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Recovering marbled murrelets via corvid management: A population viability analysis approach

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ABSTRACT

The expansion of human activities into rural areas and natural landscapes has resulted in widespread increases in the abundance of synanthropic species that threaten rarer native species. Quantitative assessments of how much impacts need to be reduced to reach acceptable levels of risk to the affected species are rarely conducted prior to the implementation of control measures, and it is perhaps not surprising that many efforts have not yielded the desired outcome. Here, we used matrix-based population viability analysis models to show that reducing predation by rapidly growing corvid populations on marbled murrelet (*Brachyramphus marmoratus*) nests likely constitutes an effective means for recovering a declining murrelet population in central California. For example, a modest 40% reduction in predation reduced extinction risk dramatically from 95.8% to 4.6% over 100 years and a 60% reduction resulted in a stable population ($\lambda = 1$) when the proportion of breeders, renesting rates, and corvid predation rates were assumed to be 0.77, 0.13, and 0.69, respectively. However, nest predation would only need to be reduced by 40% to produce a stable population if corvid management was coupled with a modest increase in after-hatch-year survival from 0.896 to 0.910. Corvid control resulted in greater gains in murrelet population size when the maximum number of breeders was allowed to increase over the projection period, as might be expected if the amount of old-growth nesting habitat increased over time, but extinction risk was insensitive to the presence of a carrying capacity. Approximately half of known murrelet nests in central California are within 1 km of heavily used campgrounds in a single state park, indicating that significant gains in viability could be achieved by targeting efforts in small areas providing corvid food subsidies. Risk assessments such as ours can provide quantitative prioritization rationale for efforts intended to mitigate the impacts of synanthropic species on threatened species.

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1. Introduction

Urbanization and the expansion of human activities into natural landscapes have resulted in widespread increases in the abundance of synanthropic species that threaten rare, native species (Garrott et al., 1993). As is the case with exotic species, overabundant species impact native species through a number of mechanisms including predation, competition for food or breeding sites, disease, habitat alteration, and hybridization (Côté et al., 2004; Gutiérrez et al., 2007; Kyle et al., 2006). Of recent concern, dramatic increases in the abundance and distribution of species in the family Corvidae in response to urbanization and habitat modification increasingly threaten less common native species via predation on nests and juveniles (Jerzak, 2001; Konstantinov, 1996; Marzluff et al., 1994). While corvid densities and their effects on

native species are typically greater in areas heavily used by humans due to the availability of food subsidies (Marzluff and Neath-erlin, 2006), “spill-over” effects where corvids immigrate into adjacent habitat are increasingly impacting native species in relatively unaltered landscapes (Kristan and Boarman, 2003; Marzluff et al., 1994). In western North America, corvids have contributed to the endangerment of a number of federally protected species including snowy plovers (*Charadrius alexandrinus*) (USFWS, 2007), California least terns (*Sternula antillarum browni*) (USFWS, 1985), desert tortoises (*Gopherus agassizii*) (Kristan and Boarman, 2003), and marbled murrelets (*Brachyramphus marmoratus*) (Ralph et al., 1995).

Several proposed and implemented conservation plans contain strategies for reducing corvid predation rates on native species of concern (Boarman, 2003; USFWS, 2002, 2007). Such plans focus on identifying strategies that reduce impacts to native species, but quantitative assessments of how much predation rates need to be reduced to reach acceptable levels of risk to the affected spe-

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cies are rarely conducted. Understanding how much predation needs to be reduced is critical for assessing whether predator management is a feasible approach for recovering the species, or whether conservation resources are better invested in strategies ameliorating other limiting factors (Beissinger and Westphal, 1998; Morris and Doak, 2002). Moreover, doing so can help prioritize among alternative predator control strategies; for example, a management program based on lethal control that can at best halve predation rates will be ineffective if the complete elimination of predation is required to stabilize the population. As a result, it is perhaps not surprising that many efforts at reducing predation on species of concern have not yielded the desired outcome (Côté and Sutherland, 1997). Moreover, impacts of synanthropic species such as corvids often occur concurrently and interact with other environmental stressors such as habitat fragmentation (Fahrig, 2003). Thus, comprehensive risk assessments incorporating all potentially important stressors are needed to prioritize management options offering the greatest conservation gains (Caughley and Gunn, 1996; Perkins et al., 2008).

In this study, we used a population viability analysis approach as a conservation prioritization tool to assess the effectiveness of conserving marbled murrelets in a small, peripheral population in central California by reducing corvid nest predation rates. The marbled murrelet is a terrestrial-nesting seabird in western North America that is believed to have declined throughout much of its range primarily due to the loss of old-growth nesting habitat and nest predation by corvids (Peery et al., 2004a; Piatt et al., 2007; Ralph et al., 1995; Raphael et al., 2002a), although factors such as changes in prey availability, oil spills, and predation on adults by raptors have likely contributed to declines as well (Becker and Beissinger, 2006; Peery et al., 2006a). Predation by corvids is high (Nelson and Hamer, 1995) and appears to drive landscape-scale patterns in nest success in many regions (Luginbuhl et al., 2001; Malt and Lank, 2009; Nelson and Hamer, 1995; Raphael et al., 2002a). Indeed, abundances of Steller's jays (*Cyanocitta stelleri*) and common ravens (*Corvus corax*) and have increased dramatically in both the state of California and the Santa Cruz Mountains, the primary nesting area for central California murrelets (Fig. 1). Moreover, surveys of both corvid species in the Santa Cruz Mountains show elevated densities at known murrelet nest sites, probably due to the placement of campgrounds within murrelet habitat (Fig. 2). In central California, murrelet reproduction appears to have declined by an order of magnitude over the past century due in part to corvid predation, and is now too low to sustain the population (Beissinger and Peery, 2007; Peery et al., 2004a, 2006b, 2007). Reducing nest predation is generally considered the most effective means to recover murrelets in this and some other regions but, as is often the case with control programs for synanthropic and invasive species, (1) how much predation needs to be reduced to recover populations and (2) the relative effectiveness of reducing predation versus ameliorating other environmental stressors have not been assessed.

2. Methods

2.1. Model structure and parameterization

We used a stage-based matrix model parameterized with vital rates estimated with field studies conducted in central California from 1997 to 2003 (Peery et al., 2004a, 2006a,b, 2007) to model marbled murrelet population dynamics and assess the potential benefits of reducing corvid nest predation. We used deterministic models to explore the underlying nature of murrelet population dynamics and estimate the annual population

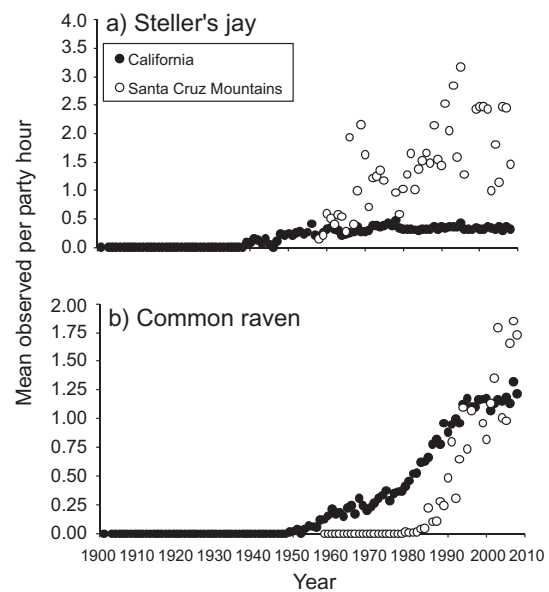


Fig. 1. Mean number of (a) Steller's jays and (b) common ravens observed per party-hour during Christmas Bird Counts (CBC; National Audubon Society, 2009) on the west slope of the Santa Cruz Mountains, California (Western Santa Cruz County CBC field) from 1958 to 2008 and California (all California CBC routes) from 1901 to 2008. Search terms included: "Steller's jay"; "coast Steller's jay" in (a) and "common raven", "American raven", and "raven sp." in (b). For surveys in the Santa Cruz Mountains, we plotted the mean number of individuals detected per party-hour across survey circles in the region. For California surveys, we plotted the geometric mean number of individuals detected per party-hour across survey circles in the region.

growth rate (λ) under varying levels of corvid nest predation, where λ was estimated as the dominant right eigenvalue of the matrix (Caswell, 2001). We also used stochastic models that incorporated both demographic and environmental stochasticity to assess extinction risk under different levels of corvid predation in a varying environment. Both deterministic and stochastic models were density dependent, were female-based, and assumed a post-breeding census. We considered five stage classes: juveniles, 1-year old subadults, 2-year old subadults, nonbreeders that were old enough to breed (≥ 3 -year olds) but did not do so because of insufficient nesting habitat, and breeders (≥ 3 -year olds; Fig. 3; Beissinger, 1995). Note that ≥ 1 -year olds (non-juveniles) are collectively referred to as after-hatch-year individuals.

We used an annual survival rate of 0.896 for female after-hatch-year murrelets (s_{ahy}) based on a mark-recapture study of 331 individuals in the region (Peery et al., 2006a). A pooled survival rate was used for these four stages classes because it was not possible to assign after-hatch-year murrelets to individual stages at the time of the mark-recapture study. We assumed that annual juvenile survival (s_{juv}) was 70% of s_{ahy} (0.627) based on the differences in juvenile and adult survival rate estimated in other alcid species (Beissinger and Nur, 1997) because insufficient juveniles were captured to estimate s_{juv} directly (Peery et al., 2006a).

Fecundity (m), the number of female young produced per female in the breeding stage class, was expressed as a function of the proportion of females that attempted to nest at least once in a given year (P_{nest}), the probability that a nest failed (P_{fail}), the probability that nest failure was due to predation by corvids given that failure occurred ($P_{fail-corvid}$), the probability that nest failure was due to other causes given that failure occurred ($P_{fail-other}$), and the proportion of individuals that attempted to renest after nest failure (P_{renest}). Thus, the fecundity element in the matrix model was formulated as:

$$m = \frac{P_{nest}[(1 - P_{fail}(P_{fail-corvid}(1 - r) + (1 - P_{fail-other}))) + P_{fail}(P_{fail-corvid}(1 - r) + (1 - P_{fail-corvid}))(P_{reest})(1 - P_{fail-other}(P_{fail-corvid}(1 - r) + (1 - P_{fail-other})))]}{2}$$

r was the proportional reduction in corvid predation due to potential management actions.

P_{nest} was estimated, in part, based on the proportion of murrelets that were captured at sea and outfitted with radio-transmit-

ters at the beginning of the breeding season that were subsequently detected initiating a nest (Bradley et al., 2004; Peery et al., 2004a). However, radio-telemetry methods may have underestimated P_{nest} for two reasons. First, radio-marking could have oc-

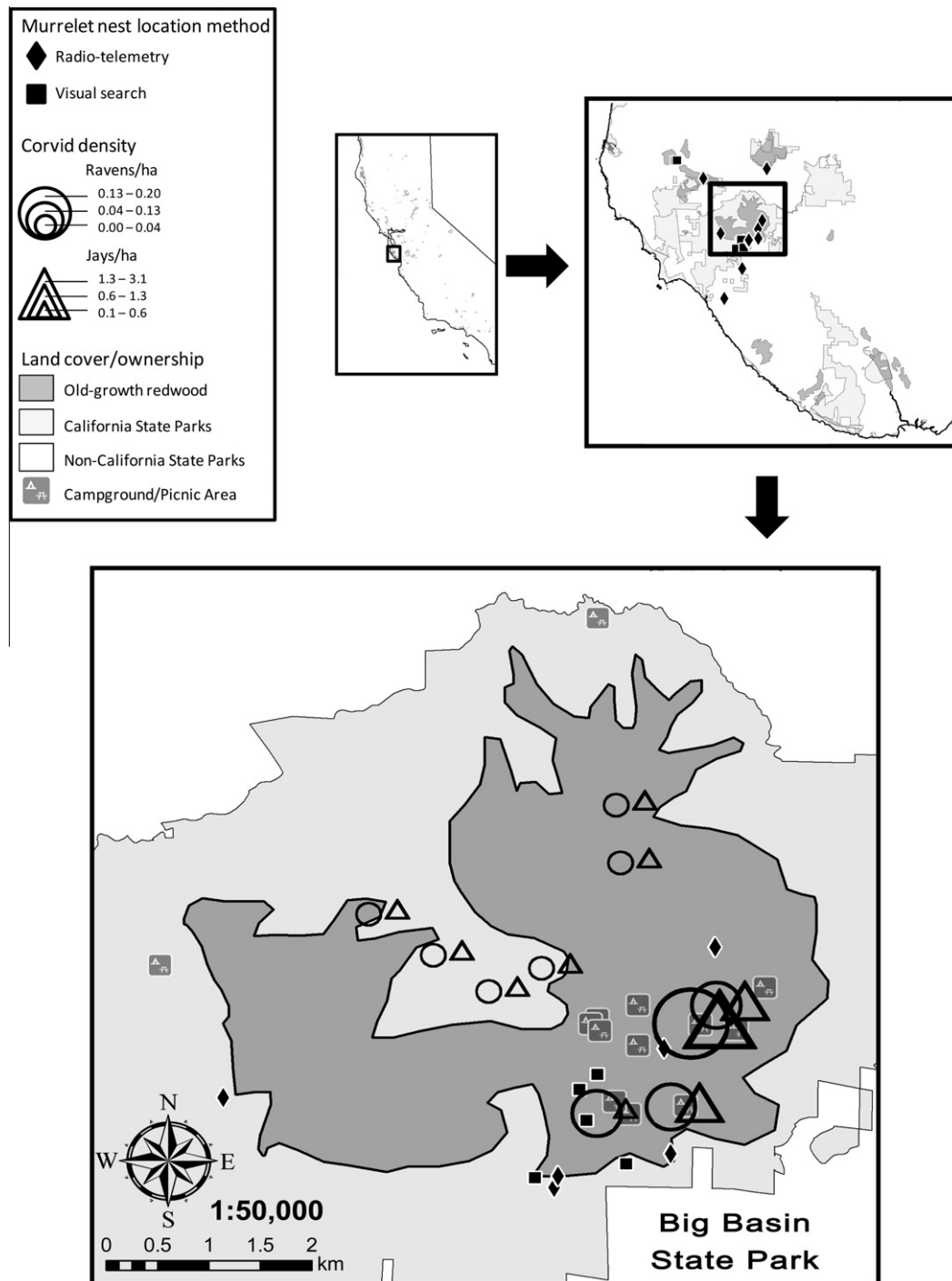


Fig. 2. Distribution of known marbled murrelet nests (Baker et al., 2006), density of Steller's jays and common ravens (Suddjian, 2003, 2005a,b), extent of old growth forest habitat (Fox, 1996), and state park boundaries in central California. Locations of campgrounds and picnic sites are detailed for the area of highest murrelet nesting density in the Santa Cruz Mountains.

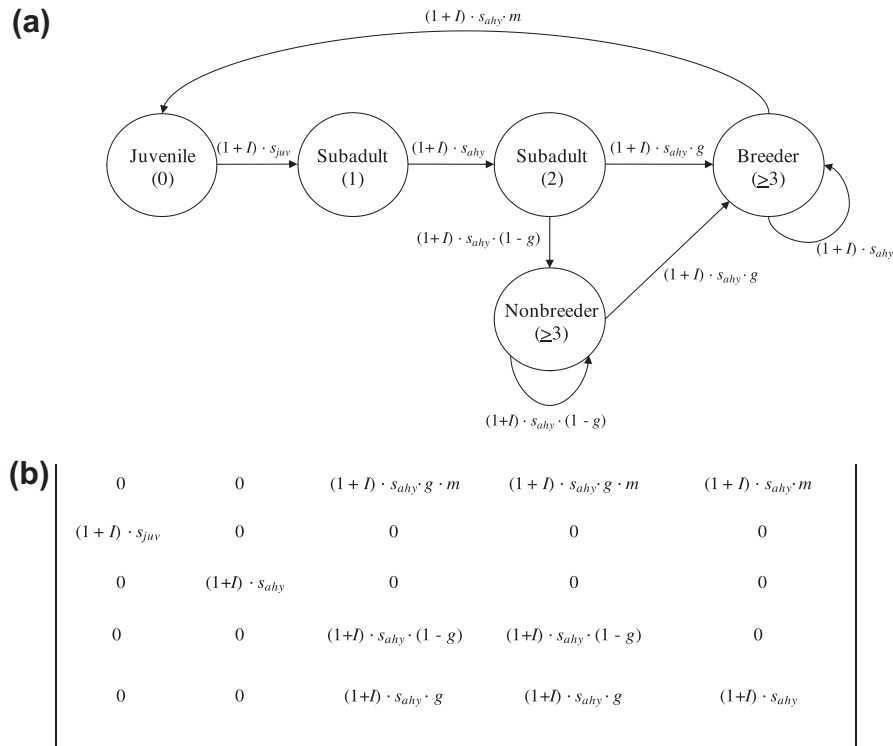


Fig. 3. Life-cycle diagram (a) and matrix model (b) for a five stage class, post-breeding marbled murrelet population model. Parameter notation is provided in the text.

curred after the marked individual's nest failed or after hatching when nests become difficult to detect. Second, the radio tags used in Peery et al. (2004a) are known to reduce breeding success in alcids including marbled murrelets (Ackerman et al., 2004; Whidden et al., 2007). To minimize these potential biases, P_{nest} was also estimated based on both radio-telemetry information and physiological criteria indicative of breeding condition. Physiological parameters considered included: (1) the presence or absence of a brood patch used to incubate eggs and brood young (McFarlane-Tranquilla et al., 2003); (2) plasma vitellogenin (an egg-yolk precursor) levels which becomes elevated during egg development (Vanderkist et al., 2000; Loughheed et al., 2002; McFarlane-Tranquilla et al., 2003); and (3) plasma calcium (used in egg-shell formation) levels which become elevated near egg-laying (Ivins et al., 1978). For this estimate of P_{nest} , we assumed that any female with a brood patch or with elevated plasma vitellogenin or calcium as having initiated nesting [i.e., potential breeders in Peery et al. (2004a,b)]. Considering these physiological criteria increased the likelihood that murrelets whose nests failed prior to radio-tagging and murrelets that stopped breeding because they were radio-marked would be considered breeders. Assuming that murrelets physiologically in breeding condition initiated nesting could upwardly bias P_{nest} if some individuals in breeding condition did not nest. Therefore, we treated P_{nest} derived from radio-telemetry only and P_{nest} derived from radio-telemetry and physiological data as minimum and maximum estimates, respectively. Approximately 5% of radio-marked individuals were below the age of first breeding (Peery et al., 2004a, 2006b), so we multiplied the proportion of murrelets that were identified as breeders by $1/(1-0.05)$ to estimate the probability that an individual at or above the age of first breeding nested (i.e., P_{nest}). This resulted in a minimum P_{nest} of 0.33 using only radio-telemetry and maximum estimate of 0.77 based on both radio-telemetry and physiological data. Because the minimum and maximum estimates represented a wide range of possible nesting probabilities and population growth was sensitive to this parameter (see below), we also estimated λ

assuming $P_{nest} = 0.55$ (i.e., the midpoint between minimum and maximum estimates). We used lower and upper P_{renew} estimates of 0.13 and 0.63 based on radio-telemetry and physiological studies of marbled murrelets in British Columbia (McFarlane-Tranquilla et al., 2003) because the probability of reneesting, P_{renew} , has not been estimated in California.

We estimated nest failure rates based on 19 nests located and monitored in central California from 1989 to 2001 using a combination of radio-telemetry, visual searches, and nest-tree climbing (Peery et al., 2004a). Only three young were successfully fledged from these nests and a value of 0.84 (16/19) was used for P_{fail} in all simulations. Of the 16 failed nests, the cause of failure was determined conclusively in nine cases, of which four nests were predated by corvids (i.e., $P_{fail-covid} = 4/9$ or 0.44; one nest was predated by Steller's jays and three by common ravens). In deriving this estimate, we treated the seven nests that failed for unknown reasons as "unknowns" and therefore did not include them in the denominator. However, while the cause of failure for these nests was not known conclusively, they may well have been predated by corvids. In these seven cases, egg shell fragments were recovered (indicative of possible predation) or no sign of the egg was detected after parents stopped attending the nest (corvids are known to remove eggs from murrelet nests; R. Golightly, pers. comm.). If indeed all seven nests of unknown fate were predated, corvid nest predation rates in central California could be as high as 0.69 (11/16) and we considered 0.44 and 0.69 as minimum and maximum estimates of $P_{fail-covid}$, respectively. The potential benefits of reducing corvid nest predation were assessed by manipulating r , the proportional reduction in corvid predation, from 0 to 1 by increments of 0.1 for both estimates of $P_{fail-covid}$. $P_{fail-other}$ was set to $1 - P_{fail-covid}$.

The probability of a second-year subadult or nonbreeder transitioning into the breeder stage class (g) was a function of the number of available nest sites and therefore provided a mechanism for incorporating density dependence in the model. Following Morris and Doak (2002), we estimated g_{t+1} as:

$$g_{t+1} = \frac{K - S_{ahy}n_{breeder(t)}}{S_{ahy}n_{subadults(t)} + S_{ahy}n_{nonbreeder(t)}}$$

Carrying capacity (K) for murrelet populations is likely a function of the amount of nesting habitat in a region as a positive correlation exists between the amount of nesting habitat in an area and the number of murrelets using that area across a range of spatial scales (Burger, 2001; Raphael et al., 2002b; Raphael, 2006). However, in good breeding years, most murrelets in California initiate nesting suggesting that sufficient nesting habitat exists for most individuals to breed given the current population size (Peery et al., 2004a). Thus, an increase in the amount of murrelet nesting habitat may or may not result in an increase in the number of breeders and we therefore modeled a range of scenarios for K and changes in K over time including (1) no carrying capacity where a lack of density dependence allowed the population to grow exponentially (i.e., g was always equal to 1), (2) $K=250$ breeding females (the approximate number currently in central California; Peery et al., 2006b) and remained constant over time, and (3) $K=250$ and increased at a rate of 0.5% or 1% per year (i.e., $K_{change}=0.005$ or 0.01) in separate model runs. The latter two scenarios were modeled to reflect possible changes in nesting habitat in response to favorable forest management practices.

We estimated I , the annual immigration rate, based on genetic studies of marbled murrelets that have shown that dispersal into central California is high, but few migrants produce offspring that recruit into the population (Hall et al., 2009; Peery et al., 2010). Specifically, based on changes in genetic population structure over the past century, ≤ 5 effective migrants enter the population per generation (assuming a generation time of 8 years), where the number of effective migrants can be considered as the number of migrants that contribute offspring at the same rate as residents. Thus, ≤ 0.63 effective migrants entered central California per year, and I was estimated to be ~ 0.001 assuming a population of approximately 600 individuals (Peery et al., 2006b). Emigration was incorporated implicitly because models were parameterized with local survival rates estimated from mark-recapture studies that discount emigrants (Peery et al., 2006b).

2.2. Stochastic population projections

Stochastic simulations were conducted using the parameters and matrix model described above (Fig. 3), but populations were projected forward in time using the following equation:

$$\mathbf{n}(t+1) = \mathbf{A}(t) \cdot \mathbf{n}(t)$$

where $\mathbf{n}(t)$ was a vector of abundances of individuals in the five stage classes in year t , and $\mathbf{A}(t)$ was the matrix of vital rates in year t . Populations were projected forward 100 years using vital rates that varied from year to year due to demographic and environmental stochasticity (see below). The probability of extinction at 100 years was estimated as the proportion of 1000 simulated populations that declined to ≤ 10 females at any time during the projection period (i.e., quasi-extinction threshold = 10).

As is typical for seabirds inhabiting the California Current, murrelet reproductive success in central California is greater in cool-water years that are characterized by greater abundances of murrelet prey species such as juvenile rockfish (*Sebastes* spp.), anchovies, and krill (Becker et al., 2007). Therefore, we treated annual variation in sea surface temperature (SST) and its effects on murrelet reproduction estimated by Becker et al. (2007) as a form of environmental stochasticity in population projections (see Supplementary materials for details). Peery et al. (2006a) found weak support for greater survival in warm water years, despite the fact that survival rates for other seabird species tend to be greater in cool-water years (Hodder and Graybill, 1985). Because of this

uncertainty, we modeled annual variability in the survival rates of both juvenile and after-hatch-year murrelets as random processes independent of environmental factors. Specifically, we randomly drew annual survival rates from beta distributions with means of 0.627 and 0.896 for juvenile and after-hatch-year murrelets, respectively, and variances equal to 0.01 (i.e., SD = 0.10). Periodic oils spills result in mortality events and can be considered a form of environmental or even catastrophic stochasticity (Peery et al., 2006a), but the frequency of oil spills and the magnitude of their impacts on murrelet survival are difficult to quantify. However, randomly drawing survival rates from a beta distribution with SD = 0.10 resulted in episodic mortality events where annual survival dropped to as low as 0.6 (see Supplementary materials), as might be expected due to major oils spills.

We incorporated demographic stochasticity in fecundity by randomly drawing the number of offspring produced in a given year from a binomial distribution with an expected value equal to m , and where the number of trials was equal to the number of breeders alive in that year. Expected values for fecundity were determined by ocean conditions and predation levels as described above. Demographic stochasticity was incorporated into survival processes by randomly drawing the number survivors for a given stage class from a binomial distribution with an expected value equal to the survival rate determined by the level of environmental stochasticity.

2.3. Sensitivity analyses

We estimated the sensitivity of λ to potential changes in vital rates using life-stage simulation analysis (Wisdom and Mills, 1997; Wisdom et al., 2000). As the objective was to assess the possibility of improving murrelet population viability by improving vital rates, we subjectively set the upper limits of the vital rates to levels that could conceivably be obtained by effective management strategies. For both S_{juv} and S_{ahy} , we set the upper limit to 0.05 plus the current (i.e., baseline) estimate (0.627 and 0.896, respectively) as it seems conceivable that improved oil spill and predator management could result in modest reductions in mortality (Peery et al., 2006a), but not much more than about 0.05 given estimated survival rates for similar-sized alcid (Beissinger and Peery, 2007). We set the upper limit for P_{nest} to 0.9, a scenario in which almost all individuals of breeding age initiate nesting, as is typical for seabirds in years with favorable environmental conditions (Ainley et al., 2002; Gaston and Hipfner, 2000). We set the upper limit for P_{renew} to 0.63, which represents the maximum estimate for a comparative “healthy” population in British Columbia, and assumed a baseline of 0.13, which represents the minimum estimate in British Columbia (Bradley et al., 2004; McFarlane-Tranquilla et al., 2003). We varied r , the proportional reduction $P_{fail-covid}$, from 0 to 1, the latter representing the complete elimination of predation by corvids on murrelet nests. We varied $P_{fail-other}$ from 50% of its current value to its current value (either 0.31 or 0.56, depending on the value used for $P_{fail-covid}$). Larger reductions in nest failure due to other causes could be challenging because these other causes are currently poorly understood and likely involve a number of factors including prey availability and predation by other species. We held I constant because increasing immigration into the region is not a viable option for increasing population growth. We assumed that $g = 1$ (i.e., that population was far enough below carry capacity that all individuals of breeding age could breed), because the population growth rate became entirely driven by survival rates when adults occupy all nesting habitat. We repeated the life-stage simulation analysis assuming that $P_{fail-covid} = 0.44$ and 0.69 (resulting in $P_{fail-other} = 0.56$ and 0.31, respectively) and for two possible lower limits (i.e., current values) for P_{nest} (0.33 and 0.77). For each of these four combinations, we generated 500

Table 1
Estimates of annual population growth rates (λ) for marbled murrelets in central California assuming different combinations of nesting probabilities (P_{nest}), reneesting probabilities (P_{renew}), and transition probabilities from the 2-year-old subadult and nonbreeder stage classes to the breeder stage class (g).

g	$P_{\text{nest}} = 0.13$		$P_{\text{nest}} = 0.55$		$P_{\text{nest}} = 0.77$	
	$P_{\text{renew}} = 0.13$	$P_{\text{renew}} = 0.63$	$P_{\text{renew}} = 0.13$	$P_{\text{renew}} = 0.63$	$P_{\text{renew}} = 0.13$	$P_{\text{renew}} = 0.63$
0	0.897	0.897	0.897	0.897	0.897	0.897
0.5	0.914	0.920	0.925	0.934	0.935	0.947
1	0.915	0.921	0.926	0.936	0.936	0.950

sets of vital rates, estimated λ for each parameter set using the matrix model, then regressed λ against each vital rate in each set. The percentage of variation in λ explained by the vital rate was used as a measure of how sensitive λ was to changes in the vital rate.

3. Results

3.1. Deterministic population projections

Assuming current levels of corvid predation (i.e., $r = 0$), λ was less than 1 for all combinations of P_{nest} , P_{renew} , and g (Table 1). Thus, the population was projected to have declined in part due to corvid predation during the period in which vital rates were estimated. The rate of decline was greatest when the population was at carrying capacity (i.e., $g = 0$), and smallest when sufficient nesting sites were available for all 2-year old subadults and nonbreeders to transition to the breeder stage class (i.e., $g = 1$). For simplicity, we only present the results of reducing corvid predation when $g = 1$, because qualitatively, results were the same across the range of values for g .

Reducing the rate of corvid predation (i.e., increasing r) significantly increased λ for all combinations of vital rates considered (Fig. 4). Achieving a stable population ($\lambda = 1$) required the smallest reduction in corvid predation when $P_{\text{nest}} = 0.77$, $P_{\text{fail-corvid}} = 0.69$,

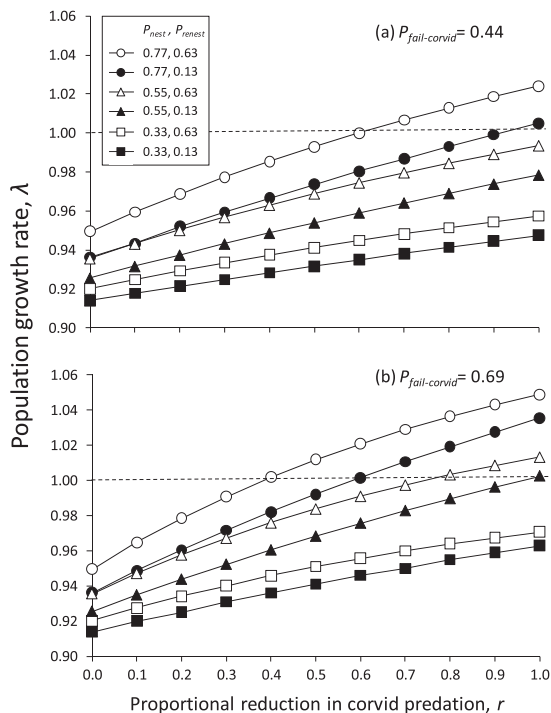


Fig. 4. Population growth rate (λ) of marbled murrelets as a function of the reduction in the rate of nest predation by corvids assuming that unmanipulated $P_{\text{fail-corvid}}$ (the probability that nest failure was due to corvid predation given that failure occurred) was (a) 0.44 and (b) 0.69. The dashed line at $\lambda = 1$ indicates the growth rate of a stable population.

and $P_{\text{renew}} = 0.63$, and in this case could be attained with only a 40% reduction in corvid predation. By contrast, corvid predation needed to be reduced by 60% ($r = 0.6$) to stabilize the population when P_{renew} was 0.13 and P_{nest} and $P_{\text{fail-corvid}}$ were held at 0.77 and 0.69, respectively. Corvid predation needed to be reduced by 70–100% in order to achieve a stable population when $P_{\text{fail-corvid}}$ was assumed to only be 0.44 and $P_{\text{nest}} = 0.77$, depending on the value assumed for P_{renew} (0.13 or 0.63).

Achieving a stable population depended strongly on value assumed for P_{nest} . Even the complete elimination of corvid predation (i.e., $r = 1$) was insufficient to generate a stable population when P_{nest} was assumed to be 0.33 for any combination of corvid predation and reneesting rates. Indeed, the maximum possible λ assuming $P_{\text{nest}} = 0.33$ was 0.971 (with $P_{\text{corvid}} = 0.69$ and $P_{\text{renew}} = 0.63$), indicative of an approximately 3% annual decline. A stable population was possible with intermediate nesting probabilities (i.e., $P_{\text{nest}} = 0.55$), but only if corvid predation and reneesting were high ($P_{\text{fail-corvid}} = 0.69$) and required an 80–100% reduction in corvid predation, depending on P_{renew} .

3.2. Stochastic population projections

How density dependence was modeled had a significant impact on mean ending population sizes (at year 100). Ending population

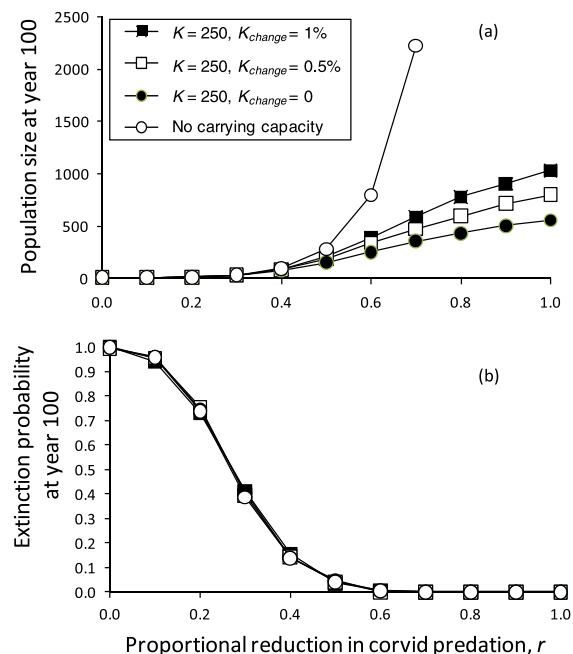


Fig. 5. (a) Mean ending population size and (b) extinction probability at year 100 for simulated marbled murrelet populations as a function of the reduction of corvid nest predation according to four competing models of density dependence. Models were run assuming $P_{\text{nest}} = 0.77$ and $P_{\text{renew}} = 0.13$. K = initial carrying capacity for the number of breeding females and K_{change} = annual percentage change in carrying capacity. When population growth was not limited by carrying capacity, ending population sizes are only presented for $r \leq 0.7$ because populations grew to very large sizes when $r > 0.7$.

size was smallest when K was held constant at 250 breeding females, increased when carrying capacity increased by 0.5% per year, and was greatest when K increased by 1% per year (Fig. 5a). However, extinction risk was not affected by how density dependence was incorporated into model projections and was identical for the four models considered, regardless of the level of reduction in corvid predation (Fig. 5b). Apparently, the level of environmental and demographic stochasticity considered here was not sufficient to increase extinction probabilities when the number of breeders was limited by the amount of available nesting habitat. Typical population trajectories from the stochastic model are presented in the Supplemental materials Fig. S1.

Because extinction risk was insensitive to density dependence, we only present estimates of extinction risk as a function of model parameters assuming a constant carrying capacity of 250. In the absence of corvid management the probability of extinction in 100 years was >90% for all combinations of vital rates considered (Fig. 6). Extinction probabilities declined rapidly as corvid predation was reduced assuming $P_{\text{nest}} = 0.77$, but effects were greater when $P_{\text{fail-corvid}} = 0.69$ (Fig. 6a) than when $P_{\text{corvid}} = 0.44$ (Fig. 6b). Indeed, extinction probabilities declined from 95.8% to 4.6% when corvid predation was reduced by 40% assuming that $P_{\text{nest}} = 0.77$ and $P_{\text{fail-corvid}} = 0.69$. However, when P_{nest} was only assumed to be 0.33, extinction probabilities declined much more slowly as corvid predation was reduced and was >0.4 even when corvid predation was completely eliminated (i.e., $r = 1$) for all combinations of $P_{\text{fail-corvid}}$ and P_{renew} . Extinction risk could be reduced to low levels (<10%) at intermediate values of P_{nest} (0.55) for most combinations of P_{renew} and $P_{\text{fail-corvid}}$, but doing so required a 60–100% reduction in corvid predation.

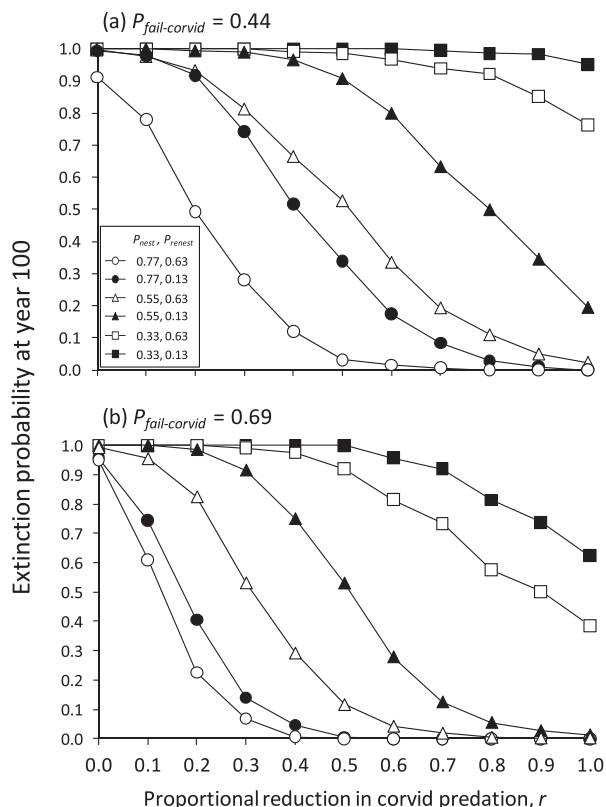


Fig. 6. Probability of extinction in 100 years for marbled murrelets as a function of the reduction in the rate of nest predation by corvids assuming that unmanipulated $P_{\text{fail-corvid}}$ (the probability that nest failure was due to corvid predation given that failure occurred) was (a) 0.44 and (b) 0.69.

3.3. Sensitivity analyses

Life-stage simulation analyses indicated that manipulating (reducing) corvid predation, increasing after-hatch-year survival, and in some cases P_{nest} yielded the greatest potential improvement in population growth (Fig. 7a). However, r was the only parameter that could be manipulated in isolation and achieve a stable population, assuming that the upper limits to the vital rates considered actually were the maximum rates achievable via management. Moreover, r explained 15–65% of the variation in λ depending on the values used for $P_{\text{fail-corvid}}$ and P_{nest} and was greatest when maximum values of $P_{\text{fail-corvid}}$ and P_{nest} were assumed (Fig. 7b). P_{nest} also explained a large amount of the variation in λ (46–61%) when the current value and upper limit of P_{nest} were assumed to be 0.33 and 0.9, respectively, compared to other parameters (Fig. 7c–h). However, increasing P_{nest} in isolation only resulted in a maximum λ of 0.946 because such a high proportion of nests failed (0.84).

4. Discussion

4.1. Effectiveness of corvid management for recovering marbled murrelets

The rapid increase of corvids in the Santa Cruz Mountains during the past 50 years (Fig. 1) suggests that their prey, such as marbled murrelets, have experienced corresponding increases in predation pressure. Our modeling results indicate that reducing the rate of corvid predation on marbled murrelet nests likely constitutes an effective means for increasing the population viability and growth rate of murrelets in central California. Indeed, reducing predation by 40% from current levels could conceivably reduce extinction risk over 100 years dramatically from 95.8% to 4.6% and result in stable population growth, depending on values assumed for vital rates. Moreover, corvid predation was the only parameter that, by itself, could be manipulated to stabilize the population given what we assumed were reasonable maximum values for demographic parameters considered in our model (Fig. 4). Nevertheless, considerable uncertainty exists in how much reducing corvid predation will impact extinction probabilities and population growth rates due to uncertainty in $P_{\text{fail-corvid}}$, P_{renew} , and particularly P_{nest} . For example, estimated extinction probabilities ranged from 0% to >90% when predation was reduced by 50%, depending on values assumed for these parameters, and indeed, even the complete elimination of corvid predation was not predicted to stabilize the population if $P_{\text{nest}} = 0.33$. If P_{nest} is low, too few murrelets breed in a given year for the increase in nest success due to corvid management to sufficiently increase population growth.

However, we consider it unlikely that P_{nest} was as low as 0.33 because this estimate was derived from breeding histories of individuals radio-marked with a subcutaneous attachment, a method that is known to reduce the breeding success of alcids (Ackerman et al., 2004; Whidden et al., 2007). Moreover, 60% of radio-marked females that did not initiate a nest exhibited physiological signs of egg production including the presence of a brood patch, elevated plasma calcium, or elevated vitellogenin levels (Peery et al., 2004a), further suggested that the proportion of breeders exceeded 0.33. Thus, we suspect that the intermediate and maximum values used for P_{nest} (0.55 and 0.77) are more likely to encompass the true probability of nesting. Indeed, the fact that stable populations and low probabilities of extinction can, theoretically, be achieved by reducing corvid predation when $P_{\text{nest}} = 0.55$ is encouraging from the perspective of implementing a successful corvid management program, even if doing so would require large reductions in predation (Figs. 4 and 6). Nevertheless, improving estimates of P_{nest}

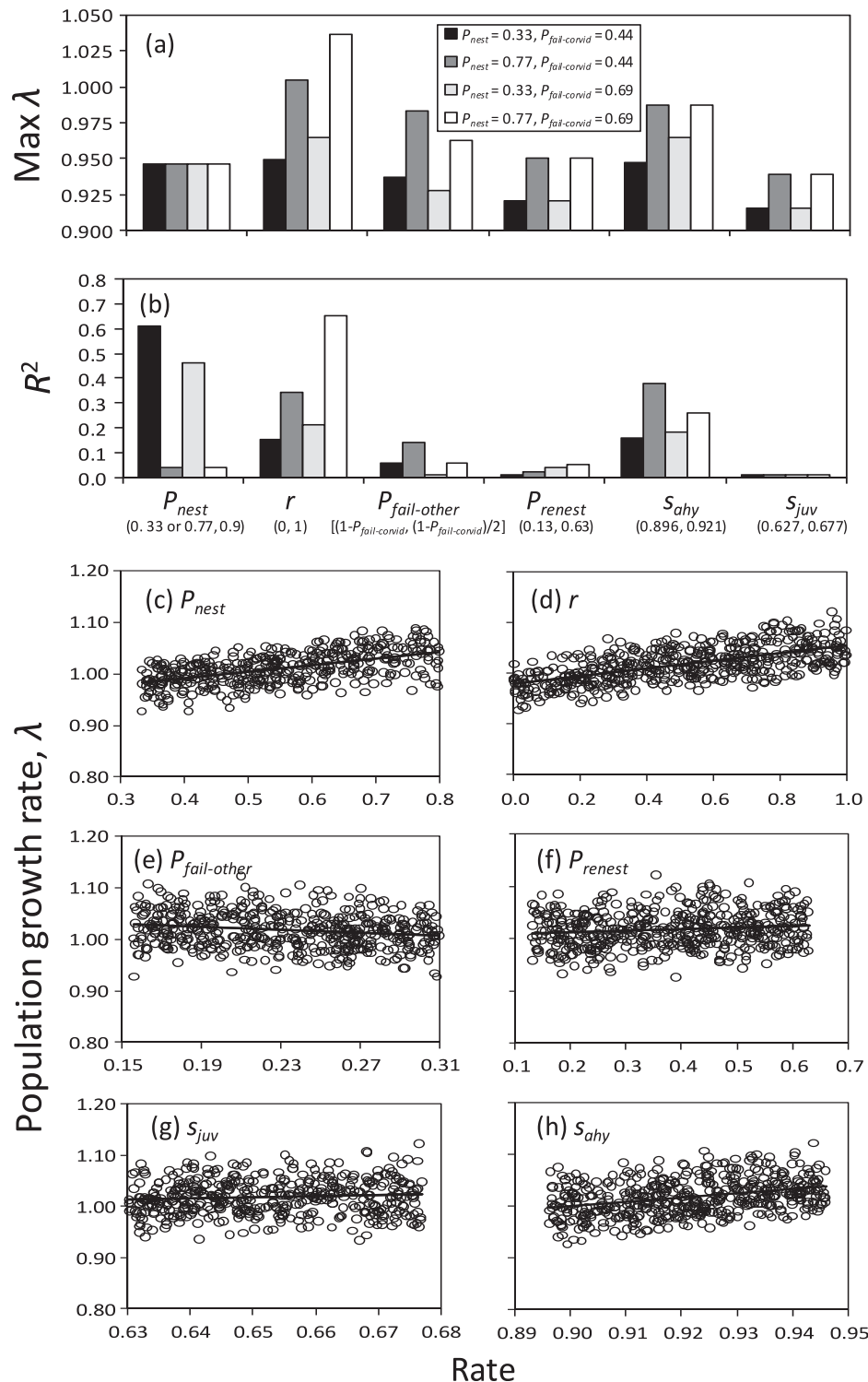


Fig. 7. Results of a life-stage simulation analysis evaluating the sensitivity of the annual population growth rate (λ) of marbled murrelets to changes in six vital rates. (a) maximum λ given likely maximum values for each vital rates assuming “baseline” values for the other model parameters and (b) variation in λ explained (R^2) by each vital rate where values were randomly drawn from a uniform distribution with a minimum equal to the baseline value. Baseline and maximum values for (a) and (b) are presented below the x-axis in (b). Fig 7c–h depict simulated ($n = 500$) λ -values generated by varying P_{nest} (c), r (d), P_{other} (e), P_{renest} (f), s_{ahy} (g), and s_{juv} (h).

should be a priority for future research as doing so will allow for more accurate predictions of the ability of corvid control and other strategies to increase reproductive success.

Despite the potential effectiveness of corvid control, a comprehensive approach that manages for multiple murrelet demographic parameters is more likely to prevent extinction than a strategy focused solely on corvid predation, particularly given the logistical

challenges of implementing effective corvid control (see below). Along these lines, management should focus on parameters that both have a relatively large influence on population growth and are reasonably amenable to manipulation. Our life-stage simulation analysis suggested that, besides the corvid predation rate, P_{nest} and s_{ahy} were the most likely parameters to meet these criteria. Moreover, corvid control resulted in the greatest gains in popula-

tion growth when nesting and renesting rates were high because increased nest success occurs across a greater number of nesting attempts. For example, the population could be stabilized ($\lambda = 1$) with only a 60% reduction in predation if P_{nest} could be increased from 0.33 to 0.77 (assuming $P_{\text{fail-corvid}} = 0.69$ and $P_{\text{renest}} = 0.13$). Without an increase in P_{nest} , a 100% reduction in corvid predation would be required to stabilize the population for this parameter set. If additional vital rates can be improved, corvid predation would need to be reduced even less. For example, predation would only need to be reduced by 40% (as opposed to 60%) if control efforts were coupled with a strategy that produced a modest increase in after-hatch-year survival from 0.896 to 0.910 (assuming $P_{\text{nest}} = 0.77$, $P_{\text{fail-corvid}} = 0.69$, $P_{\text{renest}} = 0.13$).

Management options for improving demographic rates other than the rate of nest predation vary in terms of their feasibility and effectiveness. In principle, the proportion of breeders could be increased via forest management practices that increase the area of late-seral stage nesting habitat, but doing so is not feasible on relevant time scales. The creation of nest structures in younger trees is unlikely to be effective because murrelet reproduction does not appear to be limited by habitat availability (Peery et al., 2004a) and increasing carrying capacity (i.e., the number of breeders) did not reduce extinction probabilities in this study (Fig. 5). Nevertheless, modeled populations were capable of growing to relatively large sizes in the absence of a carrying capacity and when carrying capacity was allowed to increase over time, as might be expected with an increase in the availability of nesting habitat. Thus, the absence of an effect of carrying capacity on population viability should not be used as justification for not improving the quantity and quality of nesting habitat in the region as a number of environmental factors not incorporated in model projections could certainly increase the probability of extinction in relatively small populations constrained by limited nesting habitat. Improving food resources for murrelets could constitute an effective means of increasing the proportion of breeders because this parameter seems to be limited by prey availability in some years (Peery et al., 2004a), and because overfishing during the 20th century appears to have caused murrelets to forage on smaller, less energetically valuable prey species (Becker and Beissinger, 2006). Recent implementation of Marine Protected Areas in prime murrelet at-sea habitat along the central California Coast could certainly help to increase murrelet prey in the region, but managing individual prey species for the benefit of murrelets is challenged by the fact that murrelets are generalist predators and the relative importance of individual prey species is uncertain (Becker et al., 2007).

A potentially effective means of increasing murrelet survival is by reducing predation by peregrine falcons. Peregrine falcons are known to be frequent predators of murrelets in the Santa Cruz Mountains, and indeed, seven observations of predation by peregrines, most as murrelets flew inland to visit nesting habitat, have occurred since 1994 in the region (Peery et al., 2006a). Unfortunately, observations of predation events are anecdotal and we were unable to rigorously incorporate the effect of peregrines in the population model explicitly. Thus, field studies that quantify the impacts of peregrines and assess the potential benefits of peregrine control on this murrelet population are merited. At minimum, such research should supersede ongoing subsidies of peregrine populations via hacking in the Santa Cruz Mountains region.

4.2. Strategies for controlling corvid predation

Management intended to reduce the impact of corvid predation on murrelets nesting in the Santa Cruz Mountains should focus on corvids that utilize murrelet nesting areas and are associated with areas of high human activity such as campsites in county and state parks. Indeed, five of 10 murrelet nests located with radio-teleme-

try (which presumably represent a reasonably unbiased sample) in central California occurred within 1 km of heavily used campsites in a single state park that have dramatically elevated corvid densities compared to adjacent areas low human use (Fig. 2; Baker et al., 2006; see also Marzluff and Neatherlin, 2006). In many landscapes in the Pacific Northwest, predation risk for murrelets is driven by forest structure and composition, where nests in fragmented landscapes and near edges are more likely to be predated than nests in fragmented landscapes and further from edges (Luginbuhl et al., 2001; Malt and Lank, 2009; Raphael et al., 2002a). While considerable timber harvesting has occurred in the Santa Cruz Mountains, the landscape is not characterized by a patchwork of stands of different ages and varying sizes. As a result, landscape-scale forest management is less likely to be effective in the short term than targeted strategies in specific locations containing high corvid abundances and murrelet nest densities.

A number of methods exist for reducing corvid predation on murrelet nests, each with advantages and disadvantages. Shooting and trapping are the most direct approaches, but are labor intensive, limited by the ability of corvids to learn to avoid traps and hunters, and have had limited success in other systems (Boarman, 2003; Skarphedinsson et al., 1990). Selective removal of individuals known to predate on murrelet nests or occurring in areas with high murrelet nesting densities could constitute a short-term means of reducing predation (Boarman, 2003; Goodrich and Buskirk, 1995), although removing territorial ravens could increase predation by non-territorial individuals in areas that they were previously excluded (Marzluff and Heinrich, 1991). Reducing sources of anthropogenic food subsidies in and around campsites and other human settlements is more likely to be a more effective long-term strategy, as doing so has the potential to reduce local corvid population growth rates and incentives for corvids to disperse into murrelet nesting habitat from surrounding areas. However, regional management of raven food subsidies may be required to eliminate spillover effects associated with large-scale food sources in the surrounding landscape such as waste disposal sites. In addition, taste aversion methods targeted at territorial corvids in murrelet nesting habitat could reduce the attractiveness of both murrelets eggs and young (Cox et al., 2004), but the effectiveness of such an approach in the present context is uncertain. In the case of ravens, taste aversion conditioning of dominant breeding pairs combined with sterilization may offer a longer term solution where the pair remains on territory but contributes no offspring to future generations. Ultimately, a combination of several of the above approaches will likely be the most effective means to reduce predation rates to levels that would result in an acceptably low risk of extinction for murrelets. Regardless of the approach, any effort at controlling corvids should be accompanied by a monitoring program designed to assess the effectiveness of management efforts. Moreover, robust implementation of such monitoring programs will be critical for improving the design of corvid control measures for native and threatened species in general.

Corvids and other synanthropic species have become ubiquitous in many North American regions and will likely increase in abundance as urbanization and development in native landscapes continue. Corvids have an additional advantage over native species: they are fast learners and capable of rapidly adapting to human modified landscapes. As a result, managers will increasingly be confronted with decisions about whether and how to reduce effects on native species. Population viability analysis, such as the one implemented in this study, provides perhaps the most appropriate framework for evaluating whether predator control will be effective, particularly as our understanding of the empirical linkages between habitat fragmentation, urbanization, and the population dynamics of synanthropic and native species increases.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2010.04.024.

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