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# Neighborhood and habitat effects on vital rates: expansion of the Barred Owl in the Oregon Coast Ranges

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*Abstract.* In this paper, we modify dynamic occupancy models developed for detection-nondetection data to allow for the dependence of local vital rates on neighborhood occupancy, where neighborhood is defined very flexibly. Such dependence of occupancy dynamics on the status of a relevant neighborhood is pervasive, yet frequently ignored. Our framework permits joint inference about the importance of neighborhood effects and habitat covariates in determining colonization and extinction rates. Our specific motivation is the recent expansion of the Barred Owl (*Strix varia*) in western Oregon, USA, over the period 1990–2010. Because the focal period was one of dramatic range expansion and local population increase, the use of models that incorporate regional occupancy (sources of colonists) as determinants of dynamic rate parameters is especially appropriate.

We began our analysis of 21 years of Barred Owl presence/nondetection data in the Tyee Density Study Area (TDSA) by testing a suite of six models that varied only in the covariates included in the modeling of detection probability. We then tested whether models that used regional occupancy as a covariate for colonization and extinction outperformed models with constant or year-specific colonization or extinction rates. Finally we tested whether habitat covariates improved the AIC of our models, focusing on which habitat covariates performed best, and whether the signs of habitat effects are consistent with a priori hypotheses.

We conclude that all covariates used to model detection probability lead to improved AIC, that regional occupancy influences colonization and extinction rates, and that habitat plays an important role in determining extinction and colonization rates. As occupancy increases from low levels toward equilibrium, colonization increases and extinction decreases, presumably because there are more and more dispersing juveniles. While both rates are affected, colonization increases more than extinction decreases. Colonization is higher and extinction is lower in survey polygons with more riparian forest. The effects of riparian forest on extinction rates are greater than on colonization rates. Model results have implications for management of the invading Barred Owl, both through habitat alteration and removal.

*Key words: autologistic; Barred Owl; detection; habitat; metapopulation; Northern Spotted Owl; presence.*

## INTRODUCTION

Few populations are sufficiently isolated that they are not influenced by the dynamics of neighboring populations. Neighbors serve as sources of immigrants to existing focal populations and as sources of potential colonists to locations not currently occupied by a species. Within populations of territorial species, the rates at which territories are colonized will also often be determined by the density of neighboring occupied territories. Development of models for population dynamics thus requires at least some consideration of neighborhood effects. The relevance of such effects is acknowledged in studies of metapopulation dynamics (e.g., Hanski 1999) and biological invasions (Williamson 1999), for example. Here we present a general approach to the modeling of occupancy dynamics in a manner that can accommodate neighborhood effects. While we are motivated by a specific investigation of an invading species, our approach should be useful in many other applications.

Expansions of species into previously unoccupied areas are important from both ecological and conservation perspectives. We are often only aware of invasions, and thus able to systematically collect data on them, after species are well established in new areas. As a consequence, we usually do not observe the initial stages of invasion, and our ecological understanding of most invasive species is based on static snapshots in the latter

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stages of invasions. Drawing strong inferences about structuring dynamic processes based on established, static patterns of species distribution is very difficult (e.g., Connell 1980, MacKenzie et al. 2006). Thus, we would like to take full advantage of those situations where we can make direct observations of the transient dynamics associated with species invasions, as they should permit stronger inferences about the expansion process itself and the consequences of such expansion for the preexisting ecological community (Skellam 1951, Williamson and Fitter 1996).

From a conservation perspective, invasive species represent an enormous worldwide problem (Kareiva et al. 1996, Williamson and Fitter 1996, Shigesada and Kawasaki 1997, Simberloff et al. 1997, Williamson 1999). Biologists try to develop models that can be used to predict future expansion of both currently invading species and species thought likely to invade (Williamson 1999). Such models are more likely to yield reasonable predictions if they are relatively mechanistic and based on inferences from recent expansion dynamics. Observations of a species expanding into a new area permit direct inferences about interactions with other species, especially when potentially affected species have been monitored before, as well as during and following, the invasion.

In this paper, we develop an approach for modeling occupancy dynamics based on surveys that yield detection-nondetection data. The approach is very general, and we use it to understand the local occupancy dynamics of an invading species, the Barred Owl (*Strix varia*), in Western Oregon over 21 years (1990–2010). We model changes in occupancy as a function of local rates of colonization and extinction. These rate parameters are themselves modeled as functions of site-specific habitat covariates and of current levels of occupancy in the local neighborhood, where neighborhood is defined very flexibly. These levels of neighborhood occupancy are not standard covariates, as they cannot be directly measured, but must be estimated in the face of nondetection (failure to always detect the species during surveys where the species is present). The novel methodological component of this work is development of a likelihood framework permitting inference when extinction and colonization at one patch (sample unit) are functions of occupancy of other patches within a specified neighborhood. We follow others by referring to such models as "autologistic." Although our specific ecological focus is on the dynamics of an invading species, we note that a dependence of local rates on neighborhood occupancy state is common to other population models that incorporate space (e.g., many metapopulation models; see Gotelli and Kelley 1993, Hanski 1999). Thus, we expect our inference methods to prove useful for investigators seeking to estimate metapopulation parameters in systems with habitat heterogeneity and detection probabilities less than one.

The modeling approach is related to several other recent contributions. Wikle (2003) modeled the expansion of House Finches (*Carpodacus mexicanus*) spreading from their release point on Long Island. He used autologistic modeling with North American Breeding Bird Survey data, but did not deal with nondetection, in that house finches were assumed to be absent from routes at which they were not detected. MacKenzie et al. (2006) modeled house finch expansion using the same data as Wikle (2003), but with models that directly incorporated nondetection. However, they did not use autologistic modeling, but rather used multiseason occupancy models (MacKenzie et al. 2003, Royle and Kéry 2007) to model expansion as an interaction between distance (from initial release site) and time (years since release). We view this approach as more phenomenological (less mechanistic) than the autologistic approach, and therefore less likely to produce good predictions. Barbraud et al. (2003) modeled probability of colonization for patches in one region as a function of probability of local extinction of patches in a neighboring region, accounting for detection probability in the modeling. This work was similar in some respects to that presented here, but model development applied to a very specific biological situation and did not include general effects of neighborhood occupancy. Our underlying model is most similar to the hierarchical approach of Bled et al. (2011; see related approaches of Hooten et al. 2007, Hooten and Wikle 2008) who modeled the expansion of Eurasian collared-dove (*Streptopelia decaocto*) in the United States. The chief computational difference between the work of Bled et al. (2011) and ours is the use by the other authors of Markov chain Monte Carlo methods vs. our use of maximum likelihood. The chief ecological difference is that we model focal patch vital rates as a function of occupancy of the entire study area rather than of a small neighborhood surrounding each focal site. This difference is motivated by the local spatial extent and more detailed spatial grain of our study system as compared to previous studies.

The specific motivation for our work is the recent expansion of the Barred Owl throughout the Pacific Northwest over the last few decades. The Barred Owl was historically widely distributed across south-central and southeastern parts of Canada, down through the eastern half of the United States, all the way to an isolated population in Mexico. Over the last century, researchers have noted an expansion of its geographic range (Grant 1966, Shea 1974, Wright and Hayward 1998, Holt et al. 2001, Priestley 2004, Gutiérrez et al. 2007, Livezey 2009*a*). Barred Owls were first documented in northwestern Oregon in 1974 (Taylor and Forsman 1976) and have spread through Oregon, reaching Northern California by 1981 (Dark et al. 1998). We derive our results from surveys intended primarily for monitoring of Northern Spotted Owl (*Strix occidentalis caurina*) populations. Recently, researchers have begun to survey specifically for Barred Owls leading to higher associated detection probabilities (Wiens et al. 2011) and inference at the scale of Barred Owl territories; however, data from these surveys are only available over

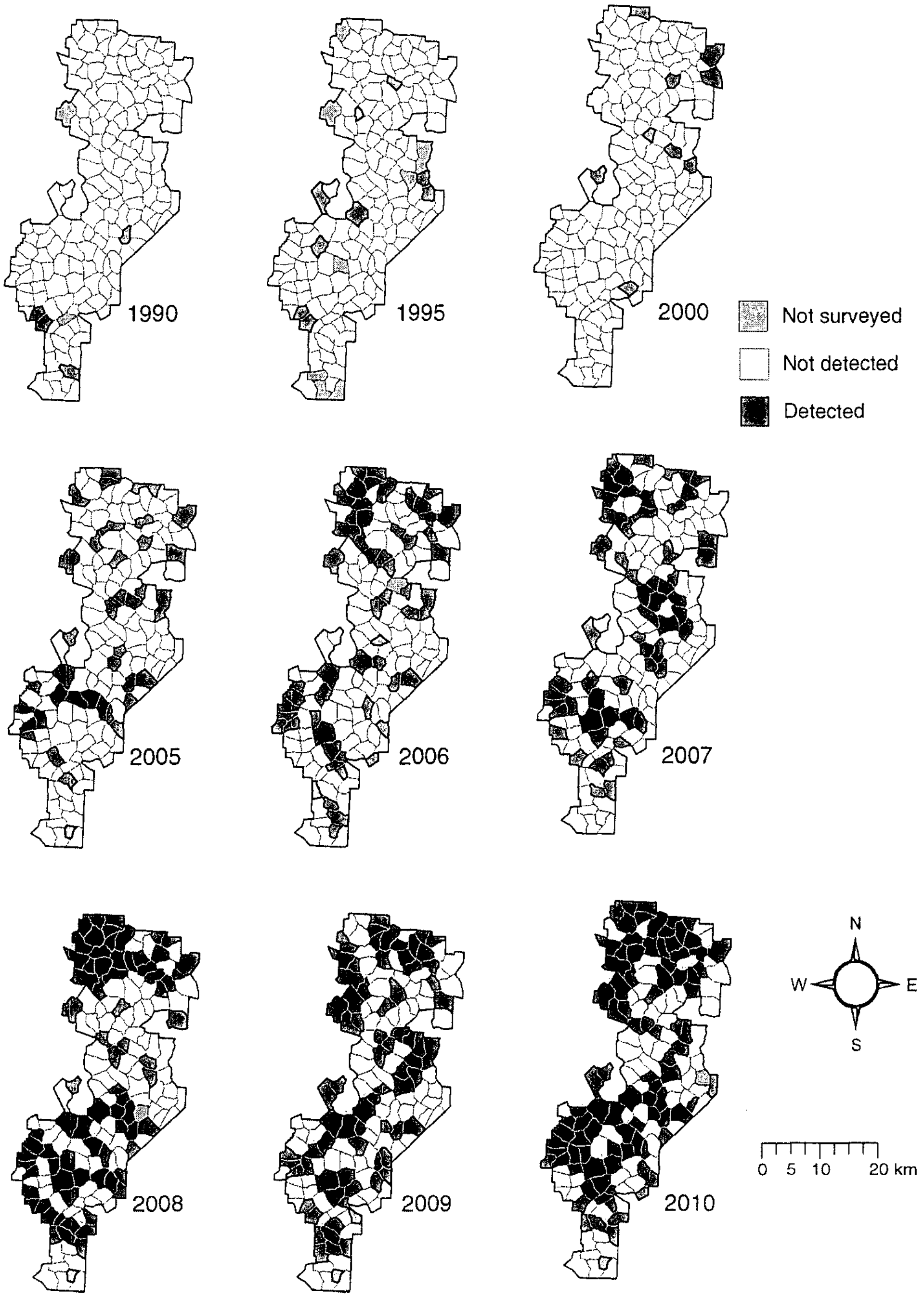

FIG. 1. Survey polygons with Barred Owl detections for selected years.

a limited time span and thus do not allow us to make inference about dynamics over the course of the invasion. Because the surveys that we use were designed for another species, occupancy is measured at a larger spatial scale than that of individual Barred Owl territories and there is considerable heterogeneity in detectability for Barred Owls. We model this heterogeneity using covariates that account for different times of day, different survey methods, the amount of time spent on the survey, and the knowledge that Barred Owl territories are smaller than the survey polygons.

The expansion of Barred Owls is of great interest because of its perceived negative impact on Northern Spotted Owl demographics (Dunbar et al. 1991, Dark et al. 1998, Kelly et al. 2003, Olson et al. 2005, Buchanan et al. 2007, Gutiérrez et al. 2007, Dugger et al. 2011, USFWS 2011, Van Lanen et al. 2011). Because the focal period was one of dramatic range expansion and local population increases for the Barred Owl (Fig. 1), the use of models that incorporate regional occupancy (sources of colonists) as determinants of dynamic rate parameters is especially appropriate. We hypothesize that models that include regional occupancy as a predictor of per-patch colonization and extinction rates will be better supported by the data then models that assume either constant rates of colonization and extinction or year-specific rates unrelated to regional occupancy. To test this hypothesis we develop a set of seven models, some of which include autologistic functions for local extinction and/or colonization and others that do not incorporate such relationships. We then test whether the best model(s) from this set can be improved by allowing extinction or colonization rates to vary with site-specific habitat covariates (in addition to regional occupancy).

We begin by describing the basic modeling approach and our maximum likelihood implementation. Next, we present results of a small simulation study designed to test the adequacy of our modeling and computational approach. We then focus on the expansion of the Barred Owl in a large study area in western Oregon Coast Ranges.

## METHODS

### *Autologistic modeling*

Our approach is an extension of the basic multiseason occupancy model of MacKenzie et al. (2003). The extension involves inclusion of a functional relationship between the vital rates (probabilities of extinction and colonization) that govern occupancy dynamics of a patch, and the occupancy status of "neighboring" patches (e.g., Wikle 2003, Royle and Dorazio 2008, Bled et al. 2011). Define the probability of extinction as $\varepsilon_{i,t} = \Pr(\text{patch } i \text{ not occupied at } t+1 \mid \text{patch } i \text{ occupied at } t)$ and the probability of colonization as $\gamma_{i,t} = \Pr(\text{patch } i \text{ occupied at } t+1 \mid \text{patch } i \text{ not occupied at } t)$. Define occupancy probability as $\psi_{i,t} = \Pr(\text{patch } i \text{ is occupied by focal species at } t)$. The probability that patch $i$ is occupied at time $t+1$ is

$$\psi_{i,t+1} = \psi_{i,t}(1-\varepsilon_{i,t}) + (1-\psi_{i,t})\gamma_{i,t}. \tag{1}$$

Under the autologistic modeling approach, probabilities of local extinction and colonization are influenced by the occupancy status of neighboring patches, where "neighbor" may be defined in a variety of ways, depending on the ecology of the modeled system. The definition of neighborhood should correspond to ecological knowledge of movement and dispersal distances of the focal species. For species with very limited movement, neighborhood of a focal patch may be restricted to the set of other patches whose borders touch those of the focal patch. For wide-ranging species, the neighborhood may include patches that are not in direct contact with the focal patch but lie within some specified distance. In some instances, such as ours, the focal species has dispersal capabilities that are roughly equivalent to the size of the study area, and it will make sense to include all other patches within the entire study area.

Depending on the nature of the biological situation, we can envisage using either the total number of occupied patches in a neighborhood or the average probability of occupancy for patches in a neighborhood to model extinction and colonization probabilities. Specifically, we can estimate the number of occupied patches ($\hat{\theta}^{n_i}_{i,t}$) in the neighborhood of focal patch $i$ as

$$\hat{\theta}^{n_i}_{i,t} = \sum_{j\in\{n_i\}} \hat{\psi}_{j,t} \tag{2}$$

where $n_i$ denotes the set of patches constituting the neighborhood of focal patch $i$, and $\hat{\psi}_{j,t}$ is the estimated probability that neighboring patch $j$ is occupied at time $t$. The average occupancy of a patch within a neighborhood can be estimated similarly:

$$\hat{\bar{\psi}}^{n_i}_t = \frac{1}{l_i}\sum_{j\in\{n_i\}} \hat{\psi}_{j,t} \tag{3}$$

where $l_i$ is the number of patches located in the neighborhood of focal patch $i$. Eqs. 2 and 3 will only lead to different inferences when individual patches have different numbers of neighbors. Although our development is general, in all our analyses, we rely on $\hat{\bar{\psi}}^{n_i}_t$, as defined in Eq. 3. However, since we calculate it over the whole study area we refer to as $\hat{\bar{\psi}}^{R}_t$.

Information available for the different patches in a neighborhood may vary, such that we can distinguish three types of occupancy parameters, $\psi_{j,t}$, that can be estimated. The first type of parameter, $\psi^{*}_{j,t}$, corresponds to predicted occupancy for a patch that was not surveyed at all. This parameter, known as the unconditional probability of occupancy, can be calculated based on the site-specific covariate values for patch $j$, or, in the absence of patch-level covariates, as the average occupancy probability for a region in which the patch is located. The next two types of parameter correspond to patches that were surveyed and found to either contain the species, $\psi^{(1)}_{j,t} = 1$, or not, $\psi^{(0)}_{j,t}$. $\psi^{(0)}_{j,t}$ is the so-called conditional probability of occupancy for cells that were surveyed, but yielded no detections (MacKenzie et al. 2006:97–98).

Autologistic modeling of probabilities of local colonization and/or extinction can then be based on either the estimated number of occupied patches in the neighborhood (Eq. 2), the average predicted probability of occupancy for a patch in the neighborhood (Eq. 3), or some weighted (e.g., by distance from focal patch, patch size, etc.) average of probabilities of occupancy for patches in the neighborhood. For example, colonization probability can be modeled as

$$\gamma_{i,t} = \frac{\exp(\beta_{0,t} + \beta_1\hat{\bar{\psi}}^{n_i}_t + \beta_2 X_{i,t})}{1+\exp(\beta_{0,t} + \beta_1\hat{\bar{\psi}}^{n_i}_t + \beta_2 X_{i,t})} \tag{4}$$

where $X_{i,t}$ specifies the value of a habitat covariate for patch $i$ at time $t$. So Eq. 4 models colonization probability for patch $i$ at time $t$ (probability that empty patch $i$ at time $t$ will contain the focal species at time $t+1$) as a function of average probability of occupancy for the patches in the neighborhood of patch $i$, as well as of the habitat covariate for patch $i$ at $t$. The intercept term in Eq. 4 is written as a function of time, but in many applications this term will be a constant. This basic model can be extended in many ways including: use of quadratic terms for neighborhood occupancy or habitat effects, use of separate parameters for initial colonization and recolonization of a patch (Bled et al. 2011), etc. We would typically expect $\beta_1 > 0$, reflecting a higher probability of colonization when average occupancy of neighboring patches (sources of colonists) is higher. Extinction probability can be modeled in the same manner as Eq. 4, and we would expect $\beta_1 < 0$, with the rescue effect (Brown and Kodric-Brown 1977) leading to lower extinction probabilities when average neighborhood occupancy was higher.

Inference is based on maximum likelihood, following the general multiseason modeling of MacKenzie et al. (2003, 2006). Several alternative parameterizations exist for the basic multiseason model, and we use the most common one, with initial occupancy parameters, $\psi_{i,1}$ for each patch, $i$, and time-specific probabilities of local extinction, $\varepsilon_{i,t}$, and colonization, $\gamma_{i,t}$, $t = 1, 2, \ldots T - 1$ (where the first and last sample periods are denoted as 1 and $T$, respectively). When using this model without the autologistic relationships, occupancy parameters are only estimated for the first sampling period. However, autologistic modeling requires tracking time-specific occupancy parameters $\psi_{i,t}$ as well. These occupancy parameters for time periods following $t = 1$ are thus computed as derived parameters using Eq. 1. Just as described for the autologistic modeling, the occupancy parameters used in Eq. 1 may be of three different types. If patch $i$ is surveyed at time $t$, and the focal species is detected, then the parameter used in Eq. 1 is $\psi_{i,t}^{(1)} = 1$. If patch $i$ is surveyed at time $t$, and the focal species is not detected, then the conditional (on no detection) occupancy parameter is used in Eq. 1, $\psi_{i,t}^{(0)}$. Finally, if patch $i$ is not surveyed, then the unconditional occupancy parameter $\psi_{i,t}^{*}$ is used in Eq. 1. If the neighborhood includes a large number of patches (e.g., the entire study area), then there will be little difference between average occupancy values obtained using conditional or unconditional estimates.

### *Equilibrium occupancy values*

The equilibrium occupancy value ($\psi_{\mathrm{eq}}$) is the value that yields $\psi_{t+1} = \psi_t = \psi_{\mathrm{eq}}$, e.g., in Eq. 1. It can be identified graphically by plotting $\psi_{t+1} - \psi_t$ as a function of $\psi_t$ and determining where $\psi_{t+1} - \psi_t = 0$. When colonization and extinction are time-constant and independent of occupancy, $\psi_{\mathrm{eq}} = \gamma/(\gamma + \varepsilon)$. For models with autologistic components we estimated the equilibrium value by calculating $\psi_{t+1} - \psi_t$ for $\psi_t$ between zero and one at each 0.001 interval and determining the interval in which the sign of $\psi_{t+1} - \psi_t$ switched from positive to negative.

### *Simulation study*

We designed a simple simulation study to investigate (1) the ability of the maximum likelihood algorithm to estimate the true parameters underlying the autologistic process, and (2) the ability of likelihood-based model selection criteria to identify the true model generating a data set. First, we chose 36 sets of parameter values (Appendix A). Parameter values were chosen to represent the nine possible combinations of three initial and three equilibrium occupancy values (i.e., 0.25, 0.50, 0.75). Within each combination of initial and equilibrium values we chose parameter values for four possible models (i.e., model 1, no effect of neighborhood occupancy on colonization or extinction; model 2, effect of neighborhood occupancy on colonization only; model 3, effect on extinction only; model 4, effect on both colonization and extinction). The simulation was tailored to our Barred Owl application, so the neighborhood was defined as the entire study area over which sampling was conducted. For each set of parameter values we then used GENPRES (Bailey et al. 2007) to simulate 100 data sets based on 200 sites over 10 years, each surveyed four times each year with a per survey probability of detection of 0.5. Simulated data sets were then fit to the four possible models in PRESENCE, and models were compared using AIC.

We hypothesized that when there were large differences between initial and equilibrium occupancy, we would be able to correctly identify the generating model in the majority of simulated data sets, however that when initial and equilibrium occupancy were similar, model 1 would be favored regardless of the model used to generate the data. Our rationale underlying this prediction is similar to that for any sort of regression. Adequate variation in the "independent" variable (in our case neighborhood occupancy) is required in order to estimate parameters of any relationship between this variable and a "dependent" variable (in our case, local probabilities of extinction and colonization). Lastly, we hypothesized that it would be easier to distinguish the effects of the neighborhood on colonization when occupancy was low initially and increasing over the course of the simulations, and easier to distinguish the effects on extinction when occupancy was initially high and declining throughout the time series. These hypotheses are based on the idea that inferences about any parameter should be more readily obtained when that parameter applies to a larger number of sites (hence more opportunities to "observe" that parameter). For example, when initial occupancy is low, more sites are available for colonization than when initial occupancy is high, and this variation in sample size is expected to produce corresponding variation in quality of inference. For model 4 and each set of parameter values, we also estimated the percent relative bias in six estimated quantities: (1) initial occupancy ($\hat{\psi}_1$), (2) initial colonization ($\hat{\gamma}_1$), (3) initial extinction ($\hat{\varepsilon}_1$), (4) equilibrium colonization ($\hat{\gamma}_{\mathrm{eq}}$), (5) equilibrium extinction ($\hat{\varepsilon}_{\mathrm{eq}}$), (6) detection probability ($p$). Equilibrium values were determined by estimating $\hat{\psi}_{eq}$ to within 0.001 by iterative replacement and then determining the $\hat{\gamma}_{eq}$ and $\hat{\varepsilon}_{eq}$ predicted for this $\hat{\psi}_{eq}$. Percent relative bias was calculated as the difference between the estimated and "true" values divided by the "true" value expressed as a percentage.

### *Application of model to Barred Owl expansion*

*Study area.*—Our analysis focuses on 159 survey polygons (the "patches" for this analysis) located either entirely or partially in the Tyee Density Study Area (TDSA) on the Roseburg District of the Bureau of Land Management (BLM), Douglas County, Oregon, USA (see Fig. 1). These contiguous polygons are believed to include all potential Spotted Owl territory sites within the study area (i.e., the 159 polygons were not a sample from some much larger number of potential territory sites). Survey polygon borders were delineated based on topography and locations of Spotted Owl home ranges and averaged 6.3 km$^2$ in size (with a standard deviation of 2.0 km$^2$). The TDSA included a mixture of federal lands and intervening sections of private land (Reid et al. 1996). TDSA consisted of a mosaic of old-growth and mature forests that had never been harvested and younger forests that were regenerating on areas that had been previously clear-cut, thinned, or burned (Olson et al. 2005).

*Field methods.*—Most, and often all, of the 159 polygons within TDSA were monitored every year from 1990–2010 using a standardized protocol to locate and band owls and determine how many young were produced by each female (Franklin et al. 1996, Lint et al. 1999). All survey polygons were visited multiple times within a year between 1 March and 31 August. We excluded sampling occasions that were less than 30 minutes in duration and/or where surveyors did not have to hoot to determine the location of Spotted Owls. Such sampling occasions could arise, for example, when a nighttime survey determined the presence and relative location of Spotted Owls, and surveyors returned the next day to visually verify that a pair was present, or if surveyors knew the location of a breeding pair and were checking on fledgling status. Surveyors targeted Spotted Owls by imitating their calls. The time spent calling and listening within any survey polygon was a function of the detection of Northern Spotted Owls (because surveys were terminated if Northern Spotted Owls were located). Detections of Barred Owls were noted at any time during this survey process. Although Barred Owls were not the target of the vocal lure surveys, they were often detected during the surveys because they responded aggressively to Spotted Owl calls (Kelly et al. 2003, Crozier et al. 2006).

*General modeling approach.*—We developed and tested models using a sequential approach to model selection. We began by developing a model set to focus on detection probability. Other model parameters were very general (full time-specificity of extinction and colonization), with the model set composed of various ways to model detection. The selected model for detection probability was then used in models that did and did not include autologistic functions for modeling extinction and/or colonization. The motivation for this step was to assess the ability of autologistic models to appropriately model the time-specificity of extinction and colonization probabilities. The final model set then explored the addition of specific habitat variables to models developed in the prior two steps. We make no claim that this sequential approach is optimal or even wise, but claim only that it provided a pragmatic approach to dealing with many potential sources of variation.

*Modeling detection probability.*—Barred Owls maintain territories that are roughly 3–4 times smaller than Spotted Owl territories (Hamer et al. 2007, Singleton et al. 2010), meaning that multiple pairs could maintain territories within a survey polygon. We hypothesized that over time as Barred Owl numbers increased not only would occupancy increase, but also detection probability would increase, as some survey polygons became home to multiple pairs of Barred Owls. Surveys occurred during the day, night, and during dusk/dawn, and past studies have shown that detection rates for Barred Owls differ between different times of day (e.g., Bailey et al. 2009). Observers also used slightly different methodologies depending on field conditions. One commonly used method was to survey intensively at call points spaced approximately 400–800 m apart and to move quickly between call points (irregular spot calls), and the other common method was to call at frequent intervals while walking along roads or through the woods (continuous transect). During some surveys, observers combined these methods leading to a mixture of methods. As a consequence of these potential sources of heterogeneity in detection probability, we modeled detection probability as a function of time of day, survey method, survey length and time (year) (Table 1). For Barred Owls, we hypothesized that (1) detection probability would increase over the course of the study period, (2) detections would be positively correlated with the amount of time spent during each survey, and (3) detection probability would vary between survey methods. Based on past studies (Bailey et al. 2009), we expected night-time detection rates to be higher than daytime rates. Barred Owls are known to hunt animals that are active diurnally (Hamer et al. 2007) and may have increased activity around dusk and dawn. We hypothesized that the detection rate around these times might be similar to or exceed nighttime detection rates. To test these hypotheses and determine which detection covariates should be included we fit a set of six models in which $\varepsilon_{i,t}$ and $\gamma_{i,t}$ were year-specific and detection probability was either constant, a function of all four detection covariates or a function of three of the detection covariates. After determining which detection

Table 1. Covariates used in different portions of model.

| Abbreviation | Covariate description | Level of variation |
|---|---|---|
| CL2 | forest cover within 120 m of second-order or greater streams† | site |
| CL4 | forest cover within 120 m of fourth-order or greater streams† | site |
| CHA | cumulative harvest from beginnings of surveys through *i*th year† | site |
| FOR | total old forest cover within survey polygon† | site |
| $\beta_{0,t}$ | year-specific intercepts | site |
| SL | survey length (h)‡ | sample |
| TOD | time of day (day, dusk, night) | sample |
| MET | survey method (continuous walk, irregular spot call, mixture) | sample |
| Year | linear trend over time | sample |

*Notes:* Site covariates varied among survey polygons within a year and were used in models of occupancy dynamics. Sample covariates varied among sampling occasions and were used to model detection probability.

† These covariates were standardized to have a mean of 0 and a standard deviation of 0.5.

‡ Survey length was centered on 90 minutes and rescaled in units of hours.

model was best supported (the model with all hypothesized detection covariates), we used these detection covariates in all additional models.

*Comparing the autologistic model to other options.*—Having determined the covariates needed to model the detection function, we compared seven models without habitat covariates to determine the performance of models where $\varepsilon_{i,t}$ and/or $\gamma_{i,t}$ were functions of $\hat{\psi}_t^R$ relative to models where $\varepsilon_{i,t}$ and $\gamma_{i,t}$ were modeled as constant or year specific. We only considered models where the neighborhood of the autologistic covariate was defined as the whole study area because Barred Owl dispersal distances are on the same scale as the study area. The study area dimensions are ~50 km by ~20 km (Fig. 1) and Livezey (2009*b*) reported that the mean distance dispersed by 200 marked Barred Owls was 41.3 km with a median distance of 22.6 km. However, we stress that our model can be applied to neighborhoods smaller than a whole study area provided that these scales are biologically relevant. Based on a priori belief that both colonization and extinction would be driven primarily by Barred Owl density in the study area during this period of invasion, we predicted that the autologistic model would fit the data better than a constant colonization and extinction model and provide year-specific estimates that were similar to those from a model with year-specific colonization and extinction parameters, but with far fewer parameters. We hypothesized that the coefficient for the autologistic covariate would be positive in the colonization ($\gamma_{i,t}$) portion of the model and negative in the extinction ($\varepsilon_{i,t}$) portion. We chose the best model from this set using AIC and used it as the base model in our habitat analyses.

To illustrate the impacts of different models on inference we used point estimates from four models to estimate occupancy, colonization, and extinction over the 21-year study period. Three of the four models considered were estimated in PRESENCE and included models in which colonization and extinction rates (1) were constant over the study period, (2) were year specific, and (3) varied with $\psi_t$. Estimates based on the fourth model, a naïve model, were calculated by assuming that all occupied territories were detected in at least one survey during a season, and then estimating the impacts of a naïve estimate of occupancy on naïve estimates of colonization and extinction via logistic regression. We also determined the equilibrium occupancies for the first, third, and fourth models based on the point estimates for all parameters.

*Habitat covariates.*—The four habitat covariates we considered are the amount of older forest (FOR), the amount of older forested area near large rivers (CL2), the amount of older forested areas near all streams and rivers (CL4), and the cumulative amount of timber harvesting within the survey polygon (CHA). Radio tracking of Barred Owls in other parts of the Pacific Northwest led to the conclusion that the species prefers forested areas in valley bottoms close to water (Buchanan et al. 2004, Hamer et al. 2007, Singleton et al. 2010), which motivated our choices of the FOR, CL2, and CL4 habitat covariates. We included the CHA because there is interest in understanding how forest management practices may influence occupancy of both Northern Spotted Owls and Barred Owls.

We used a 1988 stand age map from Cohen et al. (2001) to develop a baseline map of older forest cover in the study area by assigning all map pixels with age values ≥80 years as "old forest" (Table 1). We filtered this map using a boundary clean command in ArcGIS to eliminate isolated pixels and aggregate clusters of pixels into a stand-scale map. We then developed an old forest cover map for each year between 1988 and 2008 using LandTrendr data (Kennedy et al. 2010) to remove forest that was overlapped by stand-replacing disturbances (i.e., clearcut harvests since no wildfires occurred in TDSA during the study period). Kennedy et al. (2010) considered "moderate" and "high" loss of vegetation cover data (defined as a green vegetation cover loss of >40%) representative of a stand-replacing disturbance. Each LandTrender annual clearcut harvest map was filtered using the same process as for the older forest maps (boundary clean). Data for 2009 were not

TABLE 2. Model selection results for Barred Owl data set.

| Colonization ($\gamma$) | Extinction ($\varepsilon$) | Detection ($p$) | $\Delta$AIC† | $w$† | $K$ | AIC |
|---|---|---|---|---|---|---|
| First model set: detection probability | | | | | | |
| $\beta_{0,t}$ | $\beta_{0,t}$ | all | 0 | 0.96 | 48 | 5173.0 |
| $\beta_{0,t}$ | $\beta_{0,t}$ | SL + MET + TOD | 6.6 | 0.04 | 47 | 5179.6 |
| $\beta_{0,t}$ | $\beta_{0,t}$ | SL + TOD + year | 14 | 0 | 46 | 5186.9 |
| $\beta_{0,t}$ | $\beta_{0,t}$ | MET + TOD + year | 41 | 0 | 47 | 5214.3 |
| $\beta_{0,t}$ | $\beta_{0,t}$ | SL + MET + year | 312 | 0 | 46 | 5485.5 |
| $\beta_{0,t}$ | $\beta_{0,t}$ | | 452 | 0 | 42 | 5624.6 |
| Second model set: autologistic component | | | | | | |
| $\psi_t$ | $\psi_t$ | all | 0 | 0.70 | 12 | 5149.4 |
| $\psi_t$ | | all | 1.7 | 0.30 | 11 | 5151.1 |
| $\beta_{0,t}$ | | all | 14 | 0 | 29 | 5163.8 |
| $\beta_{0,t}$ | $\beta_{0,t}$ | all | 24 | 0 | 48 | 5173.0 |
| | $\psi_t$ | all | 59 | 0 | 11 | 5208.1 |
| | | all | 76 | 0 | 10 | 5225.6 |
| | $\beta_{0,t}$ | all | 81 | 0 | 29 | 5230.6 |
| Third model set: habitat effects | | | | | | |
| CL2 + $\psi_t$ | CL2 + $\psi_t$ | all | 0 | 0.69 | 14 | 5125.6 |
| FOR + $\psi_t$ | FOR + $\psi_t$ | all | 3.2 | 0.14 | 14 | 5128.8 |
| $\psi_t$ | CL2 + $\psi_t$ | all | 3.4 | 0.12 | 13 | 5129.1 |
| CL2 + $\psi_t$ | $\psi_t$ | all | 6.6 | 0.03 | 13 | 5132.2 |
| FOR + $\psi_t$ | $\psi_t$ | all | 7.6 | 0.02 | 13 | 5133.2 |
| $\psi_t$ | FOR + $\psi_t$ | all | 9.1 | 0.01 | 13 | 5134.7 |
| CHA + CHA$^2$ + $\psi_t$ | $\psi_t$ | all | 17 | 0 | 13 | 5142.2 |
| $\psi_t$ | CL4 + $\psi_t$ | all | 19 | 0 | 13 | 5144.8 |
| CL4 + $\psi_t$ | CL4 + $\psi_t$ | all | 20 | 0 | 14 | 5145.2 |
| CHA + CHA$^2$ + $\psi_t$ | CHA + CHA$^2$ + $\psi_t$ | all | 20 | 0 | 14 | 5146.0 |
| CL4 + $\psi_t$ | $\psi_t$ | all | 20 | 0 | 13 | 5146.1 |
| $\psi_t$ | CHA + CHA$^2$ + $\psi_t$ | all | 25 | 0 | 13 | 5150.7 |

*Notes:* Abbreviations in the first three columns are explained in Table 1, except $\psi_t$ (occupancy at time $t$). Models were compared in three sequential model sets.

† $\Delta$AIC and Akaike weight ($w$) were based only on models within each set, whereas AIC values are comparable across sets. Akaike weights were rounded at two digits. $K$ is the number of parameters. Empty cells signify that only a single intercept term was estimated for the regression associated with that particular parameter.

available, so we used the 2008 values for this year. Annual older forest maps were then used to develop maps of riparian forest habitat around second-order or greater streams (Strahler 1957) using a buffer of 120 m around the selected streams and then determining the intersection between this layer and the forest layer for each year. The amount of older forest habitat around fourth-order or greater streams, wetlands, and water impoundments was also calculated following the same procedure.

To analyze the impacts of habitat covariates on occupancy dynamics we compared AIC's for the set of 12 autologistic models that were created by including each of the four covariates independently in modeling colonization and extinction as well as in modeling both parameters concurrently. We hypothesized that FOR, CL2, and CL4 would all have positive coefficients when included in the colonization portion of the model and negative coefficients in the extinction portion. For CHA, we predicted that colonization would be greatest for intermediate values and extinction would be lowest for intermediate values and included both CHA and the square of CHA to allow for this relationship. We focused on models with single habitat covariates because most of the covariates were correlated, and we wanted to avoid issues of multicolinearity.

## RESULTS

As hypothesized, it was easy to distinguish the true autologistic model in our simulations when there were large differences between initial and equilibrium occupancies, and it was difficult to distinguish the true autologistic model when there were no differences (Appendices A and B). The neighborhood effect on extinction was more difficult to distinguish when the equilibrium occupancy value was only 0.25 larger than the initial value, and the effect of neighborhood occupancy on colonization was more difficult to distinguish when there were only small declines in occupancy (0.25) during the simulation. Relative bias was always less than 6% and was largest in estimates of initial colonization ($\hat{\gamma}_1$) and initial extinction ($\hat{\varepsilon}_1$) (Appendix C).

We began our analysis of 21 years of Barred Owl detection data in the TDSA by testing a suite of six models that varied only in the covariates included in the modeling of detection probability. The model with all covariates for detection outperformed models where single covariates were removed by a wide margin (>6 AIC, $w = 0.96$; Table 2), and all covariates were included in future models. As hypothesized, longer surveys were more likely to detect Barred Owls, probability of detection increased through time (survey year), and

TABLE 3. Estimated coefficients from selected models.

| Model set: rank within set (covariate) | AIC | $\psi_1$ | Colonization ($\gamma$) | | | | Extinction ($\varepsilon$) | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | $\beta_0$ | $\psi_t$ | $\beta_{\text{habitat}}$ | $\beta_{\text{habitat}^2}$ | $\beta_0$ | $\psi_t$ | $\beta_{\text{habitat}}$ |
| Third: 1 (CL2) | 5125.6 | −3.0 (0.5) | −3.6 (0.2) | 4.8 (0.6) | 0.5 (0.2) | | −1.5 (0.5) | −2 (1) | −2.2 (0.8) |
| Third: 2 (FOR) | 5128.8 | −3.0 (0.5) | −3.7 (0.2) | 4.8 (0.6) | 0.6 (0.2) | | −1.5 (0.5) | −2 (1) | −1.4 (0.6) |
| Third: 3 (CL2) | 5129.1 | −2.8 (0.5) | −3.5 (0.2) | 4.4 (0.5) | | | −1.5 (0.5) | −2 (1) | −3.0 (0.8) |
| Third: 4 (CL2) | 5132.2 | −3.1 (0.5) | −3.6 (0.2) | 4.6 (0.6) | 0.9 (0.2) | | −1.7 (0.5) | −2 (1) | |
| Third: 7 (CHA) | 5142.2 | −3.1 (0.5) | −3.5 (0.2) | 4.6 (0.6) | −0.1 (0.3) | −0.6 (0.4) | −1.7 (0.5) | −2 (1) | |
| Third: 8 (CL4) | 5144.8 | −3.0 (0.5) | −3.5 (0.2) | 4.1 (0.5) | | | −1.6 (0.5) | −2 (1) | −1.4 (0.6) |
| Second: 1 | 5149.4 | −3.1 (0.5) | −3.5 (0.2) | 3.9 (0.5) | | | −1.7 (0.5) | −2 (1) | |
| Second: 2 | 5151.1 | −3.0 (0.5) | −3.7 (0.2) | 4.5 (0.4) | | | −2.6 (0.3) | | |
| Second: 6 | 5225.6 | −2.9 (0.5) | −2.4 (0.1) | | | | −3.7 (0.4) | | |

*Notes:* Values in parentheses are standard errors. The coefficient $\beta_{\text{habitat}}$ is the $\beta$ associated with the standardized habitat covariate, and $\beta_{\text{habitat}^2}$ is the $\beta$ associated with the square of the standardized habitat covariate (only applies to CHA).

day surveys were less likely to yield detections than night surveys (Appendix D). Contrary to our hypothesis that dusk surveys would have similar or higher detection probabilities than night surveys, we found that dusk surveys had slightly lower detection probabilities than night surveys (but still higher than those of day surveys). Detection probabilities were lowest for continuous walks as compared to irregularly spaced spot calls and mixed spot call/walks.

As hypothesized, the model that used regional occupancy ($\hat{\psi}_t^R$) as a covariate in colonization and extinction outperformed models based on constant or year-specific colonization or extinction rates (Table 2). The model with $\hat{\psi}_t^R$ in both colonization ($\hat{\gamma}_t$) and extinction ($\hat{\varepsilon}_t$) portions of the model outperformed the model with $\hat{\psi}_t^R$ in only colonization ($\Delta$AIC of 1.7). Although the $\hat{\beta}$ associated with $\hat{\psi}_t^R$ in the extinction portion of the model was relatively high, the associated standard error was also large (Table 3). Estimates of $\hat{\psi}_t^R$, $\hat{\gamma}_t$, and $\hat{\varepsilon}_t$ from the model in which both colonization and extinction were functions of $\hat{\psi}_t^R$ were similar to estimates from the model in which colonization and extinction were estimated as annual constants (Fig. 2A–C). In contrast, the model in which colonization and extinction were constant throughout the study period overestimated $\hat{\psi}_t^R$ prior to 2006 and underestimated it afterward when compared to the other two models that accounted for imperfect detection (Fig. 2A). The naïve model underestimated $\hat{\psi}_t^R$ throughout the study period and overestimated $\hat{\varepsilon}_t$, but gave a relatively unbiased estimate of $\hat{\gamma}_t$ (Fig. 2A–C). The naïve model and the model that did not include $\hat{\psi}_t^R$ as a covariate produced lower estimates for the equilibrium value of $\hat{\gamma}_{\text{eq}}$ than the model that accounted for imperfect detection and modeled colonization and extinction as functions of $\hat{\psi}_t^R$ (Fig. 2D).

Addition of habitat covariates usually led to an improvement in AIC (Table 2). The best models that included CL4 and CHA led to modest improvements from models with only the neighborhood occupancy included, while the best models that included FOR or CL2 as habitat covariates led to drops of over 20 AIC from the best model without habitat covariates (Table 2). The best habitat model included CL2 in both colonization and extinction portions of the model with increasing CL2 having a positive effect on colonization and a negative effect on extinction (Table 3). However, a model that modeled colonization and extinction as dependent on FOR was within 3.2 AIC. Models that included CL2 had a combined Akaike weight of 0.84, whereas models that included FOR had a combined Akaike weight of 0.16, suggesting support for these covariates over the other alternatives. FOR and CL2 were highly correlated within our landscape ($r > 0.85$), and this limited our ability to more clearly distinguish whether forest per se (FOR) or forest near class 2 or greater streams and ponds (CL2) were preferred by Barred Owls. Both FOR and CL2 have bigger estimated impacts on extinction than colonization (Table 3). The signs of all habitat covariates, including the sign associated with the quadratic portion of the CHA model, were as hypothesized.

## DISCUSSION

Skellam (1951) considered the spread of biological populations and suggested that they could be usefully modeled as a diffusion process. Theoretical models based on diffusion processes typically predict invasion waves. Autologistic models can be thought of as discrete approximations to diffusion processes and have been recommended for empirical modeling (e.g., Wikle 2003). As noted above, many studies attempting to draw inferences about invasions are based on static patterns observed following invasions. Other studies that are based on data during a period of invasion dynamics have often focused on the leading edge of the invading wave. Such studies typically rely on incidental data or systematically collected data over large areas, but with sparse coverage (e.g., BBS data), requiring investigators to assume a coarse grain for analysis. Under these circumstances, autologistic models provide a useful way of characterizing how an invasion propagates. However, as demonstrated here, autologistic modeling is also useful for describing transient dynamics following initial colonization and establishment (behind the leading edge) and eventual equilibrium dynamics. We conclude that the study of population dynamics at virtually any

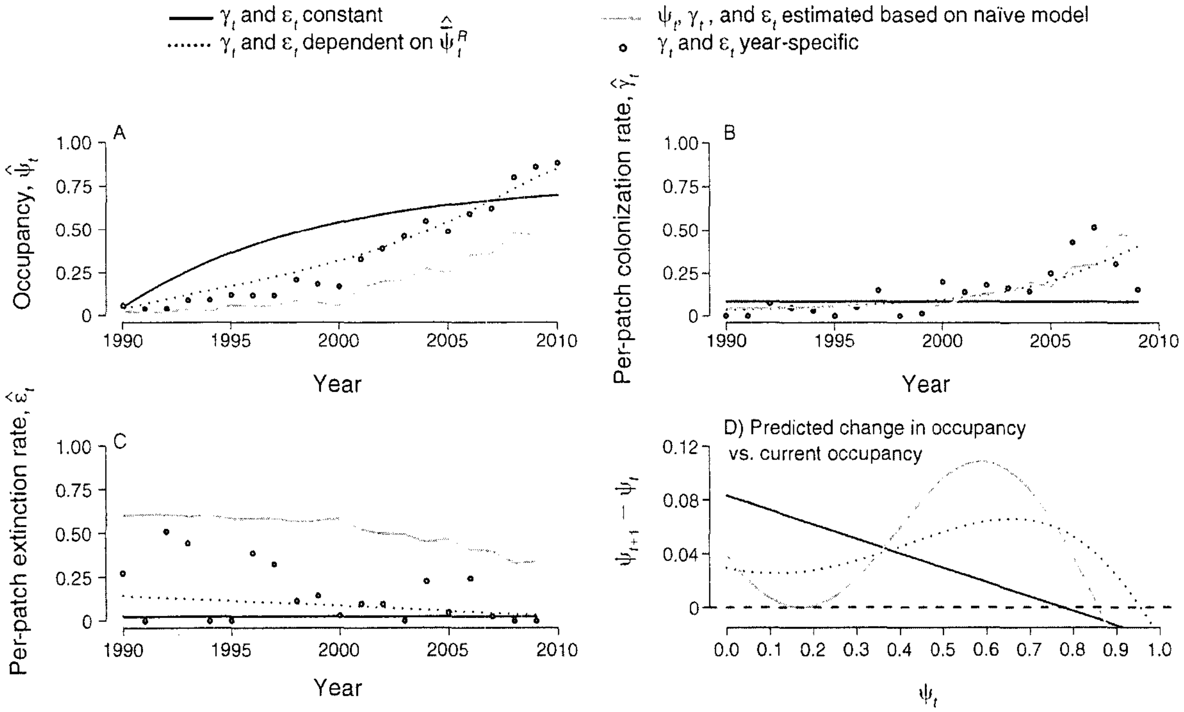

FIG. 2. Comparison of four models fit to Barred Owl (*S. varia*) data. Model estimates of (A) occupancy $\psi_t$, (B) per-patch colonization rate, $\gamma_t$, (C) per-patch extinction rate $\varepsilon_t$ and (D) the predicted change in occupancy in the next year ($y$-axis) for a given occupancy in the current year ($x$-axis). The point at which the curves cross the $y = 0$ line in panel D is the equilibrium value of $\psi$ for that model.

scale and at any stage of invasion must incorporate some consideration of colonization or immigration, and that these processes will likely be functions of the spatial distribution of potential colonists within some neighborhood defined by species-level dispersal distances. As such the potential applications of the modeling approach presented here are much more general than species expansions. For example, metapopulation theory has long recognized that per-patch colonization (and extinction) rates may be at least partially dependent on the prevalence of a species in some specified neighborhood (e.g., Hanski 1999). Indeed the concept of connectivity focuses on potential sources of immigrants for focal patches.

The complication of inference for such models is that occupancy of neighboring patches is not a standard covariate, as it is not something that is known or directly measured, but must instead be estimated. Bled et al. (2011) introduced autologistic models that deal with imperfect detection, using hierarchical models implemented using Markov chain Monte Carlo (MCMC). Here we introduce similar models, but implemented using maximum likelihood and available in user-friendly software (PRESENCE; *available online*).[5] Nearly identical estimates were derived using WinBUGS, which has the added advantage of being easily modified to introduce other modeling features (see the Supplement). However a likelihood approach requires far less computation time, which is useful for large data sets and simulation studies directed at design issues. We did not consider estimating the autologistic component in a single season occupancy model (occupancy of focal patch as function of neighborhood occupancy). This modeling can be accomplished using MCMC approaches (Augustin et al. 1996, Royle and Dorazio 2008) and, as demonstrated recently, the expectation-maximization algorithm (D. I. MacKenzie, *personal communication*).

We expect that $\hat{\psi}_t^{n_i}$ affects colonization and extinction in most populations. However, over any specific interval of time, the importance of this effect to population dynamics may be relatively small and thus difficult to detect. Our simulation studies were focused on the specific case where the neighborhood of each patch is all other patches in the region (i.e., $\hat{\psi}_t^R$). As such, we expected that our model would be better equipped to draw inferences about autologistic effects during transient, as opposed to equilibrium, dynamics (e.g., Appendix A and B). Specifically, we hypothesized that systems beginning with occupancy levels similar to equilibrium occupancy would not show important autologistic effects, simply because of the relative absence of temporal variation in $\hat{\psi}_t^R$ (inference in any regression problem requires variation in the "independent" variable). Indeed our simulation results for situations in which starting and equilibrium occupancy were identical illustrate this point well. Note that this

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[5] http://www.mbr-pwrc.usgs.gov/software/presence.shtml

discussion of relative ability to draw inference about autologistic effects applies strictly to the situation that we modeled in which the neighborhood is the entire study area. It may be possible to estimate the effect of $\psi_t^{n_i}$ on colonization and extinction in instances where the regional occupancy is constant but $n_i$ is a local (small) neighborhood and there is sufficient spatial variation in occupancy among these smaller neighborhoods. In our case study we did not focus on smaller neighborhoods than the study area for biological reasons (see *Methods*).

The direction of the difference between starting and equilibrium occupancy is also a determinant of the ability to draw inferences about effects of $\hat{\psi}_t^R$ on colonization and extinction. For example, when initial occupancy is smaller than equilibrium occupancy (the situation for invading species), the relationship between neighborhood occupancy and colonization is relatively easy to detect, as there are many opportunities for colonization (many patches begin as unoccupied; see Appendix A). In contrast, when initial occupancy is larger than equilibrium occupancy (the situation for a declining species), it is relatively easy to detect effects on local extinction, as more patches are exposed to possible extinction (Appendix A). Our estimate of the coefficient associated with the effect of $\hat{\psi}_t^R$ on $\hat{\varepsilon}_t$ in the Barred Owl data set was less precise than our estimate of the effect of $\hat{\psi}_t^R$ on $\hat{\gamma}_t$ (Table 3). This is partly a consequence of the greater number of opportunities for observing colonization vs. extinction (e.g., more unoccupied than occupied locations to begin with) when a species is invading, leading to a better ability to estimate covariates related to colonization.

We applied our autologistic model to 21 years of Barred Owl detection data in the TDSA and found strong evidence that regional occupancy was an important determinant of vital rates (Fig. 2A–C). The autologistic models outperformed models in which colonization and extinction were estimated independently for each year, but gave similar yearly estimates for $\hat{\gamma}_t$, $\hat{\psi}_t$, and to a lesser extent $\hat{\varepsilon}_t$ (Table 2, Fig. 2). Models in which colonization and to a lesser extent extinction were functions of $\hat{\psi}_t^R$ indicated that Barred Owl occupancy and colonization had been increasing through time, a result consistent with field observations. We view the autologistic models as more mechanistic and more likely to be useful for prediction than models with time-specific rate parameters. The best model suggested that the prevalence of Barred Owls was already much higher than naïve estimates and that without management intervention Barred Owls will soon be found in most survey polygons within this study area (Fig. 2A, D).

Metapopulation theory has been applied at scales ranging from individual home ranges (e.g., Lande 1987) to local populations. Regardless of scale, the defining feature of metapopulations is that focal patch dynamics are linked to occupancy of at least some other patches. In addition to this, ecological theory has long considered the importance of habitat to species occupancy and population status. Our modeling framework allowed us to integrate the metapopulation and habitat paradigms as outlined by Armstrong (2005), by analyzing the effects of habitat and neighborhood patch occupancy together in one comprehensive model. We found that models with habitat covariates (in particular CL2 and FOR) were preferred over models without habitat covariates. The best models of CL2 and FOR included the habitat covariates in both colonization and extinction portions of the model, while the best CL4 model only included it in the extinction portion, and the best CHA model only included the linear and quadratic terms in the colonization portion. CL2 was the best habitat covariate, and it had a greater effect on extinction than colonization rates. Studies of static occupancy patterns elsewhere in the Northern Spotted Owl range during early portions of the invasion suggested that habitat heterogeneity may limit the invasion of Barred Owls (Pearson and Livezey 2003, Buchanan et al. 2004, Livezey and Bednarz 2007). Our models predict lower probabilities of occupancy in survey polygons with lower values of CL2 relative to survey polygons with higher values of CL2. However, the estimated probabilities of occurrence for the least suitable survey polygons in the last year of our study period are still relatively high (0.73 in polygon with lowest value of CL2). Thus it seems unlikely that habitat segregation will occur between Barred Owls and Northern Spotted Owls within our study site (see Gutiérrez et al. 2007, Dugger et al. 2011).

While the scale of our study area was relatively large ($\sim$1000 km$^2$), Barred Owl dispersal distances are also large, and it would be naïve to treat the Barred Owl population on the study area as being closed for demographic purposes. Increases in Barred Owl occurrence in our study area occurred against a backdrop of increasing numbers in surrounding areas. As a consequence, the effects of regional occupancy on vital rates that we estimated may represent a process operating at a greater spatial scale than our study area. In fact, our use of $\hat{\psi}_t^R$ from our study area as a covariate for patches at the boundary of the study area effectively assumes similar neighbor occupancy in the interior and at edges of the study area. For situations in which this is not the case, we have considered ways to deal with patches that border non-habitat (to be presented elsewhere).

Investigating variation in invasion dynamics across multiple monitoring sites may allow us to better understand the spatial scale at which population dynamics of the Barred Owl can be treated as approximately closed. It would be useful to conduct an analysis similar to that reported here but for owl monitoring areas throughout the entire Pacific Northwest. While the issue of spatial scale does not bias our predictions of Barred Owl expansion, it will be of importance in predicting the impacts of Barred Owl removal, which is currently being discussed as a possible research experiment or management tool (Buchanan et al. 2007, Gutiérrez et al. 2007, Livezey 2010, USFWS 2011). Removal at the scale of individual survey polygons might have little impact on the regional estimates of occupancy, and we might expect recolonization at rates approximately equal to the estimates given for 2009 in Fig. 2B. Removal over large scales, however, would begin to affect regional occupancy rates as well as the status of individual territories and would thus lower recolonization rates. For example, removal at the appropriate scales to lower regional occupancy from 0.75 to 0.5 would approximately halve the recolonization rate according to parameters values reported in Table 3. Predictions of this sort require estimating the scale of the region with respect to the focal process. If the region could be defined, then curves such as Fig. 2D could help managers determine levels of annual removal levels that would be necessary to maintain Barred Owls at different levels of occupancy.

We plan to extend this model to the more complicated case of two-species occupancy, dealing with Northern Spotted Owls and Barred Owls simultaneously. Because these two species are viewed as competitors, inferences about occupancy dynamics of Spotted Owls during this period of rapid expansion of Barred Owls should be very informative. Rather than attempting to draw inferences from current patterns that reflect past competition (e.g., Connell 1980), we will model rates of local extinction and colonization of one species (e.g., Spotted Owls) as a function not only of conspecific neighborhood occupancy, but also of Barred Owl presence. This study will build on work by Olson et al. (2005) and Dugger et al. (2011) that modeled Spotted Owl dynamics and detection with respect to Barred Owl detections, but did not account for Barred Owl nondetections. Methodologically, this will require extension of the autologistic approach presented here to the case of multistate occupancy models (e.g., MacKenzie et al. 2009).

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## SUPPLEMENTAL MATERIAL

### Appendix A

Parameter values and detailed results of simulation study (*Ecological Archives* E093-172-A1.

### Appendix B

Graphical summary of simulation study (*Ecological Archives* E093-172-A2).

### Appendix C

Relative bias of estimates from simulated data (*Ecological Archives* E093-172-A3).

### Appendix D

Coefficient estimates for detection portion of model (*Ecological Archives* E093-172-A4).

### Supplement

WinBUGS code and comparison of estimates derived using Presence and WinBUGS (*Ecological Archives* E093-172-S1).