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Research Article

Demographic Response of Northern Spotted Owls to Barred Owl Removal

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ABSTRACT Federally listed as threatened in 1990 primarily because of habitat loss, the northern spotted owl (*Strix occidentalis caurina*) has continued to decline despite conservation efforts resulting in forested habitat being reserved throughout its range. Recently, there is growing evidence the congeneric invasive barred owl (*Strix varia*) may be responsible for the continued decline primarily by excluding spotted owls from their preferred habitat. We used a long-term demographic study for spotted owls in coastal northern California as the basis for a pilot barred owl removal experiment. Our demography study used capture–recapture, reproductive output, and territory occupancy data collected from 1990 to 2013 to evaluate trends in vital rates and populations. We used a classic before–after–control–impact (BACI) experimental design to investigate the demographic response of northern spotted owls to the lethal removal of barred owls. According to the best 2-species dynamic occupancy model, there was no evidence of differences in barred or northern spotted owl occupancy prior to the initiation of the treatment (barred owl removal). After treatment, barred owl occupancy was lower in the treated relative to the untreated areas and spotted owl occupancy was higher relative to the untreated areas. Barred owl removal decreased spotted owl territory extinction rates but did not affect territory colonization rates. As a result, spotted owl occupancy increased in the treated area and continued to decline in the untreated areas. Prior to and after barred owl removal, there was no evidence that average fecundity differed on the 2 study areas. However, the greater number of occupied spotted owl sites on the treated areas resulted in greater productivity in the treated areas based on empirical counts of fledged young. Prior to removal, survival was declining at a rate of approximately 0.2% per year for treated and untreated areas. Following treatment, estimated survival was 0.859 for the treated areas and 0.822 for the untreated areas. Derived estimates of population change on both study areas showed the same general decline before removal with an estimated slope of -0.0036 per year. Following removal, the rate of population change on the treated areas increased to an average of 1.029 but decreased to an average of 0.870 on the untreated areas. The results from this first experiment demonstrated that lethal removal of barred owls allowed the recovery of northern spotted owl populations in the treated portions of our study area. If additional federally funded barred owl removal experiments provide similar results, this could be the foundation for development of a long-term conservation strategy for northern spotted owls. © 2016 The Wildlife Society.

KEY WORDS barred owl, competition, demography, northern spotted owl, removal experiment.

The northern spotted owl (*Strix occidentalis caurina*) is a medium-sized owl that inhabits structurally complex forests in the coastal and Cascade ranges from southwestern British

Columbia to northern California. It is primarily a nocturnal forager of small mammals, has relatively large home ranges, and actively defends space around its nest and roosting area from conspecifics (Courtney et al. 2004). Extensive research on northern spotted owl habitat requirements, conducted during the past 4 decades, focused on understanding the structural characteristics and spatial requirements of nesting, roosting, and foraging habitat for this species. These studies

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have been conducted primarily in landscapes with significant amounts of mature or old forests, the principal seral stages used by this species in most areas where it has been studied (Courtney et al. 2004). The underlying ecological premise behind these habitat studies was that northern spotted owl populations were limited by the amount and distribution of habitat (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005).

As early as 1990 when the United States Fish and Wildlife Service (USFWS) listed the northern spotted owl as a threatened species (USFWS 1990), barred owls (*Strix varia*) were recognized as a potential threat to spotted owl populations. Similar in appearance but somewhat larger in size, the barred owl is also a territorial forest owl that historically occurred east of the Great Plains in North America. Since the listing of the spotted owl, there has been ever increasing concern about the range expansion (Livezey 2009) and increasing local populations (Yackulic et al. 2012) of the closely related barred owl. The Revised Recovery Plan for the Northern Spotted Owl (USFWS 2011:vi) stated "... it is becoming more evident that securing habitat alone will not recover the spotted owl. Based on the best available scientific information, competition from the barred owl (*S. varia*) poses a significant and complex threat to the spotted owl."

Barred owls may negatively affect spotted owl detectability, site occupancy, reproduction, and survival. Barred owls decreased detectability of spotted owls (Olson et al. 2005, Crozier et al. 2006, Dugger et al. 2009, Wiens et al. 2011), and spotted owl occupancy was significantly lower in territories where barred owls were detected within 0.8 km of the territory center (Kelly et al. 2003). Other relationships between barred owl detections and reduced site occupancy by spotted owls have been reported (Pearson and Livezey 2003, Gremel 2005, Olson et al. 2005, Kroll et al. 2010, Dugger et al. 2009) and Olson et al. (2004) reported that spotted owls had lower reproductive success on sites where barred owls had been detected. A recent range-wide analysis by Forsman et al. (2011) reported that the barred owl covariate, an annual estimate of the proportion of spotted owl territories influenced by barred owls, entered the top models with a negative coefficient for survival and fecundity in some demographic study areas throughout the owl's range. Occasional hybridization between the species is also documented (Hamer et al. 1994, Kelly and Forsman 2004), but it is not considered to be a serious threat to spotted owl populations (USFWS 2011).

Barred owls are considered habitat and prey generalists (Mazur and James 2000, Hamer et al. 2001). However, they select the same habitat for roosting and nesting as spotted owls, use similar habitat for foraging, and have a high degree of dietary overlap with spotted owls (Wiens et al. 2014). Barred owls also have comparatively smaller home ranges, greater reproductive output, and occur in higher population densities in favorable habitats (Wiens et al. 2014). Because of the slightly larger size of the barred owl, their mutual territoriality (Van Lanen et al. 2011), and similar habitat use, current hypotheses and competition theory predict that

barred owls may ultimately limit, and potentially extirpate, populations of spotted owls throughout their range (Gutiérrez et al. 2007, Yackulic et al. 2014).

As part of a monitoring commitment for a northern spotted owl Habitat Conservation Plan (HCP), Green Diamond Resource Company (Green Diamond) has conducted a demographic study for this species since 1990 within its approximately 1,600-km² ownership in northwestern California. A 2008 meta-analysis of northern spotted owl populations, including study areas from across the subspecies' range, concluded that the population on the Green Diamond study area was apparently stable or increasing until 2001, when it began to decline (Forsman et al. 2011). The 2008 meta-analysis could not determine cause and effect relationships. However, the presence of barred owls was negatively associated with fecundity and apparent survival of spotted owls. On the Green Diamond study area, the apparent decline in spotted owls coincided with an increase in barred owl numbers (Dugger et al. 2016).

Although it was the most probable hypothesis for the decline on our study area, experimental studies had not been conducted to isolate the effect of barred owls from other potential sources that may contribute to spotted owl population declines. A panel of scientists reviewed potential experimental designs and concluded that a demographic approach with a paired before-after-control-impact (BACI) experiment design where removal of barred owls was the treatment provided the greatest inference and statistical power (Johnson et al. 2008). The revised recovery plan for the northern spotted owl (USFWS 2011) expressed the need for such barred owl experimental removal experiments to be conducted.

We report the results from the first such barred owl removal experiment to address this critical research need. In 2009, the Green Diamond demographic study was partitioned into treated (barred owls lethally removed) and untreated (barred owls undisturbed) areas to estimate the impact of the treatment on spotted owl occupancy, fecundity, survival, and rate of population change. Green Diamond's demographic study has been ongoing since 1990, and they have contributed their data to the regularly conducted northern spotted owl meta-analysis since 1996 (Anthony et al. 2006, Forsman et al. 2011). Green Diamond's demographic data were also included in the most recent meta-analysis (Dugger et al., 2016) where appropriate, and where the treatment data did not compromise estimates of long-term trends. We report the specific analyses designed to test for treatment effects and integrate all of the results to draw conclusions on the effectiveness of barred owl removal for the benefit of northern spotted owls.

STUDY AREA

We conducted the study within Green Diamond's commercially managed timberlands in Humboldt and Del Norte counties, in coastal northern California. Green Diamond's lands of approximately 1,600 km² was composed predominantly of second- and third-growth stands of coast redwood (*Sequoia sempervirens*), Douglas-fir (*Pseudotsuga menziesii*),

and various hardwood species, including tanoak (*Lithocarpus densiflorus*), madrone (*Arbutus menziesii*), California bay (*Umbellularia californica*), and red alder (*Alnus rubra*). These forests were primarily harvested on a 50–70-year rotation. The primary silviculture was even-aged with historical incidental and current programmatic retention of mature and late seral elements. Light single tree selection harvest occurred within riparian zones and other sensitive areas that constituted close to 30% of the study area. Many forest stands occupied by spotted owls contained a substantial component of older, residual trees (Thome et al. 1999, Folliard et al. 2000). The entire study area was within 30 km of the Pacific Ocean, and elevation on the study area ranged from 5 m to 1,400 m. Additional details of the study area are included in Diller and Thome (1999).

Because we were interested in the effect of the barred owl invasion on spotted owls, we divided our study area into treated areas where barred owls were removed and untreated areas where they were not removed. To account for geographic differences in the history of timber harvesting, physiographic patterns, and density of barred and spotted owl sites, the relatively linear Green Diamond study area was divided into 3 roughly equivalently sized paired treated and untreated areas totaling 84,205 ha and 72,711 ha, respectively (Fig. 1). Given complications of lethal removal of barred owls with firearms, assignment of treated versus untreated areas was based on logistics and minimizing potential conflicts with adjacent landowners. As in virtually all field studies, it was impossible to ensure that all parameters such as mean density of spotted and barred owl territories of the treated and untreated areas were the same. However, this potential lack of complete symmetry was offset by 19 years of pre-treatment data such that post-treatment changes in trends or means of demographic parameters in the treated versus untreated areas could be reliably assigned to a treatment effect (i.e., barred owl removal).

METHODS

Field Methods

From 1990 to 2013, we monitored spotted owls by surveying the entire density study area (i.e., central contiguous areas where spotted owl population density could be estimated) with 100% survey coverage and territory-specific surveys for all the remaining peripheral owl sites in the demographic study area. The objectives of the surveys were to document occupancy status of owl territories, locate and confirm previously banded owls, band unmarked owls, and document the number of young produced by each territorial female (Lint et al. 1999, Reid et al. 1999). We conducted surveys using vocal imitations or playback of owl calls to incite the owls to defend their territories, thereby revealing their presence (Reid et al. 1999).

The number of surveys of each potential owl territory (i.e., owl site) in each study area was normally ≥ 3 per year, although fewer visits were allowed in cases where females were located that had no brood patch or showed no evidence of nesting during the period when they should have been

incubating or brooding young. After we became familiar with the distribution of owl territories in our study areas, it was often possible to locate owls by simply calling quietly while visually searching for owls in their traditional roost or nest areas during the day. If these diurnal surveys were unsuccessful, we surveyed the entire territory at night by calling from survey stations distributed throughout the area according to standard survey protocol. The field methods to capture, mark, and resight individual owls and to determine number of young fledged per female was the standard protocol used in all the northern spotted owl demographic study areas (Forsman et al. 2011, Dugger et al. 2016).

The pilot barred owl removal experiment within our spotted owl demographic study area was initiated on 15 February 2009 working under a permit to California Academy of Sciences that allowed 20 barred owls to be collected. Following an evaluation by the USFWS of our removal data from this pilot study, we were authorized to continue lethal removal in 2010 of ≤ 70 barred owls over a 3-year period, with ≤ 30 individuals removed in any given year.

We detected barred owls as a consequence of standard surveys to locate spotted owls from 1990 to 2009, but because these surveys were designed for detecting spotted owls, we likely underestimated the number and location of barred owls (Wiens et al. 2011). Therefore, we began barred owl-specific surveys in 2009. Barred owl-specific surveys, with similar spacing and number of visits as spotted owl surveys, included playing recordings of barred owl calls broadcast by a commercially available, remotely controlled, high-quality digital wildlife caller (Wildlife Technologies KAS-2030ML and MA 15, Manchester, NH). To reduce the potential of initiating interspecific interactions between the 2 species, we broadcast spotted owl lure calls for 8 minutes before transitioning to the barred owl-specific survey calls. If no spotted owls responded to the initial spotted owl lure broadcasts, we broadcast barred owl lure calls for 10 minutes. Following removal of barred owls from a site, we conducted additional barred owl-specific surveys to assess recolonization by barred owls at removal sites (adapted from Forsman 1983 and Bierregaard et al. 2008).

If a barred owl was detected during any survey, we returned to the site to locate it. If that location was in a known spotted owl territory, we first broadcast spotted owl calls during these follow-up visits. If spotted owls were present, we did not attempt to lure barred owls. If spotted owls did not respond within approximately 400 m of our location, we assumed there were no spotted owls present at the local site. We then broadcast a repertoire of barred owl lure calls, generally starting with male and female 2-phrased (8-note) hoots and progressed to more agitated ascending (series) hoots, pair duets, or cackling calls (Odom and Mennill 2010). We attempted to lethally remove all barred owls continuously in treatment areas that behaved in a territorial manner except barred owls that potentially had dependent nestlings or fledglings. Territoriality was assessed by aggressive hooting, flying to the source of the lure call, stooping on the calling device, and limb crashing (i.e., landing with force on a limb such that it made a loud sound). We only removed territorial

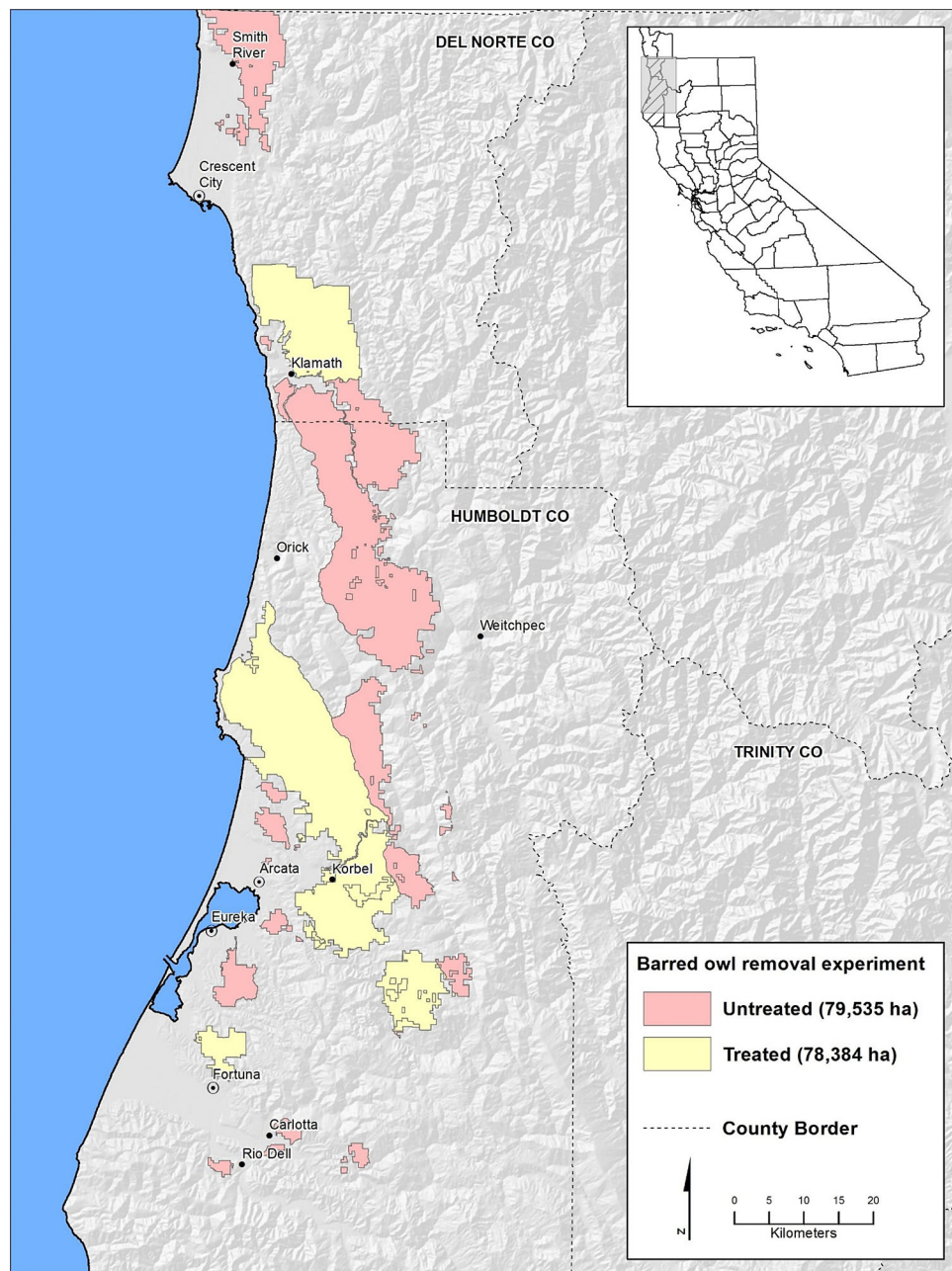


Figure 1. Treated (barred owls lethally removed) and untreated (barred owls undisturbed) areas on Green Diamond's northern spotted owl demographic study area in north coastal California, USA.

barred owls because our long-term goal was to assess impacts of territorial barred owls on spotted owls (Wiens et al. 2014) and our permits authorized a limited number of collections. We lethally removed barred owls as described in Diller et al. (2014). Lethal removal of barred owl was authorized by the following permits obtained in 2006 (USFWS permit no. MB103642-0 and California Department of Fish and Game [CDFG] permit no. SC-801126-05) issued to the California Academy of Sciences, 2009 (USFWS permit no. MB 680765-1 and CDFG permit no. SC-000687) issued to California Academy of Sciences, and 2010–2013 (USFWS no. MB 17356A-0 and CDFG Permit no. SC-000687) issued to L. V. Diller.

All territorial barred owls were continuously removed from the treated areas regardless of their proximity to known spotted owl territories. However, some barred owls occupied the same territory core, and sometimes even used the same nest site, from which the spotted owls were apparently displaced. These spotted owl sites were evaluated as case studies if the criteria were met in which a former spotted owl territory was occupied by barred owls (i.e., spotted owls no longer detected for at least a year) that inhabited the same territory center (nest or primary roost sites). In these situations, the site was surveyed at least once per month following the removal of the barred owls to determine the timing of potential re-occupancy by either barred or spotted

owls. We moused (i.e., placed a live laboratory mouse in a position to be taken by an owl; Forsman 1983) spotted owls that re-occupied (same individual owls resuming occupancy at a site that they previously occupied) or recolonized (new owls occupying a site previously occupied by different individuals) a site to determine their pair and nesting status and we captured and banded any new spotted owls.

Analytical Methods

Spatially delineated owl sites were important to the development of detection/non-detection data sets for our site occupancy analyses, and for estimation of habitat and barred owl covariates within study areas. We defined an owl site as a landscape patch that represented the cumulative area where a spotted owl or pair of spotted owls was detected. The process by which these sites were delineated using Thiessen polygons was described in Dugger et al. (2016).

Development of covariates.—We collected barred owl detection locations used in the population and site occupancy analyses incidentally during our annual northern spotted owl surveys. Barred owls were not specifically targeted during the calling surveys conducted as part of our long-term monitoring of spotted owls and detections associated with barred owl-specific surveys conducted with removal protocols were not used to develop this covariate. However, barred owls frequently responded to spotted owl calls during nocturnal surveys and, based on a calling experiment conducted by Wiens et al. (2011), we estimated that the cumulative annual detection probability of barred owls was $>85\%$ at territories in which we conducted ≥ 3 nocturnal surveys for spotted owls. For population (as opposed to occupancy) scale analyses, we calculated a barred owl covariate that was year-specific and reflected the proportion of spotted owl territories (i.e., Thiessen polygons) in which barred owls were detected ≥ 1 time per year. For occupancy analyses, we used detections at the site and survey scale to estimate barred owl detection probability and the probability of barred owl occupancy, colonization, and extinction at sites where barred owls may have been present but not detected.

We developed habitat covariates to represent the amount and distribution of northern spotted owl habitat within our study area. For population scale analyses, we calculated these covariates across the whole study area and they varied among years. For occupancy analyses, we calculated certain covariates at the scale of individual owl sites and they varied both spatially and temporally. For clarity, the covariates calculated at the population scale are capitalized and covariates calculated at the site scale are not. The covariates calculated were 1) the amount of northern spotted owl habitat (HAB for population scale; hab for individual owl site scale), 2) the change in the proportion of habitat during 3-year intervals prior to each survey year (HC/hc), 3) the proportion of the study area or owl site that contained $\geq 50\%$ habitat within an 800-m-radius circle centered on each pixel in the study area (CORE/core), and 4) the total amount of edge habitat (in m; EDGE/edge), with edge as the interface between suitable owl habitat and all other cover types.

Additional details on the development of the habitat covariates are in Dugger et al. (2016).

We used a variety of covariates to investigate possible effects of weather and climate on population-scale vital rates of northern spotted owls. All weather and climate covariates were time-specific and applied at the scale of the owl population on our study area. These variables included measures of seasonal and annual weather and long-term climatic conditions. Specific covariates included mean precipitation and temperature during various life-history stages, Palmer Drought Severity Index (PDSI), Southern Oscillation Index (SOI), and Pacific Decadal Oscillation (PDO; Franklin et al. 2000; Glenn et al. 2010, 2011a,b; Forsman et al. 2011). Additional details on the development of the weather and climate covariates are in Dugger et al. (2016).

Analysis of site occupancy.—Our analysis of site occupancy was based on 15 years (1999–2013) of detection data, including 10 years prior to initiation of treatment and 5 years during the treatment period. Detections occurred during surveys conducted from 1 March through 31 August within owl sites, but detection/non-detection was aggregated into 12 2-week periods. On a per survey visit basis, we defined a site as occupied by spotted owls when a mated pair was present. We considered a site unoccupied if no owls or only a single spotted owl was detected. However, we considered the site occupied by barred owls when 1 or a pair of territorial individuals were detected. The basis for this difference is that spotted owl pairs have the potential to reproduce and are the ecological sample unit of interest (i.e., sensu effective population size). However, either single or paired barred owls have the potential to negatively affect spotted owls; therefore, we estimated all territorial barred owls to fully quantify their impact. We used a multi-season 2-species occupancy model and Program MARK to generate estimates.

At the start of each breeding season, owl sites were in 1 of 4 mutually exclusive states: both species present (state 3), only northern spotted owls present (state 2), only barred owls present (state 1), and neither species present (state 0). As neither species was detected perfectly, the true state of a site was only known with certainty when both species were detected (state 3). When only a barred owl was detected (observed state 1), the site could also have been occupied by a spotted owl pair (state 3) or not (state 1). Likewise, when only a spotted owl pair was detected, the site could also have been occupied by barred owls (state 3) or not (state 2). When neither species was detected, the owl site could have been in any one of the 4 states.

We modeled the overall probability of detecting the state of a site, given its true state, using a matrix of probabilities, ρ , i , t , j , that varied by site (i), year (t), and sampling event (j). We assumed no false positives (e.g., detection of barred owl, but site is occupied by spotted owl only), reduced probabilities in the matrix, and modeled ρ as a function of 5 parameters that varied by site, year, and sampling event. Omitting subscripts for clarity, these 5 parameters were 1) detection probability of barred owls when spotted owls were not present, ρ^A (A = barred owl), 2) detection probability of barred owls when spotted owls were present, ρ^{Aa} , 3) detection probability

of northern spotted owls when barred owls were not present, p^B (B = northern spotted owl), 4) detection probability of northern spotted owls when barred owls were present and detected, r^{BA} , and 5) detection probability of northern spotted owls when barred owls were present but not detected, r^{Ba} . The reduced matrix was:

$$\rho = \begin{pmatrix} 1 & 0 & 0 & 0 \\ (1 - p^A) & p^A & 0 & 0 \\ (1 - p^B) & 0 & p^B & 0 \\ (1 - r^{BA})(1 - r^A) & (1 - r^{Ba})r^A & r^{BA}(1 - r^A) & r^{Ba}r^A \end{pmatrix}$$

where each row represents the probability of detecting a site in states 0 through 3 given that the true state is 0, 1, 2, or 3 (in descending order).

The 5 detection parameters could, theoretically, be modeled as independent of presence or absence of the other species; however, we assumed an additive effect on the logit scale of the presence or detection of the other species. In other words, if spotted owl detection probability in the absence of barred owls, p^B , is modeled as a function of a matrix of covariates, X , using a vector of betas, β , and an intercept, β_0 :

$$\text{logit}(p^B) = \beta_0 + \beta X$$

then detection probability of spotted owls when barred owls are present but not detected, r^{Ba} , is modeled as:

$$\text{logit}(r^{Ba}) = \beta_0 + \beta X + \beta_A$$

where β_A is the additive effect of the presence of barred owls on detection of spotted owls. Previous work has suggested that spotted owls are less likely to be detected when barred owls co-occupy an area, even if barred owls are not actively responding (Yackulic et al. 2014). When barred owls do respond, the detection probability of spotted owls is expected to decline even further. This additive effect of the detection of a barred owl, β_{DA} , in addition to the presence of a barred owl is included in the detection probability of spotted owls when barred owls are detected, r^{BA} , as follows:

$$\text{logit}(r^{BA}) = \beta_0 + \beta X + \beta_A + \beta_{DA}$$

For brevity, and because we only considered additive differences between detection parameters, hereafter we only refer to the betas, β_A or β_{DA} , as opposed to the associated parameters, r^{Ba} and r^{BA} .

Hypotheses about differences before or after treatment in either the untreated or treated areas can be tested by including interactions between indicator variables and either β_A or β_{DA} . For example, the hypothesis that detection probability of spotted owls when barred owls were present but not detected changed in the treatment area after treatment could be formulated as:

$$\text{logit}(r^{Ba}) = \beta_0 + \beta X + \beta_A + R\beta_{AR}$$

where R is an indicator variable determining whether a particular site was in the treatment group, and β_{AR} is the

estimated difference in r^{Ba} on the logit scale associated with the treated group.

The model assumes the true state of each site did not change within breeding seasons; consequently, changes in state within a season could bias parameter estimates. In particular, removal of barred owls during the breeding season would violate this assumption. In other words, removal either changes the state from occupied by both species (state 4) to occupied by spotted owls only (state 2) or changes the state from occupied by barred owls only (state 1) to occupied by neither species (state 0). Therefore, at sites in the treated area, we considered only surveys within a breeding season that occurred prior to removal of the last barred owl to avoid biasing parameter estimates.

Between breeding seasons, sites transitioned between states according to a transition matrix, $\phi_{i,t}$, that varies depending on the covariates associated with owl site i at time t . As with detection parameters, we drop subscripts and model transition probabilities as functions of the following 8 parameters: 1) colonization probability for barred owls when barred owls were not present in the previous breeding season, γ^A , 2) colonization probability for barred owls when barred owls were present in the previous breeding season, γ^{AB} , 3) colonization probability for northern spotted owls when barred owls were not present in the previous breeding season, γ^B , 4) colonization probability for northern spotted owls when barred owls were present in the previous breeding season, γ^{BA} , 5) extinction probability for barred owls when spotted owls were not present in the previous breeding season, ε^A , 6) extinction probability for barred owls when spotted owls were present in the previous breeding season, ε^{AB} , 7) extinction probability for northern spotted owls when barred owls were not present in the previous breeding season, ε^B , and 8) extinction probability for northern spotted owls when barred owls were present in the previous breeding season, ε^{BA} . The full transition matrix, ϕ , was:

$$\begin{pmatrix} (1 - \gamma^A)(1 - \gamma^B) & \gamma^A(1 - \gamma^B) & (1 - \gamma^A)\gamma^B & \gamma^A\gamma^B \\ \varepsilon^A(1 - \gamma^{BA}) & (1 - \varepsilon^A)(1 - \gamma^{BA}) & \varepsilon^A\gamma^{BA} & (1 - \varepsilon^A)\gamma^{BA} \\ (1 - \gamma^{AB})\varepsilon^B & \gamma^{AB}\varepsilon^B & (1 - \gamma^{AB})(1 - \varepsilon^B) & \gamma^{AB}(1 - \varepsilon^B) \\ \varepsilon^{AB}\varepsilon^{BA} & (1 - \varepsilon^{AB})\varepsilon^{BA} & \varepsilon^{AB}(1 - \varepsilon^{BA}) & (1 - \varepsilon^{AB})(1 - \varepsilon^{BA}) \end{pmatrix}$$

where each row corresponds to the state at time, t , and each column corresponds to the state at time, $t+1$, and states in each dimension are ordered from 0 to 3.

We modeled the effects of conspecifics as additive on the logit scale. So, for example, if extinction of spotted owls in the absence of barred owls, ε^B , is modeled via an intercept, α_0 , and the product of a vector of estimate coefficients, α , and a matrix of covariates, X according to:

$$\text{logit}(\varepsilon^B) = \alpha_0 + \alpha X$$

then extinction probability in the presence of barred owls, ε^{BA} , would be modeled as:

$$\text{logit}(\varepsilon^{BA}) = \alpha_0 + \alpha X + \alpha_A$$

where BA is the difference in extinction probability on the logit scale associated with barred owl occupancy. The primary hypotheses of interest regarding the effects of barred owl removal on spotted owl extinction probabilities are given below, after discussion of the background model.

Finally, the state of each owl site in the first year is modeled based on the probability of occupancy for barred owls, ψ_i^A , and spotted owls, ψ_i^B , where both probabilities vary based on site covariates, including potentially both habitat and pre-treatment groups. Although it is possible to differentiate between occupancy of spotted owls in sites where barred owls are present or absent, previous 2-species occupancy modeling of this dataset did not support this distinction, probably because of the low prevalence of barred owls at the beginning of the study period (Dugger et al. 2016).

Baseline model.—Dugger et al. (2016) analyzed data from our study area (and 10 other study areas) over the same time period but excluded sites in the treatment area after 2008. Their analysis tested a number of hypotheses about habitat covariates, interspecific interactions, and temporal trends in various parameters. We adopted their best model structure as the baseline model for all analyses presented here, and build on it to test hypotheses about the effects of barred owl removal. The baseline model identified by Dugger et al. (2016) contained the following sub-models: 1) barred owl detection probability included a linear temporal trend; 2) spotted owl detection probability included a year factor (i.e., year-specific intercepts), a within-year bi-week factor (different intercepts for each of the 12 2-week periods), a within-year survey effect (whether surveys had previously been done at the site in the same year), and differences depending on whether barred owls were present and not detected, β_A , or present and detected, β_{DA} ; 3) initial occupancy of barred owls did not vary between sites, 4) initial occupancy of spotted owls included the habitat change (hc) covariate, 5) barred owl colonization was a function of the edge covariate and a linear temporal trend, 6) spotted owl colonization was a function of the edge covariate, 7) barred owl extinction probability was a function of the hab covariate and whether spotted owls co-occupied the patch, β_B , and 8) spotted owl extinction was a function of the core covariate and whether barred owls co-occupied the patch, β_A .

Specific hypotheses tested in this analysis.—Past 2-species dynamic occupancy models for these species indicated that barred owls primarily affect northern spotted owl occupancy parameters by increasing local extinction rates in co-occupied patches (Yackulic et al. 2014, Dugger et al. 2016). Because barred owls were actively removed from sites in the treated area, we hypothesized that northern spotted owl extinction in the presence of barred owls would decline in the treated area to a level similar to northern spotted owl extinction in the absence of barred owls. Therefore, we modeled spotted owl extinction in the presence of barred owls using the following formula:

$$\text{logit}(\varepsilon^{BA}) = \alpha_0 + \alpha X + \alpha_A + \alpha_{AR} R$$

where X contained baseline covariates identified by Dugger et al. (2016) and hypothesized that α_{AR} would be negative

with absolute magnitude approximately the same as α_A . We also hypothesized that removals would lead to an increase in barred owl extinction in the treated area regardless of whether spotted owls were present. In other words, given:

$$\text{logit}(\varepsilon^A) = \alpha_0 + \alpha X + \alpha_R R$$

$$\text{logit}(\varepsilon^{AB}) = \alpha_0 + \alpha X + \alpha_B + \alpha_R R$$

we hypothesized that α_R would be positive.

It was more difficult to predict the effects of barred owl removals on colonization of both species because of uncertainty regarding movement rates of both species. If movement between treated and untreated was common, we reasoned that treatment effects on colonization would be difficult to detect. In addition, barred owl occupancy was steadily increasing before treatment, and it was reasonable to assume barred owl colonization rates were increasing as well (Yackulic et al. 2012). Given these uncertainties, we tentatively hypothesized that barred owl colonization rates would be lower in the treatment area than in the untreated area but had no a priori hypothesis concerning overall trends in barred owl colonization post-treatment. In addition, we hypothesized that spotted owl colonization would increase in the treatment area.

In addition to the above hypotheses regarding the effects of treatment on different groups, we also tested for pre-existing differences between the group's initial occupancy, colonization, or extinction prior to treatment. We also considered hypotheses about how detection probability may have changed either in response to treatment or to the use of digitally broadcasted northern spotted owl calls beginning in 2009. We hypothesized that the improved quality of the broadcast calls would result in an increase in detection probabilities for barred owls. We also hypothesized that improved quality of broadcast calls might affect the probability of detecting spotted owls at sites also occupied by barred owls, but we did not have an a priori expectation concerning the sign of this effect. In addition, we hypothesized that the detection probability of northern spotted owls in previously co-occupied patches within the treated areas would increase as barred owls were removed.

Occupancy model selection.—We began by fitting a full model that included all background effects and hypotheses of interest (Table 1). We then sequentially removed effects (except those included in the baseline model) and observed changes in corrected Akaike's Information Criterion (AIC_c) values. We determined the order of potential removals a priori using the following steps: 1) determine which of the hypothesized treatment effects were supported in the detection parameters; 2) determine whether there is support for any differences between treatment groups prior to initiation of treatment in the initial occupancy, colonization, or extinction of either species; 3) determine whether parameters associated with colonization and extinction changed in the untreated area after initiation of treatment; and 4) determine if parameters associated with colonization and extinction differ between treated and untreated areas

Table 1. Unique model elements and information criterion statistics for the 2-species occupancy models fitted to data on Green Diamond's northern spotted owl demographic study area in north coastal California, 1999–2013. We modeled initial occupancy (ψ^B , ψ^A [A = barred owl, B = northern spotted owl]), colonization ($\hat{\gamma}^B$, $\hat{\gamma}^A$), extinction ($\hat{\epsilon}^B$, $\hat{\epsilon}^A$), and detection ($\hat{\phi}^B$, $\hat{\phi}^A$) for northern spotted and barred owls (BO). The full model includes parameters that allow different intercepts (β_0), effects of barred owl occupancy (β_A), effects of barred owl detections (β_{D^A}), and different trends (β_T) based on pretreatment differences (R') or changes post-treatment in either the treated (R) or untreated (U) areas. Some submodels also include hypotheses that a given parameter changed after treatment and that there was no differences between treated and untreated areas with respect to the change ($U=R$). We calculated differences in Akaike's Information Criterion (ΔAIC_c) both within each model set and overall and we also report the number of parameters (K) and the deviance (twice the negative log likelihood, 2NLL). All models included habitat covariates, interspecific effects, and temporal variation in various parameters already identified as important based on a previous analysis and referred to as the base model. Dash (–) indicates that no additional parameters were added from the base model. NS = model not supported; S = model supported

Hypothesis tested	Northern spotted owl						Barred owl						Overall ΔAIC_c	Model set ΔAIC_c	K	2NLL	
	ψ_0^B	$\hat{\gamma}^B$	$\hat{\epsilon}^B$	$\hat{\rho}^B$	β_A	β_{D^A}	ψ_0^A	$\hat{\gamma}^A$	$\hat{\epsilon}^A$	$\hat{\rho}^A$							
	β_0	β_0	β_A	β_A	β_A	β_{D^A}	β_0	β_0	β_0	β_0							
First model set: detection probability hypotheses																	
Full model																	
$\hat{\rho}^A$ changes with digitally broadcasted recorders (NS).	R'	R', U, R	R', U, R	U, R	U, R	U, R	R'	R', U, R	U, R	R', U, R	U, R	R', U, R	$U=R$	17.8	5.0	67	12,620.8
$\hat{\rho}^B$ during surveys when BO are detected changes with digitally broadcasted recorders (NS).	R'	R', U, R	R', U, R	U, R	U, R	U, R	R'	R', U, R	U, R	R', U, R	U, R	R', U, R	—	16.4	3.6	66	12,621.5
$\hat{\rho}^B$ at sites where BO are present changes with treatment (S).	R'	R', U, R	R', U, R	U, R	U, R	U, R	R'	R', U, R	—	R'	R', U, R	R', U, R	—	12.8	0	64	12,622.1
$\hat{\rho}^B$ at sites where BO are present changes with treatment (S).	R'	R', U, R	R', U, R	U	U	—	R'	R', U, R	U, R	R', U, R	U, R	R', U, R	—	21.6	8.8	63	12,633.0
$\hat{\rho}^B$ at sites where BO are present changes with treatment (S).	R'	R', U, R	R', U, R	R	R	—	R'	R', U, R	U, R	R', U, R	U, R	R', U, R	—	15.0	2.2	63	12,626.4
Second model set: hypotheses concerning pretreatment differences between treated and untreated areas																	
ψ_0^A differs between areas before treatment (NS).	R'	R', U, R	R', U, R	U, R	U, R	—	—	R', U, R	U, R	R', U, R	U, R	R', U, R	—	11.0	8.4	63	12,622.4
ψ_0^B differs between areas before treatment (NS).	—	R', U, R	R', U, R	U, R	U, R	—	—	R', U, R	U, R	R', U, R	U, R	R', U, R	—	9.7	7.1	62	12,623.2
$\hat{\gamma}^A$ differs between areas before treatment (NS).	—	R', U, R	R', U, R	U, R	U, R	—	—	U, R	U, R	R', U, R	U, R	R', U, R	—	8.2	5.6	61	12,623.8
$\hat{\epsilon}^A$ differs between areas before treatment (NS).	—	R', U, R	R', U, R	U, R	U, R	—	—	U, R	U, R	U, R	U, R	U, R	—	6.5	3.9	60	12,624.2
$\hat{\gamma}^B$ differs between areas before treatment (NS).	—	U, R	R', U, R	U, R	U, R	—	—	U, R	U, R	U, R	U, R	U, R	—	4.4	1.8	59	12,624.2
$\hat{\epsilon}^B$ at sites occupied by barred owls differs between areas before treatment (NS).	—	U, R	U, R	U, R	U, R	—	—	U, R	U, R	U, R	U, R	U, R	—	2.6	0	58	12,624.5
Third model set: hypotheses concerning changes in untreated area after treatment began																	
$\hat{\gamma}^A$ intercept changes in untreated area (S).	—	U, R	U, R	U, R	U, R	U, R	—	R	U, R	U, R	U, R	U, R	—	11.2	9.2	57	12,635.2
$\hat{\gamma}^A$ trend changes in untreated area (S).	—	U, R	U, R	U, R	U, R	U, R	—	U, R	R	U, R	U, R	U, R	—	7.4	5.4	57	12,631.4
$\hat{\epsilon}^A$ changes in untreated area (S).	—	U, R	U, R	U, R	U, R	U, R	—	U, R	U, R	R	U, R	R	—	5.8	3.8	57	12,629.8
$\hat{\gamma}^B$ changes in untreated area (NS).	—	R	U, R	U, R	U, R	U, R	—	U, R	U, R	U, R	U, R	U, R	—	2.5	0.5	57	12,626.4
$\hat{\epsilon}^B$ in co-occupied sites changes in untreated area (NS).	—	R	R	U, R	U, R	U, R	—	U, R	U, R	U, R	U, R	U, R	—	2.0	0	56	12,628.1
Fourth model set: hypotheses concerning treatment effects on treated area																	
$\hat{\gamma}^A$ intercept changes after treatment were different in treated area (S).	—	R	R	U, R	U, R	U, R	—	$U=R$	U, R	U, R	U, R	U, R	—	4.7	4.7	55	12,632.9
$\hat{\gamma}^A$ trend changes after treatment were different in treated area (NS).	—	R	R	U, R	U, R	U, R	—	U, R	$U=R$	U, R	U, R	U, R	—	0.4	0.4	55	12,628.6
$\hat{\epsilon}^A$ changes after treatment were different in treated area (S).	—	R	R	U, R	U, R	U, R	—	U, R	U, R	$U=R$	U, R	U, R	—	11.3	11.3	54	12,641.6
$\hat{\gamma}^B$ changes in treatment area only (NS).	—	—	R	U, R	U, R	U, R	—	U, R	U, R	U, R	U, R	U, R	—	0	0	54	12,630.3
$\hat{\epsilon}^B$ in co-occupied sites changes in treatment area only (S).	—	—	—	U, R	U, R	U, R	—	U, R	U, R	U, R	U, R	U, R	—	8.0	8.0	53	12,630.3

following initiation of treatment. Within each set, we decided a priori to always remove parameters related to barred owls before removing parameters related to northern spotted owls and we always removed parameters related to colonization before parameters related to extinction.

Analysis of fecundity.—We conducted analysis of fecundity on the number of female young produced per territorial female per year, defined as the number of young (M + F) produced per territorial female per year divided by 2 because the sex ratio of juvenile owls at hatching was assumed to be 1:1 (Fleming et al. 1996). Spotted owls are strongly territorial, with high site fidelity and detectability, even in years when they are not breeding (Franklin et al. 1996, Reid et al. 1999). Similar to other studies (Anthony et al. 2006, Forsman et al. 2011, Dugger et al. 2016), we assumed that sampling throughout the breeding season was not biased towards birds that reproduced, and that the sample of owls used in our analyses was representative of the territorial population. During 1990 to 2013 over all sites, 90% of fledged young were produced by adult females >2 years old (other age classes included 1% produced by first-year subadults (S1), 3% produced by second-year subadults (S2), and 6% produced by unknown age birds). In addition, the number of non-adult birds was low or 0 in some years, which reduced our ability to compare fecundity for these age classes. Consequently, we dropped non-adult age classes from analysis and considered only fecundity of adult females.

Similar to previous analyses (Anthony et al. 2006, Forsman et al. 2011, Dugger et al. 2016), we analyzed mean annual fecundity using standard regression based on a normal distribution. Analysis of average fecundity helped assure the homoscedastic error assumption inherent in normal models. Furthermore, the appropriate sample units for the analysis were geographical (the treated and untreated areas), not individual owls, because both experimental areas could respond annually to effects that influenced their entirety. In addition, by averaging over owl territories occupied by females and considering treatment areas as sampling units, we reduced ill-effects of autocorrelation in reproduction through time on individual owl territories (Dugger et al. 2016).

The distribution of the underlying data (no. fledglings/female; NYF) was consistent with a truncated Poisson or multinomial distribution because spotted owl pairs almost always raise 0, 1, or 2 young. However, annual fecundity averaged over territories was not Poisson (Forsman et al. 2011), and normal models are more accurate than Poisson models when data depart from Poisson (White and Bennetts 1996, McDonald and White 2010). In addition, normal models are just as accurate as multinomial models when averages are analyzed (McDonald and White 2010). Thus, we used regression models based on a normal distribution to model mean annual NYF for study area as described in Dugger et al. (2016).

Prior analysis has shown that the spatial covariance among territories tended to be small relative to temporal variance among years and other residual effects (Forsman et al. 2011). This justified disregarding spatial covariance because it

would not seriously bias variance estimates. In addition, residual variation was relatively constant through time largely because residual variation was small relative to annual variation. Consistent with previous analyses (Anthony et al. 2006, Forsman et al. 2011, Dugger et al. 2016), we estimated the effect of barred owl removal and fit a large number of candidate models containing the effects of habitat, weather, climate, and various forms of interactions between study area (treated vs. untreated) and time period (pre-removal and post-removal). We determined the set of candidate models prior to estimation based on biologically plausible hypothesized effects. The full list included 574 models but we present only those models with a $\Delta AIC_c < 5$.

All models fitted here contained constraints on temporal trends pre- and post-removal that were, in fact, the primary goal of estimation. In addition to non-temporal covariates mentioned above, the models fitted here included year and treatment covariates that allowed the same, parallel, or non-parallel trends on the 2 study areas (treated and untreated) before treatment but parallel trends and differing magnitudes after treatment. If removal of barred owls on the treated area had no effect on average fecundity, the coefficient for the difference in magnitude between treated and non-treatment areas after removal would be 0. If the intercept coefficient measuring the mean difference post-treatment was not 0 (at $\alpha = 0.05$ level), we concluded the change in fecundity to be associated with removal of barred owls. That is, we concluded that fecundity on the 2 study areas was different following treatment.

Analysis of apparent survival.—We used capture–recapture (re-sighting) data to estimate capture probabilities and annual apparent survival probabilities of territorial owls using open population Cormack–Jolly–Seber models. We developed a set of models based on previous research and biological hypotheses (Dugger et al. 2016), and computed estimates of coefficients in those models using Program MARK (White and Burnham 1999). We considered both fixed and random effects models. Covariates considered in the fixed portion of the Cormack–Jolly–Seber model included sex and temporal effects. Covariates considered in the random portion of the model included reproduction, habitat, weather, climate, and generic time effects.

Based on the best-fitting fixed effects model, we included random effects to produce shrinkage estimates (Burnham and White 2002) of annual survival and standard error. Shrunk survival estimates were associated with the year of the field season that terminated the interval. For example, survival from field season 2011 to field season 2012 was associated with year 2012 for analysis. We discarded the final interval (2012–2013) because survival and capture were confounded during the final interval in time-dependent models (Forsman et al. 2011, Dugger et al. 2016).

We then tested for an effect of barred owl removal on survival. We exported the shrunk estimates of survival produced by the best fitting random effects model from MARK to R (R Foundation for Statistical Computing, Vienna, Austria) and used the estimates to test for an

association between survival and barred owl removal via the weighted linear model:

$$\varphi_{ij} = \beta_0 + \beta_1(Post_i) + \beta_2(Treated_j) + \beta_3(Post_i \times Treated_j) + \beta_4(Pre_i \times Year_i)$$

where φ_{ij} was the shrunk estimate of apparent survival between year i and $(i+1)$ on study area j , $Post_i$ was an indicator function for all survival intervals after removal ($Post_i = 1$ for 2008–2009 through 2011–2012, 0 otherwise, with the final interval discarded as described above). $Treated_j$ was an indicator for survival estimates on the treated areas, $Year_i$ was year of the study, and Pre_i was an indicator function for years prior to barred owl removal (i.e., $Pre_i = 1$ for 1990 through 2007). Each estimate in this model was weighted by the inverses of the standard error for individual survival estimate. This model forced parallel trends on both study areas pre-removal, and no trend post-removal. The model was constrained to estimate no trend post-removal because of the small number of observations post-removal ($n = 4$ intervals post-removal). This model allowed the difference in survival on treated and untreated areas to differ pre- and post-removal, and this was considered the effect of interest.

That is, if removal of barred owls on the treated area had no effect on survival, the coefficient for $Post \times Treated$ (i.e., β_3) would be 0 because β_3 measures the difference of differences ($\bar{\varphi}_{pre,treated} - \bar{\varphi}_{pre,non} - (\bar{\varphi}_{post,treated} - \bar{\varphi}_{post,non})$). If β_3 differed from 0 (at $\alpha = 0.05$ level), we concluded removal of barred owls was associated with a change in survival.

Analysis of annual rate of population change.—We included all banded territorial birds (S1, S2, adults) in the analysis of finite rates of population change (λ) on our study areas, the same dataset used in the survival analysis, but we did not explicitly include age effects. We used the f -parameterization of the temporal symmetry models of Pradel implemented in Program MARK (Pradel 1996) to obtain a derived estimate of λ . The rationale for using this approach instead of Leslie matrix models was based on large natal dispersal distances of spotted owls relative to the size of our study area resulting in permanent but unknown emigration of fledglings from the population, and little ability to accurately estimate juvenile survival. We assumed this reparameterization of the Jolly–Seber capture–recapture model (λ_{RJS}) produced less biased estimates of λ compared to estimates from a Leslie matrix (Anthony et al. 2006, Forsman et al. 2011).

The Pradel (1996) method assumes that study area size does not change and that survey effort is relatively constant in each sampling interval such that owls are not gained or lost because of changes in survey effort or study area size. We used consistent, established protocols on our study area for marking and resighting spotted owls each year (Franklin et al. 1996, Lint et al. 1999) to ensure that we surveyed study areas with approximately equal effort each year. Although our study area boundary increased in 1998, we corrected for the expansion through modeling in Program MARK. Full details of how we applied the Pradel method to estimating λ in our study area are in Dugger et al. (2016).

Initial effects considered for parameters in the λ_{RJS} model were general time and sex effects on recapture rates (p), general time effects on survival (φ_t), and general time effects on recruitment (f_t). We retained the best structure on p , as evidenced by the lowest AIC_c , and estimated a constant (no effect) random effects model to produce derived estimates of annual population change λ_t . The purpose behind fitting the random effects model was to reduce the number of distinct parameters without forcing them to be equal over all years, and thus shrink derived estimates of λ_t toward their mean pre- and post-removal values on both the treated and untreated areas.

We then conducted additional analyses to test for an effect of barred owl removal on the annual rate of population change. Similar to analysis of survival, we exported shrunk estimates of λ_{ij} derived from the random effects models (Burnham and White 2002) from MARK to R and tested for evidence of association with barred owl removal. We conducted the test for association with barred owl removal by estimating the weighted linear model,

$$\lambda_{ij} = \beta_0 + \beta_1(Post_i) + \beta_2(Treated_j) + \beta_3(Post_i \times Treated_j) + \beta_4(Pre_i \times Year_i)$$

where λ_{ij} was population change between years i and $(i+1)$ on study area j ; $Post_i$, $Treated_j$, $Year_i$, and Pre_i were as in the previous section; and the individual estimates were weighted with the inverses of the individual estimate's standard error. This model forced parallel trends in λ on both study areas pre-removal, and estimated no trend post-removal because of the small number of observations post-removal ($n = 4$ years post-removal). Similar to the survival model, this model allowed the difference in population change on treated and untreated areas to differ pre- and post-removal, and this was considered the effect of interest.

If removal of barred owls on the treated area had no effect on λ_{ij} , the coefficient for $Post \times Treated$ (i.e., β_3) would be 0 because β_3 measured the difference of differences. If β_3 was different from 0 (at $\alpha = 0.05$ level), we concluded removal of barred owls was associated with a change in the rate of population change.

RESULTS

Site Occupancy

Based on the analysis of 281 sites (158 treated and 123 untreated) from 1999 to 2013, the best 2-species dynamic occupancy model included 8 parameters in addition to the base model (Table 1), 5 of which concerned changes in barred owl occupancy dynamics, 1 related to spotted owl extinction in sites also occupied by barred owls, and 2 related to detection of spotted owls at sites also occupied by barred owls. According to the best model, there was no evidence of differences between treated and untreated areas for any of the barred owl occupancy parameters prior to the initiation of the treatment (barred owl removal). After treatment, barred owl occupancy parameters changed as follows: 1) estimates of

occupancy rates substantially increased in the untreated areas, whereas they remained relatively constant and much lower in the treated areas (Fig. 2A); 2) colonization rates initially increased and then declined in both treated and untreated areas, but the increase was greater in the untreated areas (Fig. 2B); and 3) extinction rates increased in the treated areas but declined in the untreated areas (Fig. 2C).

Similar to barred owls, there was no evidence of different spotted owl occupancy rates between treated and untreated areas prior to the initiation of the treatment. Following treatment, there was a slow recovery in northern spotted owl occupancy in the treated areas even as occupancy continued to decline in the untreated areas (Fig. 3A). Barred owl removal decreased overall spotted owl extinction rates to levels equivalent to spotted owls sites that had never had barred owls present (Fig. 3B). The best model estimated spotted owl colonization rates at an average of 0.19 (95% CI: 0.15–0.24) and models with different spotted

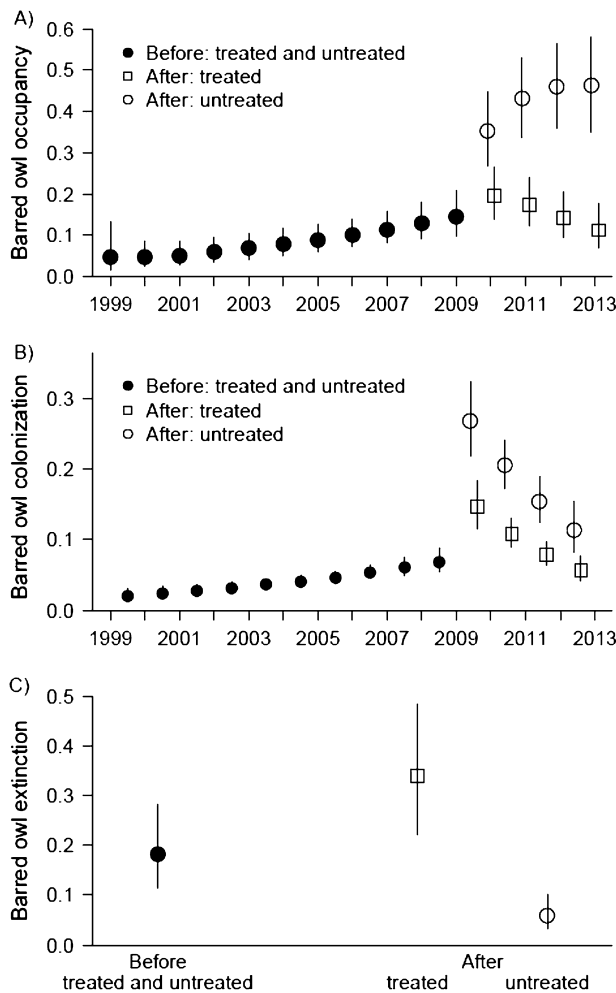


Figure 2. Changes in barred owl occupancy, colonization, and extinction on Green Diamond's northern spotted owl demographic study area in north coastal California, USA. (A) Trend in barred owl occupancy in treated and untreated areas before and after treatment (barred owl removal). (B) Trend in barred owl colonization in treated and untreated areas before and after treatment. (C) Barred owl extinction rate before treatment and after treatment in treated and untreated areas. Error bars represent 95% confidence intervals.

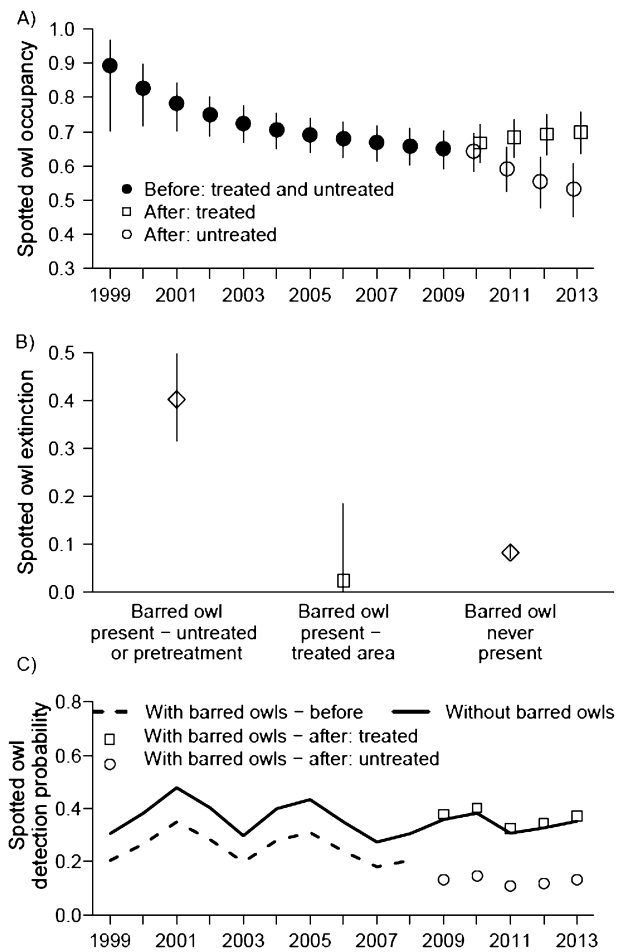


Figure 3. Changes in northern spotted owl occupancy, extinction, and detection probability on Green Diamond's demographic study area in north coastal California, USA. (A) Trend in spotted owl occupancy in treated and untreated areas before and after treatment (barred owl removal). (B) Spotted owl extinction rates when barred owls are present and not removed, barred owls are present and removed, and barred owls were never present. (C) Spotted owl detection probability with and without barred owls before treatment, without barred owls after treatment, and with barred owls after treatment in the treated and untreated areas. Error bars in panels A and B represent 95% confidence intervals.

owl colonization rates in treated and untreated areas were not supported. Northern spotted owl detection probability at sites not occupied by barred owls varied over time but showed no differences between treatments or over time (Fig. 3C). On the other hand, spotted owl detection probability at sites also occupied by barred owls increased in the treated area to the point where detection probability was nearly the same as at sites where barred owls were not present. At the same time, spotted owl detection probability in the untreated area at sites occupied by barred owls decreased to lower levels than were found prior to treatment (Fig. 3C). In agreement with Dugger et al. (2016), barred owl detection probability was estimated to be slowly increasing over the course of the study but did not show different trends with respect to treatment.

Fecundity

Estimates of fecundity (no. of female young produced/adult female/year) from 1990 to 2013 were based on records of

964 nesting attempts by adult females on the untreated study area, and 807 nesting attempts by adult females on the treated study area, for 1,771 records.

There were 19 linear models with $\Delta AIC_c < 5$ fitted to mean annual fecundity (Table 2). The top 3 models with $\Delta AIC_c < 2$ all contained a negative effect of winter precipitation and an even-odd year effect. Two of the top 3 models contained a negative effect associated with increased winter temperatures, and another 2 contained a positive effect associated with increased amounts of edge habitat. The second and third ranked models led to the same conclusions as the top model, so we focused attention on the best-fitting model (Fig. 4). After considering the effects of habitat, climate, and even-odd year trends, prior to barred owl removal, there was evidence that fecundity decreased by an annual rate of 0.01 female young per adult female ($P = 0.021$) in both treated and untreated areas, but there was no evidence that average fecundity differed between treated and untreated areas ($P = 0.1895$). After removal of barred owls on the treated area in 2009, there continued to be no significant difference in average fecundity on the treated versus untreated areas ($P = 0.860$).

Apparent Survival

We used 4,733 encounters (captures, recaptures, and resightings, excluding multiple encounters of individuals in the same year) of 982 non-juvenile owls (162 S1, 228 S2, and 592 adults) to estimate apparent survival of spotted owls on our study areas. The weighted linear model fitted to shrunk estimates of survival showed no difference in

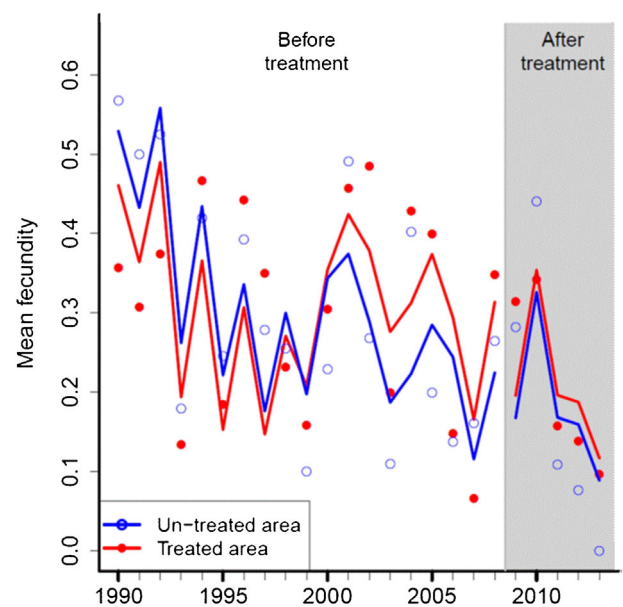


Figure 4. Observed and modeled fecundity from 1990 through 2013 on Green Diamond's northern spotted owl demographic study area in north coastal California, USA. Solid lines represent trends in fecundity estimated by the top-fitting linear model that included winter precipitation, winter temperature, an even-odd year effect, and the amount of edge habitat near the nest. An association between barred owl removal and fecundity was manifest as different lines post-treatment, but there was no evidence of an effect post-treatment ($P = 0.86$).

Table 2. Models with a difference in Akaike's Information Criterion (ΔAIC_c) < 5 from the 574 models fitted to fecundity data on Green Diamond's northern spotted owl demographic study area in north coastal California, 1990–2013. The covariates in the first parentheses indicate effects fitted to period before barred owl removal and the second parentheses indicate effects fitted after barred owl removal; effects outside parentheses were common to both periods. WT = mean winter temperature; WP = mean winter precipitation; EO = even-odd year effect; EDGE = proportion of edge habitat with the study area; T = linear time trend; Trt = treated area; CORE = amount of core high-use habitat in the study area; HAB = proportion of nesting and roosting habitat in the study area.

Model name	ΔAIC_c
WT+WP+EO+EDGE+(T+Trt)(Trt)	0
WT+WP+EO+(.) (Trt)	1.10
WP+EO+EDGE+(T+Trt)(Trt)	1.74
WT+WP+EO+CORE+(.) (Trt)	2.13
WP+EO+(.) (Trt)	2.45
WT+WP+EO+HAB+(.) (Trt)	2.58
WT+WP+EO+EDGE+(.) (Trt)	2.85
WT+WP+EO+(Trt)(Trt)	3.06
WT+WP+EO+CORE+(Trt)(Trt)	3.28
WT+WP+EO+(T+Trt)(Trt)	3.34
WP+EO+CORE+(.) (Trt)	3.46
WP+EO+HAB+(.) (Trt)	3.94
WT+WP+EO+HAB+(Trt)(Trt)	3.97
WP+EO+EDGE+(.) (Trt)	4.16
WP+EO+(Trt)(Trt)	4.41
WP+EO+CORE+(Trt)(Trt)	4.56
WT+WP+EO+HAB+(T+Trt)(Trt)	4.60
WT+WP+EO+EDGE+(Trt)(Trt)	4.64
WP+EO+(T+Trt)(Trt)	4.93

survival pre-removal (estimated difference pre-removal = 0.0004; Fig. 5) but a marked increase in survival on the treated area relative to the untreated area post-removal ($\hat{\beta}_3 = 0.0366$, $P = 0.0162$). On both treated and untreated areas, prior to barred owl removal, survival was declining at a rate of approximately 0.2% per year ($\hat{\beta}_4 = 0.0019$, $P \leq 0.001$). Following treatment, estimated survival on the untreated area was 0.822 (95% CI = 0.801–0.844), whereas survival on the treated area was 0.859 (95% CI = 0.840–0.877).

Annual Rate of Population Change

The best fitting λ_{RJS} model contained additive sex and time effects for capture probabilities (p), and general time effects in both survival (ϕ) and recruitment (γ). Derived estimates of population change on both treated and untreated areas showed a general decline before removal of barred owls on the treated area (estimated slope pre-removal = -0.0036 per year, $P = 0.013$; Fig. 6). Following removal of barred owls on the treated areas, there was evidence that the rate of population change on the treated area increased relative to that on the untreated area (difference post-removal = 0.159, $P \leq 0.001$). Following removal of barred owls, the rate of population change averaged 1.029 (95% CI = 0.982–1.075) on the treated area, whereas the rate of population change averaged 0.870 (95% CI = 0.809–0.932) on the untreated area (Fig. 6).

Empirical Observations of Northern Spotted Owl Recolonization

We evaluated 7 known spotted owl sites that barred owls subsequently occupied for ≥ 1 year before removal as case

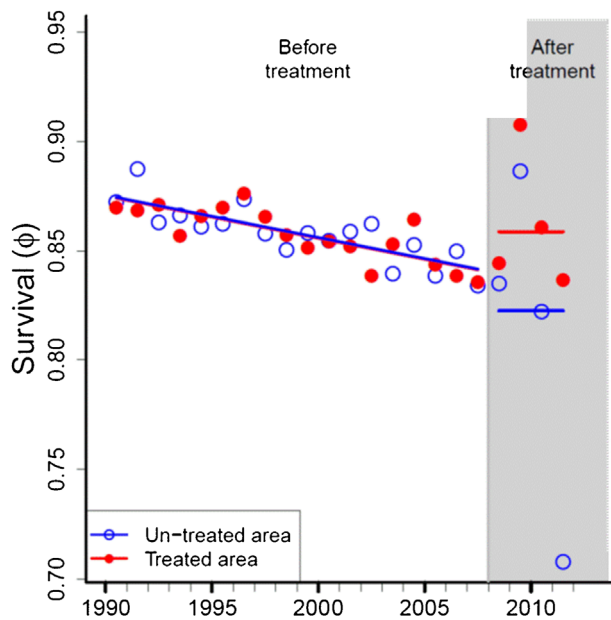


Figure 5. Shrinkage estimates of annual apparent survival from 1990 through 2013 on Green Diamond's northern spotted owl demographic study area in north coastal California, USA. Dots represent annual estimates of treated and untreated areas and trends are estimated from the weighted linear model. Survival on the treated area after removal of barred owls increased by 0.0366 (3.66%, $P = 0.016$) relative to survival on the untreated area.

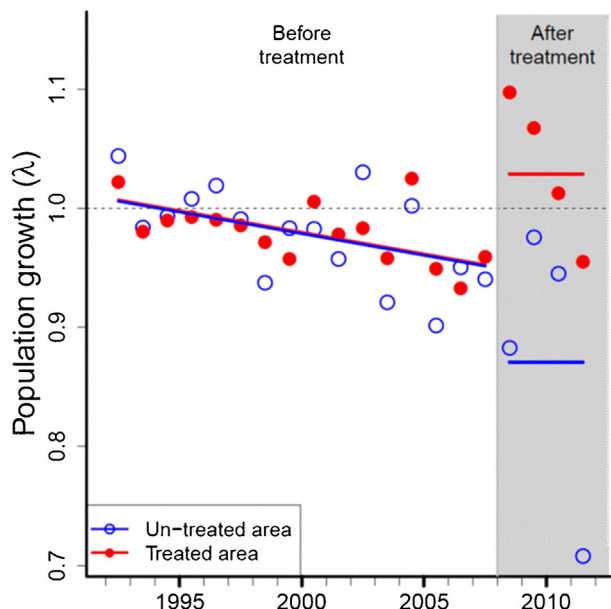


Figure 6. Shrinkage estimates of the rate of population change from 1990 through 2013 on Green Diamond's northern spotted owl demographic study area in north coastal California, USA. Shrinkage estimates are derived from the best-fitting reverse-time Cormack-Jolly-Seber model and calculated for treated and untreated areas (dots), with trends estimated from the weighted linear model. Dashed line represents a stable population, $\lambda = 1.0$. The rate of population change on the treated area increased by 0.159 ($P \leq 0.001$) after removal of barred owls relative to that on the untreated area.

studies. We documented that all were re-occupied by spotted owls with the time for re-occupation ranging from a minimum of 13 days to a maximum of 152 days after removal. Four of the sites were re-occupied by ≥ 1 of the previous resident spotted owls, including 1 female that had not been seen for 7 years. The remaining 3 sites were re-occupied by new or individuals of unknown status. Following re-occupation, the spotted owls were again displaced by barred owls at 3 sites.

There were additional barred owl removal sites that did not meet the criteria for a removal case study because the barred owls did not occupy the known spotted owl site, although they were immediately adjacent to occupied spotted owl nest sites or activity centers (i.e., the barred and spotted owl were neighbors with home ranges that likely overlapped). These neighbor case studies were more difficult to summarize, but the general pattern in all cases was for the spotted owls to either shift their territories away from the neighbor barred owls and not nest or become silent so that we had difficulty finding and determining the nesting status of the spotted owls.

DISCUSSION

The Revised Recovery Plan for the Northern Spotted Owl (USFWS 2011) noted the increasing threat of the barred owl on the northern spotted owl and called for removal experiments to quantify the impact of the invasive species on demographic parameters of spotted owls. A long-term demographic study of the spotted owl that spanned the interval when the expansion of barred owls transitioned from rare floaters on the landscape to occupying increasingly more of the available spotted owl habitat provided a unique opportunity to conduct a BACI removal experiment. However, relative to other northern spotted owl demographic study areas, the Green Diamond study area had among the lowest relative naive estimate of annual proportion of spotted owl territories with barred owl detections in Washington, Oregon, or California (Dugger et al. 2016). We hypothesized that this might reduce the magnitude of the treatment effect on all the demographic parameters, but it also facilitated the ability to remove resident barred owls from the treated areas because of their lower density compared to other areas within the range of the northern spotted owl (Diller et al. 2014).

Site Occupancy

In general, parameter estimates were consistent with our a priori hypotheses. Despite the potential for differences in physical and biological parameters, there were no differences between treated and untreated areas prior to initiation of treatment in the parameters governing either barred owl or northern spotted owl occupancy dynamics. This provides evidence that prior to treatment, the treated and untreated areas were sufficiently similar in important parameters such as occupancy, colonialization, and extinction that post-treatment differences could be assigned to the treatment effect (i.e., removal of barred owls). After the experimental removal experiment began, barred owl extinction rates

increased and barred owl occupancy rates declined in the treated areas as would be predicted given the continuous lethal removal of resident and immigrant barred owls. Occupancy of barred owls in the untreated areas continued to increase consistent with the increasing expansion of barred owls in the region (Yackulic et al. 2012, Dugger et al. 2016). The increase in barred owl colonization rates in treated and untreated areas when removal was initiated in 2009 was not expected. At the Tyee study area in Oregon, barred owl expansion proceeded slowly for many years before increasing rapidly (Yackulic et al. 2012). It is possible that treatment began just as local populations were starting to enter a similar period of rapid increases. Alternatively, environmental conditions may have been very favorable in the years prior setting the stage for a single year of high colonization. Following 2009, barred owl colonization probability declined in both treated and untreated areas. This could reflect either year-to-year variability in barred owl vital rates or could be a consequence of declines in overall regional occupancy coupled with the dependency of barred owl vital rates on regional occupancy (Yackulic et al. 2012).

Barred owls had an impact on spotted owl territory extinction with rates approximately 4 times higher where barred owls were present at spotted owl sites compared to areas where they were never present. When barred owls were removed from sites where they co-occurred, spotted owl extinction rates became comparable to sites where barred owls were never present. This provides compelling evidence that barred owls were responsible for increases in spotted owl extinction rates and that removal efforts were effective at removing this impact. This large drop in extinction rates resulted in a slight recovery from the decline in spotted owl occupancy in the treated areas. Both the speed of any recovery in spotted owl occupancy and the expected spotted owl equilibrium occupancy are dependent on colonization rates in addition to extinction rates. Because spotted owl colonization rate did not increase in the treated area and is modest (0.19), recovery is likely to be protracted. Spotted owl colonization rates may not have increased because of low fecundity rates during this period on the study area (Fig. 4) and throughout the region (R. B. Douglas, Mendocino Redwood Company, unpublished report).

Fecundity

As observed in prior studies of northern spotted owl fecundity, we observed substantial annual variation that was primarily expressed as an even-odd year effect (Anthony et al. 2006, Forsman et al. 2011). This biennial cycle is almost certainly partly an expression of the tendency of spotted owls to be facultative nesters with most females breeding in alternate years. It is not known specifically what causes the synchronization, but the fact that winter precipitation and temperature entered the top fecundity models with a negative coefficient suggests that weather may be a major contributing factor. Weather may have also contributed to the declining trend in fecundity even in the early years of this study when the annual rate of population change was not significantly different from 1.0 and before

barred owls were sufficiently abundant to affect the spotted owl population.

The lack of evidence of an effect of barred owl removal on spotted owl fecundity is likely to be at least partly caused by the high annual variation in fecundity. Furthermore, the competitive interaction between barred owls and spotted owls often results in the displacement of spotted owls (Wiens et al. 2014), and when this occurred, we were generally unable to detect the female spotted owls. This manifested itself as a reduction in occupancy in the untreated versus treated areas, but females that were not detected in a given year did not contribute to an estimate of fecundity. So although we did not find evidence of a change in the number fledged per breeding pair, the total productivity did appear to change in treated compared to untreated areas. Presumably due mostly to a reduction in the number of spotted owl sites, empirical counts of the number fledged at active (occupied at least once in the preceding 3 consecutive years) owl sites post treatment (2009–2014) indicated that only 36 fledglings were documented from an annual mean of 49.8 active owl sites in the untreated areas. In contrast, during the same period, 133 fledglings were observed from an annual mean of 104.2 active sites in the treated areas due at least partly to an increasing number of active sites following barred owl removal.

Apparent Survival

There is evidence of a pretreatment negative trend in apparent survival for spotted owls in both the treated and untreated areas. Following initiation of the removal experiment, there was evidence that survival rates recovered in the treated areas with the mean rate similar to the early years of the study when barred owls were still novel single floaters in the study area. Survival rate in the untreated areas continued to decline and was estimated at the lowest recorded level post-treatment.

The mechanism by which barred owls affect apparent survival of spotted owls is not known. Although we have observed physical attacks of barred owls on spotted owls, these attacks, although violent, did not appear to result in serious physical injury to the spotted owl. There is only one recorded case of a spotted owl purported to have been killed by a barred owl (Leskiw and Gutiérrez 1998). There is also the potential that barred owls could influence spotted owl survival through competition for mutually important prey species. Although barred owls have been shown to have substantial prey overlap with spotted owls in coastal Oregon (Wiens et al. 2014), there have been no studies of prey overlap in our study area in coastal California where spotted owls tend to specialize on dusky-footed woodrats (*Neotoma fuscipes*). Barred owls almost certainly do take some woodrats in our study area, but their more generalized food habits, relative low abundance in the study area even in the untreated areas, and the high abundance of woodrats in young managed timberlands (Hamm 1995, Hughes 2005) make it very unlikely that competition for prey could increase direct mortality or permanent emigration of spotted owls. A telemetry study of barred owls and spotted owls in coastal

Oregon indicated that interference competition for territorial space limited availability of spotted owls to their preferred habitat (Wiens et al. 2014). We also made anecdotal observations of spotted owls that no longer vocalized following occupation by barred owls at or near their territory core, but we could still observe them when they flew up to take a proffered mouse. Thus, we hypothesize that release from barred owl influence creates the appearance of increasing apparent survival by allowing displaced spotted owls in the floater population to regain a territory and become more readily detected. Our empirical observations of spotted owls recolonizing sites within as little as 13 days provides support for this hypothesis.

Annual Rate of Population Change

Because of a declining rate in both fecundity and apparent survival with apparently insufficient immigration to compensate, there was evidence of a pre-treatment negative trend in λ for spotted owls in both the treated and untreated areas. Following initiation of the removal experiment, λ significantly increased in the treated areas with the mean rate greater than 1.0, suggesting a stable or increasing population. The population continued to decline in the untreated areas and was estimated at the lowest recorded level post-treatment.

As previously noted, the Green Diamond dataset was also used in the 2013 northern spotted owl meta-analysis. One of those analyses converted estimates of λ_t to estimates of realized population change ($\hat{\Delta}_t$). This method provided a visual portrayal of the population trajectory ($\Delta_t = N_t/N_x$) in each year of the study relative to population size in year x , the first year that λ_t was estimated. The results of that analysis for Green Diamond indicated that the treated and untreated spotted owl populations were generally stable (95% CI broadly overlapped 1) until 2005 when a sharp population decline ensued. Following initiation of the experimental removal on the treated area in 2009, the treated area started to rebound and the 95% confidence interval broadly overlapped 1, whereas the trend in the untreated area continued to decline with no overlap of the 95% confidence interval (Dugger et al. 2016).

If the sharp increase in λ seen in this study were the result of increases in fecundity and actual survival within the treated population, we would have expected a delay or lag of several years in the λ response. Instead, the immediate increase suggested that similar to the effect on survival, much of the increase was probably due to displaced spotted owls in the floater population regaining territorial status and being detected. Furthermore, creating an area free of barred owls may have increased the probability that floater spotted owls rebuffed in adjacent untreated areas could colonize the treated areas.

In other areas where barred owls have been present in large numbers for a longer period of time and the population of spotted owls has been more suppressed, the demographic response of spotted owls may be protracted or delayed. If spotted owl abundance has decreased to the extent that comparatively few individuals are available on the landscape

to rapidly recolonize territories, we predict there would be a lag of several years in a positive spotted owl demographic response as survival and fecundity increases in the absence of barred owls. Furthermore, differences in habitat and climate associated with different physiographic provinces throughout the species range may play a role in the time or strength of a demographic response.

Empirical Observations of Northern Spotted Owl Recolonization

Although based on a small number of case studies ($n = 7$), these results suggested that northern spotted owls were likely to re-colonize their former territories following removal of barred owls. The very rapid re-colonization of 4 sites by the original resident spotted owls also indicated that, at least in some cases, the resident owls apparently remain in the vicinity of, or regularly investigate their former territory for years after being displaced by barred owls. These results also suggest that barred owls are not simply colonizing areas vacated by declining spotted owl populations, but rather that barred owls are actively displacing spotted owls as described by Wiens et al. (2014). The high and sometimes rapid rate of re-colonization by both original resident and new spotted owls following barred owl removal suggests that at least in some cases, barred owls were keeping the spotted owls from preferred, high quality sites. The sites that were colonized by barred owls also had high continuous occupancy by pairs of spotted owls with high reproductive success before barred owls invaded, which is further evidence that these sites were in high demand by spotted owls. For our study area, located within an intensively managed landscape where many of our spotted owls occupy young-growth sites that differed relative to other demographic study areas, the barred owls tend to occupy the sites with more classic late seral habitat elements.

MANAGEMENT IMPLICATIONS

The results from this study demonstrate that lethal removal of barred owls can allow the recovery of northern spotted owl populations. However, removal experiments may be more difficult to implement and recovery may be slower in other areas where barred owls have been present in large numbers for a longer period of time and the population of spotted owls has been more suppressed. Nevertheless, this experiment provides evidence that future management options may be developed to assist in the recovery of the northern spotted owl in at least the southern portions of its range. Unlike the substantial challenge of this removal experiment in which the objective was to continuously remove all territorial barred owls from the treated areas, long-term management options could be developed that would only require reducing barred owl population densities in selected conservation areas to allow coexistence with spotted owls. Presumably this could be done with much less cost and effort per unit area treated through an incremental decrease in adult barred owl survival or by implementing less controversial methods to decrease barred owl fecundity. At a minimum, this removal experiment provides evidence that if spotted owl populations continue to decline in the face of the barred owl threat,

refugia could be created so that extreme recovery actions like captive breeding would not be necessary while further management actions are developed and tested.

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LITERATURE CITED

- Anthony, R. G., E. D. Forsman, A. B. Franklin, D. R. Anderson, K. P. Burnham, G. C. White, C. J. Schwarz, J. D. Nichols, J. E. Hines, G. S. Olson, S. H. Ackers, L. W. Andrews, B. L. Biswell, P. C. Carlson, L. V. Diller, K. M. Dugger, K. E. Fehring, T. L. Fleming, R. P. Gearhardt, S. A. Gremel, R. J. Gutiérrez, P. J. Happe, D. R. Herter, J. M. Higley, R. B. Horn, L. L. Irwin, P. J. Loschl, J. A. Reid, and S. G. Sovern. 2006. Status and trends in demography of northern spotted owls, 1985–2003. *Wildlife Monographs* No. 163.
- Bierregaard Jr., R. O., E. S. Harrold, and M. A. McMillan. 2008. Behavioral conditioning and techniques for trapping barred owls (*Strix varia*). *Journal of Raptor Research* 42:210–214.
- Burnham, K. P., and G. C. White. 2002. Evaluation of some random effects methodology applicable to bird ringing data. *Journal of Applied Statistics* 29:245–264.
- Courtney, S. P., J. A. Blakesley, R. E. Bigley, M. L. Cody, J. P. Dumbacher, R. C. Fleischer, A. B. Franklin, J. F. Franklin, R. J. Gutiérrez, J. M. Marzluff, and L. Sztukowski. 2004. Scientific evaluation of the status of the northern spotted owl. Sustainable Ecosystems Institute, Portland, Oregon, USA.
- Crozier, M. L., M. E. Seamans, R. J. Gutiérrez, P. L. Loschl, R. B. Horn, S. G. Sovern, and E. D. Forsman. 2006. Does the presence of barred owls suppress the calling behavior of spotted owls? *Condor* 108:760–769.
- Diller, L. V., J. P. Dumbacher, R. P. Bosch, R. R. Bown, and R. J. Gutiérrez. 2014. Removing barred owls from local areas: techniques and feasibility. *Wildlife Society Bulletin* 3:211–216.
- Diller, L. V., and D. M. Thome. 1999. Population density of northern spotted owls in managed young-growth forests in coastal northern California. *Journal of Raptor Research* 33:275–286.
- Dugger, K. M., R. G. Anthony, and E. D. Forsman. 2009. Estimating northern spotted owl detection probabilities: updating the USFWS northern spotted owl survey protocol. Final report. Department of Fisheries and Wildlife, Oregon State University, Corvallis, USA.
- Dugger, K. M., E. D. Forsman, R. J. Davis, A. B. Franklin, G. C. White, C. J. Schwarz, K. P. Burnham, J. D. Nichols, J. E. Hines, C. B. Yackulic, P. F. Doherty Jr., L. Bailey, D. A. Clark, S. H. Ackers, L. S. Andrews, B. Augustine, B. L. Biswell, J. Blakesley, P. C. Carlson, M. J. Clement, L. V. Diller, E. M. Glenn, A. Green, S. A. Gremel, D. R. Herter, J. M. Higley, J. Hobson, R. B. Horn, K. P. Huyvaert, C. McCafferty, T. L. McDonald, K. McDonnell, G. S. Olson, J. A. Reid, J. Rockweit, V. Ruiz, J. Saenz, and S. G. Sovern. 2016. The effects of habitat, climate and barred owls on the long-term population demographics of northern spotted owls. *Condor* 118:57–116.
- Dugger, K. M., F. Wagner, R. G. Anthony, and G. S. Olson. 2005. The relationship between habitat characteristics and demographic performance of northern spotted owls in southern Oregon. *Condor* 107:863–878.
- Fleming, T. L., J. L. Halverson, and J. B. Buchanan. 1996. Use of DNA analysis to identify sex of northern spotted owls (*Strix occidentalis caurina*). *Journal of Raptor Research* 30:118–122.
- Folliard, L. B., K. P. Reese, and L. V. Diller. 2000. Landscape characteristics of northern spotted owl nest sites in managed forests of northwestern California. *Journal of Raptor Research* 34:75–84.
- Forsman, E. D. 1983. Methods and materials for locating and studying spotted owls. USDA Forest Service, Pacific Northwest Forest and Experiment Stations, Portland, Oregon USA.
- Forsman, E. D., R. G. Anthony, K. M. Dugger, E. M. Glenn, A. B. Franklin, G. C. White, C. J. Schwarz, K. P. Burnham, D. R. Anderson, J. D. Nichols, J. E. Hines, J. B. Lint, R. J. Davis, S. H. Ackers, L. S. Andrews, B. L. Biswell, P. C. Carlson, L. V. Diller, S. A. Gremel, D. R. Herter, J. M. Higley, R. B. Horn, J. A. Reid, J. Rockweit, J. Schaberel, T. J. Snetsinger, and S. G. Sovern. 2011. Population demography of northern spotted owls. *Studies in Avian Biology* 40:1–103.
- Franklin, A. B., D. R. Anderson, E. D. Forsman, K. P. Burnham, and F. W. Wagner. 1996. Methods for collecting and analyzing demographic data on the northern spotted owl. *Studies in Avian Biology* 17:12–20.
- Franklin, A. B., D. R. Anderson, R. J. Gutiérrez, and K. P. Burnham. 2000. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. *Ecological Monographs* 70:539–590.
- Glenn, E. M., R. G. Anthony, and E. D. Forsman. 2010. Population trends in northern spotted owls: associations with climate in the Pacific Northwest. *Biological Conservation* 143:2543–2552.
- Glenn, E. M., R. G. Anthony, E. D. Forsman, and G. S. Olson. 2011a. Local weather, regional climate and annual survival of the northern spotted owl. *Condor* 113:159–176.
- Glenn, E. M., R. G. Anthony, E. D. Forsman, and G. S. Olson. 2011b. Reproduction of northern spotted owls: the role of local weather and regional climate. *Journal of Wildlife Management* 75:1279–1294.
- Gremel, S. 2005. Factors controlling distribution and demography of northern spotted owls in a reserved landscape. Thesis, University of Washington, Seattle, USA.
- Gutiérrez, R. J., M. Cody, S. Courtney, and A. B. Franklin. 2007. The invasion of barred owls and its potential effect on the spotted owl: a conservation conundrum. *Biological Invasions* 9:181–196.
- Hamer, T. E., E. D. Forsman, A. D. Fuchs, and M. L. Walters. 1994. Hybridization between barred and spotted owls. *Auk* 111:487–492.
- Hamer, T. E., D. L. Hays, C. M. Senger, and E. D. Forsman. 2001. Diets of northern barred owls and northern spotted owls in an area of sympatry. *Journal of Raptor Research* 35:221–227.
- Hamm, K. A. 1995. Abundance of dusky-footed woodrats in managed forests of north coastal California. Thesis, Humboldt State University, Arcata, California, USA.
- Hughes, K. D. 2005. Habitat associations of dusky-footed woodrats in managed Douglas-fir / hardwood forests or northern California. Thesis, Humboldt State University, Arcata, California, USA.
- Johnson, D. H., G. C. White, A. B. Franklin, L. V. Diller, I. Blackburn, D. J. Pierce, G. S. Olson, J. B. Buchanan, J. Thraillkill, B. Woodbridge, and M. Ostwald. 2008. Study designs for barred owl removal experiments to evaluate potential effects on northern spotted owls. Report prepared for the U.S. Fish and Wildlife Service, Lacey Washington, and Yreka, California. Washington Department of Fish and Wildlife, Olympia, USA.
- Kelly, E. G., and E. D. Forsman. 2004. Recent records of hybridization between barred owls (*Strix varia*) and northern spotted owls (*S. occidentalis caurina*). *Auk* 121:806–810.
- Kelly, E. G., E. D. Forsman, and R. G. Anthony. 2003. Are barred owls replacing spotted owls? *Condor* 105:45–53.
- Kroll, A. J., T. L. Fleming, and L. L. Irvin. 2010. Site occupancy dynamics of northern spotted owls in the eastern Cascades, Washington, USA, 1990–2003. *Journal of Wildlife Management* 74:1264–1274.
- Leskiw, T., and R. J. Gutiérrez. 1998. Possible predation of a spotted owl by a barred owl. *Western Birds* 29:225–226.
- Lint, J., B. Noon, R. Anthony, E. Forsman, M. Raphael, M. Collopy, and E. Starkey. 1999. Northern spotted owl effectiveness monitoring plan for the northwest forest plan. USDA Forest Service General Technical Report PNW-GTR-440. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- Livezey, K. B. 2009. Range expansion of barred owls, part I: chronology and distribution. *American Midland Naturalist* 161:49–56.

- Mazur, K. M., and P. C. James. 2000. Barred owl (*Strix varia*). Account 508 in A. Poole, editor. The birds of North America online. Cornell Lab of Ornithology Ithaca, New York, USA.
- McDonald, T. L., and G. C. White. 2010. A comparison of regression models for small counts. *Journal of Wildlife Management* 74:514–521.
- Odom, K. J., and D. J. Mennill. 2010. A quantitative description of the vocalizations and vocal activity of the barred owl. *Condor* 112:549–560.
- Olson, G. S., R. G. Anthony, E. D. Forsman, S. H. Ackers, P. J. Loschl, J. A. Reid, K. M. Dugger, E. M. Glenn, and W. J. Ripple. 2005. Modeling of site occupancy dynamics for northern spotted owls, with emphasis on the effects of barred owls. *Journal of Wildlife Management* 69:918–932.
- Olson, G. S., E. M. Glenn, R. G. Anthony, E. D. Forsman, J. A. Reid, P. J. Loschl, and W. J. Ripple. 2004. Modeling demographic performance of northern spotted owls relative to forest habitat in Oregon. *Journal of Wildlife Management* 68:1039–1053.
- Pearson, R. R., and K. B. Livezey. 2003. Distribution, numbers, and site characteristics of spotted owls and barred owls in the Cascade Mountains of Washington. *Journal of Raptor Research* 37:265–276.
- Pradel, R. 1996. Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometrics* 52:703–709.
- Reid, J. A., R. B. Horn, and E. D. Forsman. 1999. Detection rates of spotted owls based on acoustic-lure and live-lure surveys. *Wildlife Society Bulletin* 27:986–990.
- Thome, D. M., C. J. Zabel, and L. V. Diller. 1999. Forest stand characteristics and reproduction of northern spotted owls in managed north-coastal California forests. *Journal of Wildlife Management* 63:44–59.
- U.S. Fish and Wildlife Service [USFWS]. 1990. The 1990 status review: northern spotted owl: *Strix occidentalis caurina*. U.S. Fish and Wildlife Service, Portland, Oregon, USA.
- U.S. Fish and Wildlife Service [USFWS]. 2011. Revised recovery plan for the northern spotted owl (*Strix occidentalis caurina*). U.S. Fish and Wildlife Service, Portland, Oregon, USA.
- Van Lanen, N. J., A. B. Franklin, K. P. Huyvaert, R. F. Reiser, and P. C. Carlson. 2011. Who hits and hoots at whom? Potential for interference competition between barred and northern spotted owls. *Biological Conservation* 144:2194–2201.
- White, G. C., and R. E. Bennetts. 1996. Analysis of frequency count data using the negative binomial distribution. *Ecology* 77:2549–2557.
- Wiens, J. D., R. G. Anthony, and E. D. Forsman. 2011. Barred owl occupancy surveys within the range of the northern spotted owl. *Journal of Wildlife Management* 75:531–538.
- Wiens, J. D., R. G. Anthony, and E. D. Forsman. 2014. Competitive interactions and resource partitioning between northern spotted owls and barred owls in western Oregon. *Wildlife Monographs* 185:1–50.
- Yackulic, C. B., J. Reid, J. D. Nichols, J. E. Hines, R. J. Davis, and E. Forsman. 2012. Neighborhood and habitat effects on vital rates: expansion of the barred owl in the Oregon Coast Ranges. *Ecology* 93:1953–1966.
- Yackulic, C. B., J. Reid, J. D. Nichols, J. E. Hines, R. J. Davis, and E. Forsman. 2014. The roles of competition and habitat in the dynamics of populations and species distributions. *Ecology* 95:265–279.

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