

Assessing the status and trend of bat populations across broad geographic regions with dynamic distribution models

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Abstract. Bats face unprecedented threats from habitat loss, climate change, disease, and wind power development, and populations of many species are in decline. A better ability to quantify bat population status and trend is urgently needed in order to develop effective conservation strategies. We used a Bayesian autoregressive approach to develop dynamic distribution models for *Myotis lucifugus*, the little brown bat, across a large portion of northwestern USA, using a four-year detection history matrix obtained from a regional monitoring program. This widespread and abundant species has experienced precipitous local population declines in northeastern USA resulting from the novel disease white-nose syndrome, and is facing likely range-wide declines. Our models were temporally dynamic and accounted for imperfect detection. Drawing on species–energy theory, we included measures of net primary productivity (NPP) and forest cover in models, predicting that *M. lucifugus* occurrence probabilities would covary positively along those gradients.

Despite its common status, *M. lucifugus* was only detected during ~50% of the surveys in occupied sample units. The overall naïve estimate for the proportion of the study region occupied by the species was 0.69, but after accounting for imperfect detection, this increased to ~0.90. Our models provide evidence of an association between NPP and forest cover and *M. lucifugus* distribution, with implications for the projected effects of accelerated climate change in the region, which include net aridification as snowpack and stream flows decline. Annual turnover, the probability that an occupied sample unit was a newly occupied one, was estimated to be low (~0.04–0.14), resulting in flat trend estimated with relatively high precision (SD = 0.04). We mapped the variation in predicted occurrence probabilities and corresponding prediction uncertainty along the productivity gradient. Our results provide a much needed baseline against which future anticipated declines in *M. lucifugus* occurrence can be measured. The dynamic distribution modeling approach has broad applicability to regional bat monitoring efforts now underway in several countries and we suggest ways to improve and expand our grid-based monitoring program to gain robust insights into bat population status and trend across large portions of North America.

Key words: bats; Bayesian hierarchical model; Chiroptera; conservation; detectability; monitoring; *Myotis lucifugus*; net primary productivity; occupancy; species distribution; species–energy theory; trend.

INTRODUCTION

Declines in bat populations have been noted widely across many species and environments, and the cumulative effects of habitat loss, accelerated climate change, disease, and wind power development have the potential to decimate bat populations in short spans of time (Jones et al. 2009, Frick et al. 2010a). Bats are one of the most diverse groups of mammals and are functionally

important to many terrestrial ecosystems worldwide (Schipper et al. 2008, Boyles et al. 2011, Kunz et al. 2011). Regular assessments of bat populations are therefore of growing importance and necessary for the development of effective conservation strategies. However, because of their cryptic and wide-ranging behavior, bats are difficult to study, and establishing status and trends in the distribution and abundance of bats at appropriately broad regional scales has been challenging (Pierson 1998, Jaberg and Guisan 2001, O'Shea et al. 2003, Weller 2008, Hayes et al. 2009). Regional assessments are critical for bats because of their volancy and high spatiotemporal variability at local scales. Downward trends observed at a roost or foraging site may simply reflect a shift in local resource use or be the

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result of some localized environmental perturbation rather than an actual synoptic population decline. Regional-scale assessments drawing upon surveys of many sites that are representative of the region are needed that reflect true population conditions (O'Shea et al. 2003, Jones et al. 2009).

For many bat species, particularly those that do not congregate in large conspicuous colonies, measures of regional abundance and associated population vital rates are simply unattainable using survey methods currently available (Jaberg and Guisan 2001, O'Shea et al. 2003, Hayes et al. 2009). Alternatively, measures of occurrence or distribution, and the dynamic metapopulation-type metrics associated with rates of change in distribution can be more easily generated for bats (Jaberg and Guisan 2001, Wang et al. 2003, Greaves et al. 2006, Milne et al. 2006, Weller 2008). Although distribution is a less informative metric than abundance, it is widely considered a fundamental population attribute that is expected to reflect underlying abundance and to be suitable for assessing population status and trend at broad spatial scales (Holt et al. 2002, MacKenzie et al. 2005, Jones 2011). Furthermore, important mechanistic insights into the controls on species distributions can be gained by studying regional species distribution models (SDMs; Elith and Leathwick 2009). Because the predictions from SDMs can be mapped, and because maps are familiar to a wide range of audiences, SDMs are powerful communication tools with tremendous application to conservation scenario planning.

Recent advances in occupancy modeling (e.g., Royle and Kery 2007) provide a robust and flexible framework for developing SDMs appropriate for bats, particularly when approached from a hierarchical perspective. Hierarchical SDMs allow for environmental predictors, such as land cover, as well as issues such as imperfect detection, to be explicitly articulated. Imperfect detection is a widely recognized potential source of bias in SDMs (Kery et al. 2010, Jones 2011) that is problematic for bats, given their cryptic behavior (Duchamp et al. 2006, Gorresen et al. 2008, Weller 2008, Meyer et al. 2011). If imperfect detection is overlooked, estimates of species distribution and the effects of environmental predictors on distribution will be underestimated (Tyre et al. 2003, Kery et al. 2010).

Further extensions to hierarchical occupancy models are possible that incorporate temporal and spatial dependence structures (MacKenzie et al. 2003, Royle and Kery 2007, Royle et al. 2007, Royle and Dorazio 2008), offering additional rigor and biological realism for modeling bat distributions. This is an important capability particularly if SDMs are to be used to evaluate highly mobile species or species experiencing range contraction, avoiding the awkward assumptions of stationarity implicit in most SDMs (Zurell et al. 2009, Elith et al. 2010). Temporal non-stationarity has been widely described for local patterns of bat activity at

nightly and seasonal scales (Hayes 1997, Fischer et al. 2009), but the longevity of bats (Barclay et al. 2004) and the fidelity to roosting and foraging areas exhibited by many species (Pierson 1998, Hillen et al. 2010, Perry 2010) are likely to induce year-to-year stability at regional scales. If so, this would confer additional power to detect declines in occurrence probabilities induced by extrinsic forces such as disease and climate change, making for a robust long-term monitoring strategy. To date only a few attempts have been made to model regional bat distributions (Jaberg and Guisan 2001, Wang et al. 2003, Greaves et al. 2006, Milne et al. 2006, Weller 2008), and there are no examples where the temporal dynamics of bat distributions have been investigated at such scales.

We investigated the utility of the dynamic occupancy modeling approach for estimating status and trend of regional bat populations by developing summertime distribution models for *Myotis lucifugus* LeConte (Chiroptera: Vespertilionidae), the little brown bat (see Plate 1), in northwestern USA, using detection records obtained during 2006–2009 by the “Bat Grid” inter-agency bat monitoring program (Ormsbee et al. 2006, Hayes et al. 2009). *M. lucifugus* has long been considered one of the most abundant and widespread bat species in North America (Fenton and Barclay 1980), and we predicted the species would exhibit stable distributional patterns in our region, particularly at the spatiotemporal grain of our study. However, the species has suffered severe declines in the northeastern United States from the novel fungal disease white-nose syndrome (WNS; Blehert et al. 2009), and is now threatened with extinction in that region (Frick et al. 2010a). The rapidly expanding footprint of the wind power industry (Arnett et al. 2008) and the westward expansion of white-nose syndrome present populations of *M. lucifugus* in the northwest with unprecedented threats; rapid declines are likely in the future (e.g., Frick et al. 2010a, Dzal et al. 2011). Accelerated climate change is an additional threat to *M. lucifugus* in the region over longer time periods (Adams and Hayes 2008, Frick et al. 2010b).

Our primary objective was to establish baseline trend for *M. lucifugus* in the region against which future anticipated declines can be measured. Drawing on species–energy theory (Wright 1983), we also sought to evaluate the strength of evidence for annual net primary productivity (NPP) and forest cover as influential factors on *M. lucifugus* regional distribution patterns. From species–energy theory, the so-called “more individuals hypothesis” predicts that occurrence probabilities of a species will be higher in areas where “energy,” in the form of resources important for individual survival and reproduction, is more abundant (Wright 1983, Wright et al. 1993, Evans et al. 2005). *M. lucifugus*, like many temperate-region Vespertilionidae (Barclay et al. 2004), is tightly constrained by energy budgets and sensitive to climatic conditions for survival and repro-

duction (Humphries et al. 2002, Frick et al. 2010b). The summertime distribution and abundance of *M. lucifugus* populations depends on the ability of individual bats to efficiently procure large amounts of high-energy invertebrate prey. Frick et al. (2010b) recently demonstrated that *M. lucifugus* survival probabilities in a northeastern United States maternity colony covaried with cumulative precipitation during summer prior to the onset of hibernation. They attributed this to increased production of insect prey, which, in turn, enabled bats to enter winter hibernation with higher fat reserves. Because NPP provides a measure of plant biomass available to the primary consumers that insectivorous bats feed on, we predicted that *M. lucifugus* would occur more frequently in areas of high NPP. We also predicted that *M. lucifugus* would occur more frequently in areas of higher forest cover, which is positively correlated with NPP (Zhao et al. 2011), but that also reflects a structural aspect to habitat complexity that has been shown to be important for *M. lucifugus* and other forest-dwelling bats (Hayes 2003, Kalcounis-Rüppell et al. 2005). We utilized a Bayesian hierarchical autoregressive framework (Royle and Dorazio 2008) that allowed us to incorporate imperfect detection and temporal structure with these environmental predictors of distribution. Given the correlation in NPP and forest cover, we developed separate models for each, and also considered a reduced model with no environmental predictor. We provide a distribution map based on predicted occurrence probabilities as a function of productivity, and a map of prediction uncertainty (Rocchini et al. 2011). Drawing on lessons learned from the study, we provide suggestions for improving the design of future bat monitoring programs in addition to discussing the biogeographic insights provided by these models.

MATERIALS AND METHODS

Bat grid detection histories

We utilized detection records for *M. lucifugus* obtained during 2006–2009 from the “Bat Grid” interagency bat monitoring program in Oregon and Washington, USA, a study region of $\sim 427\,156\text{ km}^2$ (Fig. 1). The Bat Grid was established as a multi-method inventory and monitoring program for bats in Oregon and Washington in 2002 (Scott 2005, Ormsbee et al. 2006, Hayes et al. 2009), although it has recently expanded into Idaho and Montana, but no data from these states were included in our analysis. The Bat Grid for Oregon and Washington consists of a lattice of 4500 sampling units, each $10 \times 10\text{ km}$ in dimension, except in the case of edge units (Fig. 1). As part of the sampling design, sample units were nested within larger $50 \times 50\text{ km}$ grid cells, and a simple random sample of units within each grid cell was drawn in order to distribute effort in a representative manner across the region. Grid cells were selected in a purposive fashion (de Gruijter et al. 2006) in an attempt to obtain adequate representation of forest and shrub-steppe habitats, which are

associated with unique species assemblages (Verts and Carraway 1998), and to accommodate ownership and accessibility constraints. The size of sample units was chosen to match the scale of space use by species in the region, which invariably utilize large summertime home ranges and travel long distances between roosting and foraging areas (Pierson 1998), and in an attempt to ensure nonzero detection probabilities for as many of the suite of 15 species in the region as possible.

Annual trainings for methods outlined in an unpublished Bat Grid protocol (P. C. Ormsbee, *unpublished manuscript*) were held at the start of each field season. Observers were assigned to randomly selected sample units to conduct repeat surveys at multiple locations within the sample units. In some cases nonrandomly selected sample units were also surveyed because they fell within an area where bat surveys were ongoing, for example, by outside researchers or for local management unit assessments. In each case, however, data contributions were accepted only if observers followed the Bat Grid protocol, ensuring a basic level of quality control. Although the survey did not follow a strictly probabilistic sampling design, we assume that the sample adequately represented conditions across the region such that regional inferences from model results were justified.

Once a unit was selected, accessible water sites, meadows, and dry washes suitable for mist-netting and acoustic recording were identified. Multiple sites within units and across available habitat types (forest and shrub steppe) were visited in order to build detection histories for units that maximized the probability of detecting all species in the region. In some units, particularly in the drier portions of the study area, there were limited suitable sites for survey. Given the home range sizes of bats in the region (Pierson 1998), we assumed that each site within a sample unit provided approximately the same opportunities for detecting species.

Capture records for *M. lucifugus* were accumulated by placing mist nets over stream courses and other bat watering, commuting, or foraging routes. Captured individuals were identified using a regional key (Verts and Carraway 1998) and supplementary identification criteria to distinguish this species from the outwardly similar *Myotis yumanensis* (Weller et al. 2007, Rodhouse et al. 2008). The Bat Grid survey protocol provided for routine collection of wing tissue for genetic confirmation of species identification as well as for the recording of voucher echolocation calls that were used with forearm length to confirm species identification following Weller et al. (2007). Capture and handling procedures followed recommendations outlined by Kunz and Kurta (1988), and were consistent with updated guidance recently provided by Sikes et al. (2011).

Acoustic records for free-flying *M. lucifugus* were accumulated by placing Pettersson D240X full-spectrum time-expansion bat detectors (Pettersson Elektronik,

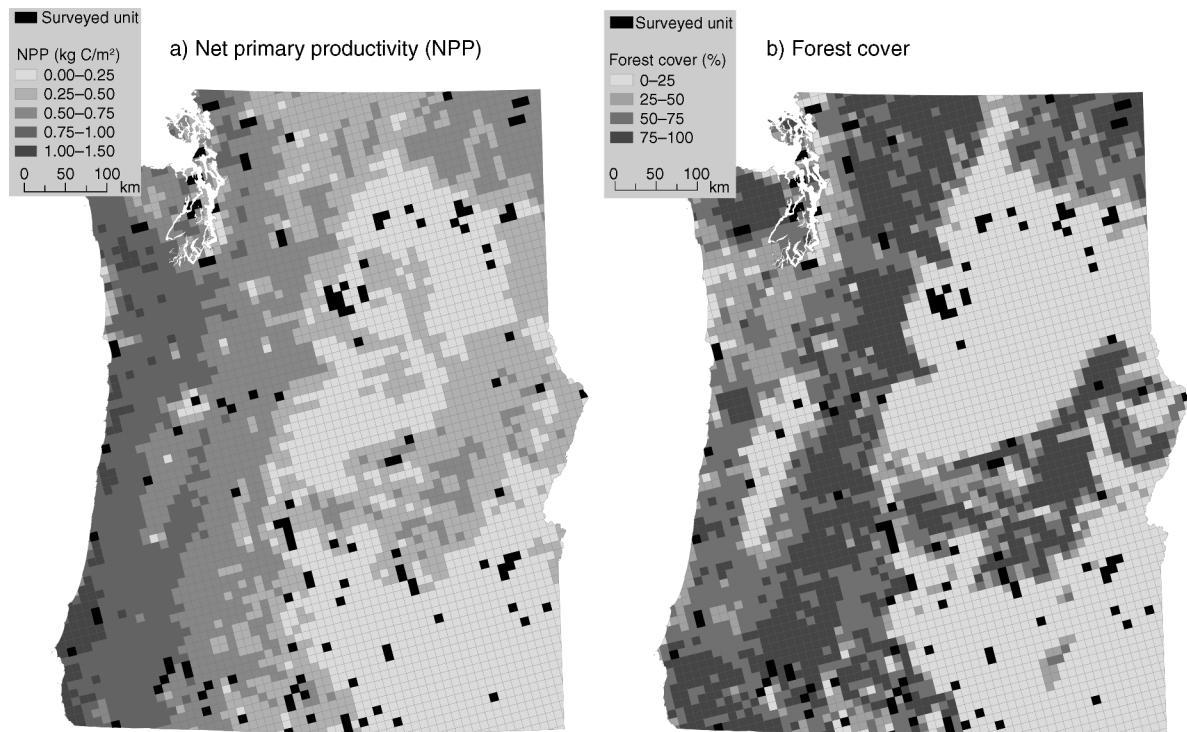


FIG. 1. Maps of (a) net primary productivity (NPP) and (b) percent forest cover across the study area encompassing Oregon and Washington, USA. The “Bat Grid” lattice of 4500 sample units, each 100 km², is shown, as are the 135 sample units surveyed at least once during 2006–2009 (black squares).

Uppsala, Sweden) along flight paths, sometimes in conjunction with capture operations. Call records were identified to species using an artificial neural network decision engine (Parsons and Szwedczak 2009, Redgwell et al. 2009) implemented in the Sonobat software program (version 3, Arcata, CA, *available online*).⁷ Sonobat 3 contains a library of ~10 000 species-known recordings from North America, with subsets of recordings organized into regional libraries that further reduce confusion in identification among allopatric species. The regional library used for our study was populated with Bat Grid voucher calls collected during the study (see Plate 1). The decision engine uses a broad suite of time–frequency and time–amplitude parameters to discriminate among species and resulting output includes discriminant function probabilities for identified species. We only accepted call records that had ≥ 0.95 probability of identification consensus among the range of decision classifiers used for *M. lucifugus*.

We established additional criteria to filter Bat Grid database records to ensure quality and to establish that detection histories were comparable across sample units and years. Records were only accepted between the dates of 1 June and 15 September and on nights where capture and recording efforts had lasted ≥ 2 hours. Detection histories were accumulated from these rec-

ords, and units that were visited >1 time per season provided information on detection probability. Our analysis was based on detection/nondetection records from 135 sample units surveyed at least once during 2006–2009. This yielded a sampling intensity of 3% of the entire lattice of 4500 sample units. Sample units were visited a maximum of 13, 8, 10, and 9 times within each of the four seasons, but most units were visited only 1–3 times per season. The number of units visited each year was 55, 56, 76, and 74, respectively. The resulting detection history matrix consisted of 135 unique sample units \times 13 potential visits for each season, arrayed over four years, but with large numbers of missing values that were estimated as part of the Bayesian inferential approach.

Productivity and forest cover

We used maps of NPP and forest cover for use as model covariates (Fig. 1). We expected the species to have higher occurrence probabilities in areas of the study region where NPP and forest cover were higher. We were particularly interested in NPP, given its relevance to species–energy theory, which has not been widely explored with bats, but we considered forest cover, which is correlated with NPP ($\rho = 0.67$ among our data sets; Fig. 1), as an alternative. *M. lucifugus* has generally been associated with forested habitats in the region (Verts and Carraway 1998, Hayes 2003, Kalcou-

⁷ <http://www.sonobat.com/>

nis-Rüppell et al. 2005), although it utilizes a range of anthropogenic and natural structures for roosting (Fenton and Barclay 1980). However, the species may also benefit from the structural complexity of forests by utilizing edge habitats and vertical canopy strata to increase foraging efficiency (Hayes 2003).

We obtained an overall estimate of NPP for each sample unit by averaging the 12-month annual NPP estimates generated from the MOD17 algorithm (Fig. 1a; Zhao et al. 2011) applied to data collected from the MODIS (Moderate Resolution Imaging Spectroradiometer) sensor. Annual variation in mean NPP during 2006–2009 was low, ranging from a high of 0.47 kg C/m² in 2006 and 2007 to a low of 0.43 kg C/m² in 2008 (SD = 0.02), and the overall average of 0.46 kg C·m⁻²·yr⁻¹ represented the four-year period well. MODIS annual NPP is served from the USGS Land Processes Distributed Active Archive Center (*available online*)⁸ at 1-km resolution. We obtained an estimate of forest cover from the Northwest Gap Analysis Program 30-m resolution land cover map (*available online*).⁹ We aggregated all areas mapped as “forest and woodland systems,” and summarized each Bat Grid sample unit by percent forest and woodland cover (Fig. 1b).

Model development

We developed multi-season occupancy models using an autoregressive parameterization described by Royle and Dorazio (2008). This approach is convenient for incorporating temporal dependence with environmental predictors, enabling us to estimate occurrence probabilities and related dynamic occupancy rate parameters, as well as to make predictions throughout the region for purposes of mapping. The hierarchical occupancy modeling approach permits the full multiparameter likelihood to be decomposed into a product of hierarchical levels, with each level representing an explicit state (e.g., occupancy) or process (e.g., observation; Cressie et al. 2009). We considered the elements of our detection history matrix as a vector of observations denoted $y_j(i, t)$, each taking a value of 1 or 0 (or “NA” for missing values) representing “detection” or “non-detection” for survey j (from 1 to 13), made in sample unit i (1 to 4500, or 1 to 135 for models not used for predicting values at unobserved sample units), during year t (2006–2009). We denote the latent, partially observed occupancy state as $z(i, t)$, and let $\psi_t = \Pr(z(i, t) = 1)$ represent the occupancy probability. Canonical dynamic occupancy rate parameters include ϕ_t , the probability of “survival” for each sample unit from t to $t + 1$, where $\phi_t = \Pr(z[i, t + 1] = 1 | z[i, t] = 1)$, and γ_t , the probability of “colonization” or recruitment from t to $t + 1$, where $\gamma_t = \Pr(z[i, t + 1] = 1 | z[i, t] = 0)$. The probability of “extinction” is $1 - \phi_t$, and with these

parameters the dynamic occupancy model can be built. We denote the initial occupancy state as $z(i, 1) \sim \text{Bern}(\psi_{2006})$, a Bernoulli trial, akin to a “coin flip,” but where the “coin” is weighted by ψ_{2006} . Occupancy states in subsequent years are denoted as $z(i, t + 1) | z(i, t) \sim \text{Bern}(\pi[i, t + 1])$, where $\pi[i, t + 1] = z(i, t) \times \phi_t + (1 - z[i, t]) \times \gamma_t$. It is in this way that the probability of occurrence “evolves” over time as a first-order Markov process, thereby accounting for temporal autocorrelation and providing a way to model the dynamics in distributional patterns and to estimate trend in ψ . In our study we focused on ψ_{2009} , the probability of occurrence in 2009, for mapping the distribution of *M. lucifugus*. This was the most recent year represented in our analysis, and ψ_{2009} provided a fully dynamic view on the contemporary status of the species in the region, conditioned on occupancy states of the previous three years. We estimated the “growth rate” in the probability of occurrence as $\lambda_t = \psi_t / \psi_{t-1}$ and trend as $\psi_{2009} / \psi_{2006}$ (MacKenzie et al. 2003, Royle and Dorazio 2008). We also considered the amount of year-to-year variability by estimating turnover, the probability that an occupied sample unit is a newly occupied one (i.e., $\Pr(z[i, t - 1] = 0 | z[i, t] = 1)$), as

$$\tau_t = \frac{\gamma_{t-1} \times (1 - \psi_{t-1})}{\gamma_{t-1} \times (1 - \psi_{t-1}) + \phi_{t-1} \times \psi_{t-1}} \quad (1)$$

(Nichols et al. 1998, Royle and Dorazio 2008).

In order to accommodate imperfect detection, we explicitly modeled the observation process as conditional on the latent occupancy state, $y_j(i, t) | z(i, t) \sim \text{Bern}(z[i, t] \times p_{ijt})$, where p_{ijt} is the probability of detecting *M. lucifugus* during survey j , given that it is present in unit i during year t . An important assumption for this model is that a species is available for observation during the entire annual survey period from 1 June to 15 September (closure), a reasonable assumption in our study region. However, assuming constant probability of detection throughout that entire annual survey period was less tenable, and we allowed detectability to vary linearly (on the logit scale) across the period by including the survey Julian date as a covariate. This represented our expectation that detectability would increase with the progression of summer, particularly as juveniles became volant. We also included the duration of each survey, in hours, as a covariate to account for variable effort, with a resulting detection model $\text{logit}(p_{ijt}) = \alpha_0 + \alpha_1 \times \text{date}_{ijt} + \alpha_2 \times \text{duration}_{ijt}$. In order to evaluate the importance of using both capture and acoustic survey methods for future monitoring study design, we estimated detection probabilities from a subset of the data representing only capture survey effort ($n = 94$, with 47, 48, 55, and 51 capture surveys in each of the four years). We compared these results with those obtained from the full multi-method data set.

We used an autoregressive reparameterization of the dynamic occupancy model in order to incorporate the

⁸ <https://lpdaac.usgs.gov/>

⁹ <http://gap.uidaho.edu/index.php/gap-home/Northwest-GAP>

additive effects of NPP and forest cover on the logit-linear scale (Royle and Dorazio 2008). Specifically, we modeled the probability of occurrence as $\text{logit}(\pi_{it}) = a_i + b_i \times z(i, t - 1) + \beta_1 \times X_1$. This model is temporally dynamic, with $\gamma_{t-1} = \text{logit}^{-1}(a_i)$ and $\phi_{t-1} = \text{logit}^{-1}(a_i + b_i)$ representing the temporal dynamics as previously described in the first paragraph of this section, and allows occurrence probabilities to vary over space as a function of X_1 , representing NPP or forest cover. Given the correlation among NPP and forest cover, we established two separate models and evaluated the predictive performance of each model. We also considered a reduced model without forest cover or NPP.

Patterns of spatial autocorrelation in bat SDMs are likely, at least for some species, due to colonial roosting behavior and the influence of environmental factors not included in SDMs that are themselves spatially structured. However, it is unlikely that residual spatial structure will persist in regional bat distribution models if the observation process (grain size) is coarser than the process(es) driving spatial autocorrelation. To test for potential spatial autocorrelation, we estimated Moran's I correlation coefficient (Cliff and Ord 1981, Wintle and Bardos 2006) for each set of model residuals, using a second-order neighborhood structure that identified the eight units adjacent to each unit i as neighbors. We computed residuals by subtracting the estimated probability of observing *M. lucifugus* at least once,

$$\psi_{it} \times \left[1 - \prod_{j=1}^j 1 - p_{ij} \right] \quad (2)$$

from observed values (either 0 or 1; Moore and Swihart 2005).

Bayesian analysis and model validation

We used WinBUGS 1.4 (Lunn et al. 2000), launched from R 2.11.0 (R Development Core Team 2010) with the R2WinBUGS library (Sturtz et al. 2005) to implement Bayesian estimation of model parameters via Markov chain Monte Carlo (MCMC) samples of posterior distributions. We used independent vague $N(0, 10)$ priors on all logit-scale parameters and a $U(0, 1)$ prior for ψ , bounded by 0 and 1 on the probability scale (Royle and Dorazio 2008, Ntzoufras 2009). We explored whether model results were sensitive to choice of prior by assigning non-informative $U(-10, 10)$ priors to all parameters, but found no meaningful differences. Posterior summaries were based on 40 000 MCMC samples of the posterior distributions from three chains run simultaneously, thinned by a factor of 10, following an initial burn-in of 5000 MCMC iterations. We assessed convergence of MCMC chains with trace plots and the Gelman-Rubin diagnostic, \hat{R} ; convergence was reached for all parameters according to the criteria $|\hat{R} - 1| < 0.1$ (Ntzoufras 2009). We compared models using the deviance information criterion (DIC),

a Bayesian analog to the more commonly used Akaike's Information Criterion (Spiegelhalter et al. 2002).

Bayesian posterior predictive P values were generated as a measure of the goodness of fit for the models (Ntzoufras 2009, Kery and Schaub 2012). These were estimated from the discrepancy between the sum of absolute values of model residuals from observed data and those from a simulated posterior predictive data set under the assumed model (Ntzoufras 2009, Kery and Schaub 2012). P values near 0.5 indicate that the model generated data similar to the observations, providing a good fit to observed data, whereas P values near 0 or 1 indicate poor fit. In order to speed MCMC convergence and improve interpretability, we input percent forest cover as proportions between 0 and 1 (e.g., 34% = 0.34) and centered the data on the mean ($\bar{X}_{\text{forest}} = 34\%$). We input NPP on original units $\text{kg C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$, but centered on the mean as well ($\bar{X}_{\text{NPP}} = 0.46 \text{ kg C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$). We also standardized survey date ($\bar{X}_{\text{date}} = \text{July 30}$) and duration ($\bar{X}_{\text{dur}} = 4.25 \text{ h}$) covariates to improve computation and interpretability of the detection model parameters.

Statistical models differ in their power to explain and predict ecological phenomena (Shmueli 2010), and the measures of convergence, DIC, goodness of fit, and parameter uncertainty used to gain insight into explanatory performance do not reflect predictive performance. To evaluate the predictive performance of models, we used k -fold cross-validation with four unique holdout subsets of data ("folds") of equal size (33 or 34 sample units) and estimated the area under the curve (AUC) of the receiver operating characteristic (Fielding and Bell 1997, Wintle and Bardos 2006, Ntzoufras 2009). The receiver operating characteristic curve plots false-positive prediction rates against true-positive prediction rates. AUC scores range from 0.5 to 1.0 and represent the percentage chance that a randomly selected unit where the target species was encountered at least once will have a higher occurrence probability than a unit where the target species was not encountered at all during the study. An AUC score of 0.5 indicates that the model discriminated among sites no better than random chance, whereas a score of 1.0 indicates that the model discriminated among sites perfectly. For each fold, models were fit to training data (101 or 102 sample units) and AUC was estimated from the fold of holdout data. This ensured that each sample unit was used once for model building and once for model validation, but not both simultaneously, which would overestimate AUC. We used the ROCR library in R to estimate AUC (R package version 1.0-4; [available online](http://CRAN.Rproject.org/package=ROCR)).¹⁰ We estimated Moran's I coefficients with the ape library in R (Paradis et al. 2004). We based inferences on the multi-season model fit to fold-1 training data ($n = 101$) with the lowest DIC and highest AUC.

¹⁰ <http://CRAN.Rproject.org/package=ROCR>

TABLE 1. Posterior summaries of parameters from the multi-season model with net primary productivity (NPP) as a spatial predictor used to make inferences on detection and occurrence probabilities and on the temporal dynamics in occurrence observed for *Myotis lucifugus* across Oregon and Washington, USA, 2006–2009.

Parameter	SD	Mean (95% CRI)
p_{2006}	0.05	0.40 (0.31, 0.50)
p_{2007}	0.04	0.47 (0.38, 0.56)
p_{2008}	0.04	0.50 (0.42, 0.58)
p_{2009}	0.04	0.52 (0.45, 0.59)
α_{date}	0.08	0.01 (−0.16, 0.15)
α_{duration}	0.04	−0.03 (−0.10, 0.04)
ψ_{2006}	0.07	0.86 (0.69, 0.97)
ψ_{2007}	0.05	0.92 (0.79, 0.99)
ψ_{2008}	0.05	0.91 (0.80, 0.98)
ψ_{2009}	0.06	0.87 (0.73, 0.98)
τ_{2007}	0.04	0.14 (0.03, 0.30)
τ_{2008}	0.04	0.04 (0.00, 0.15)
τ_{2009}	0.04	0.06 (0.01, 0.16)
λ_{2007}	0.11	1.10 (0.89, 1.34)
λ_{2008}	0.06	1.00 (0.87, 1.13)
λ_{2009}	0.08	0.96 (0.79, 1.10)
Trend	0.11	1.02 (0.82, 1.29)

Notes: Abbreviations are: p_{2006} , p_{2007} , p_{2008} , p_{2009} , detection probabilities for each year; α_{date} , coefficient of date for detection probability; α_{duration} , coefficient of duration for detection probability; ψ_{2006} , ψ_{2007} , ψ_{2008} , ψ_{2009} , occurrence probability for each year; τ_{2007} , turnover from 2006 to 2007; τ_{2008} , turnover from 2007 to 2008; τ_{2009} , turnover from 2008 to 2009; λ_{2007} , occurrence probability “growth rate” from 2006 to 2007; λ_{2008} , occurrence probability “growth rate” from 2007 to 2008; λ_{2009} , occurrence probability “growth rate” from 2008 to 2009; Trend, occurrence probability “growth rate” from 2006 to 2009; and CRI, credible interval.

RESULTS

M. lucifugus was encountered in 93 of 135 surveyed sample units during the study period 2006–2009, producing a “naïve” estimate for ψ of 0.69. Exploratory analysis indicated that these “raw” detection patterns, unadjusted for imperfect detection, were positively associated with NPP and percent forest cover, albeit only weakly so. Detectability was low relative to the assumption of perfect detection implicit in many bat distribution studies, ranging between 0.40 and 0.52, on average for a 4.25-hour survey (the mean duration) on 30 July (the mean survey date), for all years, and precisely estimated across models with SDs between 0.04 and 0.05 (Table 1). Fig. 2a shows estimated detection probabilities from the multi-season model with NPP as a covariate. There was no apparent influence of survey Julian date or survey duration on detectability (Table 1). When considering the same multi-season model with only capture data, point and precision estimates for $p_{\cdot t}$ declined substantially (Fig. 2a), as did estimates for ψ_t (Fig. 2b).

The parameter estimates among the three candidate multi-season models were similar although criteria used to evaluate the strength of evidence for each model clearly favored the NPP model. Goodness of fit was adequate and similar among models ($P = 0.37$ – 0.38). Likewise, evidence of residual spatial autocorrelation as estimated

by Moran’s I coefficients was also absent among the three models (Table 2). However, there were decreases in DIC of six units between the forest cover model and the reduced model, and a further reduction in DIC of 33 units for the NPP model. Predictive performance was poor for all models, but highest for the NPP model (Table 2). The AUC score for the NPP model for fold 1 was 0.66, but the average across all four folds was only 0.61, ranging widely from 0.50 to 0.73. Despite this variability in predictive performance, posterior distributions for parameters obtained from the NPP model varied only slightly among folds, adding confidence to the inferential reliability of the model (Fig. 3).

The estimated occurrence probability for ψ_{2009} was 0.87, providing an overall mean for the entire study region (Table 1). Occurrence probabilities trended positively with NPP and percent forest cover, and the 95% credible intervals (CRIs) for both parameters were well above 0 (Table 2). The estimated effect sizes on occurrence probabilities for NPP and forest cover were 4.8 and 2.9 (logit scale; Table 2). Therefore, an increase

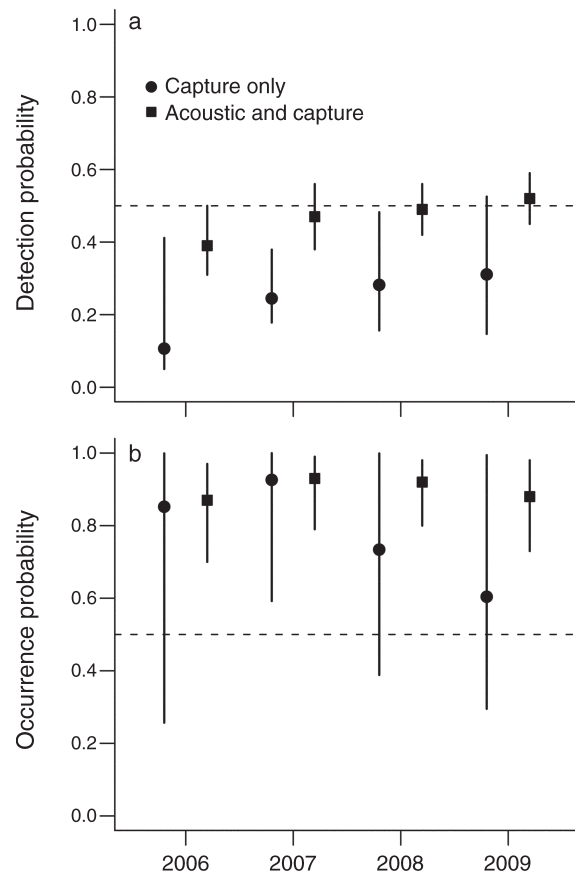


FIG. 2. A comparison of (a) detection probabilities and (b) occurrence probabilities, ψ_t , for the little brown bat *Myotis lucifugus* (with 95% credible intervals), obtained from the NPP model using fold-1 data (see *Materials and methods: Bayesian analysis and model validation* for more details) with capture only (circles) and capture and acoustic (squares) detection records.

TABLE 2. Model selection diagnostics and covariate parameter estimates (posterior summaries) for three multi-season occupancy models fit to our *Myotis lucifugus* detection history matrix.

Model	DIC	AUC	Moran's I^\dagger	Bayes P	β_1 (95% CRI)
Net primary productivity (NPP)	1049	0.66	−0.18 (0.17)	0.38	4.8 (2.0, 8.1)
Percent forest cover	1082	0.63	−0.16 (0.22)	0.37	2.9 (1.0, 5.3)
Reduced, no covariate	1088	0.50	−0.18 (0.18)	0.37	NA

Note: Abbreviations are: DIC, deviance information criterion; AUC, area under the curve; β_1 , occurrence probability model covariate; CRI, credible interval; and NA, not available.

† Parentheses include the P value for the Moran's I coefficient, indicating that these coefficients did not differ significantly from 0.

in NPP of $0.1 \text{ kg C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ was associated with an increase in the odds of *M. lucifugus* occurrence of $\exp(4.8 \times 0.1) = 1.6$ times (CRI 1.22–2.24). A 10% increase in forest cover was estimated to increase the odds by 1.3 times (CRI 1.11–1.70). However, there was uncertainty in the magnitude of the relationship with ψ_{2009} at low values of NPP and forest cover, reflected in the CRI widths. This apparently compromised the ability of the models to predict well across such a large region.

We mapped the predicted occurrence probabilities for 2009 estimated from the NPP model, which ranged from 0.38 in arid portions of Oregon and Washington to 0.99 across much of the western portion of the study region (Fig. 4a). We also mapped prediction error, the posterior density SD (Fig. 4b). Prediction error was inversely related to occurrence probabilities, reflecting the uncertainty encountered in the low end of the productivity gradient. At a cutoff value of 0.62, where the “phi” correlation coefficient (Sing et al. 2009) was highest ($\max[r_\phi] = 0.45$), the overall accuracy and error of the fold-1 NPP model was 76% and 24%. The true positive rate of prediction (sensitivity) was 100%, whereas the true negative rate (specificity) was only 27%, further illustrating the uncertainty in the low end of the productivity gradient.

We based subsequent inferences on temporal variability and trend from parameter estimates provided by the NPP model, although all three models yielded similar results for these parameters. Temporal variability was very low over the four years of observations (Fig. 5). Turnover, the probability that an occupied sample unit was a newly occupied one, was near 0 across all three yearly occupancy state transitions (Table 1). Estimates of directional change in occurrence probabilities over time provided by λ and trend indicated no change over the four-year study period, with relatively high precision (e.g., SD for trend = 0.11; Table 1, Fig. 5).

DISCUSSION

We modeled the summertime distribution of the common bat species *M. lucifugus* across a substantial portion of its range in northwestern USA. Our models are dynamic, accounting for non-stationarity over time and detectability. These are key issues that are particularly relevant for cryptic and highly mobile taxa such as bats. We demonstrated that the species is indeed widespread

across our region, but that it appears to occur with greater frequency in forested regions with higher NPP. A substantial portion of our study area is semiarid shrub steppe (Fig. 1b), and while the species also occurs in this environment, our parameter estimates suggest that the qualitative differences in productivity and structural complexity between forested and non-forested portions of the region influence *M. lucifugus* demographic rates and, therefore, its probabilities of occurrence. Such insights are not reflected in typical static range maps for this species, and the strength of evidence for forest cover and NPP increased after imperfect detection was accounted for. The occupancy modeling approach that we used provides a robust framework for developing SDMs for bats at broad, regional scales, and our study demonstrates how this can be applied widely to monitoring bat populations. The need for such an approach is compelling given the numerous and growing threats facing bat populations around the world (Jones et al. 2009) and the challenges encountered by past efforts to assess bat populations (O'Shea et al. 2003, Hayes et al. 2009).

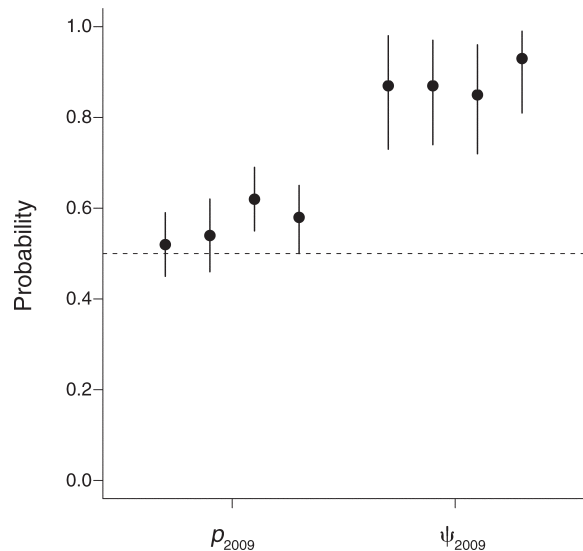


FIG. 3. Posterior means and 95% credible intervals for detection and occurrence probabilities from each of four “folds” used in k -fold cross-validation of the NPP model (see *Materials and methods: Bayesian analysis and model validation* for more details on k -fold cross-validation). The detection probability for 2009 is shown by p_{2009} , and ψ_{2009} is 2009 occurrence probability.

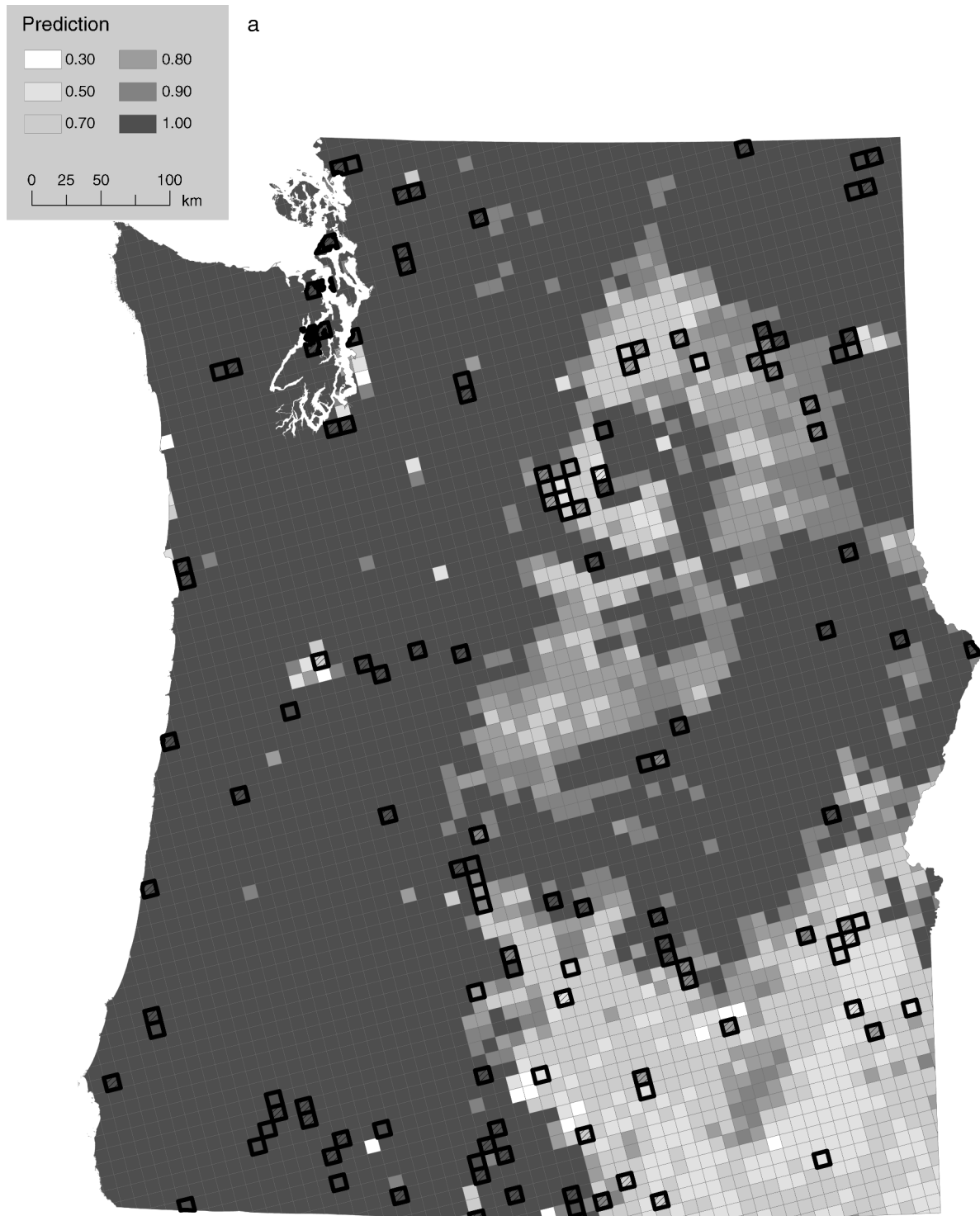


FIG. 4. Maps of (a) predicted “dynamic” occurrence probabilities and (b) prediction uncertainty for *Myotis lucifugus* based on posterior means and SDs of ψ_{2009} estimated from the NPP model. Observed sample units are outlined. Hatching in boxes indicate units where *M. lucifugus* was detected at least once. Units outlined with black boxes with no hatching indicate units where the species was never detected during the four-year survey period.

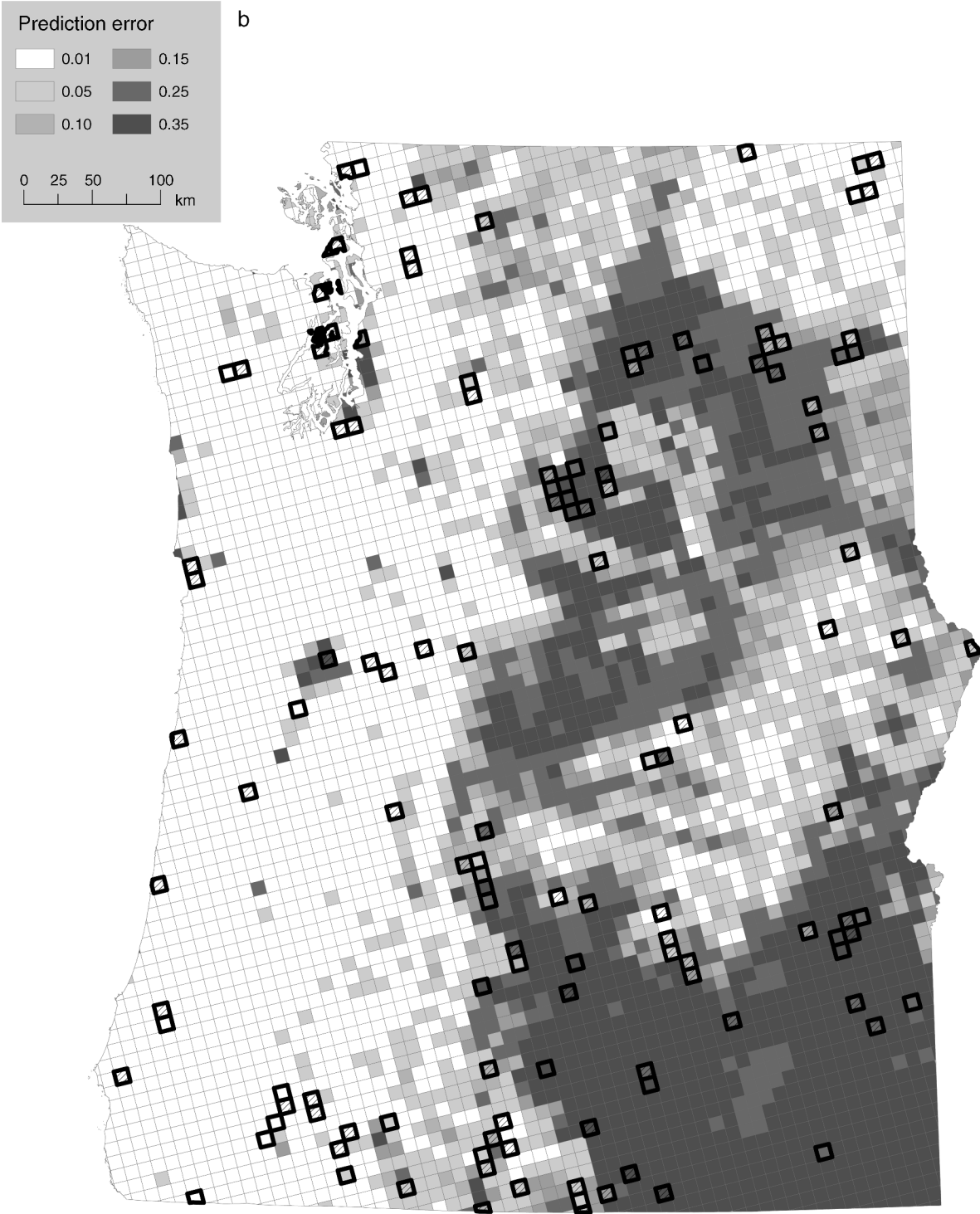


FIG. 4. Continued.

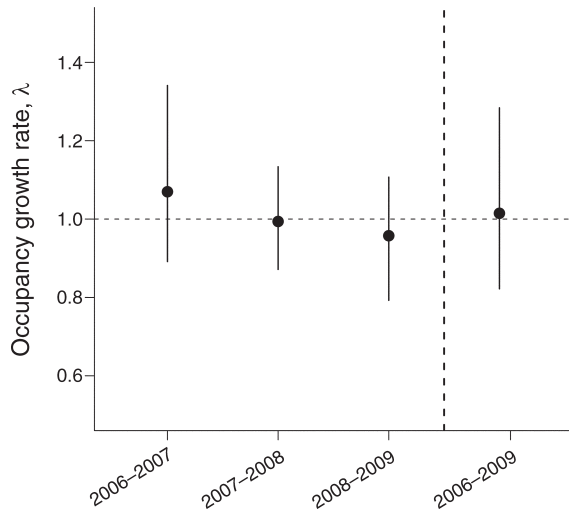


FIG. 5. The “growth rate”, λ , in *M. lucifugus* occurrence probabilities over the study period, 2006–2009. The trend for the entire period, $\lambda_{2009/2006}$, is shown to the right of the vertical dashed line.

Dynamic distribution models for bat monitoring

There were several rather surprising results from our study that have important implications for the design and interpretation of other bat distribution modeling and monitoring efforts. Despite the commonness of *M. lucifugus*, it was still detected imperfectly, with only at most a 59% average rate (upper CRI for p_{2009} ; Table 1) of detection during a typical late-July survey. Our estimates of p were strikingly similar to the estimate of 0.46 provided by Weller (2008) from a study in the western forests of our region. The naïve estimate of ψ was rather low for this abundant species (0.69), even with numerous visits to some sample units, and increased considerably after accounting for imperfect detection. Furthermore, there was considerable improvement in estimates of both p and ψ when acoustic detection methods were included, suggesting that capture surveys alone are insufficient, even for a species as common as *M. lucifugus*.

A number of studies have shown how estimates of occupancy as well as the estimated effect sizes of covariates thought to influence occupancy are biased low when imperfect detection is unaccounted for (e.g., Tyre et al. 2003, Kery et al. 2010, Kery and Schaub 2012). Our study then would suggest that most bat distribution maps are under representative, capturing only “apparent” rather than true distributional patterns (Kery et al. 2010). It is therefore imperative that the design of future bat studies accommodates the need for multiple revisits within seasons in order to permit the estimation of detection probabilities, and it seems equally important to include acoustic detection methods, even when studying species that are easily captured with mist nets (Flaquer et al. 2007, Meyer et al. 2011).

MacKenzie and Royle (2005) have provided general guidance on how to balance the trade-off in allocation of effort between overall sample size and number of within-season revisits to sample units. For a species like *M. lucifugus*, which is widespread but rather poorly detected, they recommend ≈ 4 revisits, although more may be needed if a suite of bat species are targeted that include some rarer species (MacKenzie and Royle 2005, Weller 2008). In our study, some of the effort expended on excessive revisits (e.g., 13) could be redirected to increase overall sample size. While survey date and duration did not apparently influence *M. lucifugus* detectability in our study, these factors likely affect other species such as those that migrate or those that begin foraging later at night. We encourage future studies to routinely address these and other kinds of factors such as the air temperature during surveys in order to improve estimates of detectability.

We found the temporal stability estimated by our models noteworthy, although we had suspected such a pattern might exist. Over the four years of study there was inconsequential variability observed in occurrence probabilities (Figs. 2 and 5). This is striking but consistent with our understanding of bat life history, in general. Longevity and low fecundity, particularly in temperate-region Vespertilionidae, cause bat populations to change slowly (Barclay et al. 2004). Apparently this is enhanced by the site fidelity both within and among seasons that has been observed for many bat species (Hillen et al. 2010, Perry 2010). It is for these reasons that bats have been suggested as useful bioindicators (Jones et al. 2009). Unfortunately, it is also these very same life history traits that make species like *M. lucifugus* capable of rapid and sustained declines, with very slow recovery (Frick et al. 2010a). Our estimate of trend provides an important baseline against which future anticipated declines in *M. lucifugus* occurrence can be measured.

We found no evidence of residual spatial autocorrelation in our models, despite the colonial nature of *M. lucifugus* and the likely existence of other spatially structured influential environmental factors, such as roost abundance. We suspect that this is due to the coarse scale of the Bat Grid. However, for other species and in other environments, even a 100-km² grain may not subsume spatial autocorrelation. Accounting for the phenomenon should become routine practice for future bat SDMs (Beale et al. 2010). The Bayesian autoregressive occupancy model provides a useful tool for explicitly modeling residual spatial structure (Wintle and Bardos 2006, Royle and Dorazio 2008), although large sample sizes are required to do so. We obtained a 3% survey intensity of the Bat Grid lattice (135 of 4500 sample units), which was adequate for estimating the structural parameters of our model with sufficient precision. However, in circumstances involving stronger residual autocorrelation a sampling intensity approaching 5% would provide future studies the necessary

flexibility to model spatial autocorrelation directly (Hoeting et al. 2000, Wintle and Bardos 2006). Sample size is also an important consideration if distribution maps based on predicted occurrence probabilities is desired. Statistical models rarely do both explanation and prediction equally well and prediction tends to require larger sample sizes (Shmueli 2010), an important consideration when designing multipurpose monitoring.

Productivity and species–energy theory

Our study points to environmental productivity as an important broad-scale driver of *M. lucifugus* distribution. The probabilities of *M. lucifugus* occurrence during summer at the coarse scale of the Bat Grid increased in areas of high NPP and forest cover (Fig. 4). This may be the result of higher survival rates among individuals and therefore higher abundance in mesic regions of the study area where plant biomass and invertebrate herbivore biomass is greater. This was an explanation provided by Frick et al. (2010b) for the observed correlation between higher survival probabilities of *M. lucifugus* in a New Hampshire maternity colony in years with wetter summers. *M. lucifugus* feeds on small flies, including mosquitoes, and other winged invertebrates, and many of these species have aquatic life stages whose populations increase in wet years (Landesman et al. 2007).

The relationship between *M. lucifugus* occurrence probabilities and productivity is consistent with species–energy theory and the associated “more individuals hypothesis,” which predicts that population abundance will be higher in areas of higher available energy (Wright 1983). While the hypothesis is most often applied to test patterns of species richness (Hawkins et al. 2003), it has also been used to explain occurrence patterns of individual species (Wright 1983, Wright et al. 1993). At continental scales, the negative correlation between bat species richness and the latitudinal gradient is well described (Rosenzweig 1995, Willig et al. 2003) and the gradient may be a proxy for available energy. McCain (2007) provided evidence for a general mid-elevation peak in bat species richness and in species abundance that is likely to also reflect environmental productivity. Roost habitat availability has a fundamental influence on the distribution of temperate bats at regional and local scales (Humphrey 1975) and may mediate the apparent species–energy relationship. However, this should be of less importance for species with highly plastic roosting habits like *M. lucifugus*, allowing available energy to be a stronger influence.

The apparent relationship between environmental productivity and *M. lucifugus* distribution has implications for the potential effects of accelerated climate change on the species. In our study region, climate change is projected to result in net aridification as temperatures increase and snowpack and stream flows decrease rapidly earlier in the season (Luce and Holden 2009, Mote and Salathé 2010). Frick et al. (2010b) pointed to a similar kind of scenario in the northeastern



PLATE 1. (Top) *Myotis lucifugus* captured during the study in Moses Coulee, Washington, USA. (Bottom) A Bat Grid participant collects a voucher recording of a *Myotis* captured during the study in Oregon, USA, for purposes of building the regional call library. Photo credits: Michael Durham.

United States, and Adams and Hayes (2008) have provided evidence more generally that bats in the arid western United States are likely to suffer declining reproductive success under accelerated climate change due to reduced water availability. The MOD17 algorithm used to measure NPP has proven to be sensitive to



FIG. 6. Example expansion of the Bat Grid to areas in the western USA where federal land ownership is at least 50%. Black cells (sample units) were selected using a spatially balanced random sampling algorithm (Rodhouse et al. 2011). This figure demonstrates how the Bat Grid could be used to obtain statistically valid inferences about status and trend of bat populations across large portions of North America.

El-Niño Southern Oscillation (ENSO) drought events, reflected in negative NPP anomalies (Zhao et al. 2011). This suggests both a mechanism to explain and a strategy to measure climate-induced declines in *M. lucifugus* populations in western North America over time. Our autoregressive modeling approach could readily be extended to allow NPP to vary over time, with lag effects modeled for *M. lucifugus* occurrence and sample unit “survival” probabilities (ϕ_t). Although annual NPP did not vary over the four years of our study, it is likely to do so over longer time frames. Other measures of productivity may prove even more useful than annual summaries for bats. For example, Huston

and Wolverton (2011) recently introduced the concept of “ecologically and evolutionarily significant” growing-season NPP (eNPP), which was a better predictor of body size than annual NPP. Such fine tuning of productivity offers a promising direction for future research and could lead to a stronger mechanistic linkage between species–energy theory and broadscale patterns of bat species richness and abundance.

A strategy for robust monitoring of bat populations

M. lucifugus has long been considered a very secure species, and only recently has concern for the species’ welfare arisen. Frick et al. (2010a) estimated a 73%

decline in the regional population of northeastern USA over four years following the outbreak of white-nose syndrome in 2006, and predicted that regional extinction is almost certain under current rates of decline by 2026. Dzal et al. (2011) also documented a 78% decline in summertime activity of *M. lucifugus* in an area near the epicenter of WNS. This rapid change in conservation status is startling. Although white-nose syndrome has not yet arrived in northwestern USA, it is likely to do so within the next few years given the rate of spread across eastern North America since 2006 (Foley et al. 2011). While it is unclear whether the disease will be as deadly in the west, it is likely to leave animals with wing damage, which may reduce individual fitness (Reichard and Kunz 2009, Cryan et al. 2010), making them even more vulnerable to climate-induced changes to NPP and the associated impacts on primary consumers. The additive mortality from white-nose syndrome, collision, and barotraumas at wind energy sites, and stress induced by accelerated climate change suggests that substantial declines in *M. lucifugus* and other western North American Vespertilionidae are imminent. Developing effective conservation strategies in response to this growing crisis requires an understanding of the rates of change in bat populations and the factors driving those changes at broad scales (Jones et al. 2009). Our study outlines a path forward for obtaining the necessary information to gain this understanding.

We suggest that a standardized approach to monitoring like the Bat Grid could be deployed across the USA to provide a statistical survey design for robust inference about trends in occurrence probabilities to broad regions of the country. A simple but powerful improvement to the existing Bat Grid survey design could be made by employing a spatially balanced probabilistic sampling algorithm to select units for survey, as proposed by Rodhouse et al. (2011). Spatially balanced designs result in an ordered list of sample units with the property that any ordered subset also remains spatially balanced, allowing for units to be replaced if necessary, and for sample sizes to be adjusted as available resources change. Such an approach can accommodate some of the logistical challenges that are encountered when designing bat surveys. For example, sample units could be stratified within a spatially balanced design so as to ensure adequate representation across key habitat types such as forest and non-forest land cover. The issue of accessibility can be addressed by developing a sampling frame that accounts for ownership, and an a priori rule for replacing units that are not accessible by following the order of the spatially balanced list. In Fig. 6 we illustrate such a scheme for portions of the western United States where the area of sample units contain $\geq 50\%$ federal ownership. The spatially balanced survey design can also readily accommodate nested multi-stage designs (e.g., sample sites within areal units as employed by the Bat Grid), providing even greater flexibility and statistical robustness. A flexible probabilistic design

underpinning the model assumptions inherent in the occupancy modeling approach would extend statistical inferences about bat populations across very large portions of North America. This would be an unprecedented, but desperately needed accomplishment.

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