

## VIABILITY OF BELL'S SAGE SPARROW (*AMPHISPIZA BELLI* SSP. *BELLI*): ALTERED FIRE REGIMES

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**Abstract.** We modeled the viability of a Bell's Sage Sparrow (*Amphispiza belli* ssp. *belli*) metapopulation under different fire regimes in the foothills and mountains of San Diego County, California, USA. The approach integrates a landscape model, which predicts the vegetation composition and age under three fire regimes, a habitat model, which interprets the resulting landscape in terms of its suitability for the Sage Sparrow, and a metapopulation model, which predicts the viability of the species based on a dynamic spatial structure as determined by the landscape and the habitat models. Bell's Sage Sparrow depends on early-successional shrubland (chaparral) habitat, especially when the availability of preferred open coastal subshrub vegetation is limited. The three fire rotation intervals (FRI) used in the landscape model were "current" (30-yr), representing the effect of increased human ignitions; "natural" (90-yr), representing the historic shrubland fire regime at higher elevations without the effect of human ignitions; and "long" (150-yr), representing a hypothetical endpoint (very low fire frequency for southern California shrublands). The results indicated that the viability of the Sage Sparrow was highest under the "current" fire regime scenario, slightly lower (especially when population growth rate was low) under the "natural" scenario, and lowest under the "long" fire regime scenario.

**Key words:** *Amphispiza belli* ssp. *belli*; coastal subshrub vegetation; dynamic spatial structure; fire rotation interval; habitat model; landscape model; metapopulation; Sage Sparrow; San Diego county, California; viability.

### INTRODUCTION

Natural resources management at large spatial and temporal scales requires tools for projecting the effects of natural and anthropogenic disturbances on population, community, and ecosystem processes. Computer simulation allows modeling of scenarios to test the effect of disturbance regimes on landscape patterns and, in turn, on population dynamics of wildlife species of management concern. In many cases, these simulations use metapopulation models that incorporate aspects of a dynamic landscape, such as changing carrying capacities (or other attributes) of habitat patches through time (Pulliam et al. 1992, Lindenmayer and Possingham 1996, Akçakaya and Atwood 1997, Stelter et al. 1997, Akçakaya and Raphael 1998, Gaff et al. 2000, Johst et al. 2002, Keith 2004, Kindvall and Bergman 2004). In these models, the carrying capacity changes deterministically (e.g., to simulate forest growth), stochastically (e.g., to simulate the effects of random disturbances such as fires), or both (e.g., as a deterministic function of time since a stochastic disturbance event). However, this approach does not capture the dynamics of the spatial structure of the metapopulation (e.g.,

changing number and location of habitat patches), and does not explicitly model vegetation or succession dynamics based on life history attributes of the plant species that form part of the habitat of the species being modeled. Such dynamics are especially important in early-successional habitats, which are patchy in time and space, and represent critical habitat for certain species. A recently developed approach has addressed this issue by linking a landscape model and a metapopulation model (Akçakaya et al. 2003, 2004).

The U.S. Forest Service identified Bell's Sage Sparrow (*Amphispiza belli* ssp. *belli*), a California Species of Special Concern, as currently at moderate risk of population decline, although population trends are unknown (Stephenson and Calcarone 1999). It was also designated as a species best conserved through landscape-level habitat management. The Bell's Sage Sparrow is associated with coastal sage scrub vegetation, a plant formation dominated by small, drought-deciduous shrubs, as well as open chaparral (evergreen shrubland) habitats in the interior foothills, especially young-aged, recently burned chaparral (Stephenson and Calcarone 1999). Extensive areas of coastal sage scrub have been lost to urban development in coastal southern California (Westman 1981, O'Leary 1990), while those that remain are threatened by increasing fire frequency (and conversion to exotic grassland) owing to human

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ignitions and correlated with human population growth (Keeley and Fotheringham 2003). Although frequent fire at low elevations could result in further loss of the already quite fragmented coastal sage scrub habitat (Keeley 2001), infrequent fire in foothill chaparral could also reduce available habitat. Therefore, available habitat for this species is affected directly through land cover change and indirectly via the fire regime, which is affected by humans through both increased ignitions and fire suppression efforts. Habitat could also be managed through prescribed fire.

This is one of many examples of a species whose current status is not so dire as to justify population surveys or monitoring, but one that depends not only on spatial configuration of habitat but also on habitat dynamics resulting from a natural disturbance regime. We suggest that its long-term persistence in the face of potential future land cover change and dynamics can be evaluated using an integrated landscape modeling approach. We modeled the viability of a Bell's Sage Sparrow metapopulation under different fire regimes in the foothills of San Diego County, California, USA. The approach integrates a landscape model, which predicts the vegetation composition under three fire regimes, a habitat model, which interprets the resulting landscape in terms of its suitability for the Sage Sparrow, and a metapopulation model, which predicts the viability of the species based on a dynamic spatial structure as determined by the landscape and the habitat models.

#### METHODS

We used RAMAS Landscape (Akçakaya et al. 2003), which integrates the metapopulation model RAMAS GIS (Akçakaya 2002) with the landscape model LANDIS (Mladenoff et al. 1996, He and Mladenoff 1999, He et al. 1999). In LANDIS the landscape is described by the species–age map, containing information about the presence of each species for each site (grid cell) in 10-year age classes. The conditions associated with each species' potential for establishment and with primary productivity (fuel dynamics) are approximated using a land type map (Franklin 2003). Life history parameters (longevity, maturity, dispersal distance, ability to resprout, relative shade, and fire tolerance) are used to simulate dispersal, establishment, competition, persistence, and mortality. Fire ignition and spread are stochastic, but the probability is conditioned by the rotation interval specified for each land type, and fire size is drawn from a log-normal distribution function. Fire severity is determined by the time since the last fire, and fire-induced mortality depends on species- and age-specific fire tolerance. The model operates on a 10-year time step. We made one change to the standard version of LANDIS used by other research groups, modifying the model to simulate fire-cued germination from a buried seed bank in sites where adults of the plant species are killed. These so-called “obli-

gate seeders” were also given a 50-year seed bank from which germination could take place in that site.

RAMAS Landscape uses the landscape model to create a time series of raster maps that describe the plant species composition and landscape age at each decade, and then combines these maps into a time series of patch structures by using a habitat suitability function for the species modeled. In this study, we used raster maps with cell length of 180 m. This time series of patch structures forms the dynamic spatial structure of the metapopulation, in which the patches can change at 10-year time steps in the patterns just summarized. We modeled the local dynamics of the Sage Sparrow with a matrix model at an annual time step, incorporating random environmental and demographic variation. Each step will be detailed.

#### *Study area*

The 3878-km<sup>2</sup> study area (Fig. 1) coincides with the foothills and mountains ecological subsections of the Peninsular Ranges, as defined by the U.S. Forest Service (Miles and Goudey 1997). It falls mainly within San Diego County, California (described in detail in Franklin and Woodcock 1997, Franklin 2002, 2003), and represents a major portion of the area subjected to a recent interagency assessment of species conservation issues (Stephenson and Calcarone 1999). Elevations range from 157 to 1981 m. The climate is mediterranean, with cool wet winters and warm to hot dry summers. Average annual precipitation ranges <150 to >900 mm, mean minimum January temperature ranges from  $-4^{\circ}$  to  $5^{\circ}$ C, and maximum July temperature from  $27^{\circ}$  to  $37^{\circ}$ C (Franklin 2003). On the western (ocean-facing) slopes, semideciduous coastal sage scrub is found at lower elevations, with predominantly evergreen chaparral and oak woodland at middle elevations and conifer forest at the highest elevations. To the east, in the rain shadow of the escarpment, chaparral is intermixed with some Great Basin sage scrub and annual (mainly exotic) grasslands are found in the interior valleys (Stephenson and Calcarone 1999).

#### *Landscape patterns of suitable habitat under alternative fire regimes*

Bell's Sage Sparrow occupies shrubland habitats in southern California that experience infrequent to frequent stand-replacing wildfire. Although fire has long been a part of this landscape (Byrne et al. 1977), humans have altered the fire regime in southern California prehistorically and historically by increasing ignitions on some parts of the landscape and, in the past century, through fire suppression (Mensing et al. 1999, Keeley 2002b). The main human impacts since the early 20th century have been increased frequency of small fires at the lower elevation urban–wildland interface resulting from human ignitions, and greatly reduced incidence of fire in the montane forests (above 1800 m) owing to effective fire suppression (Keeley et al. 1999,

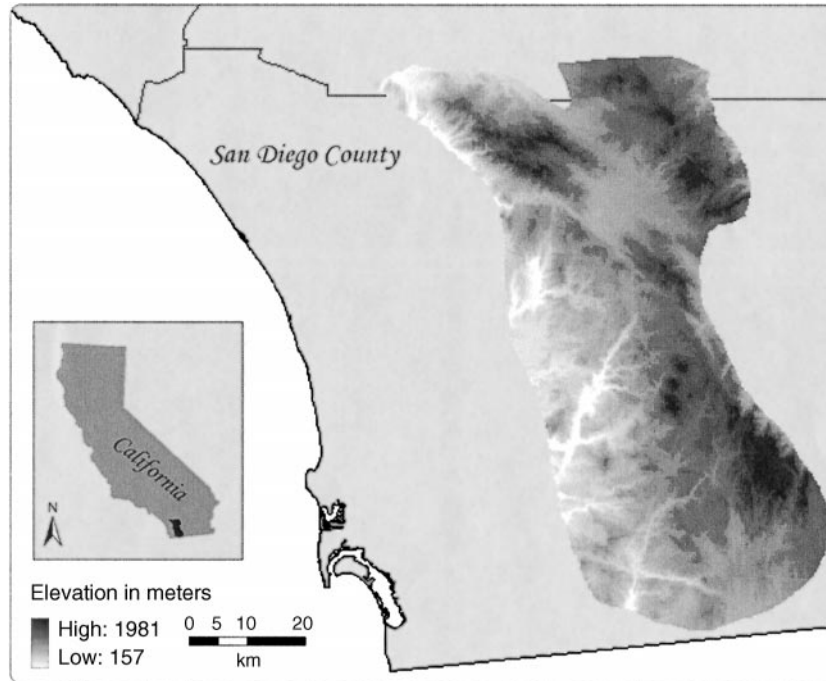


FIG. 1. The study area (3878-km<sup>2</sup>), where shading indicates relative elevation (higher is darker), coincides with the foothills and mountains ecological subsections of the Peninsular Ranges, as defined by the U.S. Forest Service, primarily within San Diego County, California, USA.

Keeley and Fotheringham 2003). A key characteristic of the crown-fire regime in California shrublands, that much of the landscape is burned in very large, infrequent fires occurring during severe fire weather (most recently in October 2003), appears to be unaffected by humans historically and prehistorically (Moritz 1997, 2003, Mensing et al. 1999).

Increased fire frequency at low elevations could reduce the availability of habitat if extensive areas of sage scrub were converted to exotic annual grasses and forbs (reviewed by Keeley and Fotheringham 2003), whereas reduced fire frequency in the montane zone could also negatively impact habitat availability if it increased the extent of old chaparral stands at the forest-chaparral ecotone. We used LANDIS to simulate three different fire regimes representing the range of con-

ditions that might occur under both high and low fire frequencies in the upper and lower parts of the elevation gradient (Table 1).

The three scenarios were developed for a related study of the impacts of human-altered fire regimes on plant community dynamics in the study area (Franklin et al. 2001). Briefly, the model was run for 27 plant species and 11 land types (Franklin 2003). The "current" fire regime scenario (Table 1) applied an average fire rotation interval (the time it takes to burn an area equivalent to the study area) of 30 years to the lower elevation foothills (ranging from 20 to 50 years from low-to-mid elevations on seven upland land types) to examine the effect of continuing the recent trend of increased fire frequency at the urban interface. The "natural" scenario applied a longer FRI, averaging 90 years (range 70–110 years), eliminating the recent effect of increased human ignitions. The "long" scenario represented a hypothetical end point: the landscape dynamics if fire were very rare (130–170 years in the foothills). Simulations were run for 250 years (recall, LANDIS operates on a 10-years time step). To explore the variability in habitat due to landscape dynamics, 10 replicates were run per scenario. The details of these landscape simulations are described in Franklin et al. (*in press*).

TABLE 1. Three fire regime treatments showing the average fire return interval (FRI), also called rotation period or fire cycle.

| Treatment | Foothills<br>(70% of area) |           | Mountains<br>(30% of area) |           |
|-----------|----------------------------|-----------|----------------------------|-----------|
|           | Specified                  | Simulated | Specified                  | Simulated |
| Current   | 30                         | 37 (2)    | 150                        | 108 (4)   |
| Natural   | 90                         | 64 (5)    | 30                         | 32 (3)    |
| Long      | 150                        | 221 (29)  | 500                        | 682 (132) |

*Note:* Mean FRI values are specified for nine foothills and two mountain land types and are simulated in 10 replicated model runs per treatment (with 1 SD in parentheses, averaged across the land types).

#### Habitat model

Because extensive survey data were not available for habitat modeling, we developed a deductive habitat

model (*sensu* Stoms et al. 1992) derived from expert opinion on habitat preferences as described in the literature and summarized here. The Sage Sparrow (*Amphispiza belli*) is found in the western United States and northern Mexico, prefers semi-open shrub habitats (Martin and Carlson 1998), and is associated with big basin sagebrush (*Artemisia tridentata*) throughout most of its range in the interior West (Wiens and Rottenberry 1981). The nonmigratory subspecies, Bell's Sage Sparrow (*A. b. belli*), occurs only on the coastal (cismontane) side of the Peninsular Ranges, and portions of western Riverside and San Diego Counties are identified as centers of abundance for the subspecies (Garrett and Dunn 1981, Stephenson and Calcarone 1999). It is uncommon to fairly common, but localized, resident breeder in coastal sage scrub and open chaparral along the coastal lowlands, inland valleys, and in the lower foothills of local mountains. Dense chaparral stands generally have fewer Sage Sparrows than shorter shrubs recovering from recent fires. Unitt (1998) writes:

*The subspecies belli of the Sage Sparrow is a characteristic bird of chaparral—especially semi-open dry chaparral. . . . It also inhabits sage scrub, though the extensive flattish tracts suitable for it are almost gone. . . . Our results so far reveal the Sage Sparrow to be most widespread in south-central San Diego County, where an extensive plateau is still covered with vast tracts of chamise [Adenostoma fasciculatum] and redshanks [A. sparsifolium].*

It was also noted (Grinnell and Miller 1944:502) that in cismontane California, Bell's Sage Sparrow frequents chaparral dominated by chamise. Lovio (1999) adds:

*. . . Bell's Sparrow tolerates a fairly broad range of shrublands, from coastal sage scrub to various types of chaparral. The sparrows prefer relatively low, dispersed shrubs. This. . . appears to favor the species' low nest placement and ground foraging. More than chaparral, "low" and "open" describe sage scrub [e.g., Artemisia californica], which. . . has been extensively replaced and fragmented by human activities on the lower coastal slope. Chaparral has the same physiognomy as sage scrub for several years as it recovers from a fire.*

Lovio (1996) also found Bell's Sparrow to be sensitive to habitat fragmentation, never found in habitat patches smaller than 160 ha.

In the Cleveland National Forest (Boyd and Stephenson 1998), a study of bird species composition in recently burned and older chaparral took place within our study area (4047 ha of mixed chaparral, from 1125 to 1625 m elevation, in the upper Pine Valley Creek watershed). Point count sampling and nest monitoring from 1993 to 1997 were used to investigate differences in bird communities in young (average age 6 years),

and old (average 31 years) mixed chaparral. As noted previously, Bell's Sage Sparrow was the only species that was substantially (three times) more abundant in the young-age chaparral, although nesting success, for all species combined, was substantially higher in old than in young stands (due to lower predation rates). Misenhelter and Rottenberry (2000) found strong habitat selection for open subshrub communities (including *A. californica*), but also noted lower nest success in preferred nest locations, possibly due to redistribution of predators as a result of human alterations of the regional land cover.

Because the preferred habitats, open subshrub vegetation communities, occupy a relatively small portion of the study area (coastal sage scrub, 3.6%; interior sage scrub, 3.6%), the much more widespread chamise/redshank chaparral (25%) and other chaparral types (37%; Franklin 2003) are potentially extensive, if lower quality, habitats for Bell's Sage Sparrow. Therefore, based on this literature review and on the distribution of shrub species in the study area, we converted the LANDIS outputs into a time series of habitat maps by defining high-, medium-, and low-quality habitat for Bell's Sage Sparrow as follows.

*High-quality habitat.*—This included all grid cells with *A. californica* or *A. tridentata* present, but all other modeled species absent (chaparral shrubs as well as trees; see Franklin et al. *in press* for complete list of modeled species). This habitat class can include any age class because these subshrub species and the communities they dominate tend to have low cover at any age.

*Medium-quality habitat.*—This included cells with the sage scrub-associated subshrubs *Salvia mellifera*, *S. apiana*, and/or *Eriogonum fasciculatum*, or with the "dry chaparral" dominants (*Adenostoma fasciculatum* and/or *A. sparsifolium*) present that were up to 30 years old (e.g., restricted to the younger age classes of the dry chaparral species), and all other species absent.

*Low-quality habitat.*—This included cells with other chaparral shrub species present (*Quercus berberidifolia*, *Ceanothus greggii*, *C. tomentosus*, *C. integerrimus*, *Cercocarpus betuloides*, *Arctostaphylos glauca*, *A. glandulosa*, and/or *Xylococcus bicolor*) that were up to 30 years old, and all other species absent.

#### Demographic model

We used RAMAS Landscape to link the landscape and habitat models to the demographic model. The spatial structure of the model was based on the predictions of the habitat and landscape models, and included a temporally varying number of patches under each scenario. Patches were identified as contiguous clusters of cells with suitable habitat (as defined in the previous section). The method of patch identification is described in Akçakaya et al. (1995) and Akçakaya (2000). The demographic component of the model included density dependence, stage and sex structure, demo-

graphic and environmental stochasticity, and dispersal among patches, which will be described.

*Density dependence.*—The Sage Sparrow is a territorial species, with territory sizes regulating populations when suitable habitat is fully saturated at optimum densities (Martin and Carlson 1998). Thus, we modeled Contest-type density dependence (Beverton-Holt function; see Akçakaya [2002]). We assumed that, at the start of the simulation, initial abundances were equal to carrying capacity for each patch. There is no evidence that territories are defended in winter (Martin and Carlson 1998), suggesting that density dependence (through territoriality) mainly operates at the reproduction stage; thus we assumed that density dependence affected fecundities. Therefore, at each time step, the density dependence function modified the fecundities based on the patch abundance at that time step, as well as on the maximum growth rate and carrying capacity. Carrying capacity estimates were based on maximum breeding densities, which ranged from 39 birds/km<sup>2</sup> to 111 birds/km<sup>2</sup> depending on the habitat (Martin and Carlson 1998). This range corresponds to a range of 1.3–3.6 birds per cell. Thus, to calculate the carrying capacity, we multiplied the number of low-, medium-, and high-quality cells belonging to each patch by 1, 2, and 4, respectively. The carrying capacity of the patch is thus determined by the area of the patch as well as its habitat quality. Patches with small populations (<40 birds) were excluded from the analysis because they would add very little to the viability but would substantially complicate the model.

*Stage structure.*—We used a two-stage, two-sex model, with juveniles and adults of the two sexes represented by four separate stages, and with a monogamous mating system (Martin and Carlson 1998), in which fecundity is a function of the minimum of the number of males and females. We assumed equal survival for males and females and equal sex ratio at fledging. The stage matrix was parameterized for postbreeding census. We used a fecundity based on 1.3 fledglings per pair (Reynolds 1981) and two broods per season (Martin and Carlson 1998). There are no data on survivorship of Sage Sparrows. Because of the assumption that initial abundances are equal to carrying capacity in our model, the initial stage matrix was set to have an eigenvalue of 1.0. Thus, the survival rates were set to result in a growth rate of 1.0, given the fecundity values previously mentioned. Assuming that adults have twice as high a survival rate as juveniles, we calculated juvenile and adult survival rates of 0.303 and 0.606, respectively, which result in an eigenvalue = 1.0. These estimates are close to the annual survival rates of other nonmigratory sparrow species. For example, Sandercock and Jaramillo (2002) estimated the annual survival rate of Song Sparrows (*Melospiza melodia*) as 0.34 and 0.56, for juveniles and adults, respectively. Lockwood et al. (2001) estimated adult Seaside Sparrow (*Ammodramus maritimus*) annual survival

TABLE 2. Stage matrix showing the average rate of transition among the four stages in the demographic model.

| Stage           | Female juvenile | Female adult | Male juvenile | Male adult |
|-----------------|-----------------|--------------|---------------|------------|
| Female juvenile | 0.394           | 0.788        | 0             | 0          |
| Female adult    | 0.303           | 0.606        | 0             | 0          |
| Male juvenile   | 0.394           | 0.788        | 0             | 0          |
| Male adult      | 0               | 0            | 0.303         | 0.606      |

*Note:* The values in the two rows for “Female juvenile” and “Male juvenile” are average annual fecundities; the rest of the values are average annual survival rates.

rate as 0.66. Estimates of annual adult return rates for nonmigratory sparrows ranged from 0.43 to 0.65 (Martin 1995, Sandercock and Jaramillo 2002). (Return rates may underestimate survival rates if recapture rates < 1.) Because the density dependence included in the model modifies the stage matrix so that the growth rate at each time step is a function of the abundance, carrying capacity, and maximum growth rate, the results of the model are very unlikely to be sensitive to survival rates (for details, see Akçakaya 2002). They are likely to be sensitive to the maximum growth rate parameter of the density dependence function. With these estimates and assumptions, the average stage matrix, when the population is at its carrying capacity, and when the number of males is equal to the number of females, is given in Table 2.

*Maximum growth rate.*—The density dependence function requires a maximum growth rate (the population's finite rate of increase at low densities). We based this value on the high fecundity observed in the San Clemente population of Sage Sparrow. Willey (1990) estimated 2.05 fledglings per nest in that population. This resulted in fecundities of 0.62 and 1.24 for juveniles and adults, respectively, and a population growth rate of 1.23, which we used as the maximum growth rate. Because the results are likely to be sensitive to this parameter, we also used plus and minus 10% of this value. During a simulation, the model modified the previous matrix in the following ways. (1) The average fecundities were modified according to the population size at that time step, using the density dependence function just described (e.g., adult fecundity changed from 1.24 when population size was small, to 0.79 when it reached the carrying capacity). (2) The number of offspring was based on the number of pairs, which was calculated as the minimum number of males and females. To do this, the average fecundity values were modified to take into account the sex ratio of the breeders at that time step. (3) The model sampled fecundities and survivals based on the means and standard deviations.

*Environmental stochasticity.*—Based on the temporal (process) variance of survival rates reported by Sandercock and Jaramillo (2002), we used standard deviations of 0.08 and 0.18 for juveniles and adults, respectively. These represent coefficients of variation of

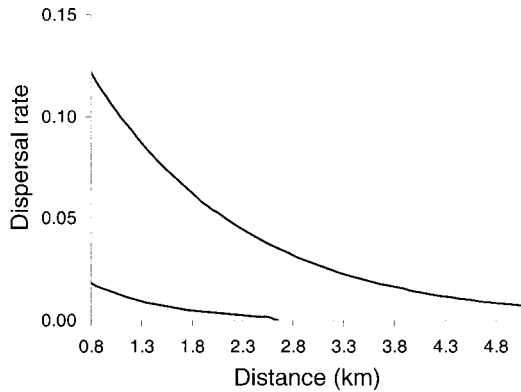


FIG. 2. Two dispersal-distance functions used to model “high” and “low” dispersal rates between pairs of Sage Sparrow populations.

26% and 30%, respectively. Fecundity can also change from year to year, for example due to changing patterns of predation (Reynolds 1981). Based on the temporal variation in the number of fledglings at one of the sites studied by Rotenberry and Wiens (1989), we set the coefficient of variation of fecundity to 40%.

**Dispersal.**—There are few data on Sage Sparrow dispersal; juvenile movement distances of 800–900 m and 75–600 m have been reported (Martin and Carlson 1998). Because of uncertainty about dispersal, we modeled a large range of dispersal rates, based on the dispersal-distance functions given in Fig. 2 for dispersing juveniles (see Akçakaya [2000, 2002] for details of how dispersal is modeled). Although there are no studies comparing adult and juvenile dispersal in this species, Lockwood et al. (2001) found that adult dispersal distance of the Cape Sable Seaside Sparrow (*A. maritimus mirabilis*) was about one-fifth of juvenile dispersal distance. Because Sage Sparrow adults also have high site fidelity (Wiens et al. 1986), we assumed that the adult dispersal rate is one-fifth of the juvenile dispersal rate.

#### Uncertainty and sensitivity analysis

The viability of species in dynamic and fragmented landscapes depends on the balance between the rate of appearance and spatial arrangement of habitat patches on the one hand, and the reproductive capacity and the dispersal ability of the species on the other. When the habitat is changing, the species must be able to reach new habitat patches, and increase in these patches fast enough to avoid extinction. Consequently, the two most important demographic properties are the population growth rate (especially from small abundances) and dispersal rate. Thus, we analyzed the sensitivity of model results to these two parameters by running 12 simulations with all combinations of the three fire regime scenarios, two maximum growth rates, and two dispersal functions (Fig. 2). We ran 1000 replications of each metapopulation simulation.

In addition, we incorporated the random variation in landscape dynamics as follows. We ran 10 replicates of the landscape simulation for each of the three fire regime scenarios, and we ran a metapopulation simulation (with 1000 replications) using each of the 10 replicate landscapes. We then combined the risk results of the 10 simulations; thus the risk results for each of the three fire regime scenarios were based on a total of 10 000 replicates.

Although the landscape models were run for 250 years to see the pattern of landscape change over a long period, we ran each metapopulation simulation for only 50 years because longer time horizons would mean that compounding uncertainties may make the results unreliable.

## RESULTS

### Landscape dynamics

The simulated fire return intervals were close to those specified for each scenario, and were well-differentiated from each other (Table 1). As expected, as the fire return interval increased, a smaller proportion of the entire landscape was in the young (1–30 years) age class (Fig. 3). The proportion of the landscape in high-, medium-, and low-quality habitat changed through time, and differed among the three scenarios (details not shown). The spatial distribution of high-, and medium-quality habitat, shown for years 30 and 50 from one simulation (Fig. 4), suggests that under shorter FRI scenarios, the high-quality habitat is less fragmented, but that habitat extent fluctuates between decades.

### Habitat dynamics

Under the “current” fire regime scenario, the total carrying capacity (in all patches) increased substantially until year 20 and then declined (Fig. 5). The other scenarios showed a similar pattern, but much smaller and slower increases. The total carrying capacity was smallest in the “long” fire regime scenario. To analyze the importance of low-quality habitat, we removed all low-quality habitat resulting from one of the replicates of the “current” fire regime scenario and repeated the population modeling experiment. In this scenario, low-quality habitat added to the carrying capacity only when  $K$  was high (Fig. 6).

### Metapopulation dynamics and viability

The “long” fire regime resulted in a higher risk of decline in the next 50 years than the “current” fire regime, which, in turn, resulted in a higher risk of decline than the “natural” fire regime (Fig. 7). These results were based on a total of 10 000 replicates incorporating variability in both landscape dynamics and metapopulation dynamics. Removing low-quality habitat (in the “current” fire regime scenario) increased the extinction risk (Fig. 7).

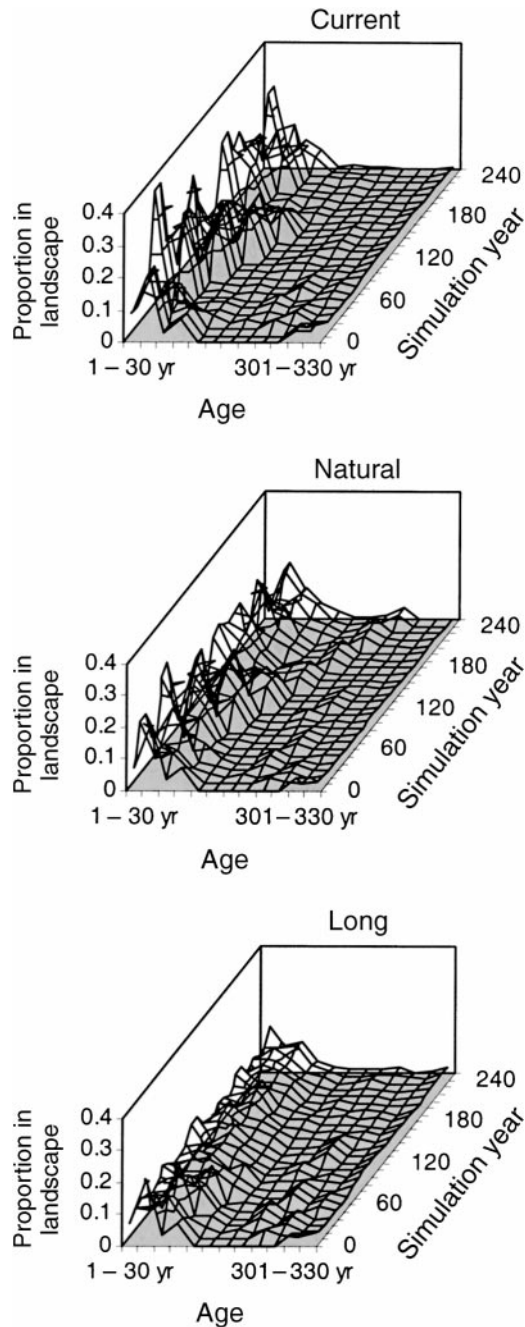


FIG. 3. Change in the proportion of age classes of the vegetation in the landscape under the three fire regime scenarios (the oldest cohort of any modeled plant species in each cell determines the age class of the cell).

#### *Sensitivity to growth rate and dispersal rate*

The sensitivities of the viability of the Sage Sparrow metapopulation to maximum population growth rate and dispersal rate are given in terms of expected minimum abundance (McCarthy and Thompson 2001). The viability results were sensitive to maximum growth rate, but not to the dispersal rate (Table 3). The effect

of growth rate and dispersal were similar under the three fire regime scenarios. The differences among the scenarios were, for the most part, similar under the different growth and dispersal rates, except that the differences in Sage Sparrow viability between the “current” and “natural” fire regimes were much less pronounced under the assumption of high growth rates (Table 3).

#### DISCUSSION

Under all three scenarios, simulations with high and low growth rate gave substantially different results. The high sensitivity of the viability results to population growth rate is not surprising. However, under any assumption of growth rate or dispersal rate, the rank of the three scenarios in terms of viability (and, to a large extent, the magnitude of the differences between the scenarios) remained the same. The fact that the differences among scenarios were not very sensitive to assumptions about growth rates and dispersal rates makes our conclusions robust, despite the uncertainties in these population dynamics parameters.

The results indicate that the viability of Bell's Sage Sparrow is highest under the “current” fire regime scenario, slightly lower (especially if population growth rate is low) under the longer FRIs of the “natural” fire regime scenario, and lowest under the “long” fire regime scenario. In other words, viability is positively correlated with the frequency of fire (within the range of values simulated) and the amount of early-successional habitat in this stand-replacing crown-fire regime. The availability of high- and, especially, medium-quality habitat, and the carrying capacity are greatest under the shorter FRI simulated in the “current” scenario. The ~20–50 year FRI simulated for the low- to mid-elevation coastal sage scrub and chaparral shrublands under this scenario maintains large blocks of high-quality habitat. The other scenarios, with longer FRIs, show a slightly lower extent, but also a more fragmented pattern of high-quality habitat (coastal sage scrub), as the short-lived subshrubs that comprise it are replaced by longer lived chaparral shrubs in the absence of fire.

The “current” scenario also results in greater extent and contiguity of medium-quality habitat comprising *Adenostoma* chaparral <30 years old. Because the foothills and mountains ecoregion does not include very much coastal low-elevation habitat (Fig. 1), much of which is fragmented by development anyway, the simulated populations may be dependent on the more extensive medium- and low-quality habitat within the study area as it has been delimited. Low-quality habitat contributed to the carrying capacity only when  $K$  was high under the “current” scenario (Fig. 6). Removing low-quality habitat increased the extinction risk and was more or less equivalent to increasing the FRI but retaining low-quality habitat (Fig. 7). Thus, low-quality habitat seems to be important, especially under sce-

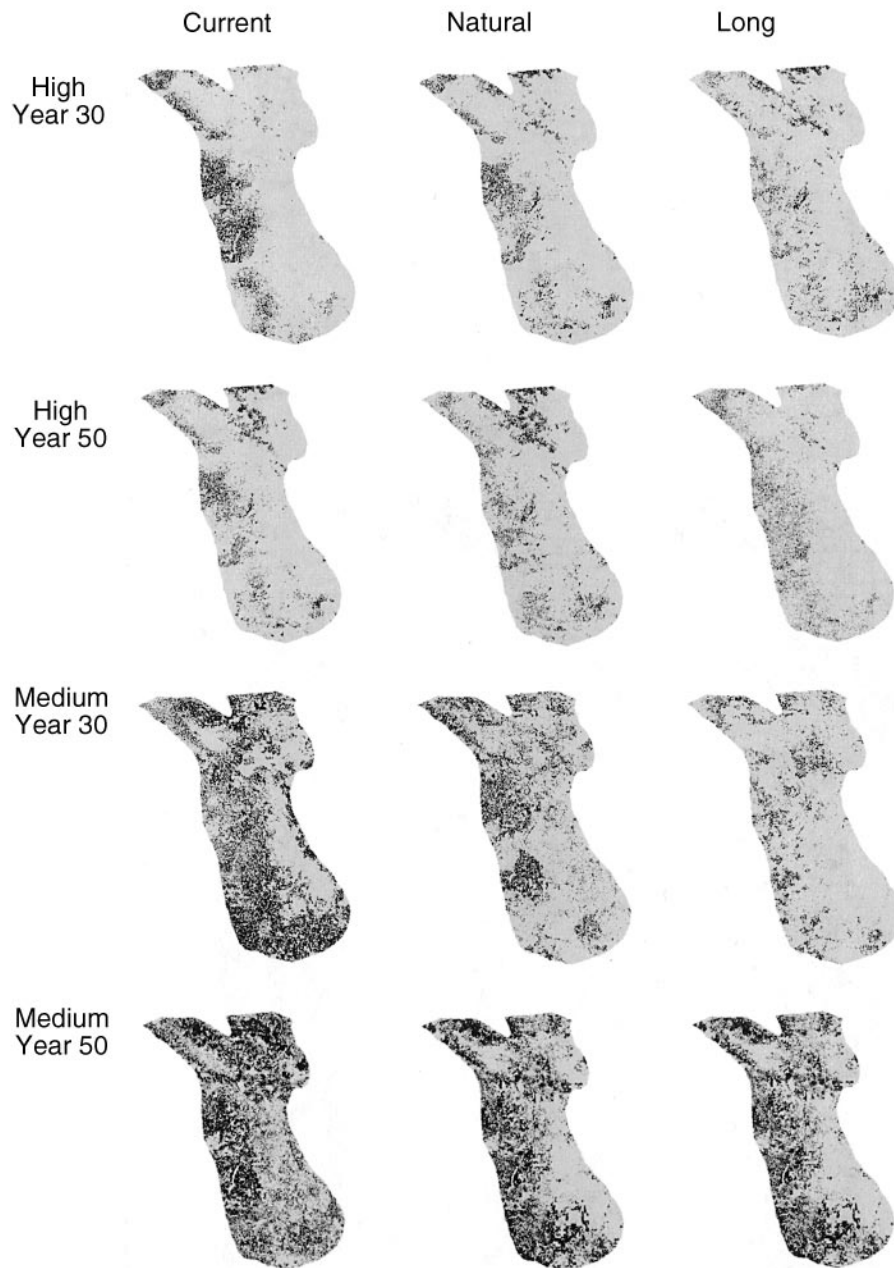


FIG. 4. The extent of high- and medium-quality habitat (black) in the study area (gray; see Fig. 1) at model years 30 and 50 for one model run of the “current,” “natural,” and “long” scenarios.

narios in which fire is less frequent on some portions of the landscape.

In spite of the names given to these fire regime scenarios, the simulated fire return interval of the “natural” scenario was actually unnaturally long (over 50 years) relative to the longevity of the dominant subshrub species, for the lowest elevations in the study area supporting the highest quality habitat. This would explain the great difference in carrying capacity and, thus, other measures of population viability between

the “current” (short) and “natural” (medium) fire return intervals (again, especially when the growth rate is low). Although the absolute difference in the fire return interval was greater between “natural” and “long,” their effective impact on the extent of suitable habitat was minimal; both FRIs were too long to maintain much short-lived coastal sage scrub or chaparral in young age classes.

Further, the shorter FRIs of the “current” regime (24–54 years for the low- to mid-elevations), although

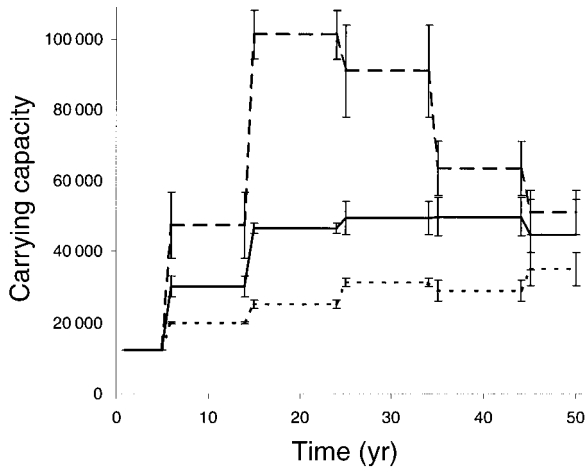


FIG. 5. The total carrying capacity of the Sage Sparrow metapopulation under the current (dashed), natural (solid), and long (dotted) fire regime scenarios. The curve for each scenario represents the average carrying capacity over 10 landscape-model replicates; the error bars indicate standard error.

designed to examine the effects of increased human-ignited fires on the southern California plant communities (Franklin et al., *in press*), did not actually simulate the very short FRIs (10–20 years) now beginning to be observed in the parts of region (Keeley et al. 1999, Wells et al. 2004). Because southern California shrublands of all age classes tend to burn in stand-replacing crown fires during severe fire weather, and fire suppression is ineffective under those conditions (Keeley 2002a, Keeley and Fotheringham 2003, Moritz 2003), there is little chance that fire will decline in this landscape under current climate conditions. A much greater risk, and one not addressed in these simulations, is the degradation of high-quality habitat (coastal sage scrub) if invaded by non-native grasses when subjected to very frequent fire (Keeley 2001). Although two annual grasses (*Avena* sp. and *Bromus* sp.) were included

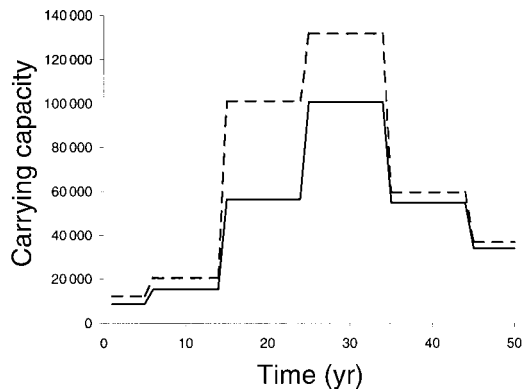


FIG. 6. The total carrying capacity of the Sage Sparrow metapopulation under the current fire regime scenario, with (dashed) and without (solid) low-quality habitat, based on the same landscape-model replicate.

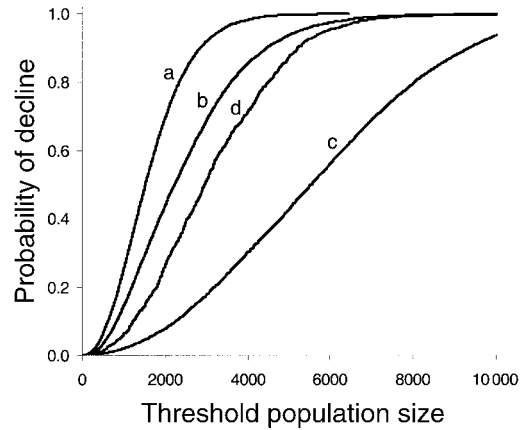


FIG. 7. Risk of decline anytime during the 50-year simulation under the following fire regime scenarios: (a) long, (b) natural, (c) current, and (d) current with no low-quality habitat (all with low growth rate and low dispersal rate assumptions).

in the LANDIS simulations, we were limited in our ability to realistically simulate high-frequency dynamics by the 10-yr time step of the landscape model.

Thus, the linked landscape and population models suggest that the risk of decline of the species is low under the fire frequencies simulated in the “current” and “natural” scenarios, because the extent and configuration of suitable habitat are adequate. The FRIs simulated under these scenarios encompass the natural range of variability in the low- to mid-elevation shrubland fire regimes for the region insofar as they can be inferred from historical records. The results for the “long” scenario also suggest that fire suppression in the montane forests could negatively impact habitat availability to the extent that it lengthens the FRI in adjacent shrublands, especially if the metapopulation in the study area becomes increasingly dependent on the medium-quality early-successional chaparral habitat as high-quality habitat at lower elevations is lost. However, we cannot determine the potential effect of even shorter FRIs at the urban-wildland interface on the availability of habitat with the current implementation of the landscape model. This is the subject of our ongoing work.

TABLE 3. Expected minimum abundance under three different fire regime scenarios, two population maximum growth rates, and two dispersal rates.

| Fire regime scenario | Growth rate | Dispersal rate |      |
|----------------------|-------------|----------------|------|
|                      |             | High           | Low  |
| Current              | high        | 8874           | 8770 |
|                      | low         | 5750           | 6186 |
| Natural              | high        | 8780           | 8651 |
|                      | low         | 3210           | 3572 |
| Long                 | high        | 5458           | 4699 |
|                      | low         | 1229           | 1339 |

Finally, the empirical evidence for lower nesting success in preferred younger shrub stands (Misenhelter and Rotenberry 2000) suggests that a fine-scale mosaic of habitat age classes could be important to the long-term security of the population. However, this effect was not simulated in our modeling experiment because so little is known about it.

This case study illustrates the potential for, and limitations of, linking a landscape, habitat, and metapopulation model to examine the effects of land management decisions on a species that is, in part, dependent on early-successional habitat, which by its very nature is dynamic in time and space. The main limitation involves the amount of uncertainty that is inherent in predicting long-term changes, because of uncertainties in data, including the habitat relationships of the species and links between habitat and demographic characteristics. In the case of the Sage Sparrow model, the lack of quantitative habitat information (e.g., productivity or density as a function of habitat variables) was the weakest aspect of the model. However, such habitat information is increasingly available for many species, and over the past decade or so there have been several developments in estimating habitat suitability and species occurrences (summarized in Morrison et al. 1992 and Scott et al. 2002). For species whose habitat relationships are based on such methods, spatially explicit, linked landscape-habitat-metapopulation dynamics models such as the one that we developed for the Sage Sparrow can examine scenarios over large spatial and temporal extents, and thus can be a useful tool for land management planning by resource and conservation agencies, especially when resources for monitoring and landscape manipulation are limited. In addition to fire regimes, we believe that this approach will be useful in evaluating the viability of target species under other types of landscape management actions or landscape-level impacts, including timber harvest (Akçakaya et al. 2004), urbanization, and habitat protection or restoration.

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