



Using spatially-explicit population models to evaluate habitat restoration plans for the San Diego cactus wren (*Campylorhynchus brunneicapillus sandiegensis*)



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ABSTRACT

A long-standing debate within conservation is how best to allocate limited management resources: should reserve area be increased, should anthropogenic disturbances be mitigated, or should connectivity be increased? We explore these issues for the San Diego cactus wren, a California Species of Special Concern. To assess the relative benefit of different post-fire habitat restoration strategies, we forecasted wren abundance over the next 100 years under three restoration strategies: (i) create new "stepping stone" habitat patches to form corridors which connect existing patches, (ii) augment existing habitat patches, and (iii) create new habitat patches in areas with low fire risk. We considered both small-scale and large-scale restoration efforts of 20 and 200 ha of habitat, respectively. To forecast wren abundance, we used a meta-population model created from maps of wren abundance, cactus abundance, land use, and estimated fire probability. Estimates of fire probability were obtained by relating previous fire locations to environmental variables and human population density. Results indicate that the best management strategy for a 20-ha restoration effort is to augment habitat in patches habitable for wrens, and that the best strategy for 180 ha of additional restoration (or 200 total hectares) is to improve wren dispersal via new corridors. Results also indicate that there is no decline in long-term wren abundance caused by planning the first 20 ha of restoration separately from planning a subsequent 180 ha. Our modeling approach provides insight into the relative benefit of several realistic restoration scenarios, providing an important tool for species conservation and habitat restoration on complex landscapes.

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1. Introduction

The spatial arrangement of reserves and the best allocation of scarce conservation resources has been rigorously debated at least since Diamond (1975) and Simberloff and Abele (1976). Environmental management must account for complex, variable, uncertain, and site-specific landscape considerations, subject to accelerating global changes (Vitousek et al., 1997). Choosing amongst the available management options requires coalescing available data into a framework that supports decision-making at the appropriate spatial scale (Addison et al., 2013). In this paper, we compare the relative benefit of three restoration strategies – creating new corridors, augmenting existing habitat, and creating new habitat in areas with low risk of human disturbance – singly and in combination, using well-established meta-population methods in a novel way.

Because habitat restoration typically proceeds under budget constraints, land managers must weigh the trade-offs of increasing the area (or spatial extent) of suitable habitat, improving the quality of existing habitat, and increasing connectivity among habitat patches (Hodgson et al., 2009). Wildlife corridors – stretches, or stepping stones, of habitat that allow wildlife to disperse among suitable habitat patches – are a frequently recommended adaptation strategy for climate change (Heller and Zavaleta, 2009), habitat fragmentation (Beier and Gregory, 2012), and post-disturbance recolonization (Noss, 1991). Many studies recommend that restoration efforts focus on increasing landscape connectivity, allowing wildlife to respond dynamically to population fluctuations and fire damage (Beier and Noss, 1998; Sauvajot, 1995). However, poorly designed corridors might fail to protect wildlife populations and might facilitate the spread of catastrophic disturbances (Brudvig et al., 2012). In models, corridors are not more effective than adding area to existing patches (Falcuy and Estades, 2007).

All restoration options come with uncertainties, and land managers choose the option they perceive to have the lowest risk of an

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undesirable outcome (Margules and Pressey, 2000). Hodgson et al. (2011) argue that constructing corridors is difficult and that the success of corridors is harder to predict than the success of simply adding area to suitable habitat. These difficulties suggest that conservation efforts focus on improving or augmenting existing habitat. However, focusing conservation efforts on a few robust populations may backfire in the face of catastrophic disturbances, such as fire (Regan et al., 2010).

A key concern in habitat restoration is to avoid the creation of population “traps” or “sinks” – areas that appear suitable and attract individuals from a population, but have more deaths than births. Since sinks are typically close to human activity (Roever et al., 2013), restoration must be particularly careful there. In a model of songbirds, Donovan and Thompson (2001) found that populations remained viable as long as sinks did not make up more than 40% of the landscape where birds preferred good, source habitat, and no more than 30% of the landscape where birds preferred sink habitat.

With limited conservation resources and limited documentation of restoration effects (Benayas et al., 2009), models are needed at the planning stage to forecast restoration effects (Addison et al., 2013). Typically, restoration choices are made locally with *ad hoc* rules designed by local experts (McIntire et al., 2007; Schultz and Crone, 2005; Pullin et al., 2004). However, expert judgments by themselves may be over-confident (McBride et al., 2012), leading to unexpected results.

Reserve design models often focus on landscape-level habitat characteristics in choosing reintroduction sites for wildlife, without considering the benefit or cost to the entire meta-population (Kuemmerle et al., 2011a). This focus neglects the importance of patch extinction and re-colonization to long-term population viability (Nicholson et al., 2006; Carroll et al., 2003a,b). The impacts of environmental and demographic stochasticity are crucial to long-term viability (Beissinger and Westphal, 1998). Thus, it is important to consider meta-population models when looking at the benefits of different management strategies (Bonnot et al., 2013; Kuemmerle et al., 2011b) or reserve designs (Bonnot et al., 2011; Haight and Travis, 2008; Moilanen and Cabeza, 2002).

Recent meta-population models have emphasized dynamic landscapes together with combinations of threats such as land use change, climate change, and altered fire frequency (Conlisk et al., 2012, 2013; Fordham et al., 2012). Here we apply this novel approach to study restoration planning, addressing a variety of interacting risks, including catastrophic wildfire, patch-specific fire frequencies, patch extinction due to small carrying capacity, and patch extinction due to isolation from other patches (see Prugh et al., 2008 on the latter two risks).

We evaluated restoration plans for the San Diego cactus wren (*Campylorhynchus brunneicapillus sandiegensis*) in the San Pasqual Valley, assuming restoration of wrens is to be accomplished by restoration of the *Opuntia* (prickly pear) or *Cylindropuntia* (cholla) cactus on which wrens depend. The San Diego cactus wren is a Species of Special Concern in Southern California and serves as an umbrella species for ecosystem health. As in other regions with hot, dry summers and cool, wet winters, extensive urban development and human-caused increases in fire frequency (Syphard et al., 2009) have created highly fragmented landscapes. Frequent fire can adversely affect plant life by shifting the competitive advantage to invasive annuals (Keeley and Brennan, 2012; Fleming et al., 2009). Since invasive annuals often burn more frequently than natives, the positive feedback between fire and invasion can lead to a new ecological equilibrium (Talluto and Suding, 2008). Such vegetation changes impact wildlife (Mendelsohn et al., 2008), necessitating conservation efforts to restore degraded habitat (Cox and Allen, 2008).

We located candidate restoration sites using GIS data on landscape characteristics. A meta-population model was created to rank the relative restoration benefits of hundreds of management plans. The model incorporates wren life history and the multiple threats to its viability, where fine scale, spatially-explicit fire frequency predictions allow for a robust analysis of disturbance risk. We considered both small-scale and large-scale restoration. Such a management model informs restoration planning before substantial resources are allocated to a project.

2. Methods

2.1. Study species

The San Diego cactus wren, *Campylorhynchus brunneicapillus sandiegensis*, is named for the nests it makes in mature *Opuntia* (paddle cactus) or *Cylindropuntia* (cholla). Non-migratory wrens use cactus nests for roosting and to protect eggs and nestlings from predation during the approximately 16-day incubation and 21-day pre-fledging periods. The monogamous, insectivorous wrens forage on bare ground under coastal sage shrubs. Although the status of the San Diego cactus wren as a subspecies is still disputed (Unitt, 2008), the wren has a distinct song as compared to the desert and Los Angeles populations of coastal cactus wrens (Atwood and Lerman, 2007).

The San Diego cactus wren faces survival challenges like those of species in similar climates world wide, especially increased fire frequency (Regan et al., 2006). The wren is frequently mentioned in California's Natural Community Conservation Planning program (Atwood et al., 1998). The wren's preferred habitat, coastal sage scrub, is arguably the most endangered ecosystem in the United States (Rubinoff, 2001). The 10–15% of coastal sage scrub that remains is home to more than 100 species classified as rare, sensitive, threatened, or endangered (Rubinoff, 2001). With the human population of Southern California expected to increase by 40% in the next 50 years (California Department of Finance, 2013), and with more frequent fires predicted due to climate-induced changes in fuel loads and precipitation (Krawchuck and Moritz, 2012), conservation and restoration of San Diego cactus wren habitat has been recognized as a regional priority. In 2007, an extremely large fire damaged the most robust meta-population of San Diego cactus wrens in the region, the San Pasqual Valley population, severely degrading wren habitat in the western half of the Valley. An estimated 90 breeding pairs still live in the Valley (Hamilton, 2008 and later surveys by the authors of this paper). In the aftermath of the fire, emergency funds were made available for restoration within the Valley, setting the stage for our case study in improved restoration modeling.

2.2. Overview

The restoration objective is to increase the population of San Diego cactus wrens by restoring cactus at well-situated sites in the San Pasqual Valley. For the primary calculations, we assumed a restoration budget of enough cactus to cover 20 ha (our current actual budget). We made further calculations assuming an addition of 180 more hectares to our budget. Data on occupied wren habitat, estimated wren abundances, and environmental variables for the Valley were coalesced from United States Geological Survey and Fish and Wildlife Service cactus surveys (Clark Winchell and John Taylor, personal communication), and from San Diego GIS databases (SanGIS, 2009). These data were used to survey the Valley for well-situated, candidate restoration sites (Fig. 1a and b). Many areas are not suitable for cactus restoration because they possess

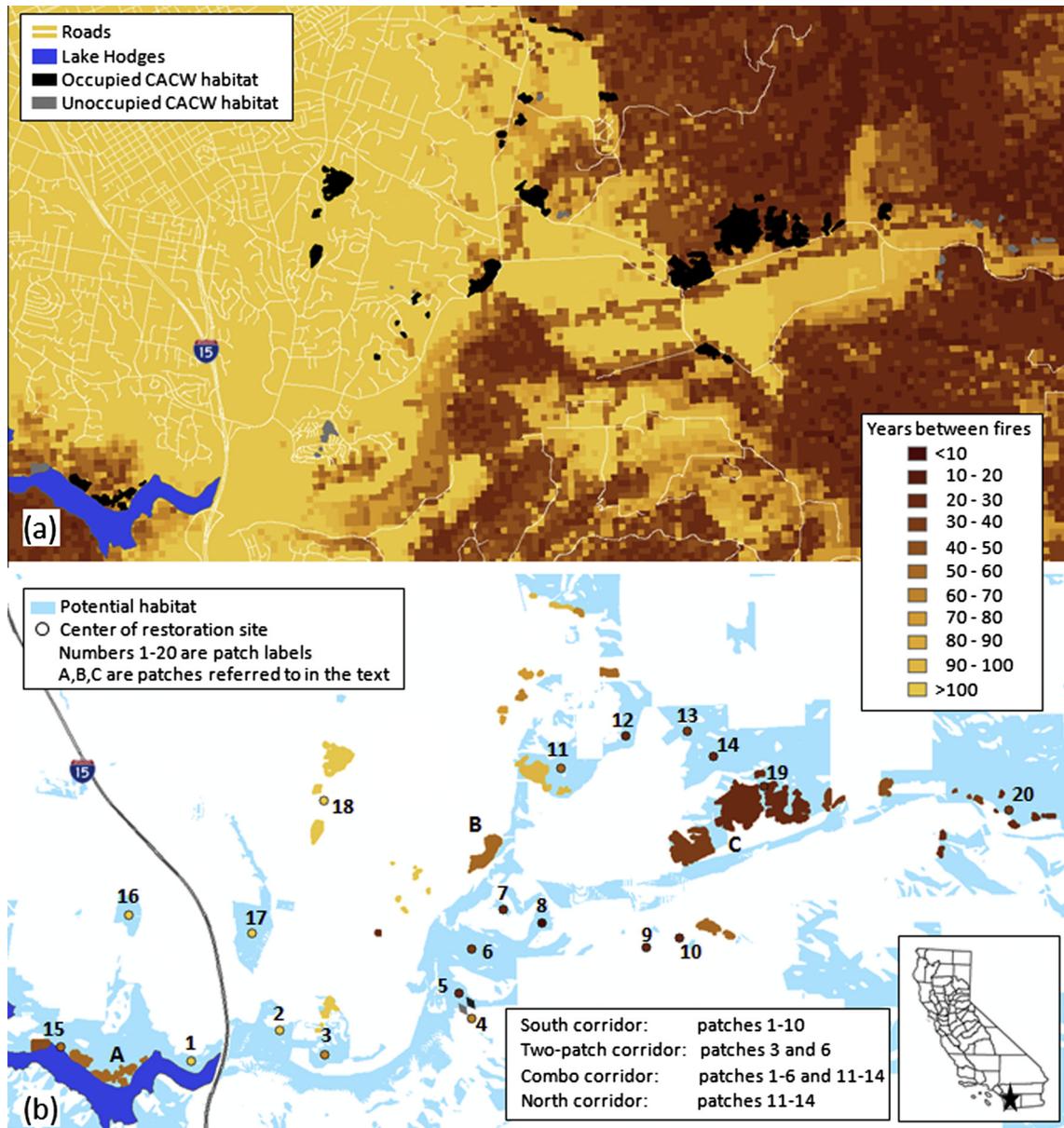


Fig. 1. Map of the study area. Fig. 1a shows the broad study area – San Pasqual Valley, Northern San Diego County, California, USA – including major roads in downtown Escondido (the northwest portion of the map) and Interstate 15 (from the northwest corner of the map to the southern edge). Fig. 1a also identifies areas currently suitable for cactus wren habitation. Suitable areas occupied by the wren are colored black, and suitable areas not known to be occupied by the wren are colored gray. For all other cells, Fig. 1a shows estimated expected fire return intervals (see *Methods*) using shades-of-orange, as interpreted on the Fig. 1a legend. Fig. 1b shows areas (highlighted in blue) where restoration would be feasible because they meet the following four criteria. (i) The elevation is low enough. (ii) The area occurs on south-facing slopes where cactus grows readily. (iii) The area is not riparian (cactus does not grow well along rivers). (iv) The area occurs on land that is set aside for open space or reserves. Fig. 1b also shows restoration patches included in simulations. Their centers are indicated by small circles with black boundaries, labeled 1–20, and with shade-of-orange-colored interiors reflecting their average expected fire return intervals from Fig. 1a. Restoration patch areas vary. Some are as small as their central circles, others are much larger. The letters A, B, and C identify large patches marking the ends of corridors.

one or more of the following characteristics: the area is urbanized (upper left of Fig. 1a); the elevation is too high for cactus wren; the area occurs on north-facing slopes where cactus does not readily grow; the area is riparian and thus does not accommodate cactus scrub; or the area occurs on land that is not available for open space or preserves. The black (occupied habitat) and gray (previously occupied habitat) areas of Fig. 1a substantially overlap the light blue areas (candidate restoration areas) of Fig. 1b. From the light blue areas (with exceptions described below), we selected 20 patches as candidate sites for restoration (numbered 1–20 on Fig. 1b).

Once the 20 patches were chosen, they were organized into a variety of restoration plans, or “scenarios”. To compare the merits

of the various scenarios, we constructed a stochastic, dynamic meta-population model of the numbers of wrens living in the San Pasqual Valley. The model was used to forecast meta-populations 100 years into the future. Computations were done on the RAMAS 5.0 platform (Akçakaya and Root, 2005). RAMAS was chosen because it is a popular, user-friendly, flexible, and well-documented meta-population platform that readily incorporates GIS habitat suitability data.

For each “scenario”, we ran the meta-population model, typically 1000 times, using a 100-year horizon for each run. The meta-population abundance at the final year, averaged over the runs, was used as a measure of restoration success for the scenario. Scenarios were ranked from highest to lowest average final

abundance. Using the same simulation output, extinction risks (fractions of runs which led to wren extinction) were also calculated. Over the scenarios considered, average final abundance and extinction risk provided almost exactly the same ranking of scenarios. Thus, we usually present only average final abundances. Extensive sensitivity analyses were performed to study the relative importance of different parameters to model results.

2.3. The meta-population model

Each of the 20 modeled patches was assigned a carrying capacity based on its actual size and based on the assumption that a breeding pair takes up 0.5 ha (Steinitz et al., 1997). A ceiling carrying capacity was employed, as is suggested for contest competition due to territoriality (Donovan and Thompson, 2001; Akçakaya and Root, 2005). For each habitat patch, the wren population was defined by stochastic births, deaths, and dispersal, subject to external forces such as fire acting on the carrying capacity of the patch. The demographic assumptions of this section will be referred to below as the “default” assumptions to which other assumptions will be compared. The two wren life stages (juveniles and adults) were chosen to mesh well with available data from field experiments (Atwood et al., 1998; Akçakaya and Atwood, 1997).

Specifically, for each patch, and for each year t , the demographic transition from t to $t + 1$ is determined by a two-equation model:

$$\begin{aligned} n_{\text{juveniles}}(t + 1) &= c_{11}(t)n_{\text{juveniles}}(t) + c_{12}(t)n_{\text{adults}}(t), \\ n_{\text{adults}}(t + 1) &= c_{21}(t)n_{\text{juveniles}}(t) + c_{22}(t)n_{\text{adults}}(t). \end{aligned} \quad (1)$$

Here $n_{\text{adults}}(t)$ and $n_{\text{juveniles}}(t)$ are the numbers of female adults and juveniles in the patch in year t . Let $C(t)$ be the 2×2 matrix of coefficients $C(t) = [c_{ij}(t)]$ that governs transitions from year t to year $t + 1$, as determined by survival, fecundity, and dispersal. For each patch in each year, each element of the 2×2 matrix $C(t)$ is separately and independently drawn from a lognormal distribution with parameters listed below. We distinguish large patches (≥ 10 ha) from small patches (< 10 ha). Wrens in small patches are assumed to suffer greater hazards due to edge effects, such as Cooper's hawk predation (Preston, personal communication). For a large patch, the means of the lognormal draws determining the elements of $C(t)$ are as shown in $\mathbf{M}_{\text{large}}$ just below; and, for a small patch, the means are as shown in $\mathbf{M}_{\text{small}}$. The standard deviations of the lognormal draws are shown in σ and assumed to be the same for both large and small patches:

$$\begin{aligned} \mathbf{M}_{\text{large}} &= \begin{bmatrix} 0.516 & 0.940 \\ 0.323 & 0.647 \end{bmatrix} & \mathbf{M}_{\text{small}} &= \begin{bmatrix} 0.394 & 0.804 \\ 0.311 & 0.623 \end{bmatrix} \\ \sigma &= \begin{bmatrix} 0.434 & 0.398 \\ 0.257 & 0.062 \end{bmatrix} \end{aligned} \quad (2)$$

The vital rates in Eq. (2) are based on vital rates reported in Preston and Kamada (2012) and Atwood et al. (1998). Environmental stochasticity, which applies equally to all individuals in a patch, is represented by the random draws, for each year, of the vital rates used in matrix $C(t)$. Appendix A1.1 describes further details of the population model.

2.4. Fire

Each patch was assigned its own expected fire return interval based on historical fire records and environmental conditions. To estimate expected fire return intervals, we obtained GIS grid cell data on fire perimeters for 1984–2011 in San Diego County from CAL FIRE's Fire and Resources Assessment Program (FRAP, 2012). To relate the number of fires in a grid cell to environmental conditions for the cell, we fit Poisson regressions with the following independent variables: July maximum temperature, January

minimum temperature, annual precipitation, slope, elevation, road density, and CALVEG (2004) categorical fuel type distinctions (such as grass, shrub and timber). The predicted fire frequencies for validation data (held back from model construction) provided a moderately good fit to observed fire frequencies ($R^2 = 0.38$). Numerous other models were constructed (including negative binomial and spatially auto-correlated models), but the Poisson model produced the best fit to the validation data. A resulting map (see Fig. 1a) shows predicted numbers of years between fires for each meta-population patch, as averaged over the GIS grid cells comprising that patch. However, for each patch and each year, actual fire occurrence within a specific patch is a random process. The probability of fire is assumed to depend on the time since the last fire according to a discrete time Weibull hazard function (see Appendix A1.2 for details).

After a fire occurs in a patch, its carrying capacity is set to 30% of its value just prior to the fire. This assumption is based on observations by Bontrager et al. (1995) for Orange County. After a fire, the carrying capacity was assumed to grow 5% for each fire-free year until an estimated maximum carrying capacity was reached. In the model, it takes 14 years for the carrying capacity to recover after a fire, in agreement with the reported 10–20 years it takes for cactus to re-grow to a height suitable for cactus wren nests (Preston and Kamada, 2009).

2.5. Dispersal

At each time step, after the demographic transitions have been applied, individual wrens are allowed to disperse to adjacent patches. Each individual wren either disperses or does not disperse based on a Bernoulli trial with a given dispersal probability. The probability of dispersal fluctuates between years depending on the carrying capacity of the receiving patch and on the number of wrens in the supplying patch. Dispersal rates also depend on factors that are constant through time, namely the distance between the two patches and the type of habitat between the patches. We also modified dispersal rates to account for difficulty in traversing urban areas. The data in Atwood et al. (1998) showed dispersing juvenile wrens moving an average of 1.59 km, with a maximum distance of 10 km. The later study by Preston and Kamada (2012), occurring after additional fires and urban development, saw dispersing juvenile cactus wrens moving an average of 0.66 km, with a maximum dispersal distance just under 5 km. A modified exponential function was fit to data from Atwood et al. (1998) for less-urbanized patches and to Preston and Kamada (2012) for patches in residential areas. Further details on dispersal are described in Appendix A1.3.

2.6. Restoration patches, strategies, scenarios, and scales

In the model, we simulate cactus restoration for the San Diego cactus wren by increasing the carrying capacity of “restored” patches proportional to the amount of habitat restored. We consider 20 candidate restoration patches, labeled by the numbers 1–20 on Fig. 1b. The center of each restoration patch is indicated by a small circle with a black edge, where the color within the circle indicates the patch's expected fire return interval. The smallest patches consist entirely of this circle. Larger patches are centered at the circle but consist of a larger area and, in some cases, connect with one or more irregular patches nearby.

“Strategy” will mean a general approach to restoration. Example strategies are “do nothing”, “create corridors”, and “augment cactus habitat in the most promising patches”. “Scenario” will mean a precise, detailed, and complete restoration plan based on one or more strategies. The broad purpose of the model is to find

the best strategy and scenario from the viewpoint of long-run wren abundance and viability.

We will focus on 11 scenarios (listed just below). One is a null scenario for which there is no restoration. Four are “corridor scenarios” involving the addition of cactus to one or more stepping stone patches to form or improve corridors, with the intent of encouraging wrens to migrate in advantageous directions. Four more are “augmentation scenarios” involving the addition of cactus to one or more patches to expand the wren habitat and population in those patches. Two more are “fire refuge scenarios” involving the addition of cactus to patches where the probability of fire is low, providing wrens with new, relatively fire-safe habitat. The following list of the 11 scenarios is in the same order as on the horizontal axis of Fig. 2.

1. No added cactus.
2. Establish the “North corridor”: northerly patches 11–14 on Fig. 1b, connecting patches in the middle of the Valley (B on Fig. 1b) to an area of patches in the far east (C on Fig. 1b).
3. Establish the “South corridor”: patches 1–10 on Fig. 1b, running along the southern edge of potentially restorable land (light blue areas) from a large area of patches in the far west (A) to an area of patches in the far east (C).
4. Establish the “Combo corridor”: southerly patches 1–6 on Fig. 1b, then crossing to northerly patches 11–14. This corridor runs from the far west (A) to the far east (C).
5. Establish the “Two-patch corridor”: a truncated version of the south corridor, involving just patches 3 and 6 on Fig. 1b.
6. Augment patch 15.
7. Augment patch 19.
8. Augment patch 20.
9. Augment patch 18.
10. Establish a fire refuge in patch 17.
11. Establish a fire refuge in patch 16.

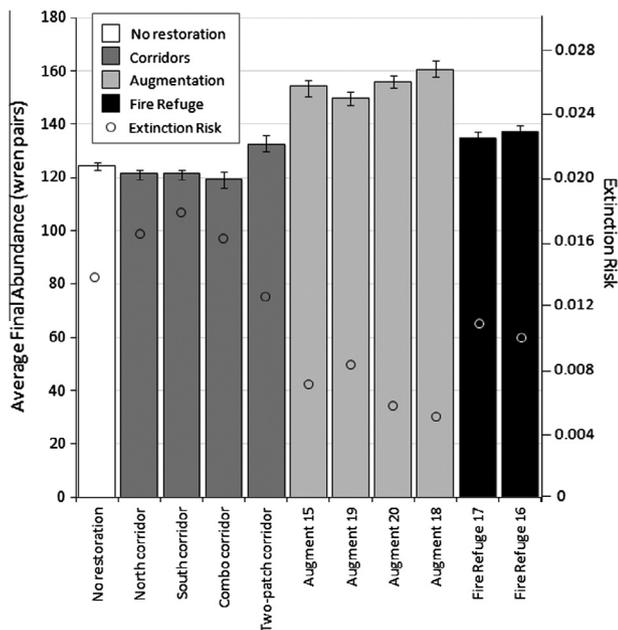


Fig. 2. Average final abundances for small scale restorations. Each of the 11 bars on the figure reports a 20-ha restoration scenario labeled along the horizontal axis. Each bar presents two pieces of information about the scenario. The height of the bar, to be read from the left vertical axis, reports the average final wren abundance (at the end of the 100-year time horizon) over 10,000 model runs of the scenario; and the height of the small circle within the block, to be read from the right vertical axis, reports the “extinction risk” of the scenario, defined as the fraction of the 10,000 runs for which the wren was extinct by the final year of the run (the 100th year). The two variables – average final abundance and extinction risk – measure wren success positively and negatively, respectively. The small error bar at the top of each main bar was constructed by computing 10 average final abundances, each an average over 1000 runs. The highest and lowest of these 10 numbers were used as the top and bottom ends of the error bar. The smallness of the error bars suggests that 1000 is an adequate number of model runs for estimating a bar’s height.

The addition of stepping stones to a corridor increases connectivity by providing more breeding habitat along the corridor and more rest area for birds travelling along the corridor. More breeding habitat increases connectivity automatically because new patches have positive carrying capacity, to which nearby breeding wrens can send emigrants. More rest area will increase connectivity through an added assumption that dispersal rates are higher along corridors. The added assumption is that dispersal rates are doubled between A and C for the south corridor and two-patch corridor, between B and C for the north corridor, and between A and B, B and C, and A and C for the combo corridor (see Appendix A1.3 for dispersal details).

In selecting scenarios, decisions were based in part on local knowledge of the area. For example, patch 18 is not in a light blue area on Fig. 1b because it is on private property and may become untenable in the near future. Nonetheless, augmenting patch 18 is considered because the land might be purchased in the near future to meet regional conservation goals. Similarly, patch 4 is on unpreserved, undeveloped land, but was considered for cactus restoration. Patches 9 and 10 are largely north-facing, which is not ideal for cactus growth; however, patches 9 and 10 are otherwise very well located as west-to-east stepping stones.

We considered these scenarios at two scales of cactus restoration, 20 ha and 200 ha, and we considered limited scenarios at intermediate scales. A 20 ha restoration will be applied to each of the 10 non-null scenarios. That represents the work we can accomplish under an existing grant. However, additional funds may become available allowing restoration of an additional 180 ha. To accommodate the additional hectares, we will extend the ten scenarios listed above, singly and in combination.

3. Results

3.1. Overview

Very little of San Pasqual Valley (Fig. 1) is available for cactus habitat restoration. The bulk of the landscape to the west has been developed and much of the landscape to the east is at elevations above the normal elevation for San Diego cactus wrens (275 m). Further, the undeveloped areas to the east have high fire frequency, limiting successful restoration there. Most of the preserved areas are on the swath of land extending east from Lake Hodges parallel to the San Dieguito River (not shown on Fig. 1). However, riparian areas themselves are too wet for cactus. Finally, there are only a few hillsides that are on protected land, are not north-facing (cactus prefer south-facing slopes), and not already cactus wren habitat. Given all these restrictions, only a few locations remain as potential cactus habitat (the light blue areas on Fig. 1b).

3.2. Small-scale restoration

When only 20 ha are restored, results indicate that augmenting a single existing patch is the best approach for maximizing average final abundance (Fig. 2). Across augmentation scenarios, average final abundance increases, on average, 24% as compared to the status quo no restoration scenario. Augmenting patch 18 alone is best from the viewpoint of providing the highest average final abundance (29% increase compared to the status quo), and the lowest extinction risk (55% decrease compared to the status quo),

although patch 18 is not on preserved land. Augmenting patch 20 is second best (25% increase in average final abundance as compared to the status quo), only slightly better than augmenting patch 15 (24% increase in average final abundance as compared to the status quo), which is third best. A corridor scenario alone is typically not effective (with an average 0.4% decrease in average final abundance as compared to the status quo). This may happen because the corridors do not provide enough habitat to sustain a viable population, or because they divert wrens from patches with more robust populations. Restoring either of the two fire refuge scenarios (patch 16 or patch 17) results in only slightly increased wren abundance (average 9.5% increase) relative to the status quo.

To give these average final abundances more meaning, an error interval was calculated for each. The average final abundance for each scenario was estimated from ten sets of 1000 runs. The highest and lowest set of 1000 runs defined the error interval (shown by the small error bars on Fig. 2). The smallness of the bars provides the important information that scenario rankings are well-justified, not just capricious random consequences of small samples.

Extinction risks (the circles within bars on Fig. 2) are highly correlated with average final abundances. With the exception of the three lowest ranked scenarios, rankings are identical between extinction risks and average final abundances. The relative differences among the scenarios are greater for extinction risk than for average final abundance. However, the standard deviation in extinction risk is relatively higher (not shown, but ranging from 0.0021 to 0.0067), indicating larger estimation error in extinction risk than in average final abundance. Because of the nearly perfect rank correlation between extinction risk and average final abundance, we present only the latter from here on.

3.3. Large-scale restoration

When the initial 20 ha restoration is followed by an additional 180 ha of restoration, there is enough land restored to create major stepping stone patches and thus major corridors. Adding a major corridor then becomes a key component of the best management scenario (Fig. 3). The best scenario is to allocate the initial 20 ha to patch 18 and the further 180 ha to the south corridor (patches 1–10). The second best scenario is to combine the third best scenario from the 20 ha case (all 20 ha to patch 15) with the same south corridor scenario. Here an initial augmentation to patch 15 is better than an initial augmentation to patch 20, although the two are nearly identical under the 20 ha scenarios. The reason is that patch 20 is more isolated and does not benefit from the south corridor. Nonetheless, augmenting patch 20 initially results in the third best 200 ha scenario, only slightly below the second best. These results are encouraging because they suggest that the best options for restoring 20 ha are still part of the best options when an additional 180 ha are restored. That is, optimal small-scale restoration does not compromise the large-scale restoration that may or may not come later.

As the amount of restored land is increased, the carrying capacity of the stepping stone patches increases. This is important for two reasons. First, the larger a patch, the less likely it will lose its population through demographic or environmental stochasticity. Second, we parameterized the model such that small patches (<10 ha) have lower survival and fecundity, reflecting the increased predation that small patches experience from Cooper's Hawks at their edges (Preston, unpublished data). Lower vital rates in smaller patches disadvantaged corridor scenarios when only 20 ha are added to the landscape. This disadvantage is no longer present under the 200 ha scenarios.

The larger error bars on Fig. 3 (as compared to the smaller error bars on Fig. 2) represent standard deviations over 1000 individual

runs (not over 10 averages of 1000 runs). Such high abundance variability suggests that the wren population is quite sensitive to environmental stochasticity.

3.4. Incremental increases in restoration area

The results from Figs. 2 and 3 suggest that, as restoration capacity increases from 20 to 200, the best strategy shifts from habitat augmentation to corridor addition. To investigate where this shift occurs, we estimated (Fig. 4) the marginal benefits of incrementally adding 20 ha (that is, moving from 20 ha to 40 ha to 60 ha ... of restoration). To investigate sensitivities of results to changes in parameters, we considered several restoration scenarios for four parameterizations: the "default" specification of the Methods section (Fig. 4a), the default specification except that all patches have mean vital rates M_{large} (Fig. 4b), the default specification except that all patches have mean vital rates M_{small} (Fig. 4c), and the default specification except that all patches have mean vital rates M_{small} and dispersal rates lowered to 10% of the default, non-urbanized dispersal rates described in Appendix A1.2 (Fig. 4d). For the one patch, we chose patch 15 rather than patch 18 (the "absolute best" strategy from Fig. 3) because patch 18 is not on preserved land. We considered combinations of augmenting patch 15 and augmenting corridors because these scenarios are among the best from Figs. 2 and 3. We also considered augmentation of patch 19 because it is the best strategy when dispersal and vital rates are low (Fig. 4d).

Under the default specification of Eq. (2), the best strategy shifts from habitat augmentation to corridor addition when enough land is added that all additional patches are ≥ 10 ha (and thus all patches shift to vital rates M_{large}). When all patches have uniformly high vital rates (Fig. 4a compared to Fig. 4b), the benefit of the south corridor occurs at a smaller amount of total land added (at 100 additional hectares instead of 160). When all vital rates are low (Fig. 4c), the relative benefit of corridors is dramatically increased. However, when both vital rates and dispersal are low (Fig. 4d), the best scenario is augmenting patch 19. Sensitivity tests, not shown, suggest that two phenomena can explain patch 19's improved performance in Fig. 4d. First, the initial abundance in patch 19 was higher than in patch 15, and adding habitat to a population that has a high extinction risk is less beneficial than adding habitat to a robust population. Second, dispersal is too weak to allow for rapid re-colonization of isolated patches; hence the more-connected patch 19 performs better than the more-isolated patch 15.

The importance of dispersal to the optimal restoration scenario can be seen in Fig. 4. When there is no dispersal, corridors convey no benefit to the meta-population. When dispersal is weakened but not suppressed, as in Fig. 4d, the best strategy shifts from corridors to augmenting habitat, and there is a reduction in the fraction of individuals dispersing out of their natal patches from approximately 25–5%. The impact of reduced dispersal becomes more pronounced when vital rates are lower (as in Fig. 4d) or when initial abundances in the augmented patches are higher (not shown). Fig. 4a and c demonstrate that, when vital rates are low and thus individual populations are more likely to become extinct, corridors become more important. Similarly, comparing the optimal strategies of Fig. 4c and d shows how lower vital rates make the model's sensitivity to dispersal more pronounced. Thus, both dispersal and vital rates are critical to the optimal management scenario.

3.5. Fragmentation and isolation

Overall, the restoration of small patches and isolated patches does not increase average final abundances. When the carrying

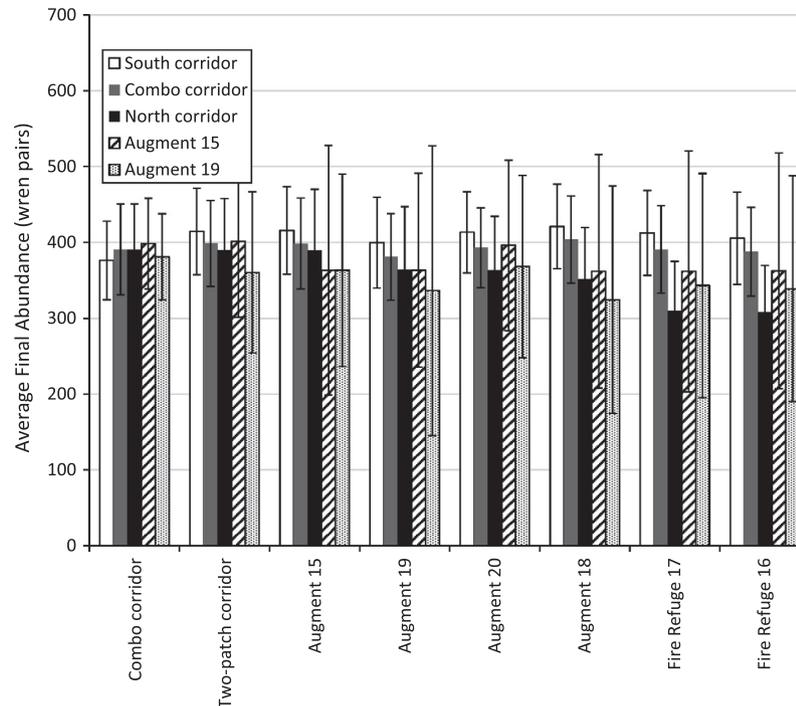


Fig. 3. Average final abundances for combinations of an initial restoration and a further restoration. The labels along the horizontal axis show the patch or patches that received the initial restoration of 20 ha. Above each label are five average final abundance bars, side by side, corresponding to the patch or patches which received an additional restoration from the further 180 ha; the caption box shows which patch or patches these are. Thus, each of the $5 \times 8 = 40$ bars on the figure corresponds to a combination of a small scale restoration (labeled on the horizontal axis) and a large scale restoration (labeled in the caption box). The large-scale restorations were spread evenly over the relevant patches, with two exceptions. Only 131 ha were available for the north corridor (the black blocks), and only 20 ha were available for augmenting patch 18 and the fire refuge patches 16 and 17 (the three right-most groups of bars). Each error bar on this figure is the standard deviation across the 1000 individual runs from which the mean final abundance (height of the corresponding main bar) was estimated.

capacity of a patch is greater than 25, patches spend at least 40% of the time occupied, even when the patch receives very few immigrants (Fig. 5). However, when a patch receives immigrants totaling 10% of its carrying capacity, then the carrying capacity could be reduced to 10 individuals and be occupied greater than 40% of the time.

3.6. Sensitivity analyses

We also considered scenarios in which (i) patch-specific fire frequencies were replaced with either no fire or a fixed fire frequency of one fire per 30 years across all patches, (ii) patches had different initial abundances, (iii) fire spread from one patch to another, (iv) specific patches were removed, testing the importance of those patches to the overall meta-population, and (v) survival and fecundity rates (in Eq. (2)) were individually changed (see Appendix A2). The alternate parameterizations (i)-(ii)-(iii) did not change the optimal strategy when only 20 ha of habitat were allocated; augmenting habitat was still the best strategy. Similarly, individual changes in survival and fecundity (v) did not change the relative rankings of the management scenarios. As discussed above, lowering dispersal in addition to lowering vital rates did result in a switch in the optimal restoration strategy when 180 ha were added. Similarly, increasing initial abundances in combination with lowering dispersal resulted in a switch of optimal strategy from corridors to augmentation when 180 ha were added. Removing habitat areas was most devastating when the patches were large and well-connected. The largest change in abundance (60% decrease) was observed when the existing habitat area C was removed, followed by the existing habitat area A. Removing existing habitat area B was least influential (less than 2% decrease in

abundance) because B is surrounded by residential areas and is thus more isolated.

4. Discussion

We used a simulation model to distill the available information on coastal cactus wren life history into a coherent framework for exploring potential restoration options. In particular, we were interested in whether conservation efforts should focus on creating corridors, augmenting individual patches, or creating patches in areas with lower probability of fire. For our area, the San Pasqual Valley, and our study species, the San Diego cactus wren, we selected 20 potential restoration patches, and we built a meta-population model over those patches, based on many natural history, urban development, climate, fire, and other sources. Using the RAMAS platform, we estimated best restoration scenarios through a competition of models over many thousand simulations.

We found that the optimal scenario differed between small-scale and large-scale restoration efforts of 20 ha and 200 ha of cactus, respectively. Small-scale restoration favored augmentation of existing habitat, whereas large-scale restoration favored the addition of stepping stone patches that would establish corridors between the western-most and eastern-most populations. Our simulations indicated no long run loss to wren abundance caused by planning the first 20 ha of restoration without regard for the 180 ha that might follow.

The reason the optimal strategy changed between the 20 ha and 200 ha budgets may be due to the behavior of population “sinks”. Small stepping stone patches offered lesser population benefits, in part, because they are more vulnerable to demographic stochasticity. Additionally, these small sink patches presented greater hazards to wrens due to edge effects, such as Cooper’s hawk

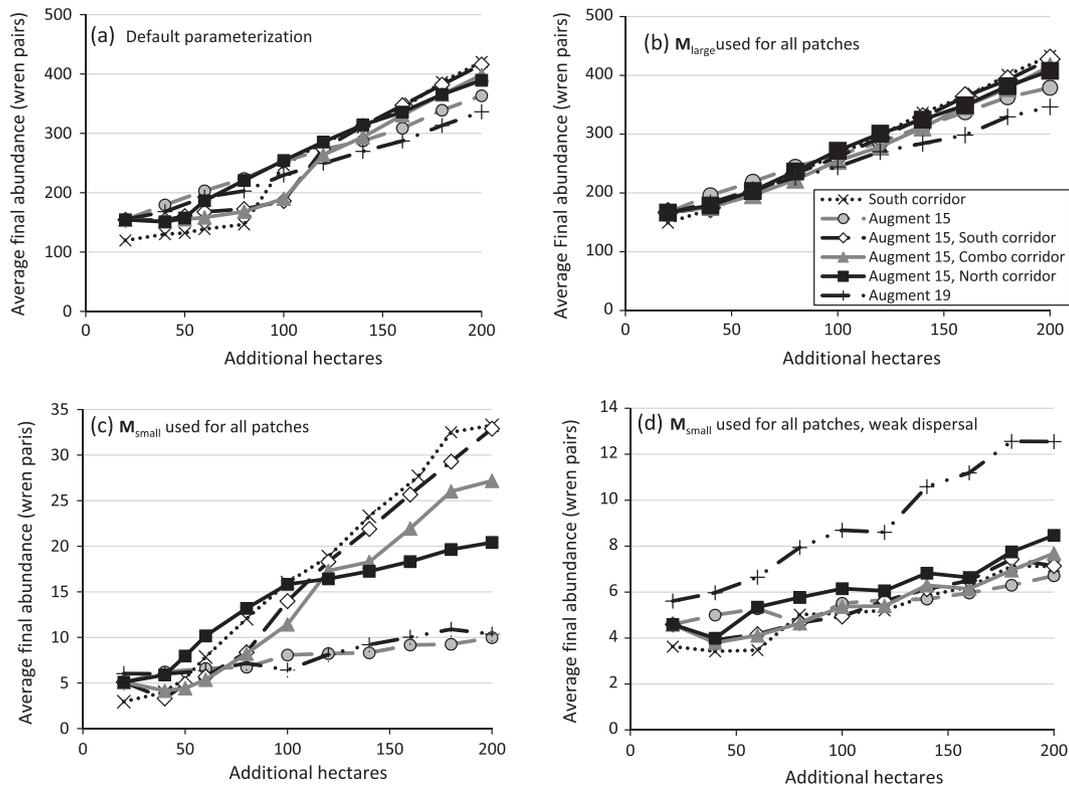


Fig. 4. Average final abundances graphed against size of restoration area. All graphs are upward sloping over most of their range since more restoration typically improves abundance. Each of the four panels (4a, 4b, 4c, 4d) contains six graphs corresponding to the six strategies listed in the legend box. The four panels (4a to 4d) differ in the assumed vital rates and dispersal parameters. Panel 4a assumes default vital rates and dispersal parameters. Panel 4b assumes the vital rates of M_{large} and the default dispersal parameters. Panel 4c assumes the vital rates of M_{small} and the default dispersal parameters. Panel 4d assumes the vital rates of M_{small} and “weak dispersal”. A stepwise increase in average final abundance occurs in Panel 4a when each restoration area is increased to more than 10 ha, since the default vital rates then change from M_{small} to M_{large} . The graphs of Panels 4a and 4b show much higher abundances than do the graphs of Panels 4c and 4d because $M = M_{large}$ applies for some or all of Panels 4a and 4b; whereas $M = M_{small}$ applies to all of Panels 4c and 4d, and because, in addition, the dispersal parameters are weakened for Panel 4d.

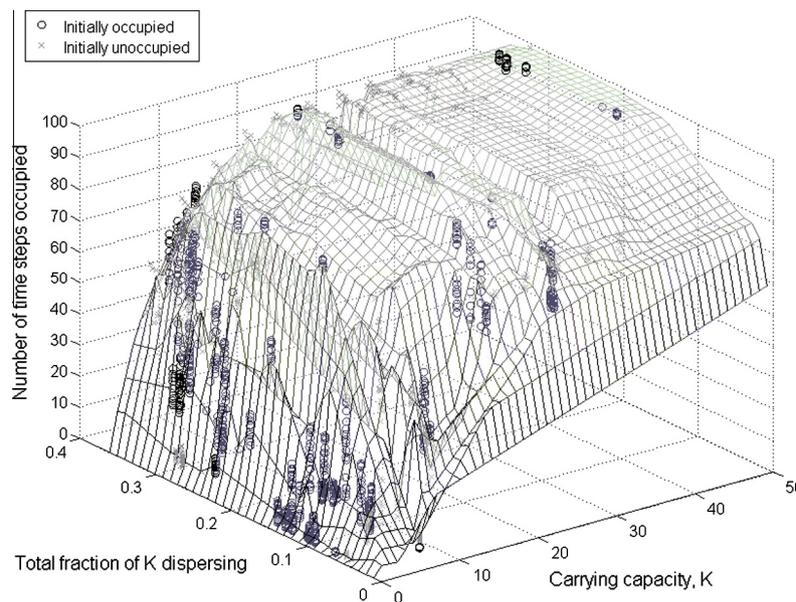


Fig. 5. Statistical surface relating the fraction of the time steps that a patch is occupied to its carrying capacity (denoted K) and the fraction of K dispersing (the immigrant fraction). The vertical axis is the fraction of time steps (years) that the patch was occupied over the 1000 simulations. The right horizontal axis (K -axis) is the carrying capacity of the patch. The left horizontal axis is the fraction of K resulting from dispersal. A linear interpolation from the datapoints gives the statistical surface shown. The datapoints are the patch occupancy data for all simulations in Fig. 4a.

predation (Preston personal communication). An alternative to creating stepping stone patches is to augment existing habitat. In a highly fragmented landscape, augmentation of existing habitat

may convert sinks to areas with constant or growing populations, stabilizing the overall meta-population (Donovan and Thompson, 2001).

When enough resources could be allocated to the creation of corridors, corridors were the optimal strategy, in part, because they mitigate high fire threats in the San Pasqual Valley (see Regan et al., 2010). Although our fire predictions are specific to our site, the complex interaction between habitat fragmentation and fire risk are common in regions with similar climate (Syphard et al., 2009), suggesting that our model is relevant to other locations and taxa.

Sensitivity analyses were performed on individual vital rates (Appendix 2) and on expected fire return intervals. Neither analysis changed the estimated benefits of corridors relative to habitat augmentations. However, reductions in fire frequency did lower the estimated relative benefits of fire refuges. In a sensitivity test with the expected fire return interval set at one fire every 30 years, the same for all patches, the average final abundance increased, suggesting that the effective average fire frequency across patches is above one fire every 30 years.

Sensitivity analyses that demonstrate the importance of specific model parameters highlight gaps in our understanding. Although dispersal rates were shown to be important in determining the benefit of corridors, the relative importance of dispersal increased as vital rates decreased (Fig. 4). In the absence of our model, intuition might suggest that future studies focus on dispersal, whereas the model suggests joint consideration with vital rates.

Using models to make decisions under uncertainty requires subjective decisions about model frameworks (Burgman et al., 2005). However, uncertainty about the impacts of parameter and model choices can be mitigated by careful analysis of how specific parameter values within a plausible range of values impact model outcomes (Fuller et al., 2008; Regan et al., 2005; Drechsler, 2000). In our model, the relative ranking of restoration strategies was robust to a variety of parameter settings when the restoration budget was held fixed at either 20 ha or 200 ha, but changed substantially when the budget increased from 20 ha to 200 ha. As pointed out in Hodgson et al., 2009, there are fewer uncertainties associated with augmenting existing habitat in practice, as compared to creating corridors. Thus, from a manager's perspective, when budgets are small, it is encouraging that the less technically difficult task – augmenting existing habitat – emerges as superior in population models.

In the model, the basic scarce resource was taken to be the area of cactus that could be planted. Implicitly, the same dollar price per unit area of cactus planted was assigned to all three strategies (augmentation, corridors, and fire refuges). However, with only small changes to the model, the basic scarce resource could have been dollars of available budget, and different prices for the three strategies could have been assigned to reflect differences in cactus planting costs across the three strategies. Intuition suggests that the price of augmenting habitat in natural areas adjacent to cactus patches would be less per hectare than creating new habitat in areas not adjacent to cactus patches (as under the corridor or fire refuge scenarios). Then, augmenting existing habitat might emerge as the preferred strategy for large-scale restoration as well as for small-scale restoration.

Although meta-analyses show that the impacts of habitat area, habitat isolation, and habitat surroundings is complex, birds as a taxonomic group appear to be most influenced by the sizes of habitat patches (Prugh et al., 2008). For our meta-population of the San Diego cactus wrens, a rough general rule emerged about adding restoration patches (see Fig. 5): Choose patches that receive roughly 10% of their carrying capacity in immigrants and have a carrying capacity of at least 10 individuals. This rule is similar to a rule suggested by Schultz and Crone (2005) for Fender's blue butterfly (butterfly sites should be <1 km away from existing sites and >2 ha in size).

Choice of a restoration plan is a highly complex decision, involving incomplete information on the relevant population dynamics and environmental threats, and typically constrained by a strict budget. Tools for planning restoration activities are sorely needed (Addison et al., 2013; Schultz and Crone, 2005). As global changes evolve, there will be a continuing need for flexible management models grounded in species-specific ecology. A simulation model provides a way to distill the available information into a coherent framework for exploring management scenarios under various assumptions about a future that is only partially predictable. Models coalesce these detailed qualitative and quantitative data into critical management decision-support tools.

Meta-population models have a long and valuable history in conservation planning, and novel uses, like the one here, are still emerging. The flexibility of meta-population models proceeds in large part from their ability to incorporate both species' life histories and multiple threats to species viability. The approach here supports restoration management by helping to avoid the potentially very high cost of poor decisions. Although there is debate about whether conservation efforts should focus on corridors or on individual patches (Doerr et al., 2011; Hodgson et al., 2011), most would agree that finding an optimal restoration scenario requires an area-specific analysis. We hope our model will be as useful in defining optimal restoration scenarios for other contexts as it was in defining the best scenario for San Pasqual Valley.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2014.04.010>.

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