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Using occupancy estimation to assess the effectiveness of a regional multiple-species conservation plan: Bats in the Pacific Northwest

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ABSTRACT

Regional conservation plans are increasingly used to plan for and protect biodiversity at large spatial scales however the means of quantitatively evaluating their effectiveness are rarely specified. Multiple-species approaches, particular those which employ site-occupancy estimation, have been proposed as robust and efficient alternatives for assessing the status of wildlife populations over large spatial scales, but implemented examples are few. I used bats as a model to evaluate design considerations for the use of occupancy estimation to assess population status and habitat associations for eight species of bats covered under a regional conservation plan. Bats were one of the groups expected to benefit from a system of reserves for species associated with late-successional/old-growth (LSOG) habitat designated under the Northwest Forest Plan (NWFP). This study produced the first estimates for probabilities of occupancy and detection for bats at a regional scale. Overall probabilities of occupancy ranged from 0.586 to 0.783 and probabilities of detection ranged from 0.239 to 0.532 among the eight species modeled. Although point estimates of occupancy suggested association with NWFP habitat categories for some species, estimate precision was low. Models that assumed constant occupancy with respect to reserve- and LSOG-status were supported for most species. I used model-averaged estimates of occupancy and detection for each species to estimate survey effort necessary to meet precision targets. Occupancy estimation was best suited to species with the highest detection probabilities. Species that are rare or difficult to detect will require enhancement in survey methods or more intensive survey effort to produce meaningful estimates. Optimizing monitoring efforts to address multiple species requires tradeoffs among survey methods, levels of effort, and acceptable levels of precision.

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1. Introduction

Regional conservation plans are increasingly used to plan for and protect biodiversity at large spatial scales where a multitude of human activities may conspire to simultaneously impact large numbers of species or their habitats (Johnson et al., 1999; Margules and Pressey, 2000; Moilanen et al., 2005). Such approaches are generally considered progressive tools for conservation because, in addition to taking a broad geographic perspective, they incorporate the needs of a wide spectrum of biodiversity as opposed to focusing on the needs of just a few species (Nicholson and Possingham, 2006). Although inclusion of a particular species or taxonomic group in a regional conservation plan is a positive step towards its

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conservation, by no means does it guarantee that the plan will protect each species and its habitats. Monitoring programs for the highest-profile organisms are sometimes included in such plans (e.g., Akçakaya, 2000). However the means for monitoring effectiveness of broader biodiversity conservation goals are often left unspecified at the time such plans are completed. The need to quantitatively evaluate the effectiveness of conservation measures is well-recognized but is challenging in practice because designing and implementing detailed monitoring plans for individual species is expensive and logistically infeasible (Manley et al., 2004; Margules and Pressey, 2000; Moilanen et al., 2005; Nicholson and Possingham, 2006; Tear et al., 2005).

The Northwest Forest Plan (NWFP), which guides the management of forests on federal land in the Pacific Northwest of the US, was one of the earliest and most ambitious regional conservation plans and embodies several of the challenges in monitoring a broad suite of biodiversity (Johnson et al., 1999; Molina et al., 2006). The NWFP was designed to protect the needs of species associated with late-successional/old-growth (LSOG) habitat while providing a predictable supply of timber. As a precursor to the NWFP, the Forest Ecosystem Management and Assessment Team (FEMAT) identified over a thousand species ranging from lichens, fungi, and mollusks to 82 vertebrates that appeared to be associated with LSOG forest conditions (FEMAT, 1993). Nevertheless, the primary driver of the wildlife/biodiversity component of the NWFP was the needs of the northern spotted owl (*Strix occidentalis caurina*) and its association with LSOG forest habitat. The NWFP defined LSOG habitat as forests 80–200 years old and designated a series of late-successional reserves (LSRs), which were intended to provide current and future habitat for the northern spotted owl and other species that were presumed to be associated with older forests (USDA Forest Service and BLM, 1994). Whereas LSOG was a vegetation type representing forests in mature or old-growth status, LSRs were administrative land allocations that contained late-successional characteristics but also included areas that were not in mature or old-growth condition. The plan formalized monitoring plans to assess changes in population trends, demographic performance, and the amount and distribution of habitat for the two species listed as threatened under the US Endangered Species Act: the northern spotted owl (Noon and Blakesley, 2006) and marbled murrelet (*Brachyramphus marmoratus*; Raphael, 2006). Over 400 more species, including five amphibians and the red tree vole (*Phenacomys longicaudus*) were included on the so-called ‘Survey and Manage’ list which required surveys to detect presence of these species prior to disturbance and prescribed a series of surveys in systematically selected locations across the NWFP area (Molina et al., 2006). Results of these systematic surveys have been used to assess the rarity of these species, their association with LSOG habitat and reserve allocations, and the extent to which reserves, designed for the spotted owl, have served as an ‘umbrella’ for their protection (Dunk et al., 2006; Molina et al., 2006).

Eleven species of bats were evaluated under FEMAT and presumed to be associated with older forests based on expert opinion and a few early studies of their habitat associations (FEMAT, 1993; Thomas, 1988). Although bats were not included in the Survey and Manage program they were expected to benefit from the system of reserves established to provide for LSOG-associated species (FEMAT, 1993). In the years since inception of the NWFP, radio-telemetry studies on several species have demonstrated that they tend to select large diameter, tall snags in early stages of decay as day roosts during summer (Baker and Lacki, 2006; Ormsbee and McComb, 1998; Waldien et al., 2000; Weller and Zabel, 2001). Although such structures occur more frequently in older forests (Ohmann et al., 1994), it remained unclear whether bats were associated with LSOG forest conditions at larger spatial scales; and the degree of protection provided by reserves was unknown. Because of their association with LSOG components (i.e., large snags) and continued concerns about their populations I was asked to design an approach for assessing their distribution and rarity within the NWFP area and their association with LSOG habitats and reserve allocations. To the extent possible, my approach was encouraged to apply the principles and methods that the Survey and Manage program used for other taxa in achieving its primary goals: identifying species associated with LSOG forests and assessing whether reserves were contributing to persistence of their populations (Molina et al., 2003, 2006).

Evaluating population status for species that are mobile, cryptic, and occur at low densities is challenging, particularly at the largest spatial scales (MacKenzie, 2005). Forest bats are a particularly challenging group because of imperfect detection methods, low site fidelity, and highly labile use of habitat over both space and time (O’Shea and Bogan, 2003; Weller, 2007). As a result, conventional metrics (e.g., abundance estimates, population demographics) cannot be generated for bats and presence/not-detected surveys are increasingly used to assess their habitat associations (Greaves et al., 2006; Ford et al., 2005, 2006). The value of such surveys can be enhanced if multiple surveys are conducted so that the probability that a species occurs at a site can be estimated while compensating for the fact that the probability of detecting it during an individual survey is <1 (Gu and Swihart, 2004; MacKenzie et al., 2002, 2006; Tyre et al., 2003). This approach, commonly known as occupancy estimation, has been proposed as a robust and cost-effective alternative to estimation of more data-intensive state variables such as abundance or demographic parameters (MacKenzie et al., 2002; Manley et al., 2004). Because a simple record of detection or non-detection of a species during an individual survey is the only data requirement, occupancy estimation has been suggested as an efficient approach for assessing population status and habitat associations for cryptic, low-density species (including bats) over large spatial scales (Bailey et al., 2004; MacKenzie et al., 2002; Manley et al., 2004; O’Connell et al., 2006; Weller, 2007).

Concomitantly, multiple-species approaches to inventory and monitoring activities that employ site-occupancy analysis methods are increasingly recommended as effective and efficient means of meeting biodiversity monitoring objectives (Manley et al., 2004). Efficiencies are generated when a single sample frame and inventory design is used to select survey sites and the survey methods applied at those sites are effective for detection of multiple-species. Although logical, there are few examples where the effectiveness of combining these approaches has been evaluated in the field (*but see* Bailey et al., 2004; O'Connell et al., 2006; Pellet and Schmidt, 2005; Tyre et al., 2003). Bats appear well-suited to a multiple-species approach because the survey methods used to detect them (e.g., capture and acoustic detection) and the locations where they are generally effective (e.g., water sources) are similar for many species. I evaluated the use of a multiple-species site-occupancy approach for assessing the effectiveness of the NWFP with respect to bats. Specific objectives of this work were to (1) generate first estimates for probabilities of occupancy and detection for bats in the Pacific Northwest, (2) use these estimates to evaluate means of optimizing efficiency of a multiple-species site-occupancy program for bats, and (3) gain initial insights into the rarity of individual species of bats and their associations with LSOG or reserve designations within the NWFP area.

2. Methods

2.1. Site selection

I stratified the NWFP area into two habitat categories (LSOG vs. non-LSOG) and two land allocation categories (reserve vs. non-reserve; Molina et al., 2003). LSOG habitat was identified based on the FEMAT map (FEMAT, 1993), which was the only seamless coverage available when this project began. Reserves include congressionally reserved lands (i.e., lands set aside by congress, e.g., wilderness), administratively withdrawn areas (i.e., lands set aside by national forests (e.g., scenic areas) that were not scheduled for timber harvest) and LSRs established specifically by the NWFP. All other lands were considered non-reserve. The NWFP also established riparian reserves along streams but I ignored this designation during sample unit selection and analyses because most survey sites for bats were located in riparian areas.

I used the Forest Inventory and Analysis Program's (FIA) systematic sample frame (Bechtold and Patterson, 2005) as the basis for distributing sample units for bats in order to maintain a measure of spatial coincidence with surveys for other taxa within the NWFP (Molina et al., 2003, 2006). The FIA system uses a seamless, 5.5 km grid of hexagons to provide spatial control on location of its vegetation plots (Bechtold and Patterson, 2005). I used 2.5 km radius (1964 ha) circular sample units with centers coincident with FIA hexagons to simplify navigation in the field. I selected 51 sample units in proportion to the distribution of FIA points among NWFP allocation/habitat categories, which resulted in selection of 19 reserve/LSOG (37.3%), 13 reserve/non-LSOG (25.5%), 5 non-reserve/LSOG (9.8%), and 14 non-reserve/non-LSOG (27.5%) sample units. I selected sample units that maximized homogeneity with respect to NWFP allocation/habitat categories so as to magnify observed differences among categories with a relatively small sample size. I assigned each sample unit to the NWFP allocation/habitat category that comprised the largest proportion of its area (Araújo, 2004). In 49 sample units, ⩾75% of the area was homogeneous with respect to reserve/LSOG designation. Sample unit locations were grouped into eight study areas (Fig. 1) to simplify field logistics and maximize the number of sample units that could be surveyed. Study area locations were selected to encompass a variety of climate and habitat conditions that occurred throughout the NWFP area and for their proximity to experienced field surveyors. Within each study area I selected sample units to maximize the number of different NWFP allocation/habitat categories represented (Fig. 1).

Within each sample unit I selected the two most suitable sites for detecting multiple-species of bats, with an emphasis on suitability for capture methods. Owing to spatio-temporal, species-specific differences in habitat use, I reasoned that surveying >1 site would improve my ability to document the species that occurred within a sample unit. On the other hand, it was difficult to locate >2 suitable sites within many sample units. I selected habitat elements as survey sites according to the following priority: low gradient streams that were medium (3–9 m wide), large (>9 m wide), or small (<3 m wide), ponds, lakes, or roads. Relative to streams and ponds, most species of bats are difficult to capture at lakes and on roads and these habitat elements were selected only when streams and ponds did not occur within the sample unit. Once the first survey site was selected, I chose a different type of habitat element as the second site wherever it was available. My method of site selection could be perceived as biased because I prioritized selection of riparian habitat types, to which bats are attracted in many areas (Ford et al., 2005; Menzel et al., 2005). However, this was a necessary concession of my study design which aimed to characterize species occurrence within sample units while minimizing survey effort.

2.2. Field methods

I surveyed each site twice within a single year, for a total of 4 surveys per sample unit. Surveys were conducted between 16 June–9 September 2003 and from 14 June–11 September 2004. On average, consecutive surveys at a site were 37.4 (SE = 1.4, range 13–83) days apart. Surveys began at sunset and continued for 3.5 h. During each survey, a combination of capture and active acoustic methods were used to detect species presence, as this general improves inventory completeness (Murray et al., 1999; O'Farrell and Gannon, 1999).

For the capture component, 2–4 (mean = 3.27, SE = 0.04), 2.6 m high mist nets were set per survey. The number and length (2.6–18 m) of mist nets were selected to suit the physical characteristics of the site. On average, 69 m^2 (range 20–140 m^2) of mist net were deployed per survey. Most captured bats were identified to species based on measurements and inspection of their external morphology. *Myotis lucifugus* and *Myotis yumanensis* were distinguished from one another via analysis of mtDNA extracted from a 3 mm tissue biopsy from the wing membrane (Zinck et al., 2004).

For the acoustic component of the survey, echolocation calls were recorded at a variety of locations at each site, focusing on areas where bats were active but unlikely to be captured with mist nets. I chose this active mode of detection because my goal was to obtain ⩾1 detection of each of the species that used the site during the survey. Active detection allows observers to orient detectors toward echolocating bats thereby improving quality of recordings which, in turn, improves the ability to identify calls to species (Milne et al.,

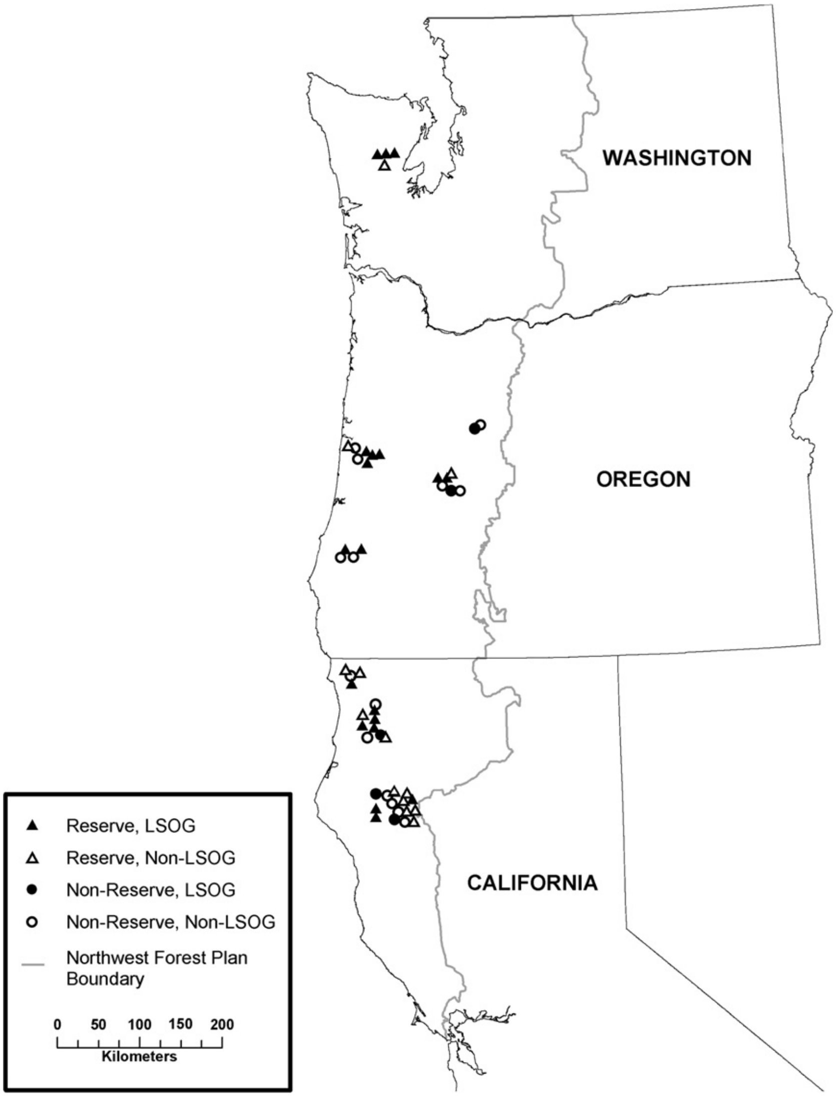

Fig. 1 – Study area locations and distribution of sample units. Sample units were characterized according to whether they occurred within a Northwest Forest Plan reserve and whether the majority of habitat was considered late-successional\old-growth (LSOG).

2004; O'Farrell et al., 1999). Echolocation calls were recorded using Pettersson D-240X time-expansion bat detectors (Pettersson Elektronik AB, Uppsala, Sweden) and transferred either to analog tape recorder or directly to the hard-drive of a laptop computer. Sequences recorded to tape recorders were later transferred to computer and all sequences were analyzed using SONOBAT software (version 2.5; DNDesign, Arcata, CA, USA). I inspected the time-versus-frequency sonogram for each echolocation sequence and separated those which contained characteristics (e.g., high signal-to-noise ratio, complete frequency information) that indicated recordings were of sufficient quality to attempt species identification. From this subset of sequences, I selected a single call and measured the following parameters: high frequency (kHz), low frequency (kHz), characteristic frequency (kHz), duration (ms), slope (kHz/ms), upper slope (kHz/ms), and lower slope (kHz/ms).

I assigned a call to species by comparing its parameter values with a key to the echolocation calls of bats in the northwestern United States (Szewczak and Weller, unpublished data). The key was created by recording echolocation calls from bats where species identity had been previously established from captured individuals. Echolocation calls were only assigned to species if one or more parameter values fell within a range considered diagnostic for a species. Because such parameter values only occurred in a small percentage of calls recorded in the field, most calls were not assigned to an individual species and the key was a conservative tool for establishing species presence during a survey.

2.3. *Data analyses*

I used program PRESENCE (version 2.0, Hines and MacKenzie, 2008) to estimate probabilities of occupancy and detection for each species. I created a detection history for each species at each of 51 sample units by combining the two surveys at each of two sites for a total of four surveys per sample unit. I considered surveys to be independent because there were generally conducted over four separate nights and the two sites were either on separate bodies of water or $\geqslant$0.5 km apart. A species was considered detected during a survey if it was captured in mist nets or its echolocation calls were recorded and identified to species at least once during the survey.

For each species, I attempted to fit 16 models which incorporated NWFP habitat categories as covariates that may affect probabilities of occupancy and detection. The 16 models were composed of the complete set of combinations that result from considering occupancy and detection constant across all sample units or variable according to the status of the sample unit with respect to NWFP habitat categories (LSOG, reserve, or their combination). I eliminated from the candidate set models that did not converge or which contained uninformative parameter estimates. I ranked models using the small-sample correction to Akaike's Information Criterion (AIC_c) and used Akaike weights to compare weight of evidence among models in the candidate set (Burnham and Anderson, 2002). I extracted the 95% confidence set of models (Burnham and Anderson, 2002), recalculated model weights using this set, and used it to generate model-averaged overall estimates of occupancy and detection for each species. I compared occupancy probabilities between NWFP allocations (reserve vs. non-reserve) and habitats (LSOG vs. non-LSOG) using models which assumed constant detection probabilities among categories.

I used overall model-averaged estimates of occupancy ($\hat{\psi}$) and detection ($\hat{p}$) for each species to evaluate sample design modifications that would improve precision of occupancy estimates. Specifically, I modified Eq. (4) of MacKenzie and Royle (2005):

$$s = \frac{\hat{\bar{\psi}}}{\mathrm{var}(\hat{\bar{\psi}})}\left[(1-\hat{\bar{\psi}}+\frac{(1-p^*)}{p^*-K\hat{\bar{p}}(1-\hat{\bar{p}})^{K-1}}\right]$$

where $p^* = 1-(1-\hat{\bar{p}})^K$, to estimate the number of sample unit (s), surveyed K times, required to achieve specified levels of precision on occupancy estimates.

3. Results

I detected 13 species of bats during 204 surveys and estimated probabilities of occupancy and detection for the eight species that were detected in $\geqslant$21 (41%) of sample units. An additional five species, *Lasiurus cinereus* ($n = 7$ sample units), *Antrozous pallidus* ($n = 3$), *Corynorhinus townsendii* ($n = 2$), *Pipistrellus hesperus* ($n = 2$), and *Tadarida brasiliensis* ($n = 2$), were detected too infrequently to generate meaningful estimates of occupancy or detection.

As expected, estimates for the proportion of occupied sample units were greater than the proportion of sample units where each species was detected in the field and the magnitude of the difference was inversely related to detection probability (Table 1). Model-averaged occupancy estimates ranged from 0.586 for *M. yumanensis* to 0.783 for *Myotis californicus* (Table 1); detection probabilities ranged from 0.239 for *Myotis evotis* to 0.532 for *M. californicus* (Table 1).

The simplest model, in which both occupancy and detection probability were assumed constant with respect to allocation and habitat, was in the 95% model confidence set for all eight species and was either the top-ranked model or within 1.1 AIC_c points of the top-ranked model for five species: *Lasionycteris noctivagans*, *M. californicus*, *M. evotis*, *Myotis thysanodes*, and *M. yumanensis* (Table 2). These five species and *M. lucifugus* had $\geqslant$2 constant occupancy models within 2 AIC_c points of their top model. However there was substantial model selection uncertainty for most species; seven species had $\geqslant$9 models in their 95% confidence set (Table 2). Models with fewer covariates generally had higher weights and this pattern was precisely evident for *M. californicus* and *M. yumanensis* (Table 2).

Estimates of occupancy were similar between reserve and non-reserve sample units for most species (Fig. 2A). Point estimates (Fig. 2A) and the model selection process (Table 2) indicated that reserve-status may affect occupancy probabilities *Eptesicus fuscus* and *M. yumanensis* (Table 2) however it is notable that occupancy estimates were lower in reserve than non-reserve for *E. fuscus*. Point estimates of occupancy were higher in LSOG than non-LSOG sample units for three species, *M. evotis*, *M. thysanodes* and *Myotis volans* (Fig. 2B) and $\psi(\text{LSOG})p(\cdot)$ was the top-ranked models for all three species (Table 2). However, variability around occupancy estimates and model selection uncertainty was high in all three cases; though the top-ranked model for *M. volans* was the highest weighted model for any species in this study. The top-ranked models for *E. fuscus*, *L. noctivagans*, and *M. lucifugus* included detection probabilities that varied according to LSOG or reserve-status. Support for inclusion of detection covariates was low for *L. noctivagans*, but higher for *M. lucifugus* and especially for *E.*

Table 1 – Overall model-averaged estimates for occupancy ($\hat{\bar{\psi}}$) and detection ($\hat{\bar{p}}$) for eight species of bats in Northwest Forest Plan planning area, 2003–2004

Species	Species code	ψ(obs)	$\hat{\bar{\psi}}$	SE $\hat{\bar{\psi}}$	SE $\hat{\bar{\psi}}/\hat{\bar{\psi}}$	$\hat{\bar{p}}$	SE $\hat{\bar{p}}$	SE $\hat{\bar{p}}/\hat{\bar{p}}$
Eptesicus fuscus	EPFU	0.588	0.691	0.100	0.144	0.402	0.070	0.173
Lasionycteris noctivagans	LANO	0.627	0.782	0.112	0.143	0.334	0.062	0.187
Myotis californicus	MYCA	0.745	0.783	0.078	0.099	0.532	0.053	0.100
M. evotis	MYEV	0.509	0.782	0.187	0.240	0.239	0.065	0.274
M. lucifugus	MYLU	0.706	0.780	0.095	0.121	0.467	0.065	0.139
M. thysanodes	MYTH	0.412	0.605	0.162	0.267	0.252	0.072	0.287
M. volans	MYVO	0.627	0.754	0.129	0.171	0.358	0.060	0.167
M. yumanensis	MYYU	0.529	0.586	0.101	0.172	0.447	0.068	0.152

ψ(obs) represents the proportion of sample units where species was detected in the field.

Table 2 – Model selection procedure for estimating probabilities of occupancy (ψ) and detection (p) for eight species of bats

Models	K	AIC_c	ΔAIC_c	w_i
Eptesicus fuscus				
ψ(Reserve) p(LSOG)	4	226.55	0.00	0.362
$\psi(\cdot)$ p(LSOG)	3	226.78	0.23	0.323
ψ(Reserve) p(Reserve + LSOG)	5	228.71	2.16	0.123
$\psi(\cdot)$ p(Reserve + LSOG)	4	229.13	2.58	0.100
$\psi(\cdot)$ $p(\cdot)$	2	231.35	4.80	0.033
ψ(Reserve) $p(\cdot)$	3	232.44	5.89	0.019
Lasionycteris noctivagans				
$\psi(\cdot)$ p(Reserve)	3	234.77	0.00	0.234
$\psi(\cdot)$ p $(\cdot)$	2	234.79	0.02	0.232
$\psi(\cdot)$ p(Reserve + LSOG)	4	236.35	1.58	0.106
ψ(LSOG) p(Reserve)	4	236.65	1.88	0.091
$\psi(\cdot)$ p(LSOG)	3	236.74	1.97	0.087
ψ(LSOG) $p(\cdot)$	3	236.89	2.12	0.081
ψ(Reserve) $p(\cdot)$	3	237.05	2.28	0.075
ψ(LSOG) p(Reserve + LSOG)	5	238.73	3.96	0.032
ψ(Reserve) p(LSOG)	4	239.09	4.32	0.027
Myotis californicus				
$\psi(\cdot)$ $p(\cdot)$	2	267.45	0.00	0.299
$\psi(\cdot)$ p(LSOG)	3	269.37	1.92	0.114
ψ(Reserve) $p(\cdot)$	3	269.39	1.94	0.113
$\psi(\cdot)$ p(Reserve)	3	269.63	2.18	0.101
ψ(LSOG) $p(\cdot)$	3	269.65	2.20	0.100
ψ(Reserve) p(LSOG)	4	271.29	3.84	0.044
$\psi(\cdot)$ p(Reserve + LSOG)	4	271.61	4.16	0.037
ψ(Reserve + LSOG) $p(\cdot)$	4	271.63	4.18	0.037
ψ(LSOG) p(LSOG)	4	271.72	4.27	0.035
ψ(Reserve) p(Reserve)	4	271.72	4.27	0.035
ψ(LSOG) p(Reserve)	4	271.91	4.46	0.032
ψ(Reserve) p(Reserve + LSOG)	5	273.71	6.26	0.013
M. evotis				
ψ(LSOG) $p(\cdot)$	3	197.38	0.00	0.214
$\psi(\cdot)$ p(LSOG)	3	198.00	0.62	0.157
$\psi(\cdot)$ $p(\cdot)$	2	198.48	1.10	0.124
$\psi(\cdot)$ p(Reserve + LSOG)	4	199.07	1.69	0.092
ψ(LSOG) p(LSOG)	4	199.59	2.21	0.071
ψ(Reserve + LSOG) $p(\cdot)$	4	199.68	2.30	0.068
ψ(Reserve) p(LSOG)	4	199.76	2.38	0.065
$\psi(\cdot)$ p(Reserve)	3	200.21	2.83	0.052
ψ(LSOG) p(Reserve + LSOG)	5	200.32	2.94	0.049
ψ(Reserve) $p(\cdot)$	3	200.71	3.33	0.041
ψ(Reserve) p(Reserve + LSOG)	5	201.53	4.15	0.027
M. lucifugus				
$\psi(\cdot)$ p(Reserve)	3	257.71	0.00	0.248
ψ(Reserve) p(Reserve)	4	258.27	0.56	0.187
$\psi(\cdot)$ p(Reserve + LSOG)	4	259.17	1.46	0.119
ψ(LSOG) p(Reserve)	4	259.67	1.96	0.093
ψ(Reserve + LSOG) p(Reserve)	5	260.11	2.40	0.075
$\psi(\cdot)$ p(LSOG)	3	260.34	2.63	0.067
$\psi(\cdot)$ $p(\cdot)$	2	260.50	2.79	0.061
ψ(LSOG) p(Reserve + LSOG)	5	261.49	3.78	0.037
ψ(LSOG) $p(\cdot)$	3	262.07	4.36	0.028
ψ(Reserve) p(LSOG)	4	262.40	4.69	0.024
ψ(LSOG) p(LSOG)	4	262.61	4.90	0.021
M. thysanodes				
ψ(LSOG) $p(\cdot)$	3	173.68	0.00	0.237
$\psi(\cdot)$ $p(\cdot)$	2	173.81	0.13	0.222
$\psi(\cdot)$ p(LSOG)	3	175.06	1.38	0.119
ψ(Reserve) $p(\cdot)$	3	175.60	1.92	0.091
ψ(LSOG) p(Reserve)	4	175.82	2.14	0.081
ψ(LSOG) p(LSOG)	4	176.03	2.35	0.073
$\psi(\cdot)$ p(Reserve)	3	176.04	2.36	0.073
ψ(Reserve) p(Reserve)	4	177.18	3.50	0.041
$\psi(\cdot)$ p(Reserve + LSOG)	4	177.39	3.71	0.037
M. volans				
ψ(LSOG) $p(\cdot)$	3	233.20	0.00	0.393
ψ(Reserve + LSOG) $p(\cdot)$	4	234.53	1.33	0.202
ψ(LSOG) p(LSOG)	4	235.53	2.33	0.123
ψ(Reserve + LSOG) p(Reserve)	5	236.98	3.78	0.059
ψ(Reserve + LSOG) p(LSOG)	5	236.99	3.79	0.059
$\psi(\cdot)$ $p(\cdot)$	2	237.38	4.18	0.049
$\psi(\cdot)$ p(LSOG)	3	237.68	4.48	0.042
ψ(Reserve) $p(\cdot)$	3	239.22	6.02	0.019
ψ(Reserve + LSOG) p(Reserve + LSOG)	6	239.56	6.36	0.016
M. yumanensis				
$\psi(\cdot)$ $p(\cdot)$	2	219.98	0.00	0.210
ψ(Reserve) $p(\cdot)$	3	220.81	0.83	0.139
ψ(LSOG) $p(\cdot)$	3	221.26	1.28	0.111
$\psi(\cdot)$ p(Reserve)	3	221.71	1.73	0.089
ψ(Reserve) p(Reserve)	4	221.91	1.93	0.080
$\psi(\cdot)$ p(LSOG)	3	222.23	2.25	0.068
ψ(Reserve + LSOG) $p(\cdot)$	4	222.74	2.76	0.053
ψ(LSOG) p(Reserve)	4	223.04	3.06	0.046
ψ(Reserve) p(LSOG)	4	223.17	3.19	0.043
ψ(LSOG) p(LSOG)	4	223.58	3.60	0.035
$\psi(\cdot)$ p(Reserve + LSOG)	4	223.82	3.84	0.031
ψ(Reserve) p(Reserve + LSOG)	5	223.84	3.86	0.030
ψ(Reserve + LSOG) p(Reserve)	5	224.02	4.04	0.028

Occupancy and detection was either constant $(\cdot)$ or varied according to a sample unit's status with respect to LSOG or reserve designations in the Northwest Forest Plan. Models shown compose the 95% confidence set for each species. Presented are the number of parameters in the model (K), Akaike's Information Criterion corrected for small sample size (AIC_c), difference between ith model and model with lowest AIC_c value (ΔAIC_c), and weight of the ith model (w_i).

fuscus where models that included LSOG as a detection covariate comprised 95% of the model weights.

A better appraisal of the relationship between occupancy estimates and NWFP allocation/habitat categories could be made if variability around occupancy estimates could be reduced. Target levels of precision were not specified by the NWFP, therefore I focused on obtaining the most precise estimates possible (MacKenzie and Royle, 2005). I selected $\text{SE}(\hat{\psi}) = 0.06$ as a low, yet attainable target for precision of occupancy estimates for all species (i.e., slightly lower than the best observed value in this study: 0.066 for *M. californicus*). At this level of precision, the probability of observing a species given that it was present (p^*) ranged from 0.66 for *M. evotis* to 0.95 for *M. californicus* using the 4-survey protocol employed during this study (Table 3). Achieving $\text{SE}(\hat{\psi}) \leqslant 0.06$ using this protocol would require surveys of 61–348 sample units (246–1392 surveys) depending on the species (Table 3). Use of a 6-survey protocol, 2 sites surveyed 3 times, would improve the probability of observing each species ($p^* \geqslant 0.95$ for four species and $p^* \geqslant 0.90$ for six species) and reduce the required

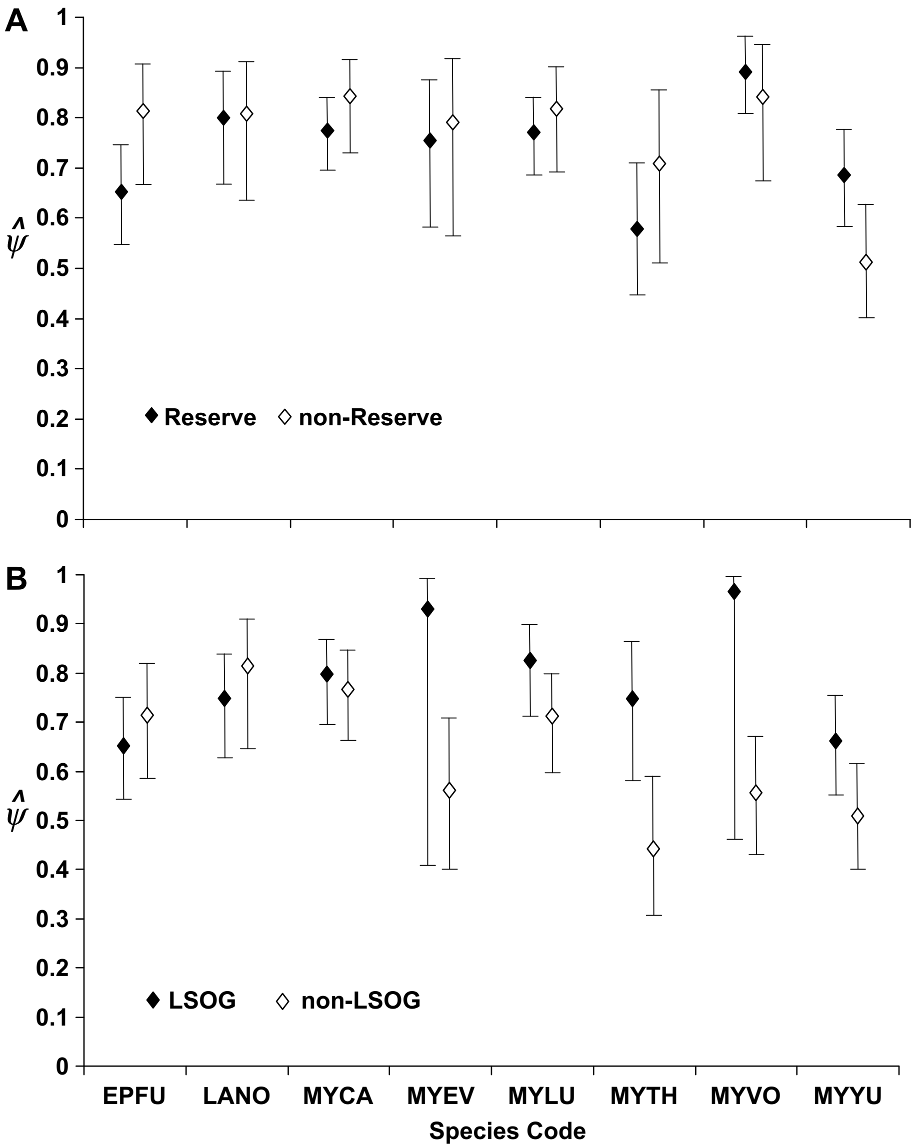

Fig. 2 – Point estimates of occupancy ($\hat{\psi}$) and standard errors for eight species of bats in the Northwest Forest Plan area. Occupancy estimates were generated for (A) reserve vs. non-reserve and (B) late-successional\old-growth (LSOG) sample units vs. non-LSOG sample units. Species codes according to Table 1.

number of sample units compared to a 4-survey protocol (Table 3). Importantly, for the four species with the lowest detection probabilities, the total number of surveys required to realize these improvements would be lower than for the 4-survey protocol.

4. Discussion

This study evaluated design considerations for assessing population status and habitat associations for multiple-species of bats within the NWFP area. It provides empirical estimates of occupancy and detection for eight species of bats across the region. Realistic estimates of these parameters are important first steps for planning effective and efficient monitoring programs (MacKenzie and Royle, 2005; MacKenzie et al., 2006). Studies in other areas have addressed the probability of detecting individual species of bats using either capture or acoustic techniques (Duchamp et al., 2006; Gorresen et al., 2008; Weller and Lee, 2007) but this is the first study to estimate probabilities of occupancy and detection for multiple-species of bats at a regional scale. Models that assumed constant occupancy with respect to reserve- or LSOG-status were highly supported for most species. Support for constant occupancy models has also been found for carnivores in northeastern US and woodland birds in South Australia (Long et al., 2007a; O'Connell et al., 2006; Tyre et al., 2003).

As has been shown in other multiple-species contexts (Bailey et al., 2004; Long et al., 2007b; O'Connell et al., 2006; Pellet and Schmidt, 2005; Tyre et al., 2003), estimates of occupancy and detection in this study varied among species. Further, estimates of both occupancy and detection for all eight species of bats met standards of 'good precision' used

Table 3 – Survey effort to achieve SE $\hat{\psi} = 0.06$ for eight species of bats using 4 or 6 surveys per sample unit

	Species Code							
	EPFU	LANO	MYCA	MYEV	MYLU	MYTH	MYVO	MYYU
K = 4 *Surveys*								
p^*	0.87	0.80	0.95	0.66	0.92	0.69	0.83	0.91
No. of sample units	106	152	61	348	75	264	130	93
Total no. of surveys	423	609	246	1392	301	1058	521	371
K = 6 *Surveys*								
p^*	0.95	0.91	0.99	0.81	0.98	0.83	0.93	0.97
No. of sample units	71	77	50	144	53	129	73	73
Total no. of surveys	424	460	298	863	320	773	436	438

Survey effort was evaluated using overall model-averaged values of occupancy and detection (Table 1). The probability of observing the species, if it used the sample unit, after *K* visits is p^*.

in other studies (SE(est)/est < 0.30; Bailey et al., 2004; Linkie et al., 2007). Nevertheless confidence intervals around estimates were too large for meaningful assessment of species' association with reserves or LSOG designations and, similar to Linkie et al. (2007), I chose a more restrictive measure of precision to evaluate required levels of survey effort.

My study joins a list of others in which the full set of a priori models could not be evaluated because they failed to converge (Long et al., 2007a; Pellet and Schmidt, 2005), models with the fewest parameters were highly weighted (Long et al., 2007a; O'Connell et al., 2006), or where model selection uncertainty was high (Long et al., 2007a; Pellet and Schmidt, 2005; Tyre et al., 2003). All of these issues arose in my study despite consideration of a relatively simple set of models that evaluated occupancy and detection probabilities as a function of two binomial covariates (reserve- and LSOG-status). A likely explanation is that the number of sample units surveyed was not sufficient to achieve stable or precise estimates when multiple covariates were considered (Long et al., 2007a). A primary goal of this and other studies (Linkie et al., 2007; O'Connell et al., 2006; Pellet and Schmidt, 2005) was to evaluate sample designs for monitoring programs that would produce precise and robust estimates of occupancy. Similarities in results of these studies, in terms of the ratio of sample units to estimable parameters, may prove useful to others designing occupancy estimation programs.

Point estimates of occupancy for three species, *Myotis evotis*, *M. thysanodes*, and *M. volans*, suggested an association with LSOG but only one, *M. yumanensis*, indicated a possible association with reserve lands. Both the variability of occupancy estimates and model selection uncertainty for each of these species prevents stronger conclusions from these data, but it is a trend to be considered further. One reason is that this result mirrors a general trend among Survey and Manage species in the NWFP: where associations have been found, many more species were associated with LSOG habitat than reserve allocation (Molina et al., 2006). Secondly a suggestion of association with LSOG habitat supports radio-telemetry work at finer spatial scales which found that all three of these species selected tall, large diameter snags to meet their summer, day-roosting needs when such structures were available (Baker and Lacki, 2006; Ormsbee and McComb, 1998; Waldien et al., 2000; Weller and Zabel, 2001). In fact, these three were among seven priority species that inspired the need to evaluate strategies for determining whether bats were associated with reserve allocation or LSOG habitat at broader spatial scales. Nevertheless, more precise estimates of occupancy, generated from sample units selected from a statistical framework, are necessary to conclude association or non-association for any of the species evaluated in this study.

Among the eight species considered in this study, the optimal number of surveys per sample unit to meet precision objectives varied from 4 to 10. Multiple-species estimates of occupancy and detection probabilities have been generated for birds in Australia (Field et al., 2005), salamanders in southeastern US (Bailey et al., 2004), frogs in Switzerland (Pellet and Schmidt, 2005) and carnivores in northeastern US (Long et al., 2007b; Agosta, 2002). In each case differences in occupancy and detection among species, sometimes with respect to survey methods, suggested that optimal survey protocols would vary among species. It is unlikely that a single design will be efficient for all species in a multiple-species program and tradeoffs in design will be necessary. Whereas protocols for species with the lowest detection probabilities will be optimized by surveying a larger number of sites, those with the highest detection probabilities require more surveys per site (MacKenzie and Royle, 2005). Field et al. (2005) recommended optimizing study design around the more data-intensive of two species though it would exceed the effort necessary to meet the needs of the other. I found that three surveys at each of two sites within a sample unit would result in a reasonable probability of observing all eight species, if they occurred within a sample unit ($p^* \geqslant 0.82$; MacKenzie and Royle, 2005) and generate precise occupancy estimates for six species of bats using approximately 75 sample units. This represents the number of sample units necessary to produce precise estimates for a single stratum, so 4–6 times the number of surveys conducted in this study might be necessary to rigorously evaluate associations with both LSOG habitats and reserve allocations. Inclusion of the two species with the lowest detection probabilities (i.e., *M. evotis* and *M. thysanodes*) would require up to 50% more effort. Further, it is important to recall that five additional species were detected so infrequently that occupancy and detection probabilities could not be estimated. This presents a conundrum as data-deficient species that are either rare, difficult to detect, or both, are often of high-priority in regional conservation plans. Evaluating population status or habitat associations for uncommon species of bats may require intensive efforts focused on sub-regions within the NWFP area, the use of alternative methods (e.g., roost searches), or both.

Whether the level of effort necessary to assess the status of uncommon species is acceptable to managers will depend on their budget and the importance of bats relative to other inventory and monitoring objectives. Cost of conducting field surveys is an important consideration in design of inventory and monitoring programs (Field et al., 2005; Joseph et al., 2006; MacKenzie and Royle, 2005). In this study, capture was the most reliable way to document presence of some species but required $\geqslant 1$ biologist to conduct the field survey. Hence capture methods for bats are relatively expensive especially compared to remote-detection methods used for other mammals (e.g., cameras, track plates). Remotely-deployed echolocation detectors are capable of generating detection histories for bats over multiple nights with minimal attention from biologists (Gorresen et al., 2008). Survey sites for echolocation detector surveys can be selected from a statistical framework (e.g., random or systematic) as opposed to capture surveys which require sites to be pre-screened by a biologist to evaluate their suitability. Hence an acoustic-only protocol has potential to improve both data collection efficiency and study design rigor. Nevertheless, because some species are difficult to detect or identify with echolocation detectors (Barclay, 1999; Fenton, 2003) an acoustic-only survey protocol might favor rigor in study design at the expense of lower detection probabilities for these species. Improvements in the ability to identify species from their calls, and to automate and standardize the process of species identification from large volumes of data generated from remotely-deployed echolocation detectors, are needed before an acoustic-only protocol can be implemented in the Pacific Northwest.

Higher probabilities of detection for individual species will improve precision of occupancy estimates and lower survey effort requirements. Therefore development of techniques that enhance the ability to detect individual species, without reducing the ability to detect others, will improve prospects for applying an occupancy approach for bats in a multiple-species context. As an example, I was only able to assign species to about 14% of high-quality echolocation sequences recorded in the field. Development of methods that improve the ability to assign echolocation calls to species will produce corresponding increases in detection probabilities. In forests of Australia, lights were used to draw bats closer to echolocation detectors which improved quality of recordings and, consequently, the ability to identify calls to species (Adams et al., 2005). Such an approach might be especially useful for species such as *Myotis evotis* and *M. thysanodes* which use low intensity echolocation calls and had the lowest detection probabilities in this study. Similarly, methods that improve capture success would improve detection probabilities. In woodlands of England broadcast of their social calls resulted in more captures of *Myotis bechsteinii* (Hill and Greenaway, 2005). If such methods were shown to be effective in the Pacific Northwest, they may provide important means for improving detection probabilities for some species.

4.1. *Conclusions*

Regional multiple-species conservation plans are important tools for incorporating the needs of a broad suite of biodiversity into land-use planning decisions. Inclusion of bats in such plans is a positive first step toward increasing recognition of their contribution to biodiversity and, potentially, for improving their conservation. Ultimately, however, the effectiveness of such efforts can only be judged by whether they produce tangible conservation results. Quantitative assessment of the effectiveness of such plans can be difficult to achieve for the large number of species considered under them especially for more cryptic and mobile taxa, such as bats. Site-occupancy methods are commonly portrayed as effective means of monitoring species which are rare, cryptic, or difficult to detect (Bailey et al., 2004; Linkie et al., 2007; MacKenzie, 2005; O'Connell et al., 2006). Nevertheless several authors have noted that these methods will be ineffective or prohibitively expensive for species with detection probabilities <0.15 (Bailey et al., 2004; O'Connell et al., 2006; Pellet and Schmidt, 2005). My results indicate that, even for species with higher detection probabilities ($p \sim 0.25$), the survey effort necessary to assess broad habitat associations may require substantial resources. This is because the required number of sample units is essentially doubled even for the simple case of a binomial habitat covariate. Similarly, simulation studies have demonstrated that power to detect change in occupancy status over time is generally low unless sampling effort is large (Joseph et al., 2006; Pollock, 2006; Rhodes et al., 2006).

The sampling requirements to assess population status or habitat associations using occupancy estimation may exceed the expectations of some managers. However it remains one of the few options available for meeting such objectives in taxa, including bats, for which estimates of abundance or demographic parameters can be very difficult to attain (Manley et al., 2004; Pollock, 2006; Weller, 2007). This is particularly true at the spatial scales considered under regional conservation plans. Occupancy estimation is likely to be most cost-effective for common species, a potentially useful approach for uncommon species (depending on costs), but unlikely to be an affordable alternative for assessing the rarest or most difficult to detect species. I arrived at these conclusions by applying such an approach for bats in a single region. However because they were based on a quantitative assessment of survey effort necessary to achieve precision targets they should apply to species of any taxonomic group with similar estimates of occupancy and detection; though the economic viability may change depending on costs of conducting surveys for a particular taxon. These conclusions should not be viewed as a condemnation of the site-occupancy approach as assessment and monitoring of common species are increasingly recognized as valid and important conservation goals (Agosta, 2002; Devictor et al., 2007; Manley et al., 2004). The decision on whether to invest in this approach for less common species must be weighed against the costs of not having quantitative information to evaluate effectiveness of conservation plans for such species.

The challenges of optimizing a protocol for detecting multiple-species, using multiple survey methods, are not unique to bats. For example, detection devices were differentially effective among carnivore species in northeastern US and the optimal number of weeks to deploy devices varied according to species and detection technique (Long et al., 2007b; O'Connell et al., 2006). Owing to such differences, multiple-species monitoring efforts will inevitably involve tradeoffs among field logistics, detection devices, and levels of survey effort in order to provide efficient and accurate estimates for target species. The issues raised in this paper are not intended to imply that multiple-species conservation plans are ineffective for protecting species or their habitats; however the costs and challenges associated with quantitatively demonstrating their effectiveness need to be acknowledged. Even if conservation plans are found to provide inadequate protection for a particular species or taxonomic group, it would not invalidate their use to conserve a wide variety of species under a single umbrella.

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