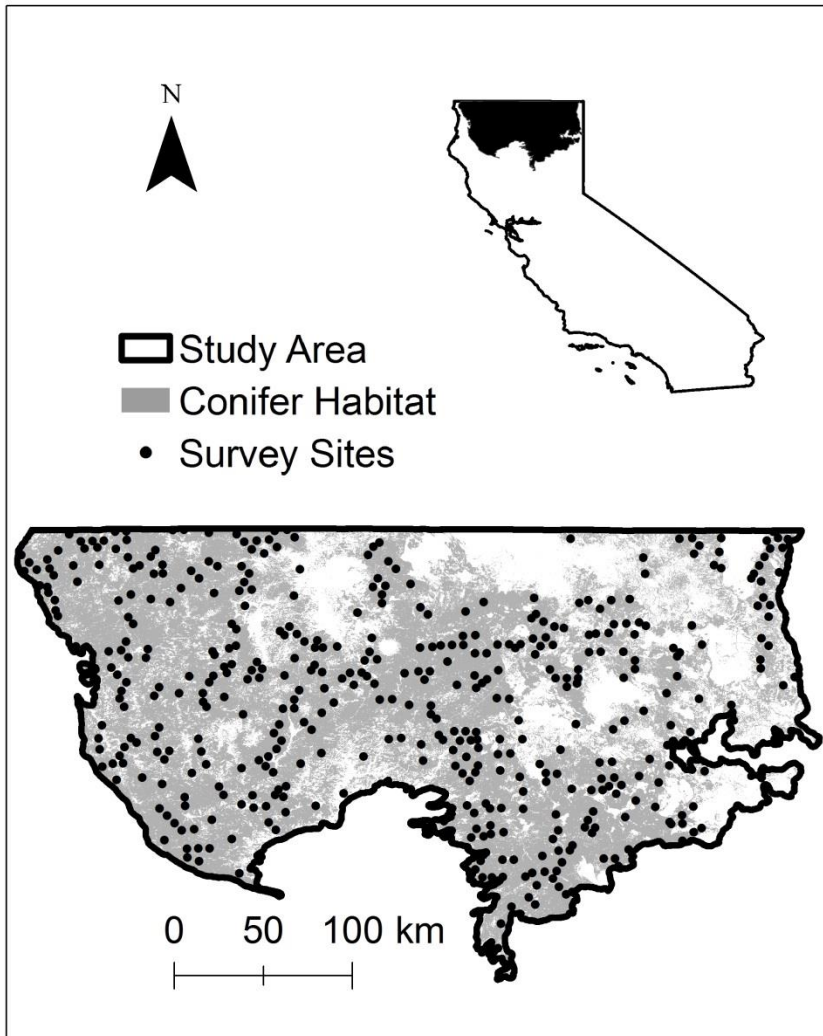


Figure 1. Northern California study area where bird surveys using automated recorders occurred from 2006 through 2010, USA.

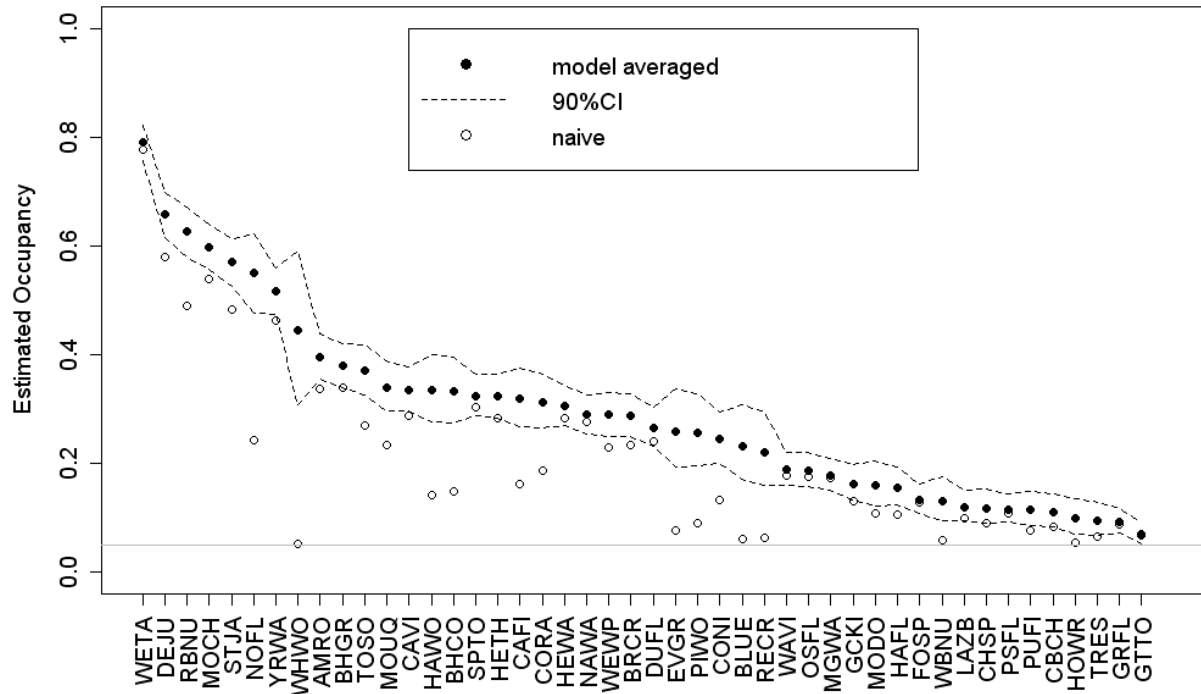


Figure 2. Model-averaged, single-species, single-season occupancy estimates for conifer sites (n=453 sites), based on automated recorder surveys in northern California from 2006 through 2010. See Table 2 for species codes. BLUE represents a genus-level taxon including both mountain bluebird (*Sialia currucoides*) and western bluebird (*Sialia mexicana*).

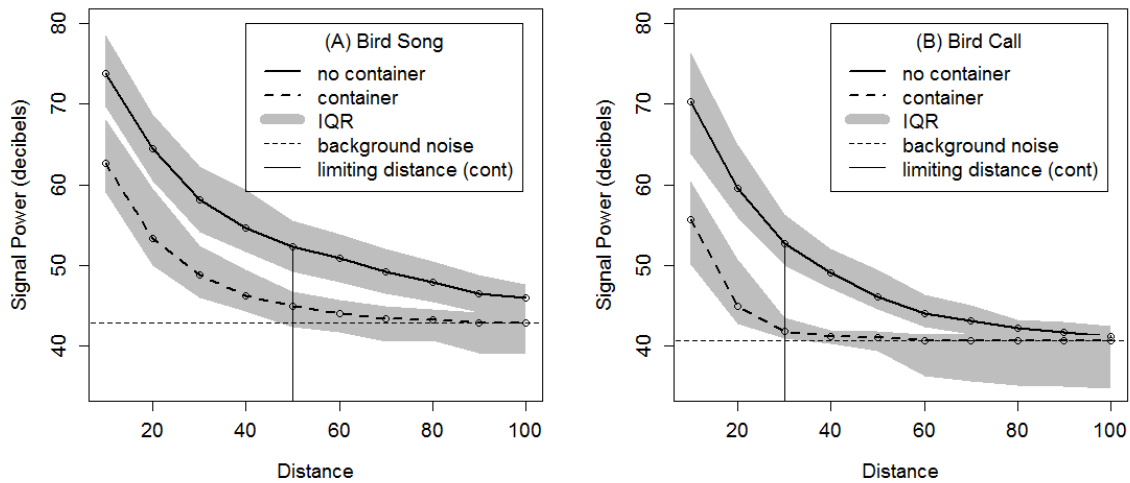


Figure 3. Distance-related decay of signal received by automated recorders. A field experiment was conducted in August 2013, whereby playback of bird song (A, American robin [*Turdus migratorius*] and hermit warbler [*Setophaga occidentalis*]) and bird call (B, brown creeper [*Certhia americana*]) were recorded from different distances at 8 montane conifer locations in northern California. The experiment compared automated recorders with and without protective containers. Results suggest a limiting distance of 30 m to 50 m for automated recorders in protective containers, and that protective containers reduced audibility by 10 decibels at 50 m.

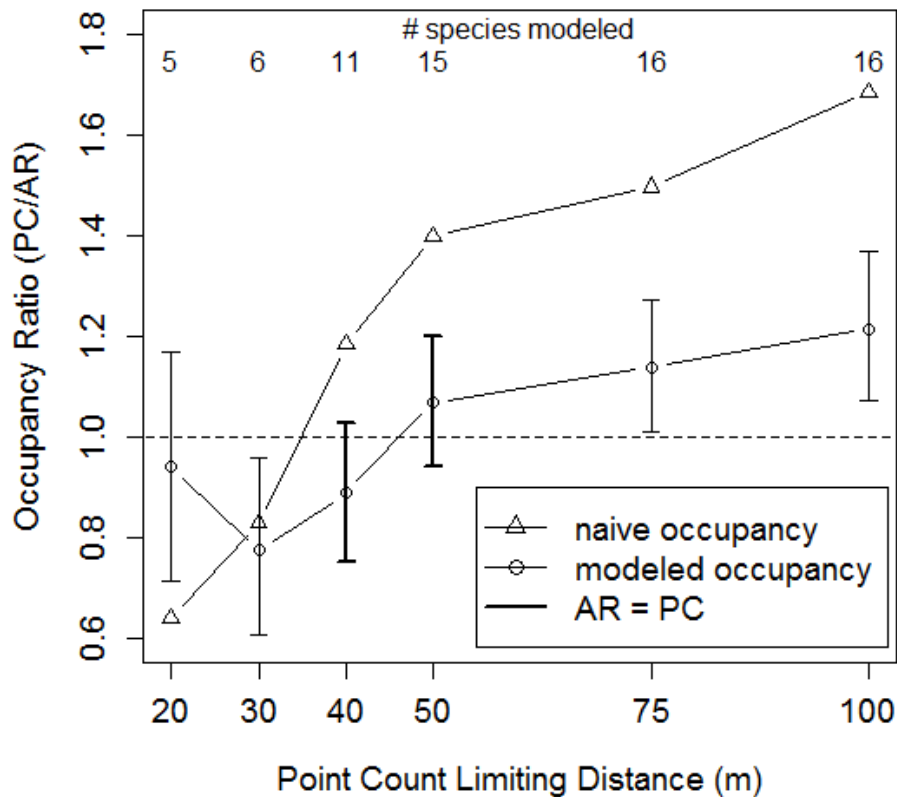


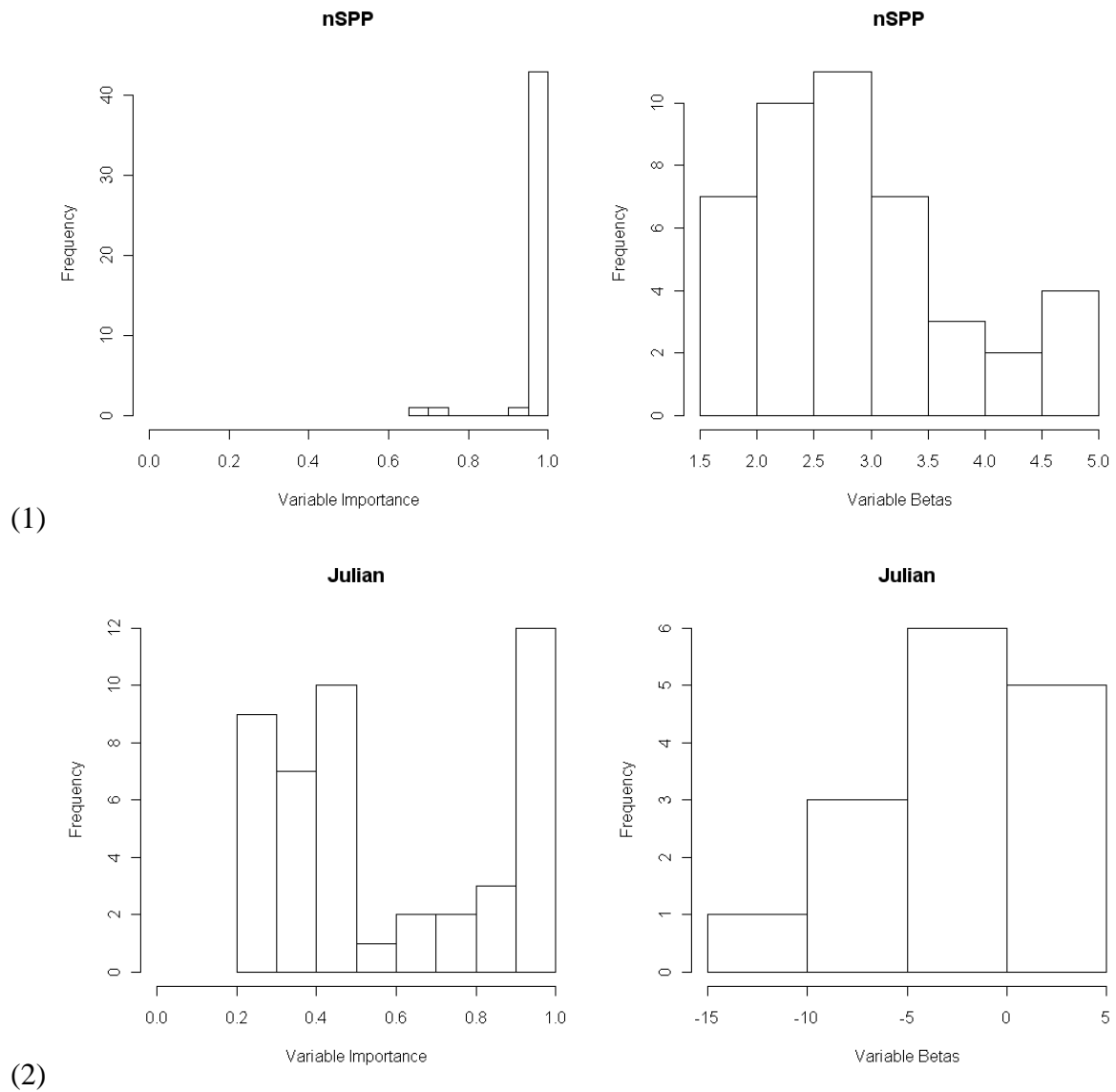
Figure 4. Comparison of concurrent automated recorder (AR) and point count (PC) surveys. Surveys occurred twice on different days at 60 sites from 6 montane conifer locations in northern California during 2008. Naïve occupancy and modeled occupancies correcting for methodological differences in detection probability were estimated. A “modeled” ratio of one represents agreement between occupancy estimates provided by the 2 methods despite differences in detection probability. The data were modeled separately for different truncation distances on the point count data, such that the distance where agreement was closest to one represents an estimate for the effective distance of the automated recorders.

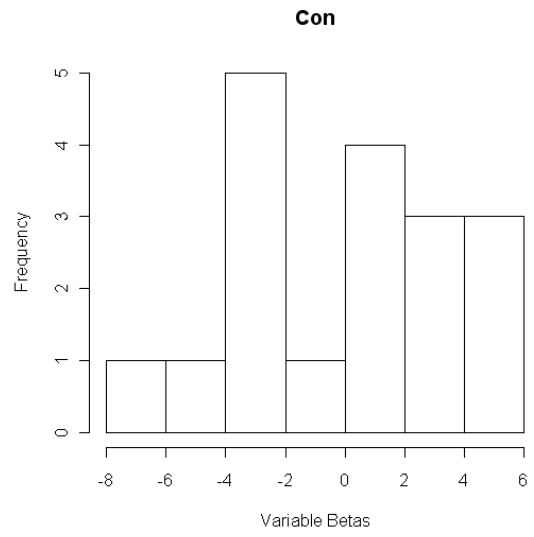
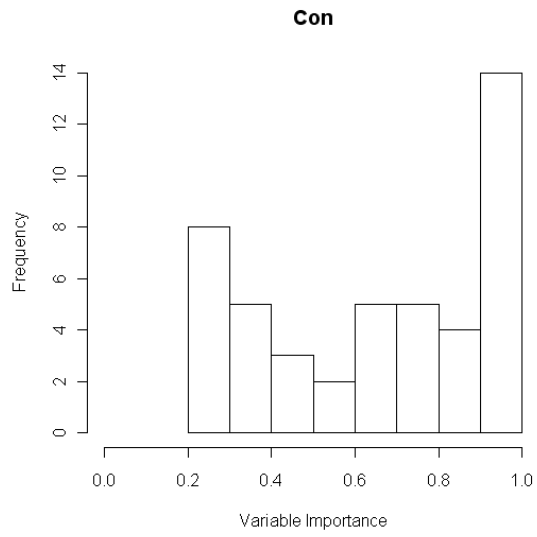
Figure S1. An automated recorder (Olympus DS-40 digital voice recorder, www.olympusamerica.com) and its protective container used for surveying common forest birds in northern California. Each device was programmed to automatically record sounds during 5-minute survey periods at 3 times each morning repeated over 3 consecutive days.



Figure S2. Relative importance values of detection covariates used in occupancy models of automated recorder bird survey data from northern California forests from 2006 through 2010.

Relative importance values (Burnham and Anderson 2002, p. 168) of detection covariates were calculated for each covariate for each bird species ($n = 46$) using the Akaike's Information Criterion model weights. The distributions of these variable importance values are shown as histograms below. The distributions of the logit-scale parameter estimates ("Betas") are also shown for species for which variable importance exceeded 0.8. The detection covariates were: (1) the total number of species detected in a 5-minute survey (nSPP), (2) the Julian date of a survey and, (3) the proportion of the 400 m radius area surrounding a survey site in conifer forest land cover. The data for the models were from automated recorder surveys at 453 sites in northern California conifer forests.





(3)

Figure S3. Survey-level detection probability by bird species from occupancy models of automated recorder survey data from northern California forests from 2006 through 2010.

Only the most detectable (site-level $p^* \geq 0.8$) species are shown here. Estimates of survey-level detection probability (MacKenzie et al. 2006) incorporate spatial and temporal variation in explanatory covariates by averaging fitted values across sites where surveys occurred. Detection probability was calculated per a single 5-minute survey for the 3 daily times: beginning 30 minutes before sunrise, sunrise, and 15 or 30 minutes after sunrise. Error bars represent upper bounds of 90% confidence intervals. The data for the models were from automated recorder surveys at 453 sites in northern California conifer forests. See Table 2 for species codes.

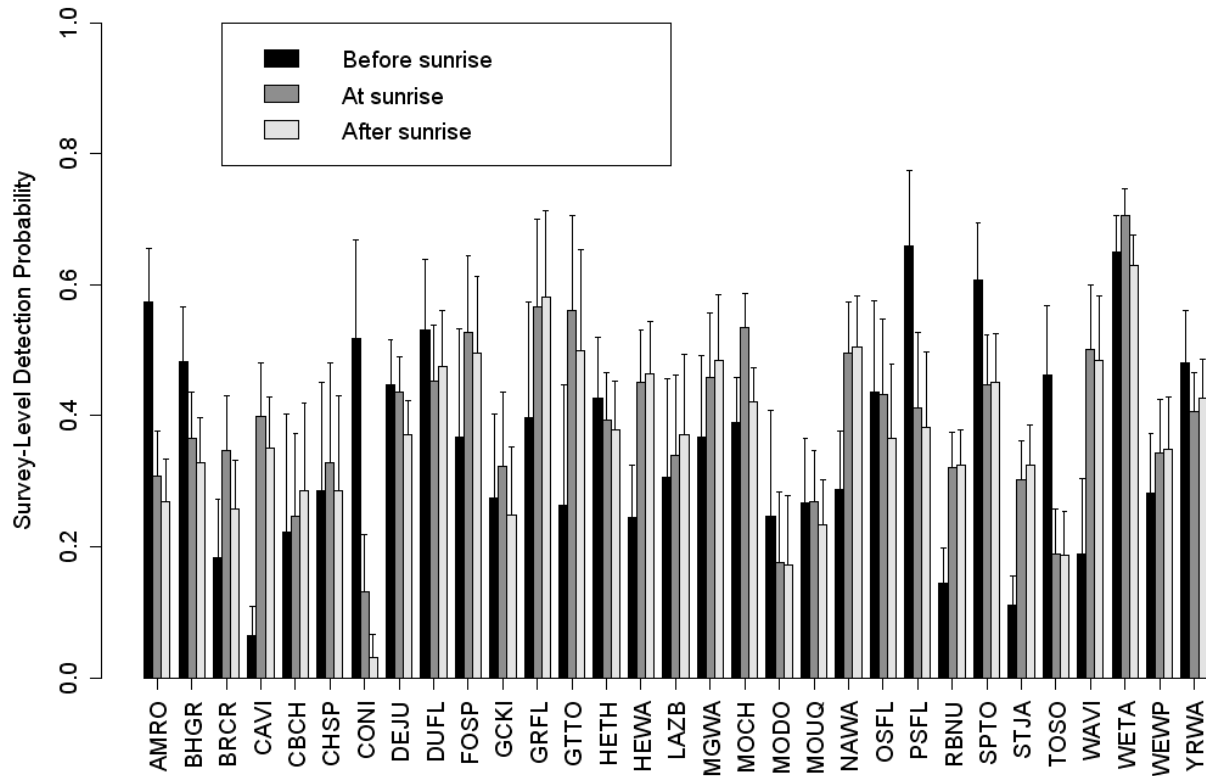


Figure S4. Site-level detection probability by bird species from occupancy modeling of automated recorder survey data from northern California forests from 2006 through 2010.

Site-level estimates of detection probability (MacKenzie et al. 2006) incorporate spatial and temporal variation in explanatory covariates by averaging across sites where surveys occurred. Site-level detection probability was calculated cumulatively after 9 replicate surveys 3 times daily repeated over 3 consecutive days: $p^* = 1 - [(1 - p_1)^3(1 - p_2)^3(1 - p_3)^3]$. The data for the models were from automated recorder surveys at 453 sites in northern California conifer forests. See Table 2 for species codes.

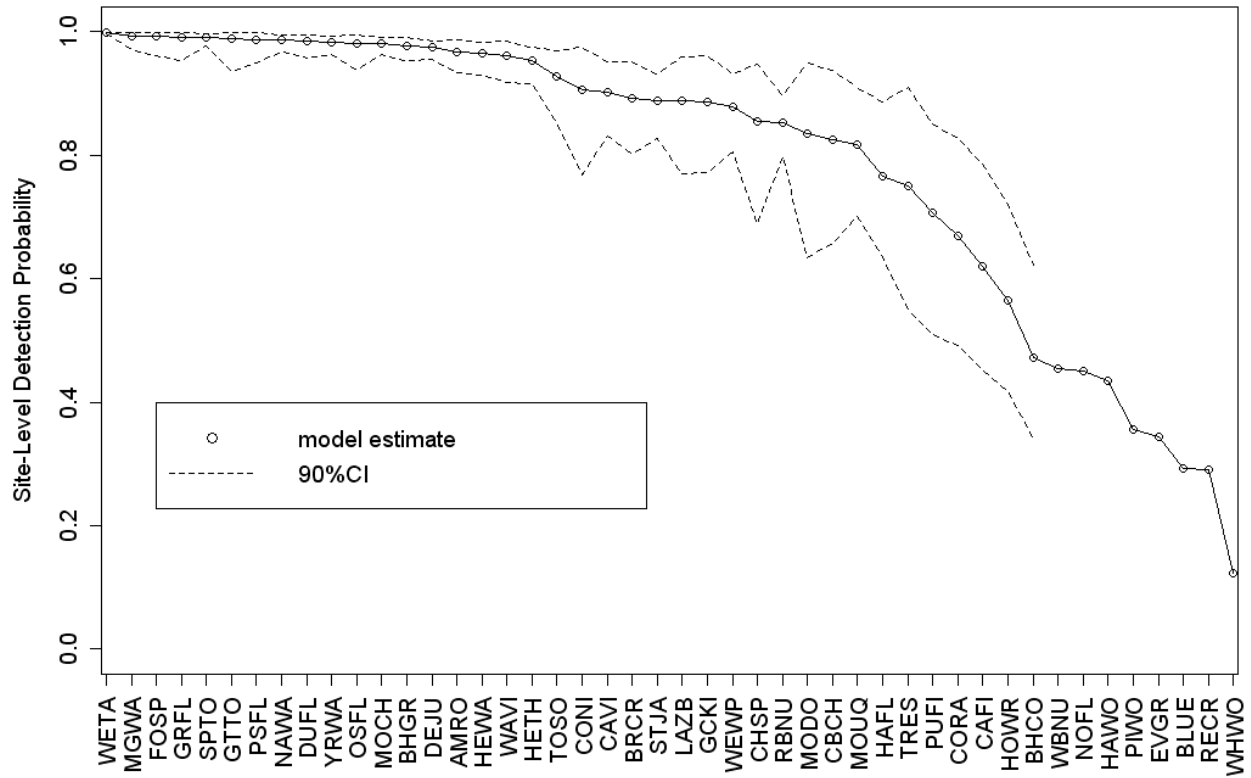
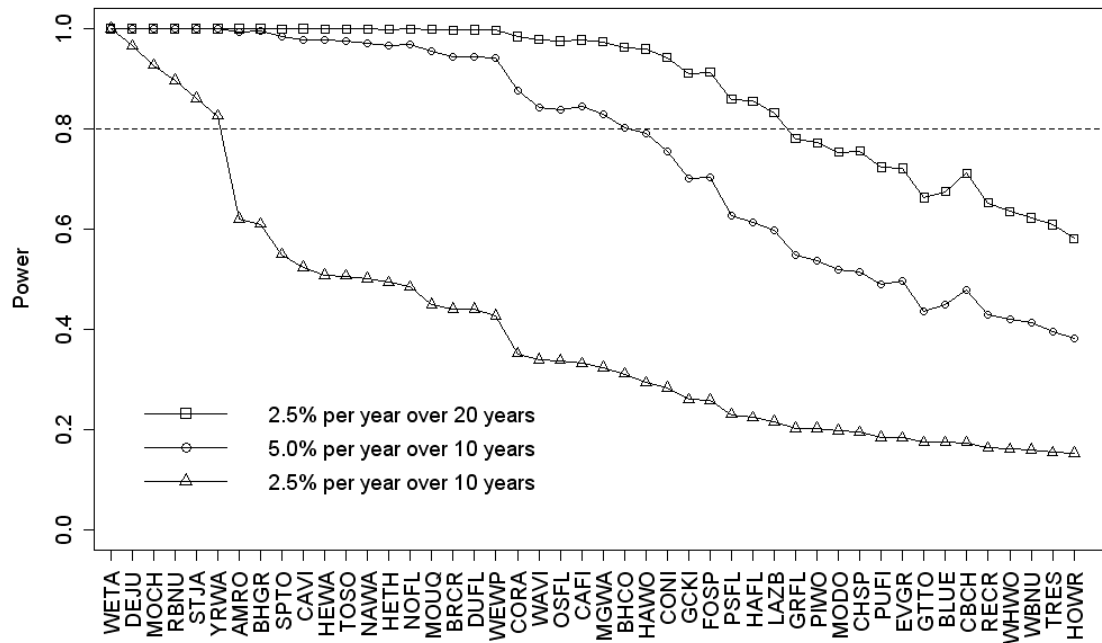


Figure S5. Statistical power to detect a trend in occupancy from regional-scale monitoring via surveys using automated recorders.

Power analyses (Purcell et al. 2005, Nielsen et al. 2009, Meyer et al. 2010) demonstrating the ability of automated recorder to monitor long-term occupancy trends of birds in northern California forests. For 46 species I assessed power to detect average annual declines in occupancy assuming an annual sampling of effort of 100 sites across the study area addressed in the main article (power ≥ 0.8 based on 10,000 Monte Carlo simulations and a type I error rate of 0.1). Starting occupancies and standard error for species for calibrating the power analysis were from occupancy modeling described in the main article. See Table 2 for species codes.



Chapter 2

Multi-species occupancy models for estimating the evenness of a forest songbird metacommunity

ABSTRACT

Biodiversity analyses are increasingly considering the importance of survey detection probability in the estimation of species richness and turnover. Less attention has been given to the effect of detection bias on the shape of rank abundance distributions. Evenness is a popular measure for describing the shape of this distribution. I used simulation and Bayesian hierarchical multi-species occupancy models for California avian surveys to demonstrate that the general effect of ignoring survey detection probability heterogeneity among species was an underestimation of the evenness of a metacommunity. I justified occupancy as a reasonable surrogate for abundance because of the small area associated with the survey method used in this study. By comparing rank occupancy distributions of different avian genera, I found that the relative occurrences of different flycatcher species (*Tyrannidae*) were evenner than for wood warblers (*Parulidae*) or woodpeckers (*Picadae*), and that all 3 groups were evenner than sparrows (*Emberizidae*).

INTRODUCTION

Habitat loss and climate change are expected to reduce biodiversity at the global (Fahrig 2003, Thomas et al. 2004) and regional scales (Radeloff et al. 2005, Stralberg et al. 2009). Scientifically-rigorous, multi-species monitoring is needed for effectively adapting to these threats (Bianchi and Morri 2000, Thomas 2005, DeWan and Zipkin 2010). The refinement of analytical techniques for community-level occurrence or abundance data is an active research field (Pueyo 2006, McGill et al. 2007, Magurran and McGill 2011, Iknayan et al. in press) rooted in concepts of alpha, beta and gamma diversity (Whitaker 1960) and the evenness of rank abundance distributions (Shannon 1948, Simpson 1949). In recent years researchers have begun to address the issue of detection probability in the estimation of species richness (Dorazio and Royle 2005, Kéry and Royle 2008) and turnover (Ruiz-Gutiérrez and Zipkin 2011, Tingley and Beissinger 2013) resulting in a more accurate understanding of how diversity is distributed and impacted by anthropogenic disturbance. These approaches for addressing detection probability have shared a Bayesian hierarchical state-space structure that treats the true ecological state and observed survey data as 2 separate but linked process models (Link et al. 2002).

In this study I considered the effects of detection probability on evaluating the evenness of species diversity. I began by using occupancy as a surrogate for abundance (MacKenzie and Nichols 2004). The rationale for doing so in this case was that I used bird survey data from automated recorders characterized by a small survey area (30 m to 50 m) for detecting forest songbird species (see Chapter One). Next, I simulated the general effect of ignoring detection probability on the evenness of species diversity. Then, I expanded the application of occupancy modeling (MacKenzie et al. 2006, Royle and Dorazio 2008, Kéry and Schaub 2012) to the estimation of a rank occupancy distribution (see Chapter One) at the metacommunity level of

assembly (Wilson 1992, Holyoak et al. 2005). I compared the performance of 2 different hierarchical Bayesian approaches to modeling detection probability for the bird survey data, and evaluated their measures of evenness to that of the uncorrected, naïve occupancies. Finally, I compared evenness among several families (*Parulidae*, *Picadae*, *Tyrannidae*, and *Emberizidae*), and discussed the ecological and conservation implications of these results.

STUDY AREA

Since 2002 the California Department of Fish and Wildlife has surveyed multiple avian species across a 5.4-million-ha area of northern California in the USA (Fig.1) as part of the Ecoregion Biodiversity Monitoring (EBM) project. Conifer-dominated forests covering 64% of this region were primarily Klamath Mixed Conifer, Sierran Mixed Conifer, Douglas Fir (*Pseudotsuga menziesii*), White Fir (*Abies concolor*), Red Fir (*Abies magnifica*), Lodgepole Pine (*Pinus contorta*), Ponderosa Pine (*Pinus ponderosa*), Jeffrey Pine (*Pinus jeffreyi*), Eastside Pine, Montane Hardwood-Conifer, and Juniper (*Juniperus spp.*) forest types (Mayer and Laudenslayer 1988). Elevations range from 60 m to 4,270 m. The geology is a mix of steep mountains and volcanic plateaus, and average annual precipitation varied from 20 cm to 300 cm (Schoenherr 1992). Forest ownership was a mix of public (64%) and private (36%) lands.

METHODS

Survey Design

Survey sites were randomly selected without replacement each year from the U.S. Forest Service hexagon grid for the Forest and Inventory and Analysis (FIA) program (Bechtold and Patterson 2005), which completely overlaps the EBM study area. The distance between adjacent hexagon centroids was 5.35 km. Permission was granted for surveying public agency and private industrial forestland ownerships in the study area.

Although EBM is an ongoing effort, data analysis in this study was limited to sites surveyed from 2006 through 2010. A post-stratification procedure was adopted to limit inference to montane conifer habitats. Using land-use, land-cover information derived from satellite imagery (U.S. Forest Service 2012b), I calculated the proportion of the 400-m-radius surrounding area in conifer forest cover and excluded all sites with < 0.5 conifer forest cover. Following these adjustments, the sample size was 453 sites.

Avian Surveys

Bird surveys were conducted using inexpensive digital voice recorders manufactured by Olympus Corporation (www.olympusamerica.com). These devices were programmable to allow automated recordings to be made at preset times. The models varied by year (e.g., DS-2, DS-40, DS-61). Recording was set to the highest quality with a sampling rate of 44.1 KHz. Microphones also varied by year. In the initial years external omni-directional microphones were purchased separately; recently factory-provided stereo microphones attached to the recording units were used instead. For all configurations, the frequency range for the combined recorder and microphone set was at least 100 Hz to 14,000 Hz. To protect the devices from rain,

condensation and small mammals, they were placed in a lightweight, plastic food container, or the external microphone was placed in a plastic bag.

Devices were programmed to automatically record sounds at up to 3 specified times each morning on 3 consecutive days during the breeding season when songbirds were singing from territories. Each survey period was 5 minutes in length and generally began 30 minutes before sunrise, at sunrise, or at either 15 or 30 minutes after sunrise. Prior to 2009 there were typically only 2 surveys periods per day occurring at sunrise and after sunrise. Surveys were conducted from the middle of May through the first week of July. After completion of the field season a biologist reviewed the recordings and listed all species detected during each 5-minute survey. The interpretation work was accomplished by listening to the recordings while simultaneously viewing the spectrograms using Raven Pro software (Cornell Lab of Ornithology, Ithaca, NY, USA). Only biologists who scored at least 70% on a test interpreting species from sample recordings worked on this task.

To study birds competing on a similar trophic level, I considered only those species belonging to *Passeriformes*, *Columbidae*, *Odontophoridae* or *Picadae*, which included 101 species that were detected at least once (Table 1).

Simulation

Monte Carlo simulation (Metropolis and Ulam 1949) was employed to examine the general effect of detection probability on the apparent shape and evenness of rank occupancy distributions. The true occupancy states of 100 hypothetical species were modeled as, $\Psi_{\text{true } i} = \exp(-0.03(x_i+5))$, for species i where x was drawn from a uniform distribution spanning 1 through 100. The observed occupancies were first modeled under heterogeneous detection probability, $\Psi_{\text{obs1 } i} = p_{1i} \Psi_{\text{true } i}$, where p_1 was drawn from a uniform distribution ranging from 0.2 to 0.9. The observed occupancies were also modeled under homogeneous detection probability, $\Psi_{\text{obs2 } i} = p_{2i} \Psi_{\text{true } i}$, where $p_2 = E[p_1]$. Simulations were repeated 10,000 times. The average values from these simulations were computed and rank sorted to create true versus observed occupancy distributions. Simpson's Measure of Evenness (E_s , Smith and Wilson 1996) was calculated for each simulation. The average value was taken and confidence intervals were constructed from the 5th and 95th percentile values, corresponding to a Type I error rate of 0.1, to test for differences among rank occupancy distributions. The null hypothesis was rejected if the average evenness from one distribution was not contained within the interval of the other distribution or vice-versa.

Occupancy Modeling

Occupancy represents the true proportion of the study area in which a species occurs, or the probability that a given site is occupied by the species. Occupancy modeling allows simultaneous estimation of detection and occupancy probabilities for providing an unbiased estimate of the latter (MacKenzie et al. 2006).

I used Bayesian hierarchical multi-species, single-season occupancy models (Dorazio and Royle 2005, Zipkin et al. 2009, Tingley and Beissinger 2013) to simultaneously estimate

occupancies of all 101 species detected at least once. The models did not include data augmentation (Dorazio and Royle 2005) for estimating the number of species potentially occurring but never detected. For occupancy (Ψ) and detection probability (p):

$$\text{logit}(\Psi_i) = \beta_i \text{ for species } i, \text{ and} \quad \text{eq. 1}$$

$$\text{logit}(p_{i,j,k}) = \beta_{i,j,k} x_{i,j,k} \quad \text{eq. 2}$$

for species i at site j on survey occasion k where x were covariates for explaining detection. The true occurrence state (z) for each site and species was assumed to follow a Bernoulli distribution, $z_{i,j} \sim \text{Bern}(\Psi_i)$, whereas the observation state (y) was modeled as a zero-inflated Bernoulli distribution, $y_{i,j,k} \sim \text{Bern}(p_{i,j,k} z_{i,j}) \text{ I}[z=1]$.

Two models were fit for comparing different approaches for addressing detection heterogeneity among species. Using hyper-parameters (Zipkin et al. 2009, Tingley and Beissinger 2013) the first model treated inter-species variability as normal random effects, $\beta_{s,i} \sim \text{Norm}(\mu_s, \sigma_s)$, for covariate s and species i . The covariates included categorical variables for time of day, year, and total number of species heard in a 5-minute survey, an indicator representing latent weather and location factors affecting avian singing behavior (see Chapter One).

The second model included fixed effects for the same covariates in the first model, but no hyper-parameters. It also included variables representing a set of *a priori* hypotheses about how species traits and taxonomic identity affected detection probability: (1) Rooted in distance sampling (Buckland et al. 2001), I predicted that a species' detection probability should be negatively correlated with territory size, because birds that move around larger territories are more likely to be farther away from the automated recorder during a survey. As complete information on territory size was missing for most species, body mass was used as a proxy for territory size (Palmqvist et al. 1996, Keeley and McPhail 1998, Polishchuk and Tseitlin 1999, Iossa et al. 2008); (2) I tested whether species that actively defend Type A territories (Nice 1941), and that should have greater site fidelity, had higher detectability than other birds; (3) I predicted species that forage higher in the canopy were more detectable, because they sing more continuously while feeding from heights where sound transmission properties are better (Bradbury and Vehrencamp 1998 – Chapter 5). I compared ground, middle canopy/no specialization and high canopy foragers; and (4) I tested whether migratory birds were more detectable than resident birds, because the former group has less time to establish territories upon arrival on the summer range, necessitating more frequent singing to attract mates. I compared species groups representing no migration, local migration and long-distance migration. Species trait data for the variables representing each of these hypotheses listed above were gathered from the Birds of North America species accounts (BNA, www.bna.birds.cornell.edu) or from Tingley et al. (2012) which had already compiled this data from the BNA accounts.

Two taxonomic covariates were also included in the species-traits model. They represented woodpeckers (*Picadae*) and finches (*Fringilidae*). The former was because of lower detectability for this group from previous analyses (see Chapter One), whereas the latter was added after initial analyses improved model fit.

Finally, single-species models for the most common species ($\Psi_{\text{naive}} \geq 0.05$) were fit for assessing accuracy of the 2 multi-species models. These intercept-only occupancy models included detection probability modeled with fixed effects for survey time, year and the number of species detected per survey.

All models were solved through a Markov Chain Monte Carlo algorithm (Link et al. 2002) implemented in WinBUGS (Version 1.4, www.mrc-bsu.cam.ac.uk/bugs) accessed using R statistical software (Version 2.12, www.r-project.org) with the R2WinBUGS package (Sturtz et al. 2005). Uninformative priors were assumed for all parameters. Three independent chains each of 10,000 samples were run with a burn-in period of 5,000 and a thinning rate of 3. Effective mixing of these chains was assessed visually and by means of the Gelman-Rubin convergence statistic (≤ 1.1 , Gelman et al. 2004). Significance tests for model covariates were made using 90 percent credible intervals of posterior distributions.

Rank Occupancy Distributions

Estimates of species' occupancies were first compared among multi-species models and against naïve values. Results from the single-species models provided an additional comparison for common species. Rank occupancy distributions were then assembled by rank sorting and plotting results from the hyper-distribution and species-traits models, and from the naïve estimates. As with the simulation exercise, evennesses of these distributions were quantified via Simpson's Measure of Evenness (E_s). The standard errors from posterior distributions of model parameters were applied in Monte Carlo simulation. Confidence intervals were constructed from the 5th and 95th percentile values corresponding to a Type I error rate of 0.1. Differences between species occupancy distributions were tested using these intervals, and the null hypothesis was rejected if the average evenness from one distribution was not contained within the interval for the other distribution or vice-versa.

Lastly, rank occupancy distributions were evaluated separately for *Parulidae* (wood warblers), *Picadae* (woodpeckers), *Tyrannidae* (flycatchers) and *Emberizidae* (sparrows). I hypothesized that warblers and woodpeckers would display more even distributions than sparrows, and that flycatchers would be intermediate. I reasoned that warblers and woodpeckers are better adapted to breeding and foraging in forested habitats than sparrows leading to less competition, greater resource partitioning and more evenness within the first 2 groups (Cotgreave and Harvey 1994). Rank occupancy distributions by family were assembled from occupancy estimates from the hyper-distribution model.

RESULTS

Simulation

Apparent alpha diversity was similarly reduced under both homogeneous and heterogeneous assumptions of detection probability (Fig. 2). However, apparent evenness was significantly ($P < 0.1$) lower for the heterogeneous ($E_s = 0.54$) versus the true distribution ($E_s = 0.61$). The evenness of the homogeneous distribution was identical to that of the true distribution.

Occupancy Models

For common species ($\Psi \geq 0.1$, Fig. 3a) the hyper-parameter multi-species model increased each species's occupancy estimate above the naïve estimate by 34% on average. The species-traits, multi-species model increased occupancy estimates of common species by 26% on average. Single-species models increased occupancy estimates by 42% on average. This pattern in magnitude was mirrored by a similar pattern in the difference in variance between modeled and naïve estimates (sd = 43%, 39% and 57% respectively); the variation was strongly right-skewed.

For rare species ($\Psi < 0.1$, Fig. 3b) occupancy estimates from the hyper-distribution, multi-species model were an average of 134% higher than naïve estimates, and 104% higher for the species traits, multi-species model. However, these large percentage increases corresponded to much smaller increases on the occupancy scale (0.01 and 0.005 respectively).

The species-traits model confirmed ($P < 0.1$) all *a priori* hypotheses about detection probability. For each 10 g increase in average species mass the per-survey odds of detection given occupancy decreased by 1%. The odds increased by 19% for neotropical migrants versus yearlong residents. They increased by 36% for species with Type A territories, and by 47% for high canopy versus ground foragers. The odds of detection were 71% lower for finches and 84% lower for woodpeckers than for other birds.

Evenness of Rank Occupancy Distributions

Ocular comparisons suggested occupancies from the 2 multi-species models were more even than from naïve estimates (Fig. 4). Formal assessment via Simpson's Measure of Evenness confirmed this impression. Modeled occupancies were significantly ($P < 0.1$) more even than the naïve estimates. Occupancies from the hyper-distribution model were 15% even, whereas occupancies from the species-traits model were 5% more even. Furthermore, occupancies from the hyper-distribution model were significantly ($P < 0.1$) more even than those from the species-traits model.

The construction of partial rank occupancy distributions for different avian families confirmed my hypotheses that warbler and woodpecker occupancies within metacommunities would be significantly ($P < 0.1$) more even than for sparrows (Fig. 5). Unexpectedly, flycatcher evenness ($E_s = 0.63$) was substantially higher than for warblers ($E_s = 0.45$), woodpeckers ($E_s = 0.43$) and sparrows ($E_s = 0.29$). Evenness of each family declined slightly (but not significantly, $P > 0.1$) when detection probability was not addressed. However, the use of naïve occupancy estimates in the Simpson's measure resulted in a significant ($P < 0.1$) difference in apparent evenness between warblers and woodpeckers that was not supported by the modeled data.

DISCUSSION

Occupancy as a Surrogate for Abundance when Estimating Evenness

One reason that there have been few evenness-related studies applying state space modeling solutions to detection probability might be that most ecologists use count (not incidence) data for calculating evenness (Magurran 2004, Magurran and McGill 2011). Multi-species hierarchical models for estimating abundance exist (Yamaura et al. 2012, Chandler et al. 2013), but they require strong assumptions about the detection of individuals and how counts vary between sites which can lead to overestimation of abundance. Theoretical relationships between occupancy and abundance (He and Gaston 2000, Harte 2011) tend to differentiate these 2 metrics more at higher occupancies. As a result one would expect occupancy-based measures of evenness to be greater in magnitude than abundance-based measures for the same community. For this reason it would be problematic to compare evenness across studies that are inconsistent in the use of count and incidence data. Alternatively, occupancy-abundance relationships (e.g., negative binomial, maximum entropy) could be used to transform occupancy to abundance estimates prior to calculation of evenness. Some researchers are directly considering theoretical relationships between the shape of species occupancy distributions and ecological process (McGeoch and Gaston 2002, Hieno 2008, Jenkins 2011).

On the other hand, occupancy may be a good, direct surrogate for abundance in some situations. The automated recorders used in this study were characterized by a small survey area (e.g., 30 m to 50 m radius) for detecting most songbird species (see Chapter One), such that site-level occurrences were expected to most frequently equate to a single territory (see Chapter Three). Incidence is more feasible than abundance to survey when using automated recorders and other automated methods (e.g., remote cameras, see Chapter Four) that make repeat surveys without the presence of a surveyor. Furthermore, incidence data and automated methods are more practical for surveying consistently across large geographical areas, as was the case with EBM. For all these reasons I believe multi-species occupancy modeling provided a good means of evaluating the evenness of the northern California forest songbird metacommunity addressed in this study.

Evenness and Detection Probability

Simulations clearly illustrated that the general effect of ignoring survey detection probability heterogeneity among wildlife species underestimates true evenness of communities. This bias was also demonstrated for real data from avian surveys in montane conifer forests. Inaccuracy in estimating community-level diversity has been addressed for species richness (Dorazio and Royle 2005, Kéry and Royle 2008) and turnover (Tingley and Beissinger 2013), but this study may be the first to quantify the role of detection probability in the assessment of evenness. At least one review has raised the question of sampling intensity affecting the shape of species occupancy distributions (McGeoch and Gaston 2002). At least one other study (Ahumada et al. 2011) has used occupancy modeling to evaluate the evenness of wildlife survey incidence data.

Species Traits and Detection Probability

This study demonstrated the importance of species traits (e.g., body size, foraging height, migration, territoriality, taxonomy) in explaining detection probability in automated recorder surveys. The species-traits observation model (eq. 2) violated an assumption of complete independence of observations among species; it did not include fixed or random effects distinguishing species identity. However, it attempted to control for differences in detection among species through the use of 7 species trait variables differentiating 101 species. I initially attempted a model that included both species trait variables and species identity random effects, but the solution was unable to split species-level variation between these components; all of the variation was assigned to species identity (i.e., hyper-parameter intercept versus hyper-parameter species traits covariates). In theory, species trait information should improve the ability of a hyper-parameter model to adjust the occupancies of rare species. For example, the knowledge that common woodpeckers are much less detectable than other species should upwardly adjust the occupancy of a rare woodpecker better than a random effect borrowing information from all species. Evidence of this prediction was provided by acorn woodpecker in Fig. 3b. Proponents of multi-species hierarchical models have pointed to the value of borrowing information across species, but previous published examples have not attempted species-trait covariates (Zipkin et al. 2009, Zipkin et al. 2010, Ruiz-Gutiérrez et al. 2010, Ruiz-Gutiérrez and Zipkin 2011, Burton et al. 2012, Tingley and Beissinger 2013). Further investigation of species-traits models is needed.

Predictable differences in detectability among species may be useful in planning future wildlife surveys. For single-species studies, for example, survey effort could be customized to optimize site-level detection probability versus replication of surveys at other sites. My results are especially relevant to the use of automated recorders, but many of the same detectability factors are expected to affect point counts (Bibby et al. 2000).

Accuracy of Multi-Species Occupancy Models

The ability of occupancy models to provide less biased estimates of community evenness was complicated by variation in results from the models I used. For common species ($\Psi > 0.1$) both forms of the multi-species model underestimated average occupancy compared to single-species models. Even the hyper-parameters model was unable to fully address inter-species variation in detection probability. Although it is possible that site and temporal explanatory covariates may have mitigated this problem, Bayesian analysis improved precision at the expense of “shrinking” individual species estimates towards the community mean (Link et al. 2002, Zipkin et al. 2009). For rare species, differentiation between the 2 multispecies models was more pronounced, but there were no single-species model results available for comparison. Further investigation of the causes of these differences is needed, because differences in occupancy estimates of rare species affect the evenness of the entire distribution (e.g., E_s was greater for the hyper-parameter model than for the species-traits model).

Ecological and Conservation Implications

Species diversity distributions (e.g., abundance or occupancy) are centrally important to the study of biodiversity. Their shapes have been linked to niche partitioning (MacArthur 1957, Whitaker 1965, Bazzaz 1975, Tokeshi 1996) and neutral theories (Watterson 1974, Hubbell 2001, Harte 2011). Biodiversity monitoring efforts have been criticized for failing to address detection probability, because inferences about rank abundance distributions can be affected by heterogeneity in detection probability among species (Yoccoz et al. 2001, Iknayan et al. in press). The present study demonstrated this problem using both simulated and real data. Unless heterogeneity in detection probability is addressed, the evenness of communities will be underestimated. Recently there has been greater attention to empirical comparisons of diversity as means of evaluating differences between places or changes over time. It is essential that these assessments (e.g., managed versus unmanaged landscapes, or before and after an impact) not be confounded by coincident differences in survey detectability. For example, it is not difficult to envision a case in which a difference in vegetation density alters inter-species heterogeneity in detectability thereby masking or accentuating the true difference in evenness between 2 communities being compared with respect to their conservation value.

Table 1. Bird species included in multi-species occupancy models

AOU Code ^a	Common Name	Scientific Name	AOU Code ^a	Common Name	Scientific Name
ACWO	Acorn Woodpecker	<i>Melanerpes formicivorus</i>	MGWA	MacGillivray's Warbler	<i>Geothlypis tolmiei</i>
AMCR	American Crow	<i>Corvus brachyrhynchos</i>	MOBL	Mountain Bluebird	<i>Sialia currucoides</i>
AMGO	American Goldfinch	<i>Spinus tristis</i>	MOCH	Mountain Chickadee	<i>Poecile gambeli</i>
AMRO	American Robin	<i>Turdus migratorius</i>	MODO	Mourning Dove	<i>Zenaidura macroura</i>
ATFL	Ash-throated Flycatcher	<i>Myiarchus cinerascens</i>	MOUQ	Mountain Quail	<i>Oreortyx pictus</i>
BARS	Barn Swallow	<i>Hirundo rustica</i>	NAWA	Nashville Warbler	<i>Oreothlypis ruficapilla</i>
BTPI	Band-tailed Pigeon	<i>Patagioenas fasciata</i>	NOFL	Northern Flicker	<i>Colaptes auratus</i>
BEWR	Bewick's Wren	<i>Thryomanes bewickii</i>	NUWO	Nuttall's Woodpecker	<i>Picoides nuttallii</i>
BBMA	Black-billed Magpie	<i>Pica hudsonia</i>	OATI	Oak Titmouse	<i>Baeolophus inornatus</i>
BBWO	Black-backed Woodpecker	<i>Picoides arcticus</i>	OSFL	Olive-sided Flycatcher	<i>Contopus cooperi</i>
BHGR	Black-headed Grosbeak	<i>Pheucticus melanocephalus</i>	OCWA	Orange-crowned Warbler	<i>Oreothlypis celata</i>
BLGR	Blue Grosbeak	<i>Passerina caerulea</i>	PSFL	Pacific-slope Flycatcher	<i>Empidonax difficilis</i>
BHCO	Brown-headed Cowbird	<i>Molothrus ater</i>	PIWO	Pileated Woodpecker	<i>Dryocopus pileatus</i>
BRBL	Brewer's Blackbird	<i>Euphagus cyanocephalus</i>	PIJA	Pinyon Jay	<i>Gymnorhinus cyanocephalus</i>
BRSP	Brewer's Sparrow	<i>Spizella breweri</i>	PISI	Pine Siskin	<i>Spinus pinus</i>
BRCR	Brown Creeper	<i>Certhia americana</i>	PUIF	Purple Finch	<i>Haemorhous purpureus</i>
BTYW	Black-throated Gray Warbler	<i>Setophaga nigrescens</i>	PUMA	Purple Martin	<i>Progne subis</i>
BGGN	Blue-gray Gnatcatcher	<i>Poliopitila caerulea</i>	PYNU	Pygmy Nuthatch	<i>Sitta pygmaea</i>
BUOR	Bullock's Oriole	<i>Icterus bullockii</i>	RBNU	Red-breasted Nuthatch	<i>Sitta canadensis</i>
BUSH	Bushit	<i>Psaltriparus minimus</i>	RBSA	Red-breasted Sapsucker	<i>Sphyrapicus rubber</i>
CAQU	California Quail	<i>Callipepla californica</i>	RECR	Red Crossbill	<i>Loxia curvirostra</i>
CALT	California Towhee	<i>Melospiza crissalis</i>	RWBL	Red-winged Blackbird	<i>Agelaius phoeniceus</i>
CAFI	Cassin's Finch	<i>Haemorhous cassinii</i>	ROWR	Rock Wren	<i>Salpinctes obsoletus</i>
CAVI	Cassin's Vireo	<i>Vireo cassinii</i>	SAGS	Sage Sparrow	<i>Artemisiospiza belli</i>
CBCH	Chestnut-backed Chickadee	<i>Poecile rufescens</i>	SOSP	Song Sparrow	<i>Melospiza melodia</i>
CHSP	Chipping Sparrow	<i>Spizella passerine</i>	SPTO	Spotted Towhee	<i>Pipilo maculatus</i>
CLNU	Clark's Nutcracker	<i>Nucifraga columbiana</i>	STJA	Steller's Jay	<i>Cyanocitta stelleri</i>
CORA	Common Raven	<i>Corvus corax</i>	SWTH	Swainson's Thrush	<i>Catharus ustulatus</i>
COYE	Common Yellowthroat	<i>Geothlypis trichas</i>	TOSO	Townsend's Solitaire	<i>Myadestes townsendi</i>
COFL	Cordilleran Flycatcher	<i>Empidonax occidentalis</i>	TRES	Tree Swallow	<i>Tachycineta bicolor</i>
DEJU	Dark-eyed Junco	<i>Junco hyemalis</i>	VATH	Varied Thrush	<i>Ixoreus naevius</i>
DOWO	Downy Woodpecker	<i>Picoides pubescens</i>	VESP	Vesper Sparrow	<i>Pooecetes gramineus</i>
DUFL	Dusky Flycatcher	<i>Empidonax oberholseri</i>	VGSW	Violet-green Swallow	<i>Tachycineta thalassina</i>
EUST	European Starling	<i>Sturnus vulgaris</i>	WAVI	Warbling Vireo	<i>Vireo gilvus</i>
EVGR	Evening Grosbeak	<i>Coccothraustes vespertinus</i>	WEBL	Western Bluebird	<i>Sialia mexicana</i>
FOSP	Fox Sparrow	<i>Passerella iliaca</i>	WESJ	Western Scrub-Jay	<i>Aphelocoma californica</i>
GTTO	Green-tailed Towhee	<i>Pipilo chlorurus</i>	WEME	Western Meadowlark	<i>Sturnella neglecta</i>
GCKI	Golden-crowned Kinglet	<i>Regulus satrapa</i>	WETA	Western Tanager	<i>Piranga ludoviciana</i>
GRFL	Gray Flycatcher	<i>Empidonax wrightii</i>	WEWP	Western Wood-Pewee	<i>Contopus sordidulus</i>
GRAJ	Gray Jay	<i>Perisoreus canadensis</i>	WBNU	White-breasted Nuthatch	<i>Sitta carolinensis</i>
HAWO	Hairy Woodpecker	<i>Picoides villosus</i>	WHWO	White-headed Woodpecker	<i>Picoides albolarvatus</i>
HAFL	Hammond's Flycatcher	<i>Empidonax hammondi</i>	WIFL	Willow Flycatcher	<i>Empidonax traillii</i>
HETH	Hermit Thrush	<i>Catharus guttatus</i>	WISA	Williamson's Sapsucker	<i>Sphyrapicus thyroideus</i>
HEWA	Hermit Warbler	<i>Setophaga occidentalis</i>	WIWR	Winter Wren	<i>Troglodytes hiemalis</i>
HOFI	House Finch	<i>Haemorhous mexicanus</i>	WIWA	Wilson's Warbler	<i>Cardellina pusilla</i>
HOWR	House Wren	<i>Troglodytes aedon</i>	WREN	Wrentit	<i>Chamaea fasciata</i>
HUVI	Hutton's Vireo	<i>Vireo huttoni</i>	YBCH	Yellow-breasted Chat	<i>Icteria virens</i>
JUTI	Juniper Titmouse	<i>Baeolophus ridgwayi</i>	YHBL	Yellow-headed Blackbird	<i>Xanthocephalus xanthocephalus</i>
LASP	Lark Sparrow	<i>Chondestes grammacus</i>	YEWA	Yellow Warbler	<i>Setophaga petechia</i>
LAZB	Lazuli Bunting	<i>Passerina amoena</i>	YRWA	Yellow-rumped Warbler	<i>Setophaga coronata</i>
LEGO	Lesser Goldfinch	<i>Spinus psaltria</i>			

^aAmerican Ornithologists' Union species codes (Banks et al. 2003)

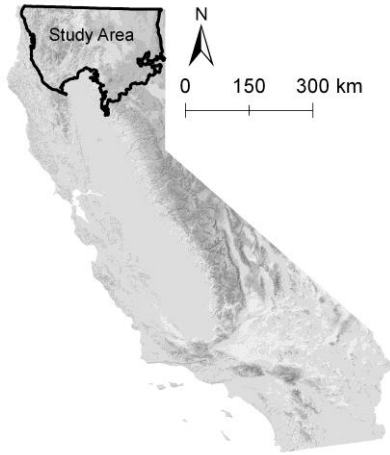


Figure 1. Northern California study area throughout which multi-species avian surveys were conducted from 2006 to 2010 using automated recorders.

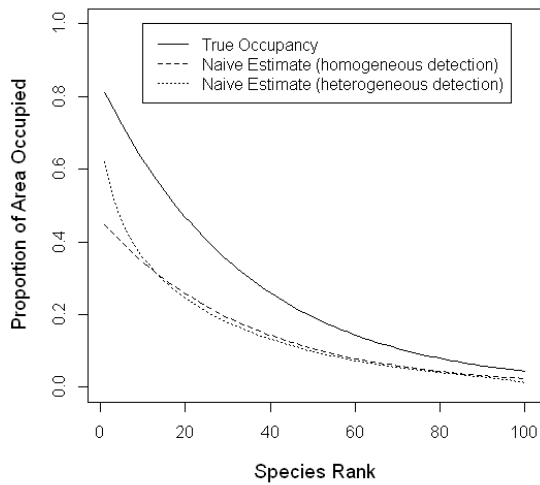


Figure 2. Simulation results demonstrating how heterogeneity of detection probability underestimates the evenness of a rank occupancy distribution.

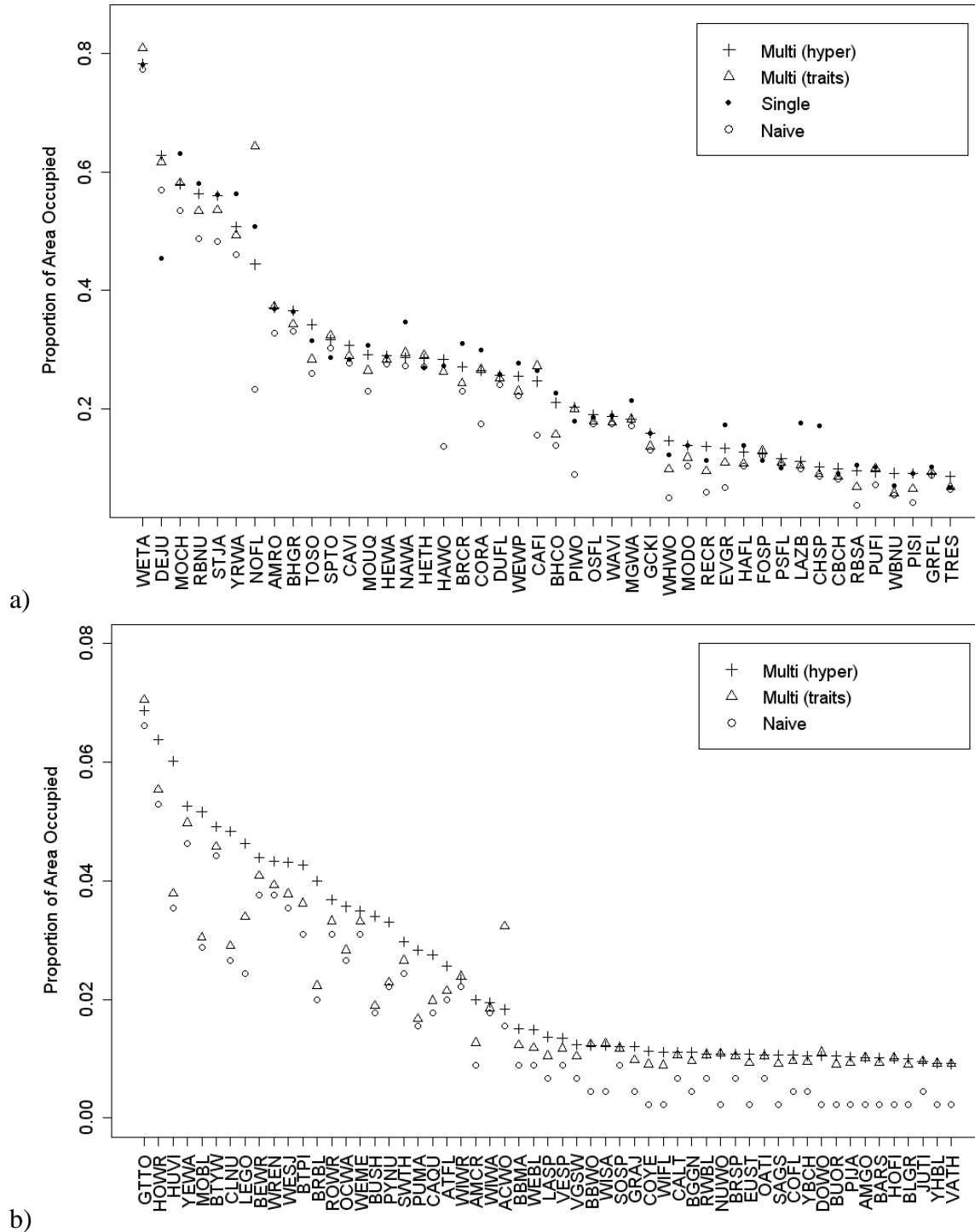


Figure 3. Occupancy estimates for common (a) and rare (b) species in a northern California conifer forest songbird metacommunity. The 2 approaches to addressing detection bias through multi-species occupancy models were hyper-parameters (e.g., random effects for differences among species) and fixed effects for species-traits (e.g., body size, foraging height guild, etc.) explaining detection probability. For reference, naïve and single-species estimates are also shown.

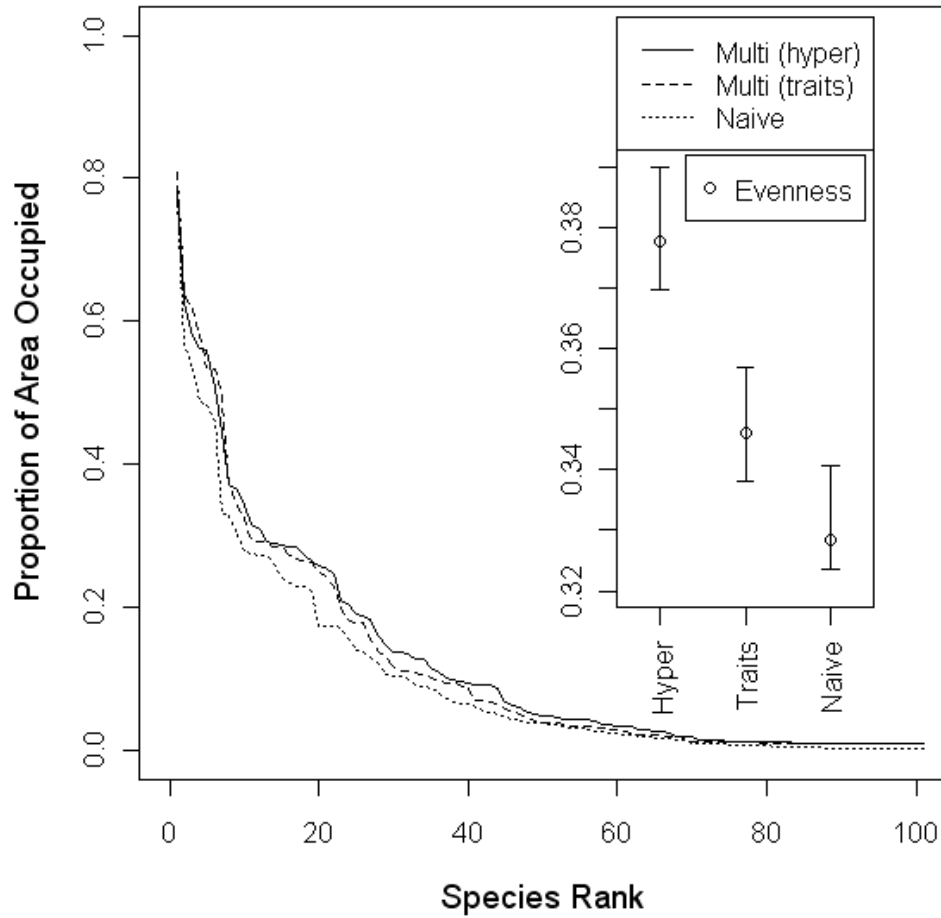


Figure 4. Comparing Simpson's measure of evenness of rank occupancy distributions for a northern California montane-conifer songbird metacommunity. The 2 approaches to addressing detection bias through multi-species occupancy models were hyper-parameters (e.g., random effects for difference between species) and fixed effects for species-traits (e.g., body size, foraging height guild, etc.). The observed rank occupancy distribution using naïve estimates is provided for reference.

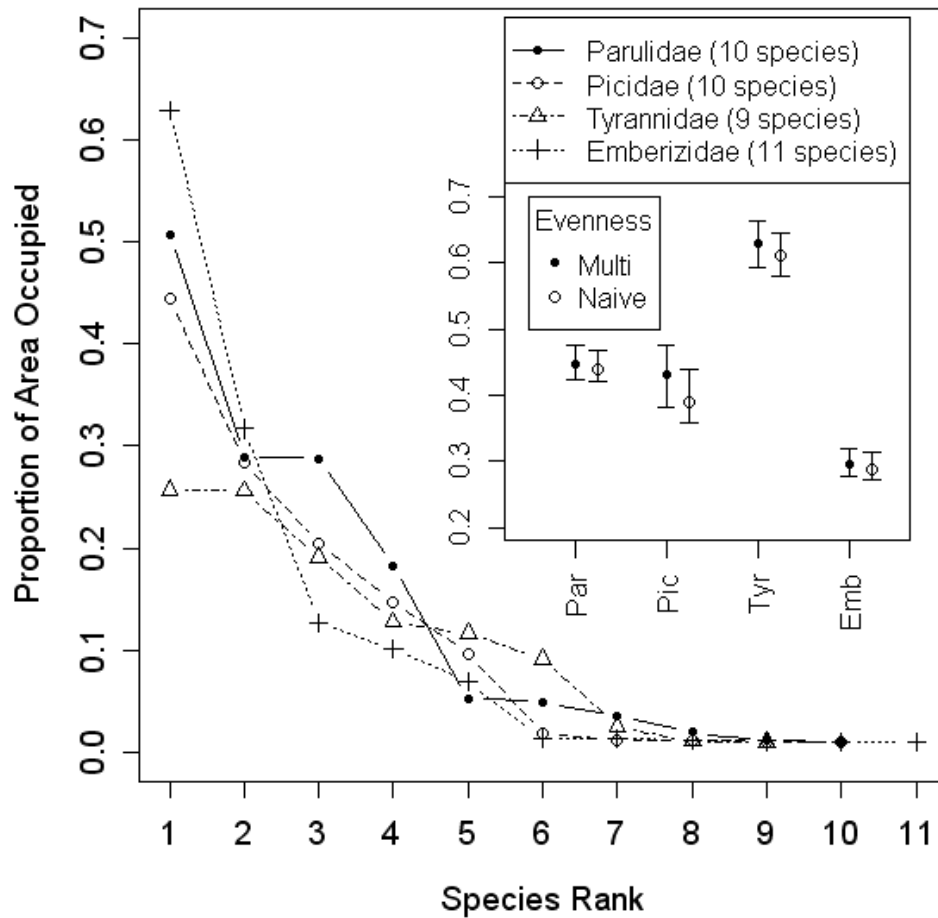


Figure 5. Comparing evenness of rank occupancy distributions among genera for a northern California conifer forest songbird metacommunity. Simpson’s measure of evenness was used. Non-detection bias was addressed with a multi-species occupancy model using hyper-parameters (e.g., random effects) to explain difference in detection probability among species.

Chapter 3

Bootstrap comparisons of avian rank abundance distributions from four California forests

ABSTRACT

Biodiversity indices, such as those that measure species richness or evenness, provide limited information about ecological communities. The species abundance distributions from which these indices are derived contain greater detail about community structure. For this reason conservation planners and land managers would benefit from methods that allow more nuanced comparisons of these distributions than offered by traditional indices. I used bird survey data from 4 research forests in California to construct rank abundance distributions. I then combined data from all these forests to investigate differences in abundance between migratory and resident species. Using bootstrap re-sampling, I created uncertainty bands associated with the empirical shapes of these curves, allowing identification of significant ($P < 0.1$) differences between distributions over a portion of their ranks. I found higher abundances of intermediately-common species on 2 of the forests, and ascribe this finding to differences in forest productivity and habitat complexity leading to greater niche partitioning of resources. At the metacommunity level, I found higher abundances of intermediately-common species for neotropical migrants compared to resident birds. Biodiversity indices derived from these data were less informative.

INTRODUCTION

Many researchers have advocated species diversity indices for quantifying and assessing biodiversity. The simplest index, species richness, formed the basis of MacArthur and Wilson's (1967) landmark theory of island biogeography. Other indices (Simpson 1949, Shannon and Weaver 1963) furnish relative abundance derived information on evenness (or dominance) among species in a community.

Species abundance distributions (Motomura 1932, Fisher et al. 1943, Preston 1948, Hubbell 2001, Harte 2011) provide a richer source of information than indices for quantifying biodiversity. One way of displaying these data, known as a rank abundance distribution (RAD), is to plot species abundances in rank order. Whittaker (1965) was one of the first to use the RAD to connect concepts of resource competition and ecological niche to differences in abundance for dominant, intermediate and rare species. Beedy (1981) applied this method to comparing bird communities and forest structure in California. He drew RADs of different forest types and concluded that the lognormal form (Preston 1948) of the associated species abundance distribution in structurally complex habitats was indicative of greater resource partitioning (and food availability) supporting greater numbers of intermediately common species. One shortcoming of Beedy's results was the lack of a formal test of these differences.

I modified Beedy's approach comparing the avian communities from 4 montane conifer forest locations in California. Rather than using indices or fitting functional forms of species abundance distributions, I compared empirical shapes of RADs by means of bootstrap re-

sampling (Efron 1982). Instead of evaluating entire curves, I focused attention on intermediate ranks (6 to 20) perhaps most pertinent to niche differentiation. Aggregating data from all forests, I also evaluated differences between migratory and resident bird metacommunities (Holyoak et al. 2005). Results were compared also with diversity indices of the data pertaining to species richness and evenness.

The methods developed here offer an alternative to traditional biodiversity indices and fitting forms to species abundance distributions for assessing differences between ecological communities and metacommunities. They provide detail on nuanced differences in species abundances, and may be more useful than parametric approaches for estimating species diversity because they allow one to focus on a portion of ranks.

METHODS

Study Area

The avian survey data were from 4 research forests owned and managed by the University of California at Berkeley or the California Department of Forestry and Fire Protection (Fig. 1). Management objectives for these forests included timber production and research. The 3,650-ha Latour State Demonstration Forest is located 70 km east of Redding in the Southern Cascades mountains. Elevations range from 1,200 m to 2,050 m. Average annual precipitation was 117 cm on volcanic soils. The forest was predominantly mixed conifer and true fir forest punctuated by a few wet meadows and some post-fire brush fields. The forest was generally even-aged with sparse understory vegetation except along creeks and in brush fields. Average forest productivity was characterized as a low Dunning Site Class II (Ronald 1992, Barrett and Bise 1993).

The 1,175-ha Blodgett Forest is located 18 km east of Georgetown in the central Sierra Nevada mountains. Elevations range from 1,200 m to 1,500 m across gently rolling, highly productive terrain. Average annual precipitation was 166 cm. The forest was primarily mixed conifer with some oak stands and brush fields. Average forest productivity was characterized as a high Dunning Site Class I (R. York, UC Berkeley, personal communication).

The 3,280-ha Sagehen Experimental Forest is located 16 km north of Truckee in the central Sierra Nevada mountains. Elevations range from 1,450 m to 2,300 m. Average annual precipitation was 85 cm. The forest was a mosaic of mixed conifer and white fir stands, post-fire plantations, grassy meadows and rocky shrublands. Average forest productivity was characterized as Dunning Site Class III or IV (S. Conway, U.S. Forest Service, personal communication).

The 1,870-ha Mountain Home State Demonstration Forest is located 35 km northeast of Porterville in the southern Sierra Nevada mountains. Elevations range from 1,450 m to 2,300 m. Average annual precipitation was 102 cm. The forest was predominantly mixed conifer forest with approximately 5,000 giant sequoia (*Sequoiadendron giganteum*) trees in excess of 1 m in diameter spread across half of the property. The forest was generally uneven-aged with more understory vegetation than at Latour. Springs supporting wet meadows occurred at numerous

locations. Average forest productivity was characterized as a high Dunning Site Class II (Ronald 1992, Barrett and Bise 1993).

Bird Surveys

Breeding bird surveys were part of a comprehensive wildlife and wildlife habitat inventory undertaken by the University of California at 10 study sites throughout the State beginning in 1977 (Dedon and Barrett 1982). At Sagehen 80 sites were surveyed in 1979 or 1981. At Latour and Mountain Home 80 sites and 79 sites, respectively, were surveyed in 1993 or 1994. At Blodgett 81 sites were surveyed in 1996 or 1997. Sites were distributed evenly across each forest using a systematic design (Thompson 2012), and they were generally spaced at least 400 m apart. Each survey consisted of 20 consecutive 10-minute periods beginning 30 minutes after sunrise on a single morning by a single surveyor during the breeding season from the middle of May through the middle of July (Dedon and Barrett 1982, Barrett and Bise 1993).

Statistical Analyses

For analysis purposes I limited detections to those birds the surveyor judged to have breeding territories intersecting at least half of the 30-m-radial area surrounding the point count site. As surveys at each site occurred on a single day, I did not attempt to address detection probability via a model-based approach (Royle 2004). Instead I used the highest count from the 20 consecutive survey replicates to represent the true abundance of each species at the site. Counts were converted into densities (birds/ha) by dividing by the 30-m-radial area to which surveys applied. Species estimates of densities were calculated as averages at the community (for each forest) and metacommunity (for all forests) levels of organization.

I rank sorted and plotted point estimates of species abundance. Considering the small survey area (0.28 ha) for the point counts and because most counts were unitary, I did not log transform abundances as is usually done for these distributions (Whittaker 1965). RAD curves were constructed as such for each forest, and also from the combined data representing all forests. For the metacommunity, ranks for neotropical migrants and resident birds were highlighted. Information for distinguishing migratory guilds was from review of the Birds of North America species accounts (BNA: www.bna.birds.cornell.edu, Table 1).

To assess differences between RADs, I bootstrap re-sampled (Efron 1982) from the ~80 sites on each forest 10,000 times. A new distribution was constructed for each re-sample such that each rank had a new abundance estimate regardless of species identity. Lastly, I estimated the uncertainty of these curves using the 5th and 95th percentiles for each rank. These corresponded to a 90% confidence interval. The lower and upper bounds were connected separately by rank for graphing an uncertainty band associated with each RAD. This process was repeated for the combined data set across all forests.

Pairs of forest-level RADs were considered significantly ($P < 0.1$) different over a portion of their ranks as indicated by the bootstrapped uncertainty bands. Differentiation for each rank was determined only if both point estimates lay outside of the uncertainty band of the other. In this study, I focused attention on differences for ranks 6 through 20 representing moderately

common species. To evaluate how well the uncertainty band technique worked with respect to traditional biodiversity indices, I also computed Simpson's measure of evenness, average site-level species richness (alpha diversity), and forest-level species richness (gamma diversity). I used the same bootstrap re-samples to create 90% confidence intervals for these indices. Next, I created a dichotomous variable, $INDEX_{i,j}$ which was 1 if a biodiversity index was significantly different ($P < 0.1$) between forest pairs, otherwise it was 0, where i represented the forest pair comparison and j denoted which index (e.g. evenness, alpha, or gamma). I created another variable, $INTER_{i,j}$ representing the proportion of significantly different ($P < 0.1$) intermediate ranks for each forest pair comparison. To test for an association between results from the uncertainty band method and traditional biodiversity indices, I fit a linear mixed-effect model as follows: $INTER_{i,j} = \beta_0 + \beta_1 * INDEX_{i,j} + \beta_3 + \epsilon_{i,j}$, where β_0 was the intercept, β_1 represented the tested association, $\beta_3 \sim \text{Norm}(0, \sigma_{\beta_3})$, and ϵ were the residual errors.

For the RAD representing the avian metacommunity across forests, probabilistic comparisons were made between ranks from this single curve. In particular, the migratory guild composition of intermediate ranks was compared against the composition of very common and rare ranks.

My *a priori* hypotheses about differences in RADs for intermediately-common species were based on ideas of niches and resource partitioning (Grinnell 1917, MacArthur 1958, Hutchinson 1959, Whittaker et al. 1973, Schoener 1974, Chesson 2000). First, I hypothesized that higher forest productivity would lead to higher abundances of intermediately-common species because larger trees, taller forests and greater structural complexity should lead to an increased potential for resource partitioning with respect to nesting and foraging habitat. Second, I posited that migratory birds should have higher abundances than resident birds for the intermediate ranks, because migrants are better adapted to take advantage of and partition resources on breeding season ranges (Lovette and Bermingham 1999).

RESULTS

Abundance Estimation

A total of 47 species were detected at least once at Latour, 57 at Blodgett, 62 Sagehen, and 62 at Mountain Home. A total of 91 species was detected at least once across all forests. Species in the top 5 abundance ranks in at least one of the forests were American robin (*Turdus migratorius*), black-headed grosbeak (*Pheucticus melanocephalus*), dark-eyed junco (*Junco hyemalis*), golden-crowned kinglet (*Regulus satrapa*), mountain chickadee (*Poecile gambeli*), Nashville warbler (*Oreothlypis ruficapilla*), pine siskin (*Spinus pinus*), red-breasted nuthatch (*Sitta canadensis*), red crossbill (*Loxia curvirostra*), spotted towhee (*Pipilo maculatus*), Steller's jay (*Cyanocitta stelleri*), western tanager (*Piranga ludoviciana*), and yellow-rumped warbler (*Setophaga coronata*). Dark-eyed junco was the only species in the top 5 ranks in all forests.

Species in the intermediate ranks (6 through 15) in at least one of the forests were American robin, band-tailed pigeon (*Patagioenas fasciata*), black-headed grosbeak, brown-headed cowbird (*Molothrus ater*), Brewer's blackbird (*Euphagus cyanocephalus*), brown creeper (*Certhia americana*), Calliope hummingbird (*Selasphorus calliope*), Cassin's finch (*Haemorhous cassinii*), Cassin's vireo (*Vireo cassinii*), chipping sparrow (*Spizella passerina*),

common raven (*Corvus corax*), dusky flycatcher (*Empidonax oberholseri*), fox sparrow (*Passerella iliaca*), golden-crowned kinglet, hairy woodpecker (*Picoides villosus*), Hammond's flycatcher (*Empidonax hammondi*), hermit thrush (*Catharus guttatus*), hermit warbler (*Setophaga occidentalis*), house wren (*Troglodytes aedon*), MacGillivray's warbler (*Geothlypis tolmiei*), mountain chickadee, Nashville warbler, northern flicker (*Colaptes auratus*), purple finch (*Haemorhous purpureus*), red-breasted nuthatch, Steller's jay, warbling vireo (*Vireo gilvus*), western tanager, white-headed woodpecker (*Picoides albolarvatus*), Wilson's warbler (*Cardellina pusilla*), yellow warbler (*Setophaga petechia*), and yellow-rumped warbler. Brown creeper and fox sparrow were the only species in the intermediate ranks of all forests, despite the fact that 24 of the 33 intermediately-ranked species listed above were detected at least once at every forest.

Based on visual inspection of natural breaks in the "all forests" RAD, I re-classified intermediately-common species as ranks 10 through 25. The only neotropical bird in the top 9 ranks was western tanager, whereas 3 resident species (brown creeper, mountain chickadee, Steller's Jay) filled these ranks. However, there were 8 intermediately-common neotropical migrants (black-headed grosbeak, Cassin's vireo, dusky flycatcher, Hammond's flycatcher, hermit warbler, MacGillivray's warbler, Nashville warbler, and warbling vireo), versus 3 residents (hairy woodpecker, northern flicker, and white-headed woodpecker).

A full reporting of abundances by forest and across forests is provided in Table 1.

Rank Abundance Distributions

Bootstrap comparisons of RADs among forests demonstrated significant ($P < 0.1$) differentiation between the majority intermediate ranks (6 to 20) for the Blodgett and Mountain Home forests versus Latour and Sagehen (Fig. 2a through 2d). On the other hand, there were only 2 intermediate rank differences between Blodgett and Mountain Home, and only 5 between Sagehen and Latour (Fig. 2e through 2f). Using the linear mixed-effects model, I found no significant association ($P = 0.28$) between the results of the uncertainty band comparisons of intermediately-common species and traditional biodiversity indices.

I constructed a single RAD representing the metacommunity across all forests, and differentiated its composition in terms of neotropical migrants, residents and other species (Fig. 3). There were 5 migratory species in the intermediate ranks that had significantly higher ($P > 0.1$) abundances than 2 of the 3 resident birds in these ranks. On the other hand, there were 3 very common resident birds at higher abundances, and a greater proportion of residents (74%) than migrants (65%) were rare.

DISCUSSION

Ecologists have proposed a confusing variety of biodiversity indices over the past century (Magurran and McGill 2011), accompanied by some criticism of the usefulness of this approach (Hurlbert 1971, Schwartz et al. 2000). Others have focused on the functional forms of species abundance distributions (Wilson 1991), for example, theorizing that lognormal-shaped

distributions are associated with more structurally complex habitats and support greater resource partitioning than geometric-shaped ones (Preston 1948, Whittaker 1965, Beedy 1981).

Rather than choosing indices or fitting functional forms, I directly compared RADs using bootstrap re-sampling to construct uncertainty bands for differentiating pairs of curves. The results suggest that the avian communities at Blodgett and Mountain Home had higher abundances of intermediately-common species than at Sagehen and Latour. These findings are consistent with the hypothesis that higher productivity forests provide the potential for greater structural diversity and enable more intermediately-common species to rise to higher abundances, because niche partitioning reduces interspecies competition for resources. All forests experienced similar timber management histories, but Blodgett and Mountain Home lay on more productive grounds than the other 2 forests. In particular, the Blodgett forest is on some of the most productive soils on the west slope of the Sierras which supports rapid growth of tall, large-diameter conifers, whereas the seeps and springs at Mountain Home nurture a mosaic of mature giant sequoias and small wet meadows.

A second, metacommunity-level finding from this study was that migratory birds dominated and rose to higher abundances within the intermediate ranks than resident species. Consistent with this hypothesis, there was additional evidence of resource partitioning within these ranks. For example, the 3 intermediately-common warbler species (hermit warbler, Nashville warbler, MacGillivray's warbler) tend to partition their feeding activities within the high canopy, middle story and ground layers, respectively (see BNA species accounts). All of the intermediately-common resident species were woodpeckers, which are also known to display a high degree of niche partitioning (Bull et al. 1986). Two additional, yet not inconsistent, findings were that resident species dominated the very common ranks, whereas the reverse was true for rare species.

The story that emerges from all 3 metacommunity findings is that resident species may face more resource limitations in California conifer forests, because they need to survive there throughout the winter when competitive interactions may be the most intense (Fretwell 1972). This could lead to a stable condition of lower abundances for most species, and higher abundances for a few dominant species. There were some exceptions to this pattern, including woodpeckers. On the other hand, migratory visitors may be better adapted to temporary partitioning of resources, behaviorally (MacArthur 1958) and via other evolved traits (Lovette and Bermingham 1999). These factors may allow migrants to temporarily rise to higher intermediate-abundances than residents during the breeding season. However, except for western tanager, these factors may have been insufficient to allow migrants to rise to the higher abundances manifested by the 3 most abundant resident species, brown creeper, mountain chickadee, and Steller's Jay.

I have shown that empirical evaluation of RAD shapes can furnish a data rich alternative to biodiversity indices or the fitting of functional forms for evaluating and comparing communities. Indices and forms can describe characteristics of the entire RAD, whereas the uncertainty band method allows one to evaluate more nuanced differences over a portion of ranks. In particular, it is possible to deconstruct patterns related to common, intermediate and rare species, as well as interactions between these segments as demonstrated in the migratory

versus resident example. MacArthur's (1957) broken stick hypothesis and other theories about RAD shapes (Fisher et al. 1943, Preston 1948) provide a mechanism for less direct inferences about resource partitioning affecting the abundances of common, intermediate and rare species. The method proposed here provides a more direct means of assessing the composition of differentiated ranks among communities, as was the case for warblers and woodpeckers, thereby strengthening the explanation of how resources were likely partitioned.

There was no consistency between biodiversity indices and my findings on how middle ranks were differentiated. This discrepancy highlights that use of indices versus the uncertainty band method may illuminate different community properties. Although alpha diversity and evenness across an entire community may also be associated with greater productivity and resource partitioning, these metrics might not be optimal for isolating effects over a portion of ranks or by guild. This is important in that resource partitioning may not be universal. In this study, I found that resident birds were bifurcated between very common and rare species, whereas migratory birds displayed greater clustering within intermediate ranks.

Results from this study are qualified by some limitations related to study design. First, these data only reflected avian community structure over 2-year timeframes, and the survey years were different by forest. Only one of the survey years was preceded by a strong El Nino or La Nina event that might have confounded results (Sillett et al. 2000). A sensitivity analysis in which I removed the 1996 surveys from the Blodgett forest did weaken abundance differences in intermediate ranks between Blodgett and Sagehen, but this may have been due to the reduced sample size ($n=40$ sites) resulting from the omission. Second, this study utilized raw survey data to which I was unable to apply hierarchical modeling for addressing heterogeneity in survey detection probability (Royle 2004) beyond taking the maximum count during a single day. It is possible that systematic differences in detectability (e.g., different surveyors, years, habitat conditions) may have confounded the conclusion that apparent difference in RADs were due to differences in forest productivity. This problem was compounded by the small sample size ($n=4$ forests) of the comparison among forests. Furthermore, the forests differed in area, which was likely to have underrepresented differences between the larger, more productive forests (e.g., Blodgett and Mountain Home) and the smaller, less productive forests (e.g., Latour and Sagehen). Despite these study limitations the RAD bootstrapping has diverse applications for evaluating and comparing communities.

Scale is another issue to consider when evaluating my results. The point counts used for estimating density covered a small area (0.28-ha), leading to generally small survey counts. In particular, 89% of non-zero counts per species per survey period were $= 1$, and 99% were ≤ 2 . It is unclear whether the rank differences reported here would have been the same for larger survey units. Nevertheless, the methodological advantages of bootstrapping discussed above for comparing a portion of ranks are not especially related to scale. Furthermore, considering the dominance of ones and zeros in the data set I used, the RAD uncertainty band approach taken here may also be appropriate for applying to rank occupancy distributions derived from incidence data.

In conclusion, the bootstrap-uncertainty band comparison method developed here allows for greater empirical examination of how RADs differ over portions of their ranks. By

evaluating finer distinctions between very common, intermediate and rare species, there is greater potential for drawing ecological inferences, particularly in regard to resource partitioning. This approach may be especially relevant to biodiversity monitoring and conservation planning (see Chapters One and Two). Declines of individual species may be better understood in context of their relationship to other species and niches within the community using RAD uncertainty bands. In particular, rank segments could be monitored for changes in differentiation and composition (Collins et al. 2008) over time. For example, assuming the metacommunity-level RAD estimated in this study was valid, this information may provide greater insight into how the expected invasion of Townsend's warbler into California (Krosby and Rohwer 2010) might displace hermit warbler from its current role dominating a foraging niche among intermediately-abundant migratory species.

Table 1. Abundance estimates for avian species surveyed at Latour, Blodgett, Sagehen and Mountain Home forests in California. These species were assigned to migratory guilds (NM – neotropical migrant, RE - resident) based on a review of the Birds of North America species accounts.

Common Name	Scientific Name	Migratory Guild	All Forests	Density (birds/ha)			
				Latour	Blodgett	Sagehen	Mt. Home
Acorn Woodpecker	<i>Melanerpes formicivorus</i>	RE	0.055	0.000	0.217	0.000	0.000
American Dipper	<i>Cinclus mexicanus</i>		0.011	0.000	0.000	0.044	0.000
American Kestrel	<i>Falco sparverius</i>		0.056	0.000	0.131	0.089	0.000
American Robin	<i>Turdus migratorius</i>		2.032	0.221	3.843	2.032	2.013
Anna's Hummingbird	<i>Calypte anna</i>		0.122	0.044	0.176	0.000	0.268
Ash-throated Flycatcher	<i>Myiarchus cinerascens</i>	NM	0.033	0.000	0.000	0.045	0.091
Band-tailed Pigeon	<i>Patagioenas fasciata</i>		0.465	0.533	0.218	0.355	0.756
Bewick's Wren	<i>Thryomanes bewickii</i>	RE	0.099	0.000	0.351	0.000	0.045
Black-headed Grosbeak	<i>Pheucticus melanocephalus</i>	NM	1.392	0.044	2.836	0.000	2.688
Black-backed Woodpecker	<i>Picoides arcticus</i>		0.022	0.000	0.000	0.089	0.000
Brown-headed Cowbird	<i>Molothrus ater</i>	NM	0.618	0.220	0.698	1.367	0.179
Brewer's Blackbird	<i>Euphagus cyanocephalus</i>		0.411	0.000	0.000	0.000	1.664
Brewer's Sparrow	<i>Spizella breweri</i>	NM	0.089	0.000	0.000	0.353	0.000
Brown Creeper	<i>Certhia americana</i>	RE	1.977	1.902	2.011	1.809	2.195
Blk.-throated Gray Warbler	<i>Setophaga nigrescens</i>		0.044	0.000	0.133	0.000	0.044
Bullock's Oriole	<i>Icterus bullockii</i>	NM	0.110	0.000	0.000	0.000	0.447
Bushtit	<i>Psaltriparus minimus</i>	RE	0.144	0.000	0.390	0.000	0.178
Calliope Hummingbird	<i>Selasphorus calliope</i>	RE	0.529	0.000	0.000	2.123	0.000
California Towhee	<i>Melospiza crissalis</i>		0.011	0.000	0.000	0.000	0.045
Cassin's Finch	<i>Haemorhous cassinii</i>		0.972	0.356	0.131	1.849	1.566
Cassin's Vireo	<i>Vireo cassinii</i>	NM	0.706	0.223	2.579	0.000	0.000
Chestnut-backed Chickadee	<i>Poecile rufescens</i>	RE	0.168	0.000	0.660	0.000	0.000
Chipping Sparrow	<i>Spizella passerine</i>	NM	0.453	0.000	0.831	0.665	0.314
Clark's Nutcracker	<i>Nucifraga columbiana</i>	RE	0.156	0.089	0.000	0.528	0.000
Common Nighthawk	<i>Chordeiles minor</i>	NM	0.045	0.132	0.000	0.000	0.045
Common Raven	<i>Corvus corax</i>	RE	0.321	0.440	0.000	0.000	0.849
Cooper's Hawk	<i>Accipiter cooperii</i>	NM	0.055	0.132	0.043	0.044	0.000
Dark-eyed Junco	<i>Junco hyemalis</i>		5.060	4.022	5.844	4.068	6.309
Downy Woodpecker	<i>Picoides pubescens</i>	RE	0.089	0.132	0.131	0.000	0.089
Dusky Flycatcher	<i>Empidonax oberholseri</i>	NM	1.038	1.594	0.918	0.881	0.764
Evening Grosbeak	<i>Coccothraustes vespertinus</i>		0.364	0.134	0.350	0.616	0.357
Forster's Tern	<i>Sterna forsteri</i>		0.011	0.044	0.000	0.000	0.000
Fox Sparrow	<i>Passerella iliaca</i>		1.555	0.930	1.137	1.637	2.548
Green-tailed Towhee	<i>Ardea herodias</i>	NM	0.143	0.045	0.000	0.308	0.224
Golden-crowned Kinglet	<i>Pipilo chlorurus</i>		2.735	2.610	2.489	2.204	3.673
Great Blue Heron	<i>Regulus satrapa</i>		0.022	0.000	0.088	0.000	0.000
Hairy Woodpecker	<i>Picoides villosus</i>	RE	0.772	0.531	0.955	0.967	0.629
Hammond's Flycatcher	<i>Empidonax hammondi</i>	NM	0.739	1.108	0.612	0.926	0.312
Hermit Thrush	<i>Catharus guttatus</i>		0.596	0.929	0.611	0.576	0.267
Hermit Warbler	<i>Setophaga occidentalis</i>	NM	1.127	1.413	1.832	0.044	1.211
House Wren	<i>Troglodytes aedon</i>	NM	0.242	0.000	0.173	0.000	0.807
Hutton's Vireo	<i>Vireo huttoni</i>	RE	0.056	0.044	0.130	0.000	0.045
Lazuli Bunting	<i>Passerina amoena</i>	NM	0.067	0.000	0.000	0.132	0.136
Lincoln's Sparrow	<i>Melospiza lincolnii</i>		0.044	0.000	0.000	0.044	0.134
MacGillivray's Warbler	<i>Geothlypis tolmiei</i>	NM	1.147	0.265	2.317	0.132	1.880
Mountain Bluebird	<i>Sialia currucoides</i>		0.122	0.133	0.000	0.351	0.000
Mountain Chickadee	<i>Poecile gambeli</i>	RE	3.270	3.798	2.405	4.194	2.683
Mourning Dove	<i>Oreortyx pictus</i>	RE	0.044	0.000	0.087	0.000	0.090
Mountain Quail	<i>Zenaidura macroura</i>		0.066	0.089	0.088	0.043	0.045
Nashville Warbler	<i>Oreothlypis ruficapilla</i>	NM	1.371	0.577	1.746	0.353	2.824
Northern Flicker	<i>Colaptes auratus</i>	RE	0.786	0.531	1.528	0.309	0.762
Northern Goshawk	<i>Accipiter gentilis</i>		0.011	0.000	0.000	0.045	0.000
Olive-sided Flycatcher	<i>Contopus cooperi</i>	NM	0.353	0.264	0.918	0.088	0.134
Orange-crowned Warbler	<i>Oreothlypis celata</i>		0.110	0.000	0.000	0.267	0.178
Pacific-slope Flycatcher	<i>Empidonax difficilis</i>	NM	0.033	0.000	0.000	0.000	0.135
Pileated Woodpecker	<i>Dryocopus pileatus</i>	RE	0.100	0.045	0.263	0.045	0.045
Pine Grosbeak	<i>Pinicola enucleator</i>		0.022	0.000	0.000	0.089	0.000
Pine Siskin	<i>Carduelis pinus</i>		0.752	0.000	0.087	2.913	0.000
Plumbeous Vireo	<i>Vireo plumbeus</i>		0.022	0.000	0.000	0.088	0.000

Purple Finch	<i>Haemorhous purpureus</i>		0.311	0.796	0.000	0.000	0.449
Pygmy Nuthatch	<i>Sitta pygmaea</i>	RE	0.044	0.000	0.000	0.176	0.000
Red-breasted Nuthatch	<i>Sitta canadensis</i>		1.936	2.298	1.967	1.062	2.416
Red-breasted Sapsucker	<i>Sphyrapicus ruber</i>		0.552	0.354	0.962	0.484	0.401
Red Crossbill	<i>Loxia curvirostra</i>		0.736	0.177	0.000	2.746	0.000
Red-tailed Hawk	<i>Buteo jamaicensis</i>		0.066	0.000	0.044	0.000	0.224
Rock Wren	<i>Salpinctes obsoletus</i>		0.023	0.000	0.000	0.089	0.000
Ruby-crowned Kinglet	<i>Regulus calendula</i>		0.067	0.000	0.000	0.267	0.000
Rufous Hummingbird	<i>Selasphorus rufus</i>		0.065	0.000	0.000	0.268	0.000
Sharp-shinned Hawk	<i>Accipiter striatus</i>		0.022	0.000	0.000	0.088	0.000
Song Sparrow	<i>Melospiza melodia</i>	RE	0.067	0.000	0.000	0.266	0.000
Sooty Grouse	<i>Dendragapus fuliginosus</i>		0.044	0.000	0.088	0.000	0.088
Spotted Towhee	<i>Pipilo maculatus</i>		0.806	0.133	3.018	0.000	0.044
Steller's Jay	<i>Cyanocitta stelleri</i>	RE	1.933	1.327	2.620	0.616	3.187
Swainson's Thrush	<i>Catharus ustulatus</i>	NM	0.044	0.000	0.131	0.044	0.000
Townsend's Solitaire	<i>Myadestes townsendi</i>		0.288	0.443	0.131	0.485	0.090
Townsend's Warbler	<i>Setophaga townsendi</i>		0.022	0.000	0.044	0.000	0.045
Tree Swallow	<i>Tachycineta bicolor</i>		0.011	0.000	0.000	0.044	0.000
Warbling Vireo	<i>Vireo gilvus</i>	NM	0.771	0.618	1.709	0.399	0.357
Western Bluebird	<i>Sialia mexicana</i>		0.022	0.000	0.000	0.000	0.091
Western Tanager	<i>Piranga ludoviciana</i>	NM	2.296	1.946	2.531	1.457	3.272
Western Wood-Pewee	<i>Contopus sordidulus</i>	NM	0.199	0.000	0.174	0.355	0.270
White-breasted Nuthatch	<i>Sitta carolinensis</i>	RE	0.176	0.045	0.000	0.526	0.134
White-crowned Sparrow	<i>Zonotrichia leucophrys</i>		0.022	0.000	0.044	0.044	0.000
White-headed Woodpecker	<i>Picoides albolarvatus</i>	RE	0.961	0.573	0.699	0.352	2.241
Willow Flycatcher	<i>Empidonax traillii</i>	NM	0.066	0.000	0.219	0.000	0.045
Williamson's Sapsucker	<i>Sphyrapicus thyroideus</i>	RE	0.099	0.000	0.000	0.400	0.000
Winter Wren	<i>Troglodytes hiemalis</i>	RE	0.286	0.000	0.872	0.000	0.270
Wilson's Warbler	<i>Cardellina pusilla</i>	NM	0.343	0.664	0.044	0.533	0.135
Wrentit	<i>Chamaea fasciata</i>	RE	0.144	0.000	0.566	0.000	0.000
Yellow Warbler	<i>Setophaga petechia</i>	NM	0.366	0.353	0.000	1.016	0.089
Yellow-rumped Warbler	<i>Setophaga coronata</i>		2.143	2.653	2.755	2.301	0.851

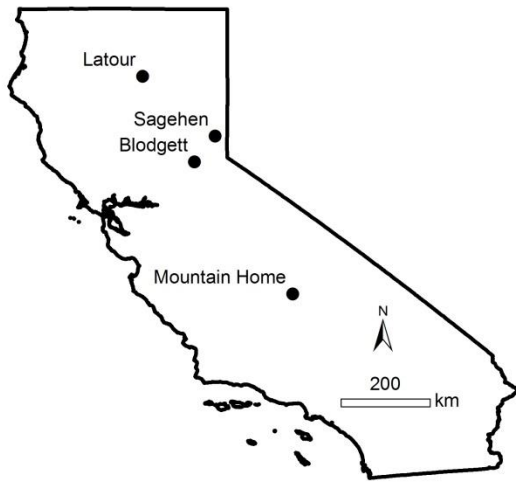
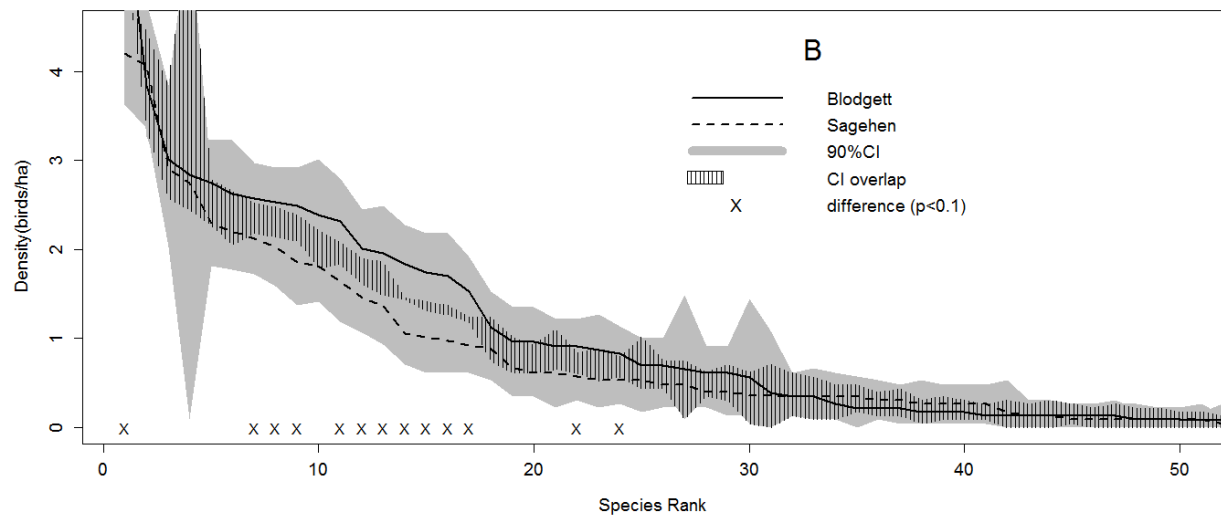
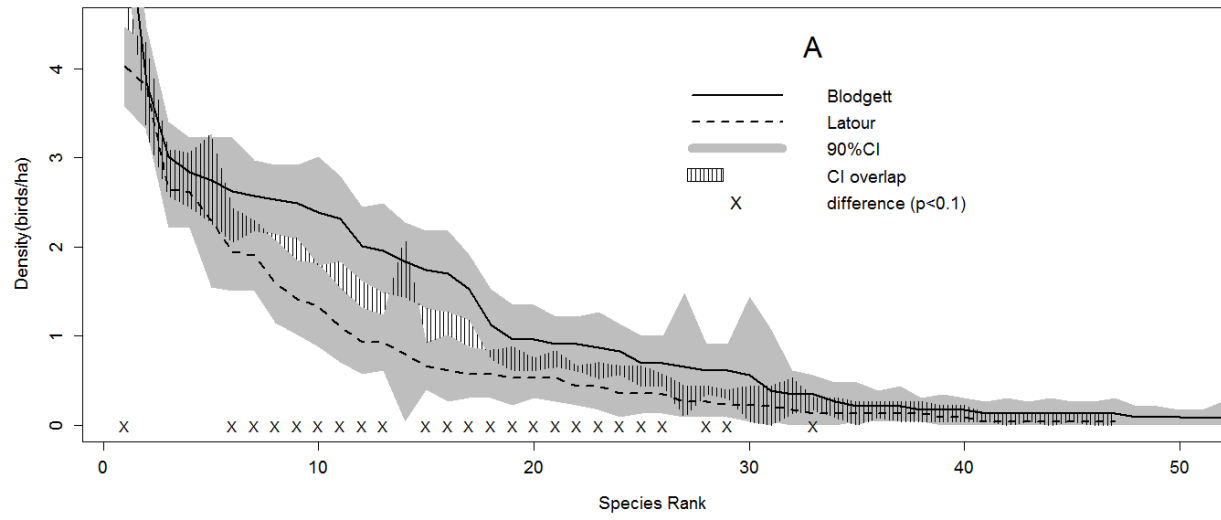
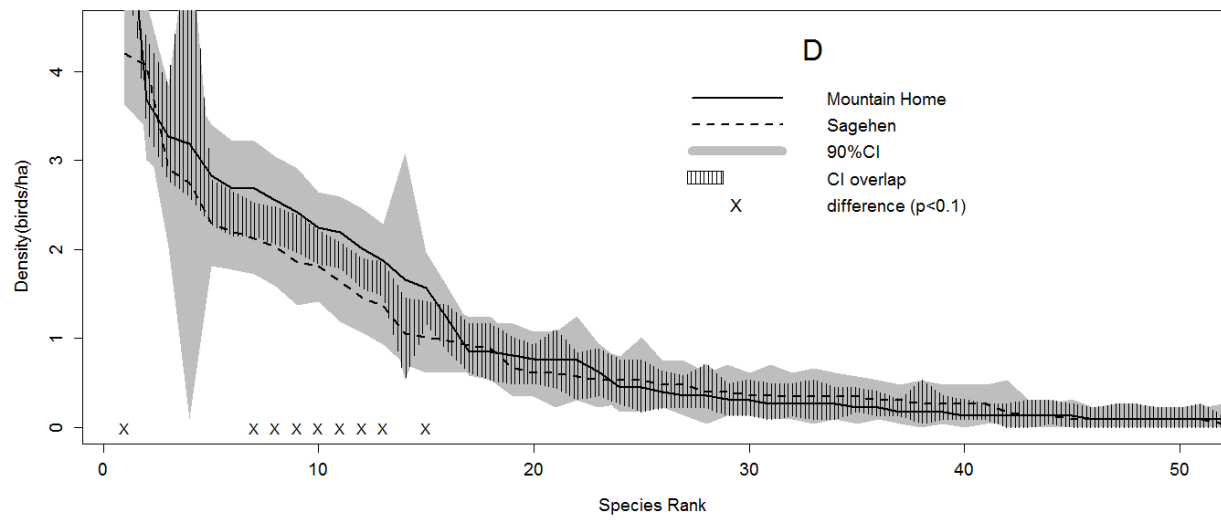
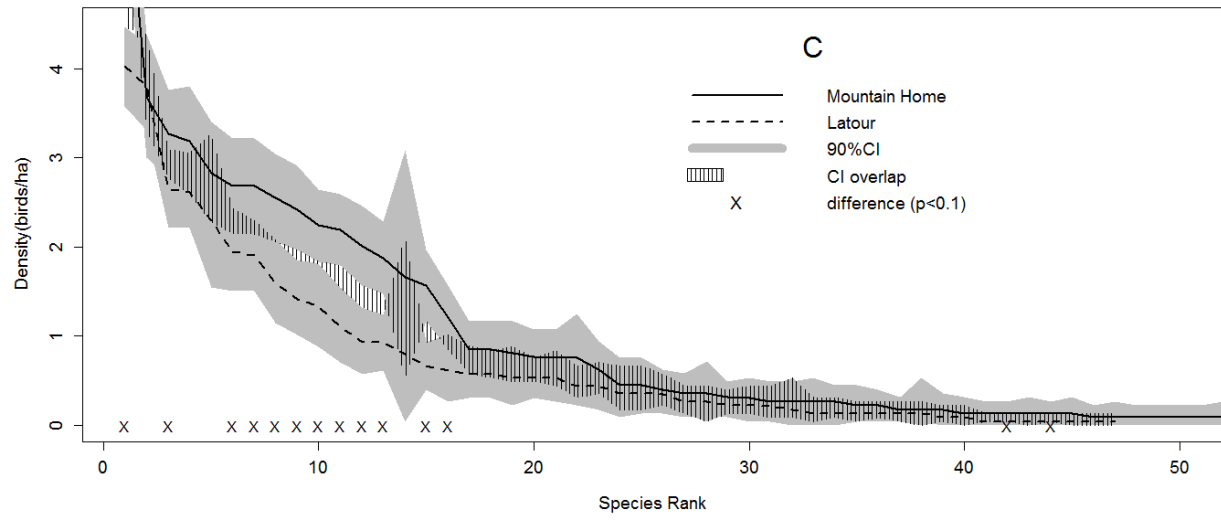


Figure 1. Research forests where birds surveys occurred over the course of 2 breeding seasons at approximately 80 sites on each forest, 1979 through 1996.





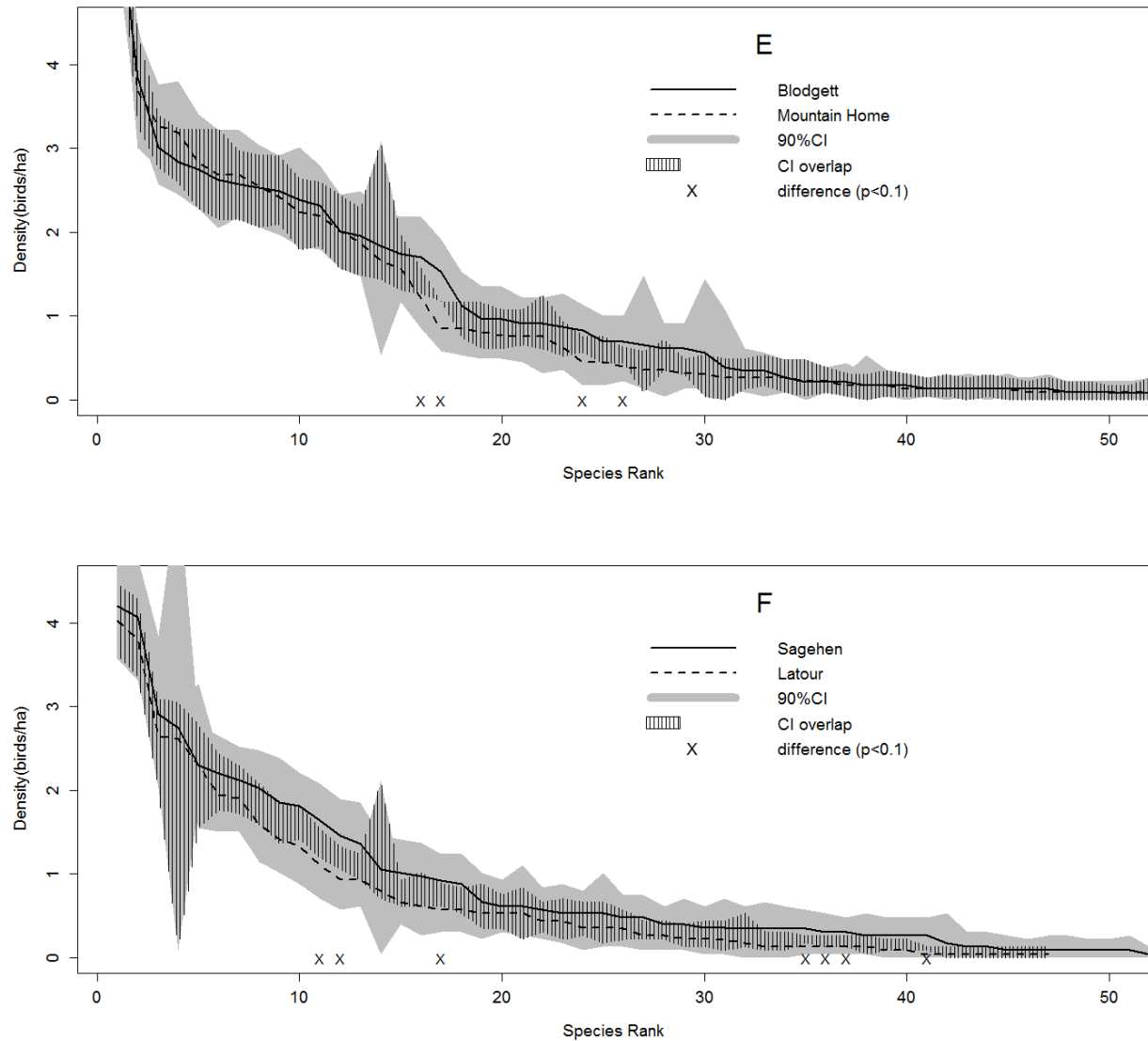


Figure 2. Pairwise of comparisons of avian rank abundance distributions using bootstrapped confidence intervals to represent uncertainty bands. Segments where these distributions lie outside of regions of confidence interval overlap represent ranks for which there was significant ($P < 0.1$) differentiation in abundance.

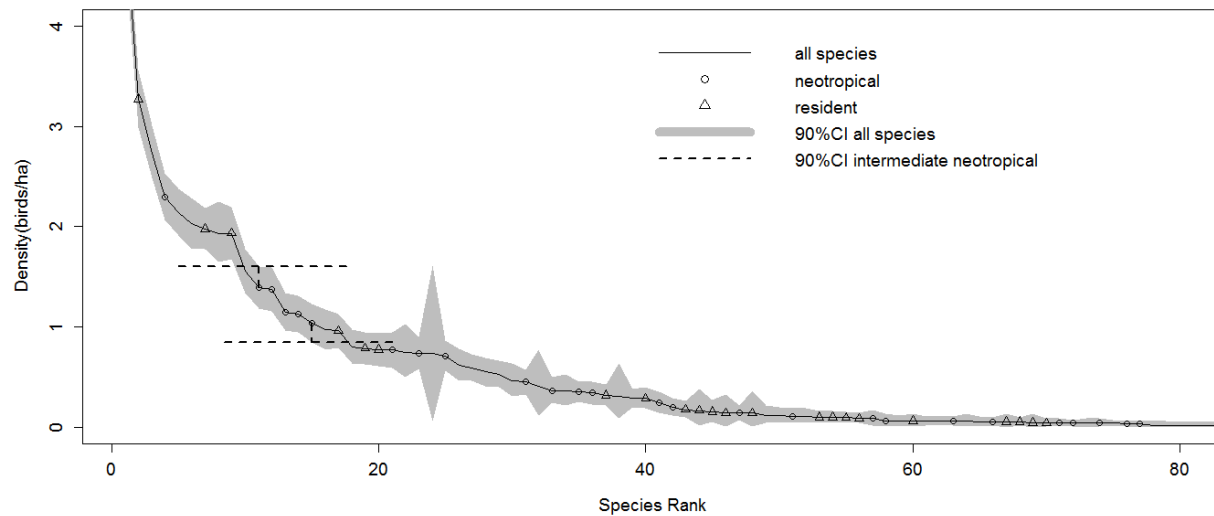


Figure 3. Rank abundance distribution for the avian metacommunity represented by all 4 research forests. The 90% confidence bars show the abundance range for a cluster of intermediately-common neotropical migrants. These 5 species (black-headed grosbeak, dusky flycatcher, hermit warbler, MacGillivray’s warbler, Nashville warbler) were significantly more abundant ($P < 0.1$) than all but one other resident bird (white-headed woodpecker) in the intermediate ranks, but less abundant than several very common resident species (brown creeper, mountain chickadee, Steller’s Jay).

Chapter 4

Monitoring Pacific fisher (*Pekania pennant pacifica*) and other mammals at the regional scale using camera traps and occupancy modeling

ABSTRACT

The Pacific fisher (*Pekania pennant pacifica*) is a forest carnivore of conservation concern in California due to a variety of anthropogenic stressors. Here I report on the initiation of a monitoring effort for this species at the regional scale using baited camera stations. Over 2 years beginning in 2011, 172 stations were surveyed at random forest locations in northwestern California. I used hierarchical modeling to estimate occupancy at 2 survey scales (i.e., for stations and pairs of stations 1.6 km apart). Latitude was negatively associated with detection probability, whereas occupancy was not, both possibly due to larger home ranges to the north. Throughout the 2.8-million-ha study area, fisher occupancy was estimated at 0.465 [90% CI: 0.372-0.599] for stations, and 0.651 [90% CI: 0.535-0.791] for station pairs. Simulations calibrated from these estimates suggest that continuation of this monitoring approach could provide 80% power for measuring occupancy declines as small as 2% per year over 20 years. Furthermore, the ability to estimate occupancy at more than one survey scale is likely to improve inferences linking occupancy to abundance as required for better informing conservation planners about fisher population status. I discuss how camera station surveys can expand single-species monitoring to multiple species.

INTRODUCTION

The Pacific fisher (*Pekania pennant pacifica*) is a mesocarnivore of conservation concern, because of a combination of stressors including historical trapping (Dixon 1925, Grinnell et al 1937, Lewis and Zielinski 1996), timber harvesting (Lefroth et al. 2010), disease (Gabriel et al. 2012a), poisoning (Gabriel et al. 2012b) and climate change (Lawler et al. 2012). For these reasons and because of potential listing of fisher under the federal Endangered Species Act (USFWS 2004) and the California Endangered Species Act (Fish and Game Commission 2013), there is an immediate need for sustained monitoring of this subspecies at the regional scale and across its range. Although there have been some studies estimating fisher abundance at the local or landscape scale (Matthews et al. 2011, Thompson 2008, Jordan 2007), there are few examples of long-term monitoring at larger spatial scales (Zielinski et al. 2005, Zielinski et al. 2013).

In this study I report on the initiation of a regional-scale, multi-species, long-term monitoring program that uses baited camera traps (Kay and Slauson 2008) in northern California to monitor metapopulations of fisher and other mammalian species. I demonstrated how hierarchical occupancy models (Royle and Dorazio 2008, Kéry and Schaub 2012) can be applied to a design where more than one camera station is included at a survey location, thereby allowing estimation of occupancy at more than one survey scale. I investigated sources of detection probability heterogeneity at the regional scale, and tested the statistical power of camera traps to

monitor long-term population trends of fisher. Finally, I considered the applicability of this method to multi-species monitoring.

METHODS

Study Area

Since 2009 the California Department of Fish and Wildlife has used baited camera traps to survey fisher and other mammals across a 4.4-million-ha northern California assessment area. The surveys were part of the State Wildlife Grant-funded, Ecoregion Biodiversity Monitoring project for informing conservation planning. The survey area encompassed conifer- and hardwood-dominated habitats in the Klamath Mountains, East Franciscan, Southern Cascades and Northern Sierra Nevada USDA-defined ecoregions (Miles and Goudey 1997) truncated to California boundaries.

This study limited reporting to data collected from the Klamath Mountains and East Franciscan ecoregions, a combined area of 2.8-million-ha (Fig. 1). Habitats in these ecoregions were primarily montane conifer forest dominated by Douglas fir (*Pseudotsuga menziesii*), Ponderosa pine (*Pinus ponderosa*), and white fir (*Abies concolor*) intergrading with oak (*Quercus spp.*) dominated forests at lower elevations. Pockets of chaparral and annual grasslands punctuated this mosaic across generally steep slopes (Schoenherr 1992).

Camera Trap Surveys

Sampling Design. Survey hexagons were randomly sampled each year without replacement from the Forest and Inventory Analysis sampling frame (Bechtold and Patterson 2005). The distance between adjacent hexagon centers from this grid was 5.35 km. An array of 2 camera stations 1.6 km apart was placed within each selected hexagon. Permission for surveys was granted for surveying most public agency and private industrial forestland ownerships within the study area. The primary camera station was usually located at a hexagon centroid, but private property, steep terrain, and other logistical issues often required relocating survey sites to more accessible, offset locations still within selected hexagons. When this situation occurred, a supplemental random distance and direction procedure was followed. In cases where relocation was not feasible, the selected hexagon was not sampled. A final constraint was that crews were instructed to limit survey sites to areas surrounded by at least 20 ha of forest in excess of 10% canopy cover as deemed necessary for finding trees on which to place cameras. There was also a randomization procedure for locating the secondary camera stations. For all the reasons listed above, the sampling design is best described as quasi-random.

Surveys in the Klamath Mountains occurred in 2011 and 2012, but only during 2012 in the East Franciscan ecoregion. A total of 86 hexagons were surveyed, 65 in the Klamath Mountains and 21 in the East Franciscan. Geographical information systems (GIS) and land-use land-cover data derived from Satellite imagery (U.S. Forest Service 2012b) were used to assess the amount of forest cover surrounding each survey location.

Survey Protocol. A “stealth mode” Reconyx PC 90 or PC 900 infra-red sensor, motion activated, digital camera (www.reconyx.com) was affixed to a tree at each station. It was typically placed approximately 1 m above the ground aimed at a shallow angle (<20 degrees) towards a bait tree 3 m to 5 m distant. The camera settings were set to high trigger sensitivity, 3 pictures per trigger, 1-second trigger interval and no delay quiet period. The resolution of each image was 3.2 megapixels. During the day these images were color, at night they were black and white illuminated by an infra-red flash.

Bait items included chicken parts and “fishy” cat food in a sock nailed approximately 1 m up the bait tree bole, half an apple impaled on a nail below the sock, 2 cups of oatmeal-peanut butter mixture on a plate surrounded by a ring of sliced apple at the base of the tree, and a salt lick placed next to the grain. To assist in the identification of individual animals and by gender, a measuring board with marks every 10 cm was attached to the tree vertically below the sock bait. Finally, “Gusto” scent lure (www.minntrapprod.com) was applied to the sock and low hanging branches of at least 2 nearby trees behind the bait tree.

The majority (>95%) of camera stations was never re-baited, which has been done on a weekly basis by other researchers (Zielinski and Kucera 1995). The survey season began in the middle of August, and continued through the middle of November or whenever snow and winter weather prevented safe access to survey locations by field crews. The durations of surveys at stations varied between 2 and 4 weeks, and both stations within a hexagon were always surveyed concurrently.

Data Interpretation. All photos were downloaded and stored electronically in Mapview software (www.reconyx.com). Metadata imbedded in the header code of every photograph (e.g., image number, date, time, temperature) were automatically exported to an electronic database. A technician then viewed and interpreted all images. She entered information (species identification, bait condition, camera operation status) for every photograph into the database. For fisher, she also entered best guesses about gender and the number of unique animals. Additionally, field crews independently reviewed all the images to identify at which stations fishers were detected; this provided a quality check to ensure that no fishers were overlooked in the interpretation process.

Data Processing. Data were first truncated to ≤ 30 days, and a detection history was created for each station that indicated whether a fisher was detected in each survey day (i.e., 00000110101000). If the survey duration was < 30 days, or if the camera was not functional some of the time, these days were treated as missing data in a full 30-day detection history. Each survey day was the 24-hr period commencing upon camera set-up.

Covariates pertaining to station locations and survey days for potentially explaining variation in fisher occupancy and detection probability were created as follows. To address changes in animal behavior upon discovery of a station, I created a covariate array for testing a 1st order Markov dependency (Hines et al. 2010, Slauson et al. 2012) between detection history days at each station; the covariate value at day_k was the detection history at day_{k-1} , or it was zero if this data was not available. To address seasonal changes in detection and occupancy there was also a covariate vector for the start date of each station survey. To address potential regional-

level heterogeneity in occupancy and detectability, I created a covariate vector of station latitudes. Information on weather, bait condition, fisher gender, topography and vegetation cover was not used for creating additional model covariates due to the small sample size ($n=172$ stations).

Occupancy Modeling

Model Structure. Occupancy represents the true proportion of a study area in which a particular species occurs, or probability that a given location is occupied by the species. Occupancy modeling allows simultaneous estimation of detection and unbiased occupancy probabilities, based on the frequency of detections from temporally-replicated surveys occurring over a time period for which occupancy is assumed to remain constant (MacKenzie et al. 2006).

I used a Bayesian hierarchical, single-species, single-season occupancy model structure (Royle and Dorazio 2008, Kéry and Schaub 2012) to estimate fisher occupancy and detection probabilities at the regional scale represented by the forested locations throughout Klamath Mountains and East Franciscan ecoregions. The fully saturated models for occupancy (Ψ) and detection probability (p) were:

$$\begin{aligned} \text{logit}(\Psi_j) &= \beta_{\Psi 0} + \beta_{RE} + \beta_{\Psi 1} X_{\text{latitude } j} + \beta_{\Psi 2} X_{\text{start } j} & \text{eq. 1} \\ \text{logit}(p_{j, k}) &= \beta_{p 0} + \beta_{MA} y_{j, k-1} + \beta_{p 1} X_{\text{latitude } j} + \beta_{p 2} X_{\text{start } j} & \text{eq. 2} \end{aligned}$$

for station j on survey day k where y was the detection history and x were covariates. A random normal effect (β_{RE}) with an expectation = 0 was included in the occupancy model to account for non-independence of stations nested within sampling hexagons. The detection model included a Markov dependency (β_{MA}) on the previous day's detection history. The true occurrence state (z) at each station was assumed to follow a Bernoulli distribution, $z_j \sim \text{Bern}(\Psi_j)$, whereas the observation state (y) was modeled as a zero-inflated Bernoulli distribution, $y_{j, k} \sim \text{Bern}(p_{j, k} * z_j)$.

All models were solved through a Markov Chain Monte Carlo algorithm (Link et al. 2002) implemented in WinBUGS (Version 1.4, www.mrc-bsu.cam.ac.uk/bugs) accessed via R statistical software (Version 2.12, www.r-project.org) with the R2WinBUGS package (Sturtz et al. 2005). Uninformative priors were assumed for all parameters. Three independent chains each of 40,000 samples were run with a burn-in period of 10,000 and a thinning rate of 3. Effective mixing of these chains was assessed visually and by means of the Gelman-Rubin convergence statistic (< 1.1 , Gelman et al. 2004). Average occupancy across the study region was estimated at the station and hexagon scales by averaging z among stations and hexagons, and including these additional parameters as derived quantities in the algorithm. Applying a “Bayesian P -value” approach, significance tests for model covariates were made using 90 percent credible intervals of posterior distributions.

Model Selection. Rather than just fitting the fully saturated model (eq. 1 & 2), I first fit simpler detection models always including the intercept (β_{p0}), but only including one of the remaining detection covariate effects (β_{MA} , β_{p1} , β_{p2}) at a time. I considered an effect to be “significant” if the 90% credible interval did not include zero. If an effect was “significant,” I

advanced to combining it with other such effects in more complicated models. Once a final detection model was selected, I repeated the process for testing potential effects (β_{ψ_1} , β_{ψ_2}) on occupancy given the final detection model.

Power Analysis

Statistical power to detect a trend (Purcell et al. 2005, Nielsen et al. 2009, Meyer et al. 2010) in fisher occupancy was assessed via Monte Carlo simulation. I simulated time series over 10 and 20 years based on the station- and hexagon-scale occupancy estimates and their uncertainties from this study and different scenarios for average annual declines in occupancy. The true starting occupancy (ψ_1) for each scale was the point estimate from this study. The true occupancy state for each subsequent year (t) in the time series was modeled as $\psi_t = [1 - d(t - 1)]\psi_1$, where d was the true average annual decline occupancy with respect to ψ_1 . The monitored occupancy in each year was modeled as a normal random variable with expectation ψ_t and standard deviation σ_t , where σ_t was the standard error from the fisher occupancy estimate from this study scaled to the annual sample size of stations (n) by dividing by $\sqrt{n/172}$.

I generated 50,000 simulations of each average annual decline scenario ($d=0.01$ to 0.03) and annual sample size of stations ($n=100$ to 200), and tested each simulation for a simple linear trend via ordinary least squares regression. I calculated power as the proportion of simulations where one could reject ($P < 0.1$) the null hypothesis of a zero or positive slope for the trend line. I evaluated satisfactory monitoring power as ≥ 0.8 (Cohen 1969).

Other Mammal Species

Occupancy models were only run for fisher. However, I calculated naïve occupancy estimates for all other mammal species detected $\geq 5\%$ of stations. For each species, I calculated the latency to first detection (Slauson et al. 2009) as the median number of survey days until first detection among stations at which the species was detected within 30 days. Comparison of this measure for the other species to its value for fisher provided a rudimentary means for assessing how effective camera traps would be for monitoring species other than fisher.

RESULTS

Survey Design and Methods

From GIS analysis 86% of stations were $> 40\%$ forest cover within a 250 m radial area surrounding each station, and 91% of stations surpassed this cover threshold for a 500 m radius. Less than 5% of stations from this study were re-baited between set-up and take-down of cameras. Black bears (*Ursus americanus*) rendered cameras inoperable for a portion of survey duration at 18% of stations. The median number of operable survey days per station was 15.

Occupancy Estimation

Of the covariates for explaining detection probability, 1st order Markov dependency and latitude were “significant” whereas the start date of surveys was not. The first 2 variables remained important when included in the final model. The expected probability of detection per day for before a station was discovered by a fisher declined from 0.127 at 39 degrees North to 0.035 at 42 degrees North (Fig. 2a). Cumulative, station-level detectability increased from an average of 0.624 after 14 days to 0.870 at 30 days (Fig. 2b to 2d). Latitude was not predictive of occupancy when added to this model, whereas it was predictive when the same covariate was not included in the detection model. The start date of surveys was marginally important (but not “significant”) for occupancy. Both parameters were positively correlated, but relaxation to an 84% credible interval on survey date for explaining detection was necessary to reject a null hypothesis that the effect was zero. Following the model selection process summarized earlier, I chose a final model including an intercept, Markov factor and latitude for explaining detections, and an intercept and the random effect for explaining occupancy (Table 1). Based on this model the occupancy estimate at the station scale was 0.465 [90%CI: 0.372-0.599], whereas it was 0.651 [90%CI: 0.535-0.791] at the hexagon scale. In contrast, the unmodeled, naïve occupancy estimates for these scales were 0.261 [90%CI: 0.207-0.317] and 0.407 [90%CI: 0.320-0.494], respectively.

Power Analysis

The simulations demonstrated 82% power for monitoring average annual declines as small as 2.0% per year over 20 years for fisher occupancy at the station scale. They showed 81% power for identifying a trend as small as 1.6% at the hexagon scale. For surpassing the 80% power standard, 5.9% and 4.8% were the smallest average annual declines that could be monitored over 10 years, at the station and hexagon scales respectively.

Other Mammal Species

Besides fisher a total of 22 mammalian and 14 avian species were photographed. Of these species, 14 mammals were detected $\geq 5\%$ of stations (Fig. 3). Black bear, mule deer (*Odocoileus hemionus*), and gray fox (*Urocyon cinereoargenteus*) were the most frequently detected large mammals, whereas Douglas squirrel (*Tamiasciurus douglasii*) and western gray squirrel (*Sciurus griseus*) were the most frequently detected small mammals. The median latency to first detection was ≤ 6 days for 11 of these 14 species, and this threshold was only one day more than for fisher (e.g., 5 days).

DISCUSSION

Occupancy model results suggest detectability of fishers at baited camera stations decreased with latitude in northwestern California. One explanation of this finding might be that home ranges for both genders are generally larger at higher latitudes across western North America (Lefroth et al. 2010, p. 68). This could lead to a longer period until first detection, because, as animals move throughout larger areas, they become less likely to encounter a camera station by chance. Hence, this study illustrated the importance of hierarchical modeling for

correcting methodological biases when estimating occupancy of wildlife species at large spatial scales. If latitude had not been included in the detection model, one could have mistakenly concluded that fisher were more widespread to the south of the study area (i.e., Mendocino National Forest) than in the north (i.e., along the Klamath River and near the Oregon border). In addition, naïve estimates of occupancy were substantially lower than modeled ones that corrected for non-detection bias.

Unexpectedly, survey date did not affect detectability for these data. There was a “non-significant” association, however, between survey date and increased occupancy. It is unclear whether this effect would have been more conclusive if sample size had been greater. Temporal adjustments in territoriality, especially among dispersing juveniles and females (Matthews et al. 2013, Shelley et al 2013), were expected to affect variability in occupancy during the earlier months of surveys (e.g., August and September). If there had been stronger evidence of this issue, I would have modified model structure to estimate it as increasing asymptotically over the course of the survey season.

The surveys reported on here provide evidence of relatively high, station-level cumulative detection probabilities, mostly without re-baiting visits. This point is germane in that visits to remote survey locations (whether for set-up, re-baiting, or take-down) were this project’s greatest expense. For this reason I began phasing out revisits in 2011 to concentrate on surveying more hexagons during each survey season. On the other hand, station-level detection probabilities were less than the 0.8 standard proposed by other practitioners (Slauson et al. 2009). According to other studies 30-day surveys with weekly re-baiting (Zielinski and Kucera 1995) has been required to meet this detection probability standard (Gompper et al. 2006, Slauson et al. 2009).

This study demonstrated statistical power to monitor 2% average annual declines over 20 years for surveys characterized by a median duration of 15 days and which were rarely re-baited after the initial visit. I also found that monitoring moderate declines (<5% per year) over shorter (<10 years) time frames will be challenging. This problem could presumably be addressed by some combination of dramatically increasing sample size, regularly re-baiting, and increasing survey duration. However, ecological factors are likely to add to the difficulty in identifying declines related to persistent stressors affecting limiting factors or carrying capacity. For timeframes of less than 10 years, information about steady-state declines could be easily confounded by transient or cyclical patterns in population numbers. Numerous studies have identified population cycles related to weather patterns (Lima et al. 1995, Stenseth et al. 2002), irruptive events (Koenig 2001, Linden et al. 2011), disease epidemics (Anderson and May 1991) and random variation (Cole 1951, Saether et al 2000). Some researchers (Kaitala et al. 1996, Elias et al 2006) have used autoregressive models to support the idea that random or episodic effects over a year or two can lead to population cycles that are longer (4 to 7 years) than the events that triggered them.

Occupancy has been proposed as a surrogate for monitoring abundance (MacKenzie and Nichols 2004), but the magnitudes of trends in these 2 state variables may not be the same for fisher (Tucker 2013) and other animals with large territories. The occupancy-abundance relationship is governed by how clustered a population or metapopulation is distributed in space

(He and Gaston 2000). Therefore, one cause of a disparity between occupancy and abundance trends could be an expansion in average home range size over time. Considering the theoretical link between abundance and detection probability (Royle and Nichols 2003, Royle et al 2008), the home range expansion hypothesis described above is consistent with findings from this study that fisher detectability declined with latitude. As fisher territories that partially overlap get larger, fewer individuals, on average, might contribute to the occupied status of a location. Indeed, although I found fisher occupancy invariant across northwestern California, it is possible that abundance is lower to the north. For these reasons, occupancy modeling at multiple spatial scales is especially relevant (Pavlacky et al. 2012). By modeling at 2 spatial scales (i.e., station and hexagon), this study provided an example for improving inferences about abundance trends using incidence data. Specifically, this design should allow one to make better inferences about whether a decline in occupancy is related to a decrease in abundance, by assessing whether occupancy declines occur at both scales. Alternatively, occupancy could be monitored separately by sex, because males generally have larger home ranges (Lofroth et al. 2010). Although I did not attempt to do so in this study, photo information interpreted on the minimum number of identifiably distinct fishers seen at each station could be used to help estimate abundance via a repeated counts n-mixture model (Royle 2004, Kéry et al. 2005).

The findings from this study were qualified by some limitations. The sample size was relatively small, meaning that the lack of association of some of the predictive variables I tested could be related to analytical power. For the same reason, I did not include other covariates such as bait condition which may have improved model performance of a larger data set. Along these lines, the data set spanned only 2 years and locations were not visited both years, thereby preventing application of a multi-season occupancy model. Zielinski et al. (2013) have taken the multi-season modeling approach to show that fisher sites monitored over 8 years rarely changed their occupancy states. Their finding suggests that, given the right balance between new location visits and yearly visit to a portion of sites, a multi-year occupancy model framework could further increase statistical power for detecting occupancy declines for fisher at large spatial scales.

An additional limitation was that the random effect accounting for non-independence among baited camera stations was not easily interpretable for providing a biological explanation. It would have been preferable to include a Markov dependency term in the occupancy model such that the occupancy state, z_1 , at one station was predicted by both the model intercept, β_{ψ_0} , and an effect, $\beta_{\psi_{ma}}$, representing whether the paired station was also occupied ($z_2=1$). Unfortunately, although this modeling approach worked well for simulated data, I was unable to achieve good model chain mixing when run on the real fisher data.

Bears were deleterious to sampling effort, especially in the project's early years; they frequently misaligned or damaged cameras. In a few cases, they tore cameras into pieces and chewed up all the batteries. Besides following clean handling procedures for the camera side of a sampling station, the problem was further mitigated as follows. Field crews switched from a camera mounting bracket to the use of a cable lock for tightly securing the camera to the tree bole, and used splints for aiming. This procedure appeared to reduce the bears' curiosity which might have been heightened by the bracket method which caused the camera to stick out awkwardly from the tree.

An often overlooked benefit of baited camera surveys is that they are well suited for monitoring multiple species for little additional effort. The data they provide may be viewed equally as a fisher monitoring project or a big game monitoring project or a biodiversity monitoring project. Based on a qualitative review of the survey data, the addition of grain and fruit dramatically increased the detection frequency for squirrels (*Sciuridae*) and woodrats (*Neotoma spp.*). A follow-up occupancy analysis, taking full advantage of the bait condition information collected, is warranted for formally addressing these questions. Nevertheless, the low median latency to first detection (≤ 6 days) for most (11) of the 14 mammalian species with naïve occupancy estimates >0.05 lends support to the idea that camera traps could serve as a valuable and effective survey method for implementing long-term, multi-species monitoring at large-spatial scales (Manley et al. 2005, Zielinski et al. 2005).

MANAGEMENT IMPLICATIONS

Although not a perfect surrogate for monitoring abundance, camera trap surveys provide a robust method for estimating fisher occupancy, interpreted broadly as the proportion of a large region inhabited by this species. Combined with the application of hierarchical models, this method can provide good statistical power for monitoring occupancy declines as small as 2% per year over 20 years. This approach allows occupancy estimates at multiple spatial scales for better informing inference about how an occupancy decline might be related to a long-term population trend affected by stressors including land use or climate change. Given enough resources, the regional monitoring scheme reported on here could be expanded to add enough annual revisits to increase monitoring power for fisher even further, through the application of a multi-season occupancy model approach. More importantly, cameras trap surveys at large spatial scales provide an easy opportunity for broadening single-species monitoring into multi-species monitoring.

Table 1. Bayesian hierarchical model results for fisher occupancy across northwestern California. The model was fit to data from baited camera surveys up to 30 days in duration from 2011 or 2012. Occupancy was estimated for 2 spatial scales: *stations* 1.6 km apart within randomly selected survey *hexagons*.

Parameter	Mean	SD	Median	5%	95 %	R-Hat
Occupancy						
Station	0.472	0.070	0.465	0.372	0.599	1.00
Hexagon	0.652	0.078	0.651	0.535	0.791	1.00
Occupancy Model Parameters						
Intercept	-0.148	0.433	-0.169	-0.815	0.607	1.00
SD for random effect	1.255	0.516	1.307	0.277	2.019	1.05
Detection Probability Model						
Intercept	-1.921	0.292	-1.916	-2.409	-1.446	1.00
Latitude (per 0.1 degree >39)	-4.698	1.884	-4.714	-7.776	-1.575	1.00
1 st Order Markov Dependency	1.243	0.326	1.248	0.704	1.771	1.00
Model Deviance	625.8	19.6	625.1	594.8	659.4	1.00

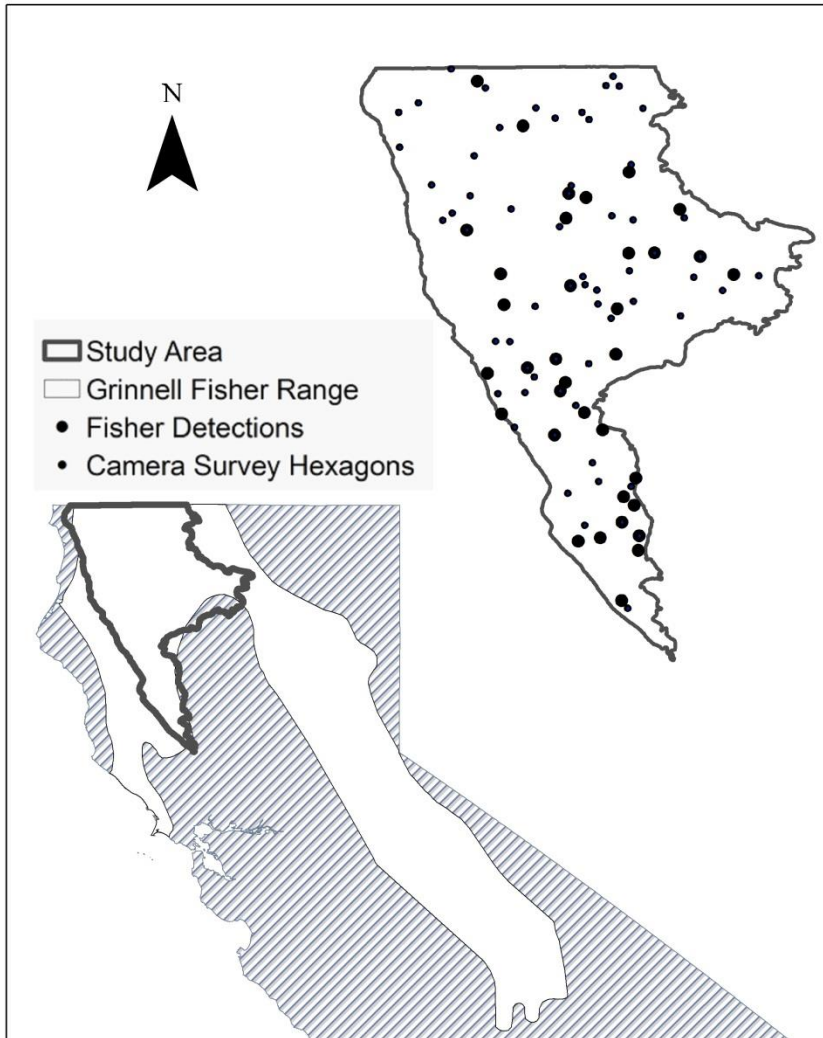


Figure 1. Northern California study area where baited camera surveys occurred in 2011 and 2012. The historic fisher range identified by Joseph Grinnell is shown for comparison.

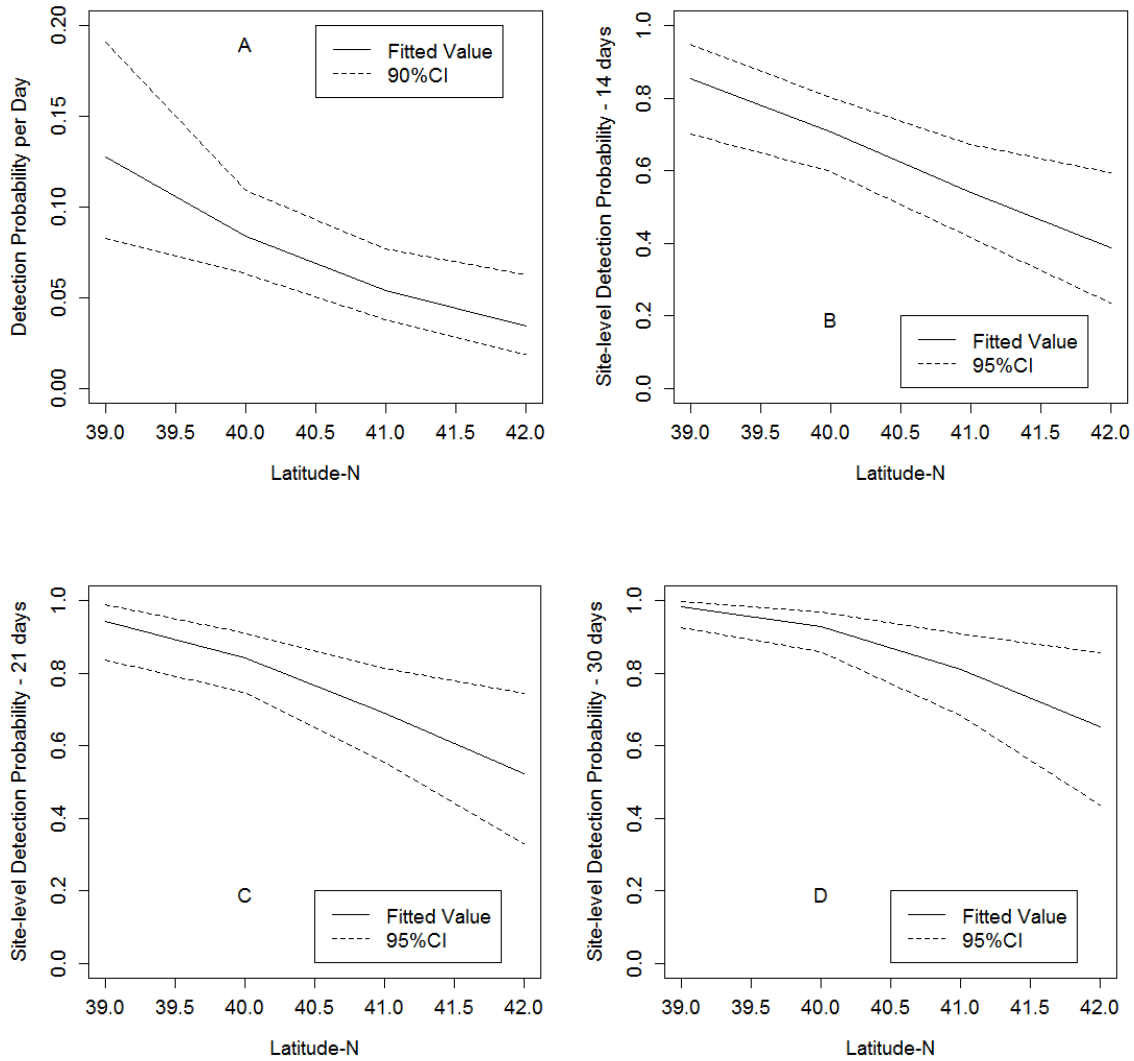


Figure 2. Estimates of detection probability and their dependency on latitude are shown for a single day (A) and for total survey duration (B through D).

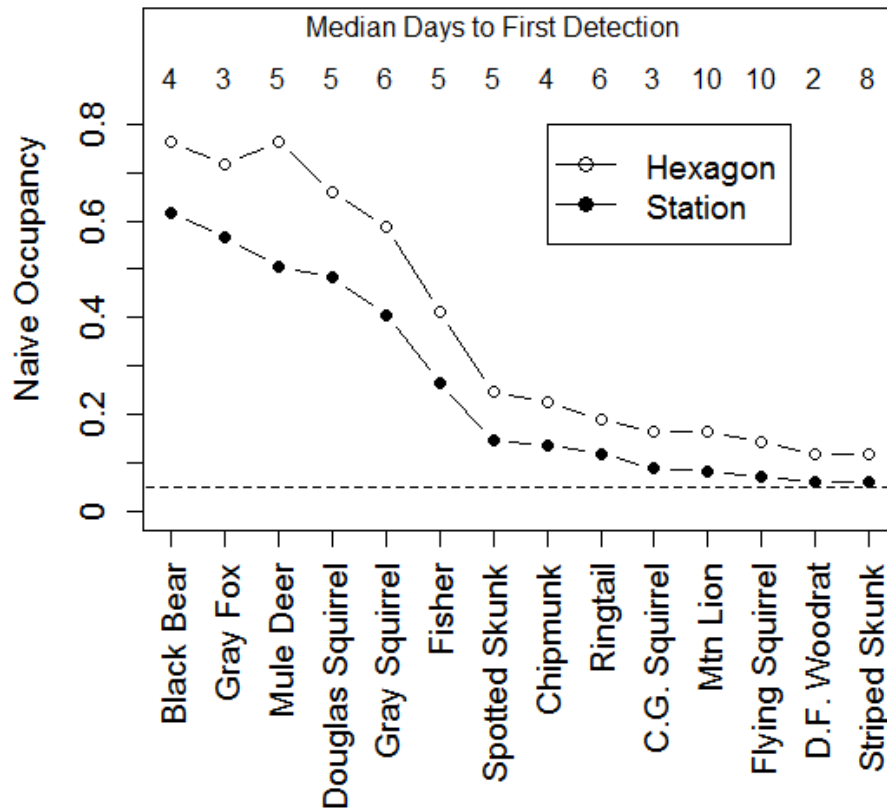


Figure 3. Naïve, unmodeled occupancy estimates for mammal species detected at baited camera stations in northwestern California forests in 2011 or 2012. Occupancy is given for stations and for sampling hexagons each consisting of a pair of stations 1.6 km apart. Additionally, the median number of days until first detection (if a detection occurred ≤ 30 days) is shown at the top for each species. The species/taxa are black bear (*Ursus americanus*), gray fox (*Urocyon cinereoargenteus*), mule deer (*Odocoileus hemionus*), Douglas squirrel (*Tamiasciurus douglasii*), western gray squirrel (*Sciurus griseus*), Pacific fisher (*Pekania pennant pacifica*), western spotted skunk (*Spilogale gracilis*), chipmunk (*Neotamias spp.*), ringtail (*Bassariscus astutus*), California ground squirrel (*Otospermophilus beecheyi*), mountain lion (*Puma concolor*), northern flying squirrel (*Glaucomys sabrinus*), dusky-footed woodrat (*Neotoma fuscipes*) and striped skunk (*Mephitis mephitis*).

Chapter 5

General conclusions

Automated survey devices such as sound recorders and cameras offer an excellent opportunity for efficiently, accurately and simultaneously monitoring population trends for multiple wildlife species. These methods are particularly amenable to occupancy modeling because repeat survey data for addressing detection probability biases can be collected from remote locations without a skilled surveyor being physically present for each survey. These incidence-based methods are appropriate for monitoring large areas for several reasons. First, gathering count data across such a large area may be prohibitively expensive. Second, for birds, the effective survey area of automated recorders may be small enough that occupancy becomes a reliable proxy for abundance. Third, for mammals with larger territories, a nested design of camera stations allows occupancy estimation at multiple survey scales for drawing more informative inferences about the connection between occupancy and abundance.

Multi-species occupancy models offer the opportunity of expanding monitoring of common species to an entire metacommunity. I applied this approach to bird survey data and found that species traits predicted detection probability and improved model accuracy. I also demonstrated the ability of a bootstrap re-sampling method to probabilistically compare abundance ranks of intermediately-common species, and reasoned that differences in these abundances provided inferences about resource partitioning within communities.

Long-term, large-scale monitoring of wildlife metacommunities is needed to recognize population declines early enough to identify environmental stressors and facilitate adaptive planning. Potential outcomes include information supporting the designation of new species of conservation concern, or better yet, conservation actions that avert the need for conferring critical statuses. The survey and analytical methods investigated in this dissertation provide a variety of tools for effective and efficient monitoring. I demonstrated their statistical power for identifying long-term trends, and provided examples of baseline results in the shorter term. However, the political and financial commitment of wildlife management agencies to sustain monitoring programs such as the Ecoregion Biodiversity Monitoring project is essential to success of conservation efforts. I liken the value of investing in monitoring to planting and nurturing orchard. One needs to wait for the trees to mature, but then new fruit becomes available each year.

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