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MODELING OF SITE OCCUPANCY DYNAMICS FOR NORTHERN SPOTTED OWLS, WITH EMPHASIS ON THE EFFECTS OF BARRED OWLS

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Abstract: Northern spotted owls (*Strix occidentalis caurina*) have been studied intensively since their listing as a threatened species by the U.S. Fish and Wildlife Service in 1990. Studies of spotted owl site occupancy have used various binary response measures, but most of these studies have made the assumption that detectability is perfect, or at least high and not variable. Further, previous studies did not consider temporal variation in site occupancy. We used relatively new methods for open population modeling of site occupancy that incorporated imperfect and variable detectability of spotted owls and allowed modeling of temporal variation in site occupancy, extinction, and colonization probabilities. We also examined the effects of barred owl (*S. varia*) presence on these parameters. We used spotted owl survey data from 1990 to 2002 for 3 study areas in Oregon, USA, and we used program MARK to develop and analyze site occupancy models. We found per visit detection probabilities averaged <0.70 and were highly variable among study years and study areas. Site occupancy probabilities for owl pairs declined greatly on 1 study area and slightly on the other 2 areas. For all owls, including singles and pairs, site occupancy was mostly stable through time. Barred owl presence had a negative effect on spotted owl detection probabilities, and it had either a positive effect on local-extinction probabilities or a negative effect on colonization probabilities. We conclude that further analyses of spotted owls must account for imperfect and variable detectability and barred owl presence to properly interpret results. Further, because barred owl presence is increasing within the range of northern spotted owls, we expect to see further declines in the proportion of sites occupied by spotted owls.

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Key words: barred owls, colonization, local-extinction, northern spotted owls, occupancy, site occupancy modeling, *Strix occidentalis caurina*, *Strix varia*.

Northern spotted owls have been studied intensively since their association with late-successional conifer forest was identified (Forsman et al. 1984). Most studies were prompted by concerns that spotted owl populations were declining, and enough evidence was accumulated to justify their listing as a threatened species by the U.S. Fish and Wildlife Service in 1990 (U.S. Fish and Wildlife Service 1990). Although population status and trends of northern spotted owls have been pri-

marily investigated using demographic studies of survival and productivity (Anderson and Burnham 1992, Burnham et al. 1996, Franklin et al. 1999, Anthony et al. 2004), there remains a need to determine site occupancy rates and the factors that affect them. Spotted owls are territorial; thus, occupancy of suitable sites is required for successful reproduction and probably survival. For long-lived species such as spotted owls, trends in occupancy rates may be an early indication of longer-term population trends. Site-occupancy models are essential for identifying the temporal and spatial fac-

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tors that impact occupancy probabilities, and estimates from these models may also be used to estimate abundance for a given set of sites.

Most studies of spotted owl site occupancy used binary response measures such as presence/absence, nest/no nest primarily for analyses of their associations with habitat (Hershey et al. 1998, Meyer et al. 1998, Swindle et al. 1999). Almost all of these studies have made the assumption that detectability is perfect or at least high and not variable. This is not a valid assumption, even for spotted owls that are relatively easy to survey compared to other wildlife species (Reid et al. 1999). Sighting a nest or an owl is a definite indication of presence, but lack of sighting does not necessarily mean absence. Differences in weather conditions, habitat, survey observers, time of day, season, and year may all affect detectability of owls (e.g., Ganey 1990, Reid et al. 1999, Hardy and Morrison 2000). Adjustments for imperfect detection are common in abundance estimation methods (Seber 1982, 1986; Williams et al. 2001), but have seldom been used in analyses of site occupancy.

Another drawback of previous occupancy studies of spotted owls was that temporal variation was usually ignored. Sometimes only 1 year of data was used, or data from consecutive years were collapsed and treated as though they were taken at the same time (e.g., Hershey et al. 1998, Swindle et al. 1999, Zabel et al. 2003) or as an average (McComb et al. 2002). All of these approaches discount possible variation in site turnover and also disregard differences in site occupancy consistency. Blakesley (2003) investigated temporal variation in site occupancy rates for California spotted owls and found a trend in such rates, but she did not account for potential differences in detectability.

MacKenzie et al. (2003) described an approach to modeling site occupancy that explicitly incorporated detection probabilities and allowed for both temporal and spatial variation in occupancy parameters. These methods, similar to Pollock's robust design for abundance and survival estimation (Pollock 1982), were particularly applicable to spotted owls because of the structure of existing survey methods for owls (see below). MacKenzie et al. (2003) included an example of these methods applied to spotted owls in northern California but without a comprehensive analysis.

We were particularly interested in assessing the effects of barred owl presence on site occupancy. Range expansion by barred owls into the Pacific Northwest has been well documented (Taylor and Forsman 1976, Dark et al. 1998, Herter and Hicks 2000, Kelly et al. 2003, Pearson and Livezey 2003).

Barred owls have been found to interbreed with spotted owls, leading to viable offspring (Hamer et al. 1994, Kelly and Forsman 2004), and this interbreeding has the potential for negative genetic effects (Haig et al. 2004). Several studies have also indicated that spotted owls may be harassed and displaced by barred owls (Hamer 1988, Kelly et al. 2003, Pearson and Livezey 2003). In all of these studies, the authors concluded that barred owls had a negative effect on spotted owls.

Recently, several studies have attempted to quantify the impact of barred owls on spotted owls, with mixed results. Kelly et al. (2003) found a decline in ranked occupancy scores of spotted owls at historical territories following the detection of barred owls in or near those territories. Olson et al. (2004) found a negative effect of territory-specific barred owl presence on spotted owl productivity in 1 study area in Oregon. Anthony et al. (2004) examined the potential effect of barred owls on spotted owl survival and productivity on 14 study areas using the annual proportion of owl territories by study area where barred owls were detected. Their results were equivocal, which they attributed to the coarse nature of their barred owl covariate. However, they did find negative effects on survivorship in areas in Washington where barred owls were most abundant and had been present for the longest time. We predicted that using a site-specific barred owl covariate, such as those used by Kelly et al. (2003) and Olson et al. (2004) would show that barred owls have a negative effect on spotted owl site occupancy even on study areas in Oregon for which Anthony et al. (2004) found no effects.

The presence of barred owls has also been hypothesized to affect the detectability of spotted owls even when displacement has not occurred (Leski and Gutiérrez 1998, Reid et al. 1999). Thus far only Anthony et al. (2004) have attempted to quantify these effects. However, they used the same annual barred owl presence covariate to model capture probabilities as they used in survival modeling and again did not find a consistent relationship. Thus, we predicted that use of a site-specific covariate would show that detectability of spotted owls would decline due to presence of barred owls, even if occupancy rates of the former did not change.

In summary, we intended to investigate annual variation, potential time trends, and the effect of barred owl presence on site occupancy of northern spotted owls on 3 study areas in Oregon using open population site occupancy models developed by MacKenzie et al. (2003). We hypothesized that spotted owl site detection and site occupancy

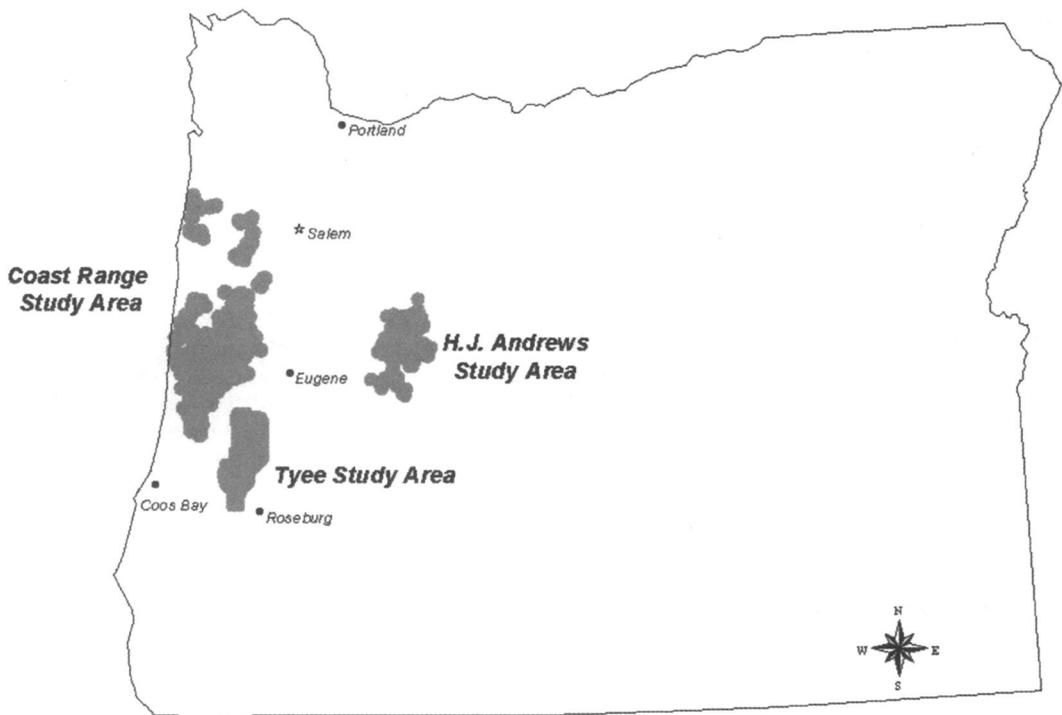


Fig. 1. Location of the HJ Andrews, Tyee, and Coast Range study areas where we modeled northern spotted owl site occupancy based on survey data 1990–2002, in Oregon, USA.

rates would be negatively affected by the presence of barred owls.

STUDY AREA

We used data from 3 study areas in western Oregon, USA (Fig. 1). The HJ Andrews study area was located on the west slope of the Oregon Cascades and included the HJ Andrews Experimental Forest and adjacent areas of the Willamette National Forest. The Coast Range and Tyee study areas were located in the central and southern Coast Ranges, respectively. Land ownership on the Tyee study area typically included a checkerboard pattern in which square-mile sections of Bureau of Land Management (BLM) lands alternated with sections of private land. The Coast Range study area included most of the Siuslaw National Forest plus adjacent areas on the Eugene and Salem Districts of the BLM, the latter of which also contained lands with checkerboard ownership patterns. All 3 areas were characterized by mountainous terrain covered by temperate coniferous forests. Vegetation on the HJ Andrews and Coast Range study areas was dominated by forests of Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*).

Vegetation on the Tyee study area included forests of Douglas-fir and western hemlock in more mesic areas. In more xeric areas, it included mixed-conifer forests of Douglas-fir, grand fir (*Abies grandis*), incense cedar (*Calocedrus decurrens*), Pacific madrone (*Arbutus menziesii*), golden chinquapin (*Castanopsis chrysophylla*), and Oregon white oak (*Quercus garryana*). Forests on all 3 study areas included a mosaic of old forests intermixed with younger forests on areas that had been clear-cut, thinned, or burned.

METHODS

Field Surveys and Data Preparation

Northern spotted owl populations have been monitored throughout much of western Oregon since the early 1980s. Because spotted owls are territorial, do not migrate, and have high site fidelity, researchers have been able to develop and maintain a master list of owl sites for many different study areas in which owls are color-banded and monitored each year, using a standard survey protocol to document survival and productivity of individuals and pairs of owls (Franklin et al. 1996, Lint et al. 1999). These surveys were primarily de-

signed to obtain information on survival and productivity of individuals and pairs of owls for population growth studies (Burnham et al. 1996). However, the structure of these surveys made it possible for us to create data sets appropriate for modeling site occupancy as well. The owl sites in our data base included all areas known to be used by spotted owls at some point during the years surveys were conducted. Added together, these sites encompassed most of what was considered potential owl habitat within each study area. Most sites corresponded roughly with spotted owl territories, in that marked owls or their replacements were assigned to the same site each year that they were located in the same general area. We identified sites with low or no occupancy based on scattered detections obtained prior to or early in the study period with subsequent monitoring, indicating those sites did not correspond to known owl territories. We also defined several areas containing suitable habitat that were consistently surveyed but never contained spotted owls. The boundaries of these areas were somewhat loosely defined, but they were generally associated with topographical and ecological features that experienced owl biologists used to assign owl locations to individual sites. The number of sites used in the occupancy analyses for each study area were HJ Andrews, 125; Tyee, 145; and Coast Range, 146.

Although spotted owl surveys for all 3 study areas were conducted in the 1980s, we constructed analysis data sets for occupancy analyses only from surveys taken in 1990–2002 (13 years). Elimination of earlier years reduced variation in survey effort and also lessened the possibility that our sample of sites was saturated (i.e., fully occupied by owls), which could have biased our results. Each year, surveys were conducted by seasonal crews of biologists (>5 per study area) supervised by a project manager. Crews were trained in spotted owl detection methods, and many of the surveyors worked for multiple years but did not work on >1 study area during a single year. Managers were responsible for ensuring adequate survey effort to meet spotted owl monitoring objectives (Lint et al. 1999), maintenance of all survey records, and construction of appropriate data summaries for subsequent analyses of spotted owl survey data, including the site occupancy analyses reported here.

The survey protocol for all study areas was standardized and consisted of multiple visits within each year to document the nesting status of spotted owl pairs and number of fledglings produced

(Franklin et al. 1996). What transpired during a visit depended on the time of year and the status of the birds found at a site. Some surveys were conducted during daylight hours and others at night. Because weather or logistic considerations occasionally caused observers to interrupt a visit, we were concerned that such variability in visits could cause high variation among detection probabilities. To reduce this source of variation, we conferred with over a dozen owl biologists directly involved in conducting surveys and reached a consensus on a set of criteria for determining what we counted as a complete visit (Appendix A). We also defined an average maximum number of visits per year (Appendix A) because the number of visits to sites varied. Most sites were visited ≤ 6 times, but a few sites were visited many more times. Although the modeling methods we used (MacKenzie et al. 2003) allowed for differing numbers of visits to sites within a year, we believed that the additional detection parameters associated with the additional visits would be estimated with poor precision and would also decrease precision on the occupancy parameters while having little effect on our results. Using these criteria, the average maximum number of visits to sites within years varied from 5 to 9, and the total maximum number of visits recorded for each study area were 91 for HJ Andrews, 78 for Tyee, and 86 for the Coast Range. The average number of visits to each site for each study area over all years were similar: HJ Andrews 4.8, Tyee 4.6, and Coast Range 4.3. Because of the large number of visits for each study area, we did not try to use individual covariates to model the variability in visits within years that might have affected detection probabilities, but instead we sought to reduce this variation as much as possible via our visit criteria. Likewise, we did not combine data across study areas for a joint analysis because of the large number of parameters and the area-specific determination of the number of visits within years.

Detection of birds on a site is sufficient to determine site occupancy, but it does not necessarily constitute territoriality (a distinction similar to that between occupancy and use, as discussed by MacKenzie 2005). Spotted owl territories are generally held by either a mated pair or a resident single bird that is most often a male. While we could have assumed that detection of a pair was an indication of pair occupancy, we could not determine residency of a single owl on a per-visit basis. Although we were most interested in modeling pair occupancy, there was also value in determining

site occupancy by single birds regardless of residency status. Site occupancy by any single bird or pair represented the upper bound of site occupancy and could be used to estimate the upper limit of spotted owl abundance. Therefore, we created 2 data sets corresponding to different levels of site occupancy, 1 in which the presence of any owl was recorded, and the second in which the detection of the presence of a pair was required. We refer to the analyses based on these data sets as simple and pair, respectively.

To investigate the effects of barred owl presence on spotted owl site occupancy dynamics and detectability, we developed a set of year-specific binary barred owl covariates that we coded as 1 if barred owl presence was detected on a site within a year, and 0 if it was not. Barred owl presence was not consistently surveyed using the same criteria that spotted owl presence was, but it was noted in the course of conducting the spotted owl surveys. On a per visit basis this information was probably not reliable, but we assumed that within a year the probability of detecting a barred owl on a site was high. Although these covariates were somewhat flawed, as they lacked an adjustment for barred owl detectability, they were a substantial improvement over those used in previous studies because they were year- and site-specific.

Barred owl presence on all 3 study areas was low (<0.10) prior to 1997, and it remained low but gradually increased on the Tyee and HJ Andrews study areas in subsequent years (Fig. 2). There was a substantial rise in the proportion of sites occupied by barred owls within the Coast Range study area, with a maximum of 0.28 sites affected in 2001 (Fig. 2).

Site Occupancy Modeling and Parameter Estimation

We modeled site occupancy based on techniques designed for open populations as described by MacKenzie et al. (2003). The sampling structure for this method is analogous to that of

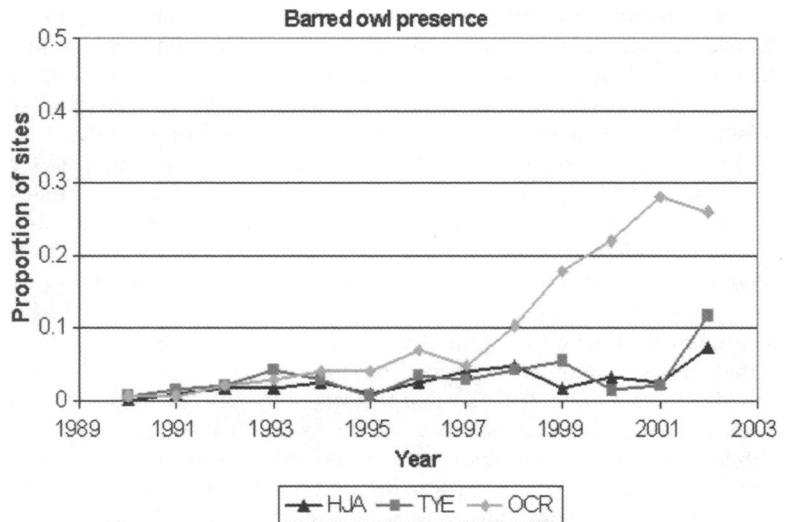


Fig. 2. Year-specific proportions of northern spotted owl sites with barred owls present within each of 3 study areas in Oregon, USA, 1990–2002: HJ Andrews (HJA), Tyee (TYE), and Coast Range (OCR).

Pollock's robust design (Pollock 1982) for survival estimation in 2 ways: (1) there are primary sampling occasions among which changes in site occupancy status may occur, and (2) there are sampling intervals between the primary occasions in which there was assumed to be a period during which site occupancy status did not change. During this time, sites are surveyed multiple times (secondary sampling occasions), and species detections are coded as 1 for a detection and 0 otherwise. If a site is not surveyed during a specific sampling occasion, a dot (.) is coded. These records are compiled into detection histories for each site, similar to the capture histories recorded for survival estimation. These detection histories, denoted as X_i , constitute the data that are used with a product multinomial likelihood model to estimate occupancy parameters (from MacKenzie et al. 2003):

$$L(\boldsymbol{\psi}_1, \boldsymbol{\varepsilon}, \boldsymbol{\gamma}, \boldsymbol{p} \mid X_1, \dots, X_n) = \prod_{i=1}^n \Pr(X_i)$$

where $\boldsymbol{\psi}_1$ is a vector of site occupancy probabilities for the first primary sampling period, $\boldsymbol{\varepsilon}$ and $\boldsymbol{\gamma}$ are matrices of local-extinction and colonization, and \boldsymbol{p} is a matrix of detection probabilities. Other parameterizations of this model may be used to directly estimate time-specific occupancy parameters ($\boldsymbol{\psi}_t$), but we chose to use this one because we wanted to directly model the processes (local-extinction and colonization) that result in site occupancy status, not the outcome.

In our study, the primary sampling occasions were years, and our secondary sampling occasions were the visits that took place during the spotted owl breeding and nesting seasons (Mar–Aug). We estimated local-extinction and colonization probabilities for the intervals between years, and they were conditional on the state of the site at the start of the interval. Local-extinction probabilities were conditional on the site being occupied, and colonization probabilities were conditional on the site being unoccupied. Thus, a site that was occupied in year i may have 1 of 2 fates in the interval between year i and year $i+1$: it may continue being occupied or go extinct. Likewise, a site that was unoccupied may either be colonized or remain unoccupied in the interval between years. The conditional nature of this model generally reduces confounding that may occur between local-extinction and colonization rates, but it does not eliminate it entirely. If a site went extinct and it was subsequently re-colonized, a factor that was positively related to site extinction might also appear to be positively related to re-colonization because otherwise the site would not be available for re-colonization. Thus, care must be taken in the development and interpretation of models to ensure this does not occur.

In general, we developed our models in a step-wise manner. First, we focused on modeling detection probabilities, and we selected a best model from that analysis to use in modeling local-extinction and colonization parameters. We then examined a set of temporal models for those parameters and then added the barred owl covariates to a selected subset (details below). We used model selection procedures as described by Burnham and Anderson (2002) to rank and compare models based on the small-sample-corrected version of Akaike's Information Criterion (AIC_c). We used program MARK (White and Burnham 1999) was used to construct and implement all models. The logit link function for all models to ensure that parameter estimates would be constrained to the interval 0–1.

Our a priori hypotheses regarding within-year detection probabilities were that they might be either constant through time (denoted as [.]), follow a linear trend (T), or follow a quadratic trend (TT). We did not consider that detection probabilities would be completely time-specific (t) within years, as those models would require too many parameters to be estimated. Among years, we considered models where detection probabilities were year-specific, and in addition we also fit a linear or quadratic trend because of potential changes in

survey effort or efficiency through time, or simply because they might be more parsimonious models (i.e., fewer parameters). Likewise, we included a model where detection probabilities were constrained to be constant across years because it might be found to be more parsimonious, and not because we thought it was plausible for biological reasons. We included barred owl presence as a covariate in 2 ways, either with the effect varying by time or with the effect remaining the same through time. We also included mean annual reproductive output (r) as a potential covariate for detection probabilities because we thought pairs in particular would be more conspicuous during years when reproduction was higher.

We did not model initial occupancy in our analyses (except by study area), as it did not vary through time. The candidate models for local-extinction and colonization parameters were similar to those used for detection probabilities, except that we did not include the reproduction covariate in these models. We ran all combinations of time effects (., T, TT, and t) for both sets of parameters for a total of 16 models. We used these models to compute model averaged estimates (Burnham and Anderson 2002) of initial occupancy, and annual estimates of local-extinction and colonization probabilities using program MARK (White and Burnham 1999). We used the estimates from program MARK to calculate year-specific (denoted as i) site occupancy probabilities using a formula from MacKenzie et al. (2003):

$$\hat{\Psi}_i = \hat{\Psi}_{i-1}(1 - \hat{\epsilon}_{i-1}) + (1 - \hat{\Psi}_{i-1})\hat{\gamma}_{i-1}$$

We then added the barred owl covariate as an additive effect to the best time trend models (lowest AIC_c and models with $\Delta AIC_c < 2.0$). As the barred owl presence covariate was an annual measure, and both local-extinction and colonization were estimated for the intervals between years, the barred owl effect could be modeled 2 ways with potentially different timing of the barred owl influence. Our first option was that barred owl presence in year i might affect local-extinction and/or colonization probabilities in the interval between years i and $i+1$. Our second option was that barred owl presence in year $i+1$ might be a better measure of the effect of barred owls on local-extinction and/or colonization in the same interval. Since we were uncertain which of these possibilities were more appropriate biologically (either could be), we modeled the barred owl covariate both ways (designated BAO and BAO $_{i+1}$, respectively). In both cases, we placed 2 con-

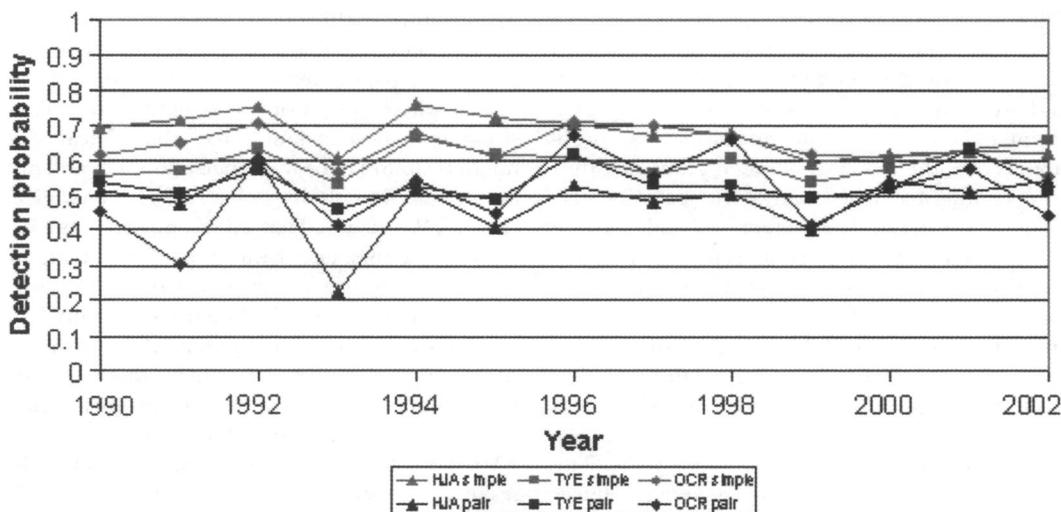


Fig. 3. Estimated year-specific detection probabilities for 2 levels of northern spotted owl site occupancy, simple (gray lines) and pair (black lines), for 3 study areas in Oregon, USA, 1990–2002: HJ Andrews (HJA), Tye (TYE), and Coast Range (OCR). We calculated estimates from the best detection probability model for each study area and occupancy level based on AIC_c . For the Tye pair analysis this model was $p_{BAO + r}$, where BAO refers to site and year-specific barred owl presence, and r is a measure of average reproductive effort. For all other analyses the best model was $p_{BAO + t}$, where t refers to study year. Effects in all models were additive.

straints on models with the barred owl covariate that were intended to reduce the potential for spurious relationships and possible confounding between local-extinction and colonization probabilities: (1) we did not use the covariate to model both local-extinction and colonization probabilities in the same model; and (2) if we found the covariate to be related to both local-extinction and colonization in the same analysis, we retained only the model for which the barred owl covariate was positively related to local-extinction or negatively related to colonization. These were the more biologically plausible relationships, and so we assumed them to be more valid.

We determined the magnitude of the barred owl effect in several ways. We considered the effect to be important if models containing the barred owl covariate reduced AIC_c values by >2.0 , and confidence intervals on the corresponding regression coefficient did not overlap 0. We also measured the impact the covariate had on site occupancy parameters by computing site occupancy estimates from the best barred owl model with and without the barred owl covariate.

RESULTS

Detection Probabilities

For all 3 study areas, the best model for detection probabilities within year was one with con-

stant probabilities for both pair and simple analyses. Among years, we selected the time-specific model (p_t) for all study areas and both levels of occupancy, with the exception that the reproductive covariate model (p_r) was better in the Tye pair occupancy analysis. As we expected, this relationship was positive ($\beta = 1.36$, $SE = 0.27$).

Annual detection probabilities were always greater for simple occupancy than for pair occupancy (Fig. 3); we did not see any other consistent patterns when comparing either levels of occupancy within study areas, or detectabilities for either occupancy level among study areas. Pair detection probabilities were lowest for the HJ Andrews study area, but simple detection probabilities for this area were the highest among our study areas. In general, detection probabilities ranged from 0.53 to 0.76 for simple occupancy and from 0.22 to 0.67 for pair occupancy (Fig. 3).

We found the barred owl covariate was important for modeling detectability among years in all analyses, and this effect was always negative. The impact was found to be constant (i.e., the magnitude of the effect did not vary among years). For all 3 study areas, the effect of barred owls was similar for both simple and pair detectability (Table 1). The effect seemed greater on the HJ Andrews study area, although 95% CIs for all areas broadly overlapped (Table 1).

Table 1. Estimates (and 95% confidence intervals) of the barred owl presence regression coefficients ($\hat{\beta}$) for the best simple and pair models of visit-specific detectability of spotted owls on 3 study areas in Oregon, USA: HJ Andrews, Tye, and Coast Range, 1990–2002.

Study area	$\hat{\beta}$ (95% CI)	
	Simple	Pair
HJ Andrews	-1.14 (-1.47 to -0.82)	-1.03 (-1.65 to -0.42)
Tye	-0.87 (-1.21 to -0.53)	-0.95 (-1.45 to -0.44)
Coast Range	-0.83 (-1.01 to -0.65)	-0.79 (-1.05 to -0.53)

Table 2. Initial occupancy probability estimates (ψ_{1990}) and 95% confidence intervals for 3 study areas in Oregon, USA, based on data from 1990 to 2002, obtained by model averaging estimates from final time trend site occupancy parameter models. Simple refers to analyses based on detections of any owl, and pair refers to analyses based on detections of pairs only.

Study area	ψ_{1990} (95% CI)	
	Simple	Pair
HJ Andrews	0.89 (0.80–0.94)	0.78 (0.68–0.86)
Tye	0.68 (0.59–0.75)	0.42 (0.34–0.50)
Coast Range	0.77 (0.67–0.85)	0.48 (0.36–0.59)

Initial Occupancy

Initial occupancy probability for the pair analysis on the HJ Andrews study area was evidently greater (based on non-overlapping confidence intervals) than on the other study areas, and initial occupancy for the simple analysis was higher than the Tye study area but not greater than on the Coast Range (Table 2). Initial occupancy probabilities were similar in the Coast Range and Tye study areas, and initial occupancy estimates for both study areas were less in the pair analyses than in the simple analyses.

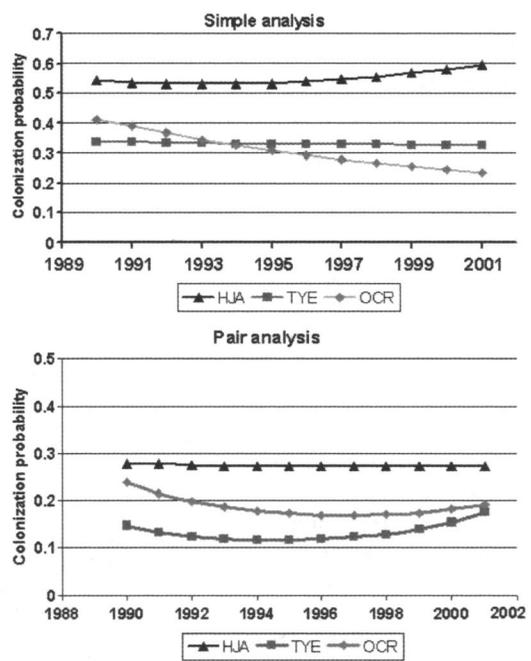
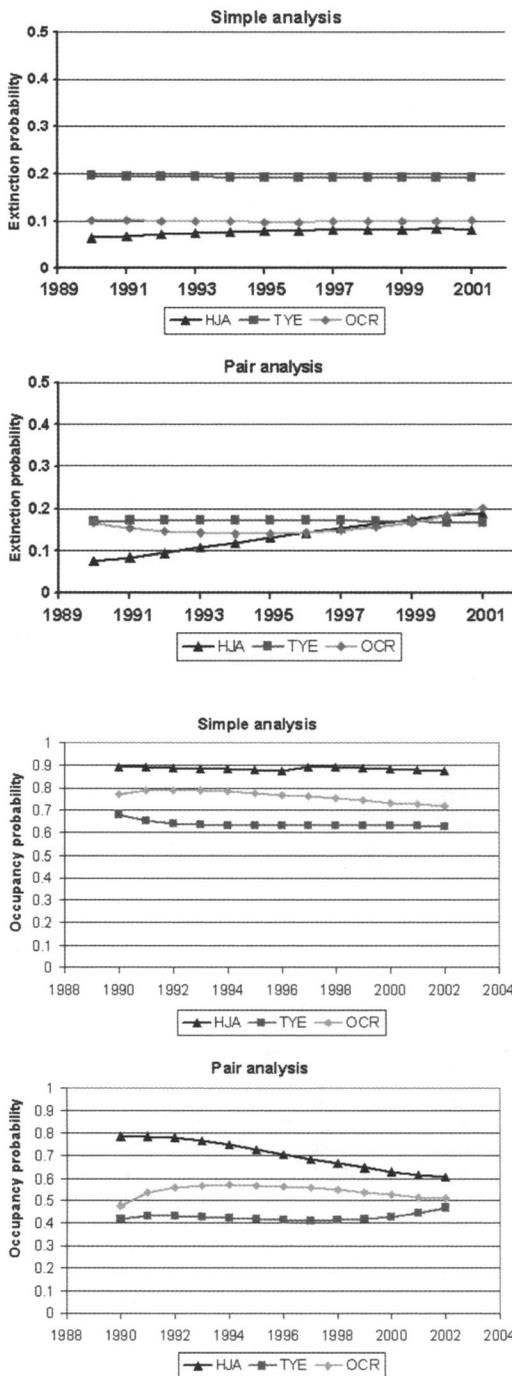
Local-extinction and Colonization Modeling

Time Trend Analyses.—In our analyses of time trends in local-extinction and colonization probabilities, we found such trends in the best model in 4 cases, and in closely competing models ($\Delta AIC_c < 2.0$) in one other case (Table 3). Colonization probabilities had a negative linear trend ($\hat{\beta} = -0.09$, 95% CI = -0.17 to -0.01) in the Coast Range in the simple analysis, and local-extinction probabilities had a positive trend ($\hat{\beta} = 0.10$, 0.03 to 0.16) in the HJ Andrews pair analysis. We found a quadratic

trend in colonization parameters in the Tye pair analysis that was initially decreasing but later increasing ($\hat{\beta}_1 = -0.24$, -0.48 to 0.00; $\hat{\beta}_2 = 0.02$, 0.00 to

Table 3. Best ranked northern spotted owl time trend site occupancy models (cumulative model weights ≥ 0.95) for 3 study areas in Oregon, USA, 1990–2002. For all study area and type combinations the model for capture probabilities was p_{BAO+r} except the Tye pair occupancy which was p_{BAO+r} and the initial occupancy parameter (ψ_{1990}) is constant.

Study area	Occupancy level	Model	K	AIC _c	ΔAIC_c	w_i	Deviance	
HJ Andrews	Simple	$\epsilon(\cdot)\gamma(\cdot)$	17	8037.05	0.00	0.34	7994.31	
		$\epsilon(T)\gamma(\cdot)$	18	8038.39	1.34	0.18	7992.47	
		$\epsilon(\cdot)\gamma(T)$	18	8039.31	2.26	0.11	7993.40	
		$\epsilon(TT)\gamma(\cdot)$	19	8039.43	2.38	0.10	7990.26	
		$\epsilon(\cdot)\gamma(TT)$	19	8039.69	2.64	0.09	7990.52	
		$\epsilon(T)\gamma(T)$	19	8040.49	3.44	0.06	7991.31	
	Pair	$\epsilon(T)\gamma(TT)$	20	8040.88	3.83	0.05	7988.35	
		$\epsilon(T)\gamma(\cdot)$	18	7249.65	0.00	0.49	7203.74	
		$\epsilon(TT)\gamma(\cdot)$	19	7250.84	1.18	0.27	7201.66	
		$\epsilon(T)\gamma(T)$	19	7252.88	3.22	0.10	7203.70	
		$\epsilon(TT)\gamma(T)$	20	7254.20	4.54	0.05	7201.66	
		$\epsilon(T)\gamma(TT)$	20	7255.06	5.40	0.03	7202.52	
Tye	Simple	$\epsilon(\cdot)\gamma(\cdot)$	17	9526.67	0.00	0.52	9487.52	
		$\epsilon(\cdot)\gamma(T)$	18	9529.01	2.34	0.16	9487.21	
		$\epsilon(T)\gamma(\cdot)$	18	9529.19	2.53	0.15	9487.40	
		$\epsilon(TT)\gamma(\cdot)$	19	9531.43	4.76	0.05	9486.93	
		$\epsilon(\cdot)\gamma(TT)$	19	9531.45	4.79	0.05	9486.90	
		Pair	$\epsilon(\cdot)\gamma(TT)$	8	6628.64	0.00	0.39	6611.51
	$\epsilon(\cdot)\gamma(\cdot)$		6	6630.23	1.59	0.18	6617.58	
	$\epsilon(T)\gamma(TT)$		9	6630.85	2.21	0.13	6611.43	
	$\epsilon(\cdot)\gamma(T)$		7	6631.37	2.74	0.10	6616.51	
	$\epsilon(T)\gamma(\cdot)$		7	6632.30	3.66	0.06	6617.43	
	$\epsilon(TT)\gamma(TT)$		10	6632.46	3.83	0.06	6610.72	
	Coast Range	Simple	$\epsilon(T)\gamma(T)$	8	6633.56	4.93	0.03	6616.44
			$\epsilon(\cdot)\gamma(T)$	18	8326.13	0.00	0.46	8281.01
			$\epsilon(\cdot)\gamma(\cdot)$	17	8328.43	2.30	0.15	8286.38
			$\epsilon(\cdot)\gamma(TT)$	19	8328.47	2.34	0.14	8280.20
			$\epsilon(T)\gamma(T)$	19	8329.24	3.11	0.10	8280.97
			$\epsilon(TT)\gamma(T)$	20	8330.43	4.30	0.05	8278.92
		Pair	$\epsilon(T)\gamma(\cdot)$	18	8331.46	5.32	0.03	8286.34
$\epsilon(TT)\gamma(TT)$			21	6761.21	0.00	0.19	6706.38	
$\epsilon(\cdot)\gamma(\cdot)$			17	6761.30	0.09	0.18	6719.25	
$\epsilon(TT)\gamma(\cdot)$			19	6761.59	0.39	0.15	6713.32	
$\epsilon(\cdot)\gamma(TT)$			19	6761.95	0.74	0.13	6713.68	
$\epsilon(T)\gamma(\cdot)$			18	6762.23	1.02	0.11	6717.11	
		$\epsilon(\cdot)\gamma(T)$	18	6762.80	1.59	0.08	6717.68	
		$\epsilon(TT)\gamma(T)$	20	6763.53	2.32	0.06	6712.03	



0.04; linear and quadratic coefficients, respectively), and a quadratic trend in both local-extinction and colonization probabilities for the pair analysis on the Coast Range that had the same trends (local-extinction: $\beta_1 = -0.33, -0.63$ to $-0.02, \beta_2 = 0.03, 0.01$ to 0.05 ; colonization: $\beta_1 = -0.38, -0.67$ to $-0.10, \beta_2 = 0.03, 0.00$ to 0.05). The second best model from the simple analysis for HJ Andrews ($\Delta AIC_c = 1.34$) had a positive linear trend in local-extinction probabilities, but the 95% CI for this coefficient overlapped 0 ($\beta = 0.05, -0.02$ to 0.11).

We calculated time-specific model averaged estimates of local-extinction and colonization probabilities (Fig. 4). Local-extinction probabilities were highest for Tyee for the simple analysis and lower but similar for the HJ Andrews and Coast Range areas. Local-extinction probabilities for the pair analyses were lowest for HJ Andrews during the early 1990s but similar for all 3 areas during the later years of the study. Colonization probabilities were highest for the HJ Andrews area for both simple and pair analyses.

Barred Owl Analyses.—Barred owls had an impact on local-extinction and colonization probabilities in all but 1 analysis (HJ Andrews simple analysis; Table 4). For the Coast Range study area (both simple and pair analyses) the barred owl effect was more important for modeling local-extinction, but for HJ Andrews pair analysis, colonization probabilities were more affected. Barred owl effects were also more evident in the extinction probab-

Fig. 4 (above left and right). Estimated year-specific local-extinction, colonization, and occupancy parameters for 2 levels of northern spotted owl occupancy, simple and pair, for 3 study areas in Oregon, USA, 1990–2002. Estimates of local-extinction and colonization probabilities were model averaged over all time trend models within each analysis set. Occupancy probabilities were calculated using the model averaged estimates of initial occupancy, local-extinction, and colonization and formulae from MacKenzie et al. (2003).

ity model for pair analysis of the Tyee study area, but for the simple analyses the models for local-extinction and colonization were essentially tied. However, in this case, the relationship between the barred owl covariate was positive in both extinction and colonization models, so we eliminated the latter model based on our a priori criteria. We included it in the results only to fully disclose what the outcome of this model was.

There was not a clear preference in the timing of the barred owl effect as determined by the relative ranking of immediate effects vs. effects delayed by 1 year (Table 4). The BAO covariate was clearly more favored for the Tyee study area for both simple and pair analyses, whereas the BAO_{t+1} covariate was better for the Coast Range pair analysis. In the HJ Andrews pair analysis and the Coast Range simple analysis, models with either covariate were ranked similarly. For either covariate, the effect of barred owl presence on local-extinction probabilities was always positive, and usually negative for colonization probabilities, with the exception as noted above (Table 5). Only 1 of the 95% CI on the regression coefficients overlapped 0, further supporting that this was a strong effect. The exception was the HJ Andrews pair analysis, in which the regression coefficient had a very broad CI that barely contained 0; we considered this also an indication of a barred owl effect but slightly less strong than that for the other study areas. In general, the magnitude

Table 4. Northern spotted owl site occupancy models with barred owl covariates added to the best ranked ($\Delta AIC_c < 2.0$) time trend models in Table 3, for 3 study areas in Oregon, 1990–2002. For all study area and type combinations the model for capture probabilities was p_{BAO+t} except the Tyee pair occupancy which was p_{BAO+r} . For all models the initial occupancy parameter (ψ_{1990}) is constant.

Study area	Occupancy level	Model	K	AIC _c	ΔAIC_c	w_i	Deviance
HJ Andrews	Simple	$\in (T) \gamma(\cdot)$	17	8037.05	0.00	0.35	7994.31
		$\in (\cdot) \gamma(\cdot)$	18	8038.39	1.34	0.18	7992.47
		$\in (\cdot) \gamma(BAO_{i+1})$	18	8039.93	2.88	0.08	7994.02
		$\in (BAO) \gamma(\cdot)$	18	8039.97	2.92	0.08	7994.06
		$\in (\cdot) \gamma(BAO)$	18	8040.10	3.05	0.08	7994.19
		$\in (BAO_{i+1}) \gamma(\cdot)$	18	8040.16	3.11	0.07	7994.24
		$\in (T) \gamma(BAO_{i+1})$	19	8041.38	4.33	0.04	7992.20
		$\in (T+BAO) \gamma(\cdot)$	19	8041.43	4.38	0.04	7992.25
		$\in (T+BAO_{i+1}) \gamma(\cdot)$	19	8041.53	4.48	0.04	7992.36
		$\in (T) \gamma(BAO)$	19	8041.55	4.50	0.04	7992.37
	Pair	$\in (T) \gamma(BAO)$	19	7246.17	0.00	0.30	7196.99
		$\in (T) \gamma(BAO_{i+1})$	19	7246.47	0.30	0.26	7197.29
		$\in (TT) \gamma(BAO)$	20	7247.38	1.21	0.17	7194.84
		$\in (TT) \gamma(BAO_{i+1})$	20	7247.73	1.56	0.14	7195.19
		$\in (T) \gamma(\cdot)$	18	7249.65	3.49	0.05	7203.74
		$\in (TT) \gamma(\cdot)$	19	7250.84	4.67	0.03	7201.66
		$\in (T+BAO_{i+1}) \gamma(\cdot)$	19	7251.35	5.18	0.02	7202.17
		$\in (T+BAO) \gamma(\cdot)$	19	7252.62	6.46	0.01	7203.45
		$\in (T+BAO_{i+1}) \gamma(\cdot)$	20	7252.71	6.55	0.01	7200.17
		$\in (T+BAO) \gamma(\cdot)$	20	7253.97	7.80	0.01	7201.43
Tyee	Simple	$\in (\cdot) \gamma(BAO)$	18	9523.99	0.00	0.43	9482.20
		$\in (BAO) \gamma(\cdot)$	18	9524.15	0.16	0.40	9482.36
		$\in (\cdot) \gamma(\cdot)$	17	9526.67	2.67	0.11	9487.52
		$\in (\cdot) \gamma(BAO_{i+1})$	18	9529.22	5.23	0.03	9487.42
		$\in (BAO_{i+1}) \gamma(\cdot)$	18	9529.32	5.33	0.03	9487.52
		Pair	$\in (BAO) \gamma(TT)$	9	6623.27	0.00	0.50
	$\in (BAO) \gamma(\cdot)$		7	6624.91	1.64	0.22	6610.04
	$\in (BAO_{i+1}) \gamma(TT)$		9	6626.05	2.78	0.12	6606.63
	$\in (BAO_{i+1}) \gamma(\cdot)$		7	6627.23	3.96	0.07	6612.36
	$\in (\cdot) \gamma(TT)$		8	6628.64	5.37	0.03	6611.51
	$\in (\cdot) \gamma(TT+BAO_{i+1})$		9	6630.12	6.85	0.02	6610.70
	$\in (\cdot) \gamma(\cdot)$		6	6630.23	6.96	0.02	6617.58
	$\in (\cdot) \gamma(TT+BAO)$		9	6630.36	7.09	0.01	6610.94
	$\in (\cdot) \gamma(BAO_{i+1})$	7	6631.26	7.99	0.01	6616.39	
$\in (\cdot) \gamma(BAO)$	7	6632.01	8.75	0.01	6617.15		
Coast Range	Simple	$\in (BAO_{i+1}) \gamma(T)$	19	8322.67	0.00	0.45	8274.40
		$\in (BAO) \gamma(T)$	19	8323.21	0.54	0.35	8274.94
		$\in (\cdot) \gamma(T)$	18	8326.13	3.46	0.08	8281.01
		$\in (\cdot) \gamma(T+BAO)$	19	8326.25	3.58	0.08	8277.98
		$\in (\cdot) \gamma(T+BAO_{i+1})$	19	8327.24	4.57	0.05	8278.97
		Pair	$\in (BAO_{i+1}) \gamma(\cdot)$	18	6744.75	0.00	0.31
	$\in (BAO_{i+1}) \gamma(TT)$		20	6745.22	0.48	0.24	6693.72
	$\in (TT+BAO_{i+1}) \gamma(TT)$		22	6745.78	1.03	0.18	6687.52
	$\in (TT+BAO_{i+1}) \gamma(\cdot)$		20	6746.92	2.17	0.10	6695.41
	$\in (BAO_{i+1}) \gamma(T)$		19	6747.19	2.44	0.09	6698.92
	$\in (T+BAO_{i+1}) \gamma(\cdot)$		19	6747.55	2.81	0.08	6699.28

of the barred owl effect was greater for the pair analysis than simple analysis, but confidence intervals overlapped broadly (Table 5). Likewise, the confidence intervals among study areas overlapped each other, even though the Tyee study area seemed to be more affected by barred owl presence.

Table 5. Regression coefficients (and 95% confidence intervals) for the barred owl covariate from the best model (lowest AIC_c) of site occupancy model sets for 3 study areas in Oregon, USA, 1990–2002. Probabilities are the set of parameters modeled with the barred owl covariate. Simple and pair refer to whether analyses were based on detections of any owl or pairs only, respectively.

Study area	Probabilities	$\hat{\beta}$ (95% CI)	
		Simple	Pair
HJ Andrews	Colonization	NA	-2.15 ^a (-4.52 to 0.22)
Tyee	Local-extinction	1.08 (0.22 to 1.95)	1.72 (0.58 to 2.85)
Coast Range	Local-extinction	0.83 (0.23 to 1.43)	1.38 (0.83 to 1.94)

^a The barred owl covariate for this model was a lagged effect.

Site Occupancy Probabilities

We calculated estimates of site occupancy probabilities for years subsequent to 1990 from the model-averaged estimates of initial occupancy, local-extinction, and colonization for each study area (Fig. 4). Simple and pair site occupancy probabilities were highest for HJ Andrews, intermediate for the Coast Range, and lowest for the Tyee study area. There was temporal variation in both simple and pair occupancy, but there was more variation in the latter.

The effect of barred owl presence on northern spotted owl site occupancy probabilities varied by study area and levels of occupancy (Table 6). The difference between site occupancy estimates with and without the barred owl effect was greatest on the Tyee study area that had a 0.15 decline in site occupancy probability due to the barred owl covariate for both simple and pair analyses. Barred owls had the least effect on HJ Andrews site occupancy probabilities, with 0.00 difference (no barred owl covariate) for simple occupancy, and 0.05 for pair occupancy. The Coast Range was intermediate with a 0.08 reduction in simple occupancy and a 0.12 reduction in pair occupancy due to the barred owl covariate.

DISCUSSION

Our study was the first to extensively examine time-specific site occupancy trends in northern spotted owls, to incorporate estimates of detectability into spotted owl site occupancy analyses, and to assess the impact of barred owl presence on both spotted owl site occupancy dynamics and detectability. In general, we found the methods developed by MacKenzie et al. (2003) to be well suited for all of these purposes. We highly recommend these methods be used by others with similar study objectives.

As we expected, barred owls had a notable impact on spotted owl site occupancy dynamics. Although the proportion of sites affected by barred owls was low for all areas, the effect of barred owls was substantial when it occurred. Barred owl pres-

ence led to increases in local-extinction probabilities on 2 of our study areas and a decline in colonization probabilities on the third area. The resulting effect on occupancy probabilities were substantial, with average declines over the period of our study of up to 15%. This suggests

that increased presence of barred owls on spotted owl sites will lead to further declines in the proportion of those sites occupied in the future. This supports the findings of Kelly et al. (2003) who used different methodology but also found a negative effect of barred owl presence on spotted owl site occupancy rates. A key element in both studies appeared to be the use of a barred owl covariate in the analyses that was site-specific, indicating that this was a local effect (site scale) rather than a broader one (study area scale).

We found no clear preference in the timing of the barred owl effect among study areas, and results were also mixed within study areas. For the Tyee study area, the BAO covariate was definitely better in both simple and pair analyses, but within the Coast Range study area, only the pair analysis indicated a better fit from 1 covariate (the lagged covariate BAO_{i+1}). We did not expect these results, since any temporal patterns in barred owl movements should have been consistent among

Table 6. Estimates of mean site occupancy probabilities for 3 study areas in Oregon, USA, 1990–2002, computed with and without the barred owl effect from the best barred owl model of local-extinction and colonization probabilities, and averaged over any temporal effects. Occupancy level refers to whether the estimates are for any owl or for pairs of birds. For the HJ Andrews study area, the barred owl effect was on colonization probabilities and for the other areas, the effect was on local-extinction probabilities. Site occupancy estimates were computed based on formulae in MacKenzie et al. (2003).

Study area	Occupancy level	Mean occupancy probability		Difference
		Without barred owls	With barred owls	
HJ Andrews	Simple ^a	NA	NA	0.00
	Pair	0.75	0.70	0.05
Tyee	Simple	0.66	0.51	0.15
	Pair	0.41	0.26	0.15
Coast Range	Simple	0.78	0.70	0.08
	Pair	0.52	0.40	0.12

^a The best model for HJ Andrews simple occupancy did not contain a barred owl effect.

our study areas. One possible explanation for the better fit from the BAO covariate on the Tyee study area could be due the difference in study area types. Tyee was a density study area (DSA), and it was more intensively surveyed for spotted owls across the entire area. The other study areas were territorial study areas (TSA; Anthony et al. 2004) that were more specifically surveyed within historical owl territories, but the entire area was not completely searched for spotted owls. Greater survey intensity within the DSA may have made it more likely that barred owl presence was discovered within the same year that spotted owl occupancy status was determined, whereas in the TSAs barred owl presence may not have been established until the following year. This presumes that barred owls remained on sites for at least 1 year, which we believe is a reasonable assumption. If differences in survey methods cause differences in detectability of barred owls, then it may be important to also consider estimating barred owl detection probabilities in developing spotted owl site occupancy models. Further, a more insightful analysis of the influences barred owls have on spotted owl site occupancy dynamics would likely be obtained from jointly modeling both species. Analytical methods for this type of analysis were described by MacKenzie et al. 2004 and could be considered for 2 of our study areas (HJ Andrews and Tyee), but the data required for such an analysis have not yet been compiled. Also, whereas observations of barred owls on these areas have been recorded on a per-visit basis in recent years, there has not been continuous monitoring of sites occupied by barred owls. Currently, efforts are underway to encourage collection of such data, but additional resources will be required to do so.

The most consistent effect of barred owls was on detection probabilities, as the magnitude of the barred owl covariate was the same for both levels of occupancy and all 3 study areas. This indicated that the standardized protocols used for detecting spotted owls probably were also consistent in detecting the change in their response due to barred owls. Although the magnitude of the effect was not known, these results support field observations that spotted owls were less likely to respond to taped calls when barred owls were present, probably due to increased vulnerability to harassment and predation (Leskiw and Gutiérrez 1998). If barred owl presence continues to increase as we expect, detections of spotted owls will continue to decline. This means that survey and modeling methods that do not take into account detectability will be-

come more biased and could lead to conclusions about spotted owl declines that are not valid.

Simple occupancy probabilities for all study areas appeared to be stable or to decline slightly over our study. Pair occupancy, however, declined greatly on the HJ Andrews study area, rose slightly on the Tyee study area, and declined slightly in recent years on the Coast Range area. Only HJ Andrews pair occupancy probability changed by >0.10 over time, with a decline from 0.78 to 0.60. These trends in site occupancy were comparable to trends in realized population change ($\Delta\lambda$) described by Anthony et al. (2004) that concluded that $\Delta\lambda$ was declining on the HJ Andrews and Coast Range study areas and was stationary on the Tyee study area.

The patterns in site occupancy probabilities could not be consistently attributed either to changes in local-extinction or colonization probabilities, but they mostly reflected a combination of the two. However, the decline in pair occupancy on the HJ Andrews study area appeared to be mostly driven by an increase in local-extinction probabilities. Since pair site extinction could be the result of either death or emigration from the site of 1 or both birds (and any combination of those events), it is difficult to discern what might cause increases in site extinction probabilities. If owls emigrated from sites at an increased rate, they were clearly not re-forming pairs at the same rate on unoccupied sites within the study area because colonization rates did not increase. Thus, the 3 possible explanations for increasing local-extinction probabilities are that survival has declined, migration off the study area has increased, or birds moved within the study area to sites that were not being surveyed. Survey coverage of the entire study area was nearly complete, thus the latter is not likely, and Anthony et al. (2004) did not find any changes in apparent survival for owls on the HJ Andrews study area during this same time interval. Thus, increased migration off of the study area was a possibility. Although the survival analysis of Anthony et al. (2004) should also reflect permanent emigration, their analysis was based on individual owls, not paired owls on specific sites. The HJ Andrews study area was of similar size to the Tyee study area, but it had more edge and was surrounded by areas containing spotted owl habitat that are not well surveyed for owls. Thus there was a greater potential for loss of owls to these surrounding areas; we were concerned that there was apparently not a reciprocal gain of owls from these areas.

The differences in magnitude of site occupancy probabilities among study areas are not easily ex-

plained, but they could be due to other factors that we did not include in our analysis, particularly spatial factors. Several previous studies linked habitat factors, particularly amount of old forest, to various measures of spotted owl occupancy (Ripple et al. 1997, Swindle et al. 1999, Zabel et al. 2003). Higher site occupancy rates on the HJ Andrews study area may thus be due to owl territories there having a greater proportion of older forest, on average, than do territories within the Tyee and Coast Range study areas (Olson, unpublished data). Another possible explanation (unsupported as yet) for low site occupancy rates on the Tyee study area may be the checkerboard pattern of land ownership within this area. Although public lands in that area were not logged during the time frame of our study, private lands in the area have been. Intermediate rates of site occupancy on the Coast Range area may be due to the combination of checkerboard ownership lands and larger blocks of publicly owned property within this area. We intend to explore these hypotheses, as well as others concerning habitat, in future work using the same MacKenzie et al. (2003) methodology as we employed in this study. We expect to find similar overall relationships with occupancy probabilities as in previous studies, but we also expect to be able to more specifically attribute habitat characteristics with local-extinction and colonization parameters.

Our results confirmed our contention that detection probabilities for spotted owls were <1.0 and highly variable. Average detection probabilities (over all years and study areas) were 0.64 (simple), and 0.51 (pair detections), similar to those reported by Reid et al. (1999). Our results indicated that, on average, a single visit within a year would miss the presence of a pair about half the time and miss any owl a third of the time; therefore, assumptions of perfect detectability based on a single visit would obviously be wrong. Based on the averages given, a survey consisting of at least 3 visits would detect any owl 95% of the time, but it would detect a pair of owls only 88% of the time. These rates might be acceptable for most study objectives, but based on the temporal and spatial variation we found in detection probabilities, they may be overly optimistic in other cases.

There did not seem to be any consistent pattern to the variation in detection probabilities. Annual detection probabilities (averaged across study areas) had coefficients of variation (CVs) of 6.6 and 14.5% for simple and pair occupancy, respectively. However, the greatest difference among any 2 years

was 0.13 vs. 0.24, indicating that estimates of pair occupancy, in particular, would be greatly biased if annual variation was not taken into account.

We did not fully explore possible sources of annual variation. We found that the one factor we did investigate, average reproductive effort, was an adequate covariate for only the Tyee study area. Although reproductive status might also be a source of variation in detectability for the other study areas, there must be additional temporal factors that are influencing time variation in detection probabilities. We do not believe that survey effort or observer bias were factors because, although the composition of survey crews varied among years, the number of observers was >5 in each year, and average effort and ability of the crews were similar among years.

Detection probabilities among study areas (averaged across years) did not differ much (CV for both types of occupancy were <5%), but the pattern of annual variation differed (Fig. 3), indicating there was spatial variation in detectability at the study area scale. Changes in detection probabilities from 1 year to the next were in the same direction (positive or negative) on all 3 study areas 8 out of 12 times for simple occupancy as compared to only 2 out of 12 times for pair occupancy. Since those cases were in the most recent years, it is possible that more years of dissimilarity will follow. Even in years when detectability changed in the same direction, the magnitude of the change often differed, and this was especially true for pair detectability. This further supports our contention that detection probabilities must be estimated for each analysis and that generalizations across study areas cannot be made.

Although we did not detect within-year differences among visit detection probabilities, we did not fully explore potential sources of variability such as time of visit (day or night), weather conditions, and time of year (other than via simple time trends). We tried to reduce variation from these kinds of sources with our visit criteria, but we acknowledge that this is an area where precision might be improved by a more thorough analysis.

MANAGEMENT IMPLICATIONS

Site occupancy probabilities appeared to be mostly stable for all of our study areas, but there are indications of a substantial decline in pair occupancy on the HJ Andrews study area due to increased site extinction, and this is an area that deserves further investigation. There was also evidence that site occupancy may decline on all areas in the near future. Increasing presence of barred

owls will likely lead to lowered site occupancy rates in Oregon (see also Kelly et al. 2003). If possible, our study should be repeated for study areas in Washington that have a longer history and higher frequency of barred owl presence. Results from that investigation would be useful for making predictions about future impacts of barred owls on northern spotted owls in Oregon and California.

Our finding that detection probabilities of spotted owls averaged from 0.50 to 0.67 supports the current minimum 3-visit protocol for determining site occupancy established by Lint et al. (1999) for monitoring owl population status on historical owl territories. However, there was enough temporal and spatial variability in detection rates to indicate that more visits would be needed in some years and in some areas, especially if establishing pair occupancy was the primary goal. Further, any studies that depend on owl presence as the response variable or as a covariate must consider that results may be biased if the magnitude and variation in detectability is not accounted for.

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Appendix A. Definitions of visit criteria and average maximum number of visits per year for site occupancy modeling of northern spotted owls on 3 study areas in Oregon.

Visit Criteria

1. Visits were considered "complete" if all calling points at a site (always >1, the total number determined by the topography of each site) were covered during a night survey. Spot calls were conducted for ≥10 min at each point.
2. Trips taken to the same site ≤2 days apart are considered 1 visit. This usually occurred when an owl responded to a night survey call and a daytime follow-up trip was required to determine its reproductive status.
3. If trips occurred 2 < days ≤7 then:
 - A. trips were counted as 1 visit if taken to complete a visit.
 - B. insufficient visits are dropped if a single complete visit exists within the 7-day interval.
 - C. complete visits (according to protocol) within the 7-day interval were counted as separate visits.
4. Visits made to sites where pairs were established to count and/or band number of young could be counted as occupancy visits.

Average Maximum Number of Visits Per Year

The average maximum number of visits for each year was determined after the visits for each site within a year were determined according to the visit criteria listed above. The average maximum should be chosen so that at least 90% of the sites have that number of visits or fewer.
