Linking Burrowing Owl Population Change to Interactions with a Fossorial Ecosystem Engineer, the California Ground Squirrel

By

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DISSERTATION

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Of my family, my sister Susan was the first to jump on the PhD bandwagon, although you could see the gleam in my Dad’s eye once the declaration had been made. My Mom tells me how proud she is of this accomplishment. I’d like to think that I have become who my parents raised me to be. My husband, Michael Hennessy, did everything in his power to lift responsibilities from me so that I could focus on getting to the finish line. The family we have made is the best part of my life, and reminds me every day why I chose this line of work.
ABSTRACT

Ecological studies are defined by three primary categories of activity: the collection of field data, statistical analysis, and modeling. Of the several meanings of the term “model,” it is used here in the sense of simulation modeling, when the purpose is to extend the existing state of knowledge to potential scenarios not yet encountered or impossible to evaluate with field methods. This dissertation encompasses all three types of studies.

In Chapter 1, we manipulated vegetation and squirrels in a replicated, large-scale field experiment. The intended objectives of the field experiment had a strong applied purpose, to provide managers with a cost-effective tool for restoring hybrid ecosystems with improved suitability for the recovery of Western Burrowing Owl (*Athene cunicularia hypugaea*) on protected reserve lands. We implemented short-term restoration treatments to re-establish key ecological processes provided by an ecosystem engineer, the California Ground Squirrel. The experiment produced new information about burrow availability for owls, squirrel habitat selection, and the positive feedback of squirrel activity on vegetation structure in grasslands. This chapter represents the type of focused field experiments needed to reduce uncertainty around parameters in the study system. The results can be used to inform management directly or to parameterize simulation models.

Chapter 2 presents a statistical analysis that characterizes the variability in available field data sources in order to produce precise and robust estimates of the mean and variance of demographic parameters. We employed Bayesian Markov Chain Monte Carlo estimation to estimate four key life history parameters of Western Burrowing Owl: adult and juvenile
mortality, nest success, and nest productivity. In this suite of vital rates the estimate of juvenile mortality of Burrowing Owls was least well-resolved. While our specific goal was to provide improved estimates of burrowing owl vital rates, this approach is broadly applicable to synthesizing the findings of multiple field studies, linking demographic estimates to simulation models, and informing management decisions.

In Chapter 3 we developed, parameterized, and evaluated the stability of an agent based model of burrowing owls that uses explicitly defined individual behavior to examine the relationship between owl settlement decisions and the habitat quality consequences for reproduction and population growth. In an analysis of model sensitivity, juvenile mortality consistently was the most influential input parameter, followed by adult owl mortality and squirrel mortality. We conducted an uncertainty analysis to verify the reliability of the model. Observations of density-dependent owl population growth provided evidence that the model produces biologically realistic population-level emergent behavior. We utilized the model to conduct a factorial experiment comparing the relative influences of owl density and a gradient of landscape proportions of low vs. high habitat qualities, which showed that initial owl density is also an influential driver of population persistence. The model currently enables qualitative consideration of the proximate mechanisms behind population decline, including the factors that attract owls to disturbed edge habitats.

The progression of the three types of studies is generally expected to begin with data collection in the field. The data is then evaluated with statistical analyses, which indicates whether the amount and quality of data is sufficient for inference. Simulation modeling is conducted as the
final step. Frequently, simulations are delayed until researchers believe they have a thorough understanding of the system. However, this dissertation compressed all three steps into a relatively short period of time. Proceeding directly to simulation created a feedback of valuable information to both our field efforts and statistical analyses, both by identifying the most influential parameters in the system, and by showing the potential range of model outcomes from current levels of parameter uncertainty. This identified needs for additional field data and updated analyses. This dissertation illustrates the value of planning for all three steps at the outset of research projects, to enable iterative improvement in data collection and parameter estimates, in order to provide managers with the best possible set of predictions and recommendations from modeling.
CHAPTER 1.
Grassland ecosystem restoration for burrowing owls using vegetation management and an ecosystem engineer

Abstract

Historically the ecosystem engineer California Ground Squirrel (*Otospermophilus beecheyi*) created burrows for Western Burrowing Owls (*Athene cunicularia hypugaea*) across large areas of native grasslands. Squirrel populations have been reduced by pest eradication efforts and shifts in grassland structure due to the invasion of exotic annual grasses. The overarching goal of this experiment was to provide conservation managers with a cost-effective tool for restoring degraded habitats to a hybrid ecosystem state with improved suitability for the recovery of the burrowing owl. Our objective was to implement short-term restoration treatments to re-establish key ecological processes on protected reserve lands. We manipulated vegetation and squirrels in a replicated, large-scale field experiment. We established 6 pairs of experimental plots, 0.8 hectare per plot, on 2 sites in San Diego County. Vegetation mowing and soil decompaction treatments reduced grass density and thatch depth. Squirrel translocation using soft release methods accelerated squirrel settlement and activity in target sites.

The success criteria were self-sustaining squirrel populations, creation of burrow complexes, and persistent change in vegetation structure. Nearly all burrows were concentrated in the plots that received squirrel translocation. Within plots receiving translocation, most burrows were observed in the mowed subplots (84±2%) compared to unmowed controls. The spatial footprint of squirrel activity was significantly greater when vegetation management was combined with squirrel translocation (p<0.01). The highest activity levels were observed after two years of treatments.
More than 1000 burrow entrances remained through the third year, indicating noteworthy and persistent engineering effects were achieved through squirrel activity. This field experiment demonstrates that both vegetation management and squirrel re-establishment are needed to stimulate natural processes that improve habitat for burrowing owl populations.

**Introduction**

Widespread and pervasive anthropogenic change to functioning ecosystems has led to the development of either primarily novel combinations of ecosystem components, or hybrid ecosystems incorporating a mixture of historical elements and novel components (Hobbs et al. 2009). Under this classification, much of the grasslands in the western United States can be identified as hybrid ecosystems. In many locations non-native grasses, often of Mediterranean origin, have become the dominant species (D’ Antonio et al. 2007). Non-native species can supply functions that benefit native species, such as when they provide foraging opportunities, but the vegetation structure of non-native grasses often differs from the open character of native bunch grass habitats important for predator detection and avoidance for many native animal species. Conservation management options for ecosystems such as these differ depending on the degree of anthropogenic change and difficulty associated with returning the system to historical conditions (Cox and Allen 2008, Hobbs et al. 2009). Efforts to restore these native grasslands have met with mixed success, as changing climate and fire regimes and other forms of disturbance often favor invasive species (Seabloom et al. 2003a, Seabloom et al. 2003b, Cox and Allen 2008). An alternative approach available to managers is to alter the physical structure of the plant community, by reducing the height and density of non-native grasses. In this way, increased suitability for native wildlife can be achieved through managing non-native species.
and setting restoration goals to achieve a hybrid mixture of pre-invasion and post-invasion conditions, rather than trying to undo history.

Ecosystem engineers—species that modify the environment with consequences for other species and ecosystem processes—may provide a cost-effective means of achieving some ecological restoration goals (Byers et al. 2006). The promise of this approach is twofold: reducing overall restoration cost by focusing resources on ecosystem engineer reintroduction, and the possibility of creating a more self-sustaining system that is less dependent on continuing human intervention. Success is more likely with a thorough understanding of the ecosystem’s alternative states and the strength of the engineer’s effects (Byers et al. 2006). Here, we describe a management approach for the western burrowing owl (Athene cunicularia hypugaea), utilizing native ecosystem engineers to achieve desired system states. The overarching goal of this experiment was to provide conservation managers with a cost-effective tool for restoring degraded habitats to a hybrid ecosystem state with improved suitability for the recovery of the burrowing owl.

Although the western burrowing owl is a widespread species that shows tolerance towards human disturbances, the population is declining across its range and is under consideration for listing as a protected species by several state and federal agencies (Sheffield 1997, Desmond et al. 2000, Poulin et al. 2005). In California, burrowing owl population declines and local extinctions have been recorded in southern and coastal locations undergoing urbanization (Gervais et al. 2008). In San Diego County, historical and recent surveys indicate that the number of occupied burrowing owl colonies has declined, and currently there is only one
productive cluster of breeding pairs known to managers (Unitt 2004). Three factors are likely driving burrowing owl population decline in southern California: (1) reduction in habitat area caused by urban development (Gervais et al. 2008); (2) changes in habitat composition and structure of native grasslands with the invasion of exotic annual grass species like wild oat (Avena fatua) and brome (Bromus diandrus, Bromus madritensis) (D’ Antonio et al. 2007); and (3) reductions in the distribution and abundance of an ecosystem engineer, California ground squirrel (Otospermophilus beecheyi) important for both creating burrows and maintaining vegetation structure that is beneficial for burrowing owls (Marsh 1998, Lenihan 2007).

Habitats are dynamic and the ecological processes that influence those dynamics need to be included in restoration and management plans (George and Zack 2001). Our intent was to develop a new protocol for restoring burrowing owl habitat by re-establishing colonies of California ground squirrel. For burrowing owls, squirrel burrowing activity is a key process driving burrow availability. Squirrels may also be responsible for maintenance of the low, open vegetation structure preferred by owls (Green and Anthony 1989). Currently, management for burrowing owls involves the installation of artificial burrows (Trulio 1995, Smith and Belthoff 2001, Belthoff and Smith 2003, Smith et al. 2005). However, artificial burrows habituate owls to artificial conditions in locations that may not otherwise provide appropriate habitat. This issue raises the possibility that artificial burrows will create ecological traps (sensu Battin 2004), attracting owls to nest in areas associated with lower fitness due to predation, foraging conditions, or other factors. Here we explore an alternative approach to increasing burrow availability by increasing the presence of an important grassland ecosystem engineer, the California ground squirrel.
Ground squirrels are often found occupying the margins, rather than the interior, of grasslands with mixed native and exotic species composition, suggesting that some component of the habitat is not suitable. Dense ground cover and heavy thatch may reduce the ability of ground squirrels to move, forage, detect predators, and dig burrows. We therefore hypothesized that habitat modification in the form of vegetation management would be a necessary prerequisite for the establishment of squirrels. A comprehensive restoration program to restore the native plant community, however, was beyond the scope of this initiative. Instead the focus was on altering the physical structure of the habitat to make it more favorable to squirrels and other native wildlife. We also hypothesized that these modifications, combined with the eco-engineering effects of squirrels once they were established, might alter the competitive balance between native and exotic plant communities and shift the system to a new stable equilibrium comprised of a greater proportion of native grasses and forbs (Seabloom et al. 2003b). However, since this hypothesis presumed that vegetation management would address untested mechanisms of local exotic plant dominance, native plant restoration was necessarily a secondary goal of the program.

Our restoration plans, developed with the support of a multi-agency task force, were designed primarily to reduce vegetation height and thatch depth, and to shift the current, degraded, “novel” grassland to a hybrid state with some restored native elements of the historical system. Mowing was selected as the most feasible method to achieve these goals at the target restoration sites at the spatial scale needed to create adequate amounts of habitat for both burrowing owls and squirrels in an experimental context.
Habitat modification to increase suitability for ground squirrels, however, does not guarantee squirrels will colonize the site. Active management in the form of squirrel translocations may be required if resident squirrels are not sufficiently close for natural dispersal to take place. Moreover the rate of colonization may be too slow and cause unacceptable delays in the establishment of desired ecosystem engineering effects. To contend with difficulties associated with achieving successful translocation (Griffith et al. 1989), we developed translocation protocols that address ecological and behavioral needs of animals relocated to an unfamiliar environment (Shier 2006, Shier and Swartz 2011, Shier and Swaisgood 2012). To encourage burrow establishment and to counter problems with soil compaction associated with historical land use patterns, we also used a soil auger to drill holes intended to resemble starter or refuge burrows.

These management actions, including vegetation treatments, squirrel translocations, and soil augering, were implemented in an experimental context so that the contributions of each manipulation could be measured and the lessons learned incorporated into future actions (i.e., adaptive management sensu Nichols & Williams 2006). The long-term goal of the broader program is to produce management protocols that can be implemented easily and cost-effectively by conservation managers, with the highest degree of confidence possible that their actions will have the desired outcome.
Methods

Site description

The study was conducted on two sites in southern San Diego County, both located inland 12-16 km from the ocean. The sites experience a Mediterranean climate of mild, wet winters and hot, dry summers with coastal influence through cooling afternoon winds. Rancho Jamul Ecological Reserve consists of former agricultural fields and pasture on sandy loam soils, with plant communities of non-native grasslands, riparian habitat, and coastal sage scrub on upland slopes. The San Diego-Sweetwater National Wildlife Refuge has silt loam soils with cobbles, and a plant community of native and exotic grassland species and coastal sage scrub.

Plot establishment

Six sets of paired treatment and control plots were established in grassland sites. Plots were paired based on similar vegetation community, soil type, slope, and aspect as well as proximity. Each circular plot was 100 m in diameter, with an area of 7854 m$^2$ (0.79 ha). The published literature indicates that most burrowing owl foraging activities are concentrated within 600 m of the burrow (Haug and Oliphant 1990, Gervais et al. 2003). Female California ground squirrels occupy a home range of approximately 0.24 ha, or a radius of 27 m around the burrow with extensive overlap of individual home ranges (Evans and Holdenried 1943). Each plot was divided into three equal wedges. The wedges received one of three treatments: control, mowing, and mowing plus soil augering. Squirrels were translocated into one plot from each pair (Figure 1). This design allowed us to separate the effects of vegetation manipulation and squirrel translocation, and also accounted for the possibility that burrowing activity might be attributable to resident squirrels from nearby areas rather than translocated individuals. Four pairs of plots
were established in 2011 (RJER1-3, SWTR), and two pairs of plots were established in 2012 (RJER4, RJER5).

**Figure 1.** Paired design of the habitat enhancement/squirrel translocation experiment.

*Vegetation and soil treatments*

Mowing and thatch removal was conducted without heavy motorized equipment to minimize soil compaction and extensive surface disturbance. Vegetation treatments were conducted for two consecutive years in May, at the end of the growing season for annual grasses but before the grasses had dried out. Vegetation was mowed to a height of 7.5 – 15 cm using handheld string...
trimmers, and the resulting thatch was raked and removed from the site. There was no evidence of soil disturbance from mowing or thatch removal.

Soil decompaction was implemented by augering 20 holes per wedge to produce a density of one hole every 10 m$^2$. Holes were drilled to ~0.3 m depth on a 45 degree angle with a one-person handheld auger fit with a 15 cm auger bit.

*Squirrel translocation procedures*

California ground squirrels were captured for relocation from source sites 3-16 km from the release site, with a target number of 30-50 squirrels per plot and a minimum of three adult males and six adult females, plus weaned pups. An attempt was made to maintain familiar social groups of individuals. Individuals were marked with standard ear tags and unique dye markings for individual identification. After a short holding period, squirrels were transferred to acclimation burrows with above- and below-ground protection, and provided with water and food. After one week, acclimation cages were removed, and squirrels were released.

A second year of translocations was conducted to supplement the initial squirrel populations. The supplemental translocations occurred in August (in contrast to the June timing of the initial translocations). In the second year, debris piles were also added to the plots to provide additional cover as a refuge from predators.

*Assessment methods*

In all plots, vegetation structure and composition was measured prior to the first treatment. Post-treatment assessments were conducted after both the vegetation and squirrel translocation treatments had occurred. Pre- and post-treatment assessments were also conducted in the second treatment year, and spring and fall assessments were conducted thereafter.
One 25 m permanent transect was established in each treatment wedge. We collected point intercept data by reading 50 points per transect, spaced 0.5 m apart. We recorded all species touching the point, and characterized the ground surface by cover type (bare ground, rock, litter, fine woody debris).

Vertical vegetation density was assessed, using a Robel pole vertical obstruction method, to a height of 1 m scaled for capturing the experimental effects of mowing (Herrick et al. 2005). Vertical vegetation density measures habitat structure in terms of height and density of vegetation cover, which complements the species-based cover estimates above. Vegetation density is expressed as a percentage of the vertical column from ground level to 1m. The Robel pole was placed at three points along each transect (at 5, 12, and 19 m). Two measurements were read at each position from a distance of 5 m.

Observers walked a grid pattern through each wedge and recorded California ground squirrel activity. Burrows with an opening of at least 7 cm at the point of maximum diameter were recorded as probable California ground squirrel burrows (Lenihan 2007). Burrow locations were marked with GPS, and the size and shape of both the burrow entrance and the burrow apron (the disturbed area around the burrow cleared of all vegetation) were recorded. Field notes about burrow condition and use were recorded.
Statistical Analysis

Repeated-measures general linearized modeling was used to analyze native cover, vegetation structure and ground surface disturbance. The native cover analysis combined native forb and native grass cover, and used only springtime pretreatment data to limit seasonal effects on vegetation cover. The between-plot factors for all analyses were the identity of the matched pair of experimental plots (pair ID) and squirrel translocation. Pair ID accounted for plot-level variance due to both site and the year the plot was initiated. The within-plot factors were time (number of years into the experiment: year 1, year 2, year 3), and vegetation treatment (control, mow, mow/auger).

We derived a single measure of overall ground surface disturbance from the apron areas measured at each burrow. We used a square root transformation on the data due to right (positive) skew resulting from the few established, occupied burrow complexes with larger entrances and apron areas compared to the many small “starter burrows” that had small entrances and aprons.

Results

Vegetation Cover and Structure

Across the plots we recorded: 9 species of non-native grass; 1 species of native grass; 19 species of non-native forbs; and 23 species of native forbs. There were no significant main or interaction treatment effects on native cover.

We found no strong evidence that vertical vegetation density was associated with either the vegetation treatments or squirrel translocation (Table 1). In contrast, vegetation density differed significantly through time. The main effect of year was associated with reductions in vegetation...
density during an ongoing drought ($R^2 = 0.59, F_{2,10}=26.90, p<0.01$). There was some indication that these changes through time differed among the plots ($R^2 = 0.26, F_{10,10}=2.40, p=0.09$).

We found marginal evidence of a vegetation treatment effect. Both the main effect of vegetation treatment ($R^2=0.15, F_{2,10}=2.84, p =0.11$) and the interaction of vegetation treatment and pair ($R^2=0.53, F_{10,10}=1.98, p=0.15$) indicated that vegetation density might be responding to vegetation treatment. We observed that vegetation density was higher in control wedges than in either mow or mow/auger treatments (Figure 2). This pattern was very strong in some plots (i.e., RJER2 and SWTR) and not others. Figure 2 also shows the decrease in density in all of the plots due to the drought in 2014, which resulted in a relatively small effect size from vegetation treatment that year.
Table 1. Generalized linear model repeated measures results from vertical vegetation density sampling during 2011-2014 (n=6). Vegetation density is expressed as a percentage of the vertical column from ground level to 1m. The data were square root transformed, and these results represent the effects of two years of treatments. All interactions were modeled.

<table>
<thead>
<tr>
<th>Treatment Effect</th>
<th>Vertical vegetation density</th>
<th>df</th>
<th>ΔR²</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Between Subjects</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Squirrel</td>
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<tr>
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<td>0.25</td>
</tr>
<tr>
<td>Error</td>
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<td>0.33</td>
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<td><strong>Within Subjects</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Year</td>
<td></td>
<td>2</td>
<td>0.59</td>
<td>26.90</td>
<td>&lt;0.01*</td>
</tr>
<tr>
<td>Year x Squirrel</td>
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<td>0.04</td>
<td>1.63</td>
<td>0.25</td>
</tr>
<tr>
<td>Year x Pair</td>
<td></td>
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<td>0.26</td>
<td>2.40</td>
<td>0.09</td>
</tr>
<tr>
<td>Error</td>
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<td>0.11</td>
<td></td>
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<tr>
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<tr>
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<td></td>
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<tr>
<td>Veg x Year</td>
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<td>1.91</td>
<td>0.15</td>
</tr>
<tr>
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<tr>
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</tr>
<tr>
<td>Error</td>
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<td>20</td>
<td>0.34</td>
<td></td>
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</tbody>
</table>
Figure 2. Vertical vegetation density before vegetation treatments April 2011-2014. Vegetation density is expressed as a percentage of the vertical column from ground level to 1m. The values of the squirrel translocation and control plots are averaged for each plot pair.
**Squirrel Burrowing Activity**

Throughout the experiment the overall footprint of squirrel activity on the plots continued to increase, and squirrel activity continued to be concentrated in the plots that received squirrel translocation (Figure 3). During the year 3 assessment, 974 of 1028 (94.7%) burrows were found on the plots that received translocated squirrels. The pattern of burrows in control plots was weak and patchy.

![Burrow counts from spring of year 3 for each of the paired squirrel translocation plots.](image)

_**Figure 3.**_ Burrow counts from spring of year 3 for each of the paired squirrel translocation plots.
The density of squirrel burrows was much higher in the wedges receiving vegetation treatments than the control (Figure 3). For year 3 data, the proportions of burrows in the mowing only subplot ranged between 16-50% (mean = 33%) and in the mow/auger subplots between 27-62% (mean = 47%); by contrast only 5% of burrows were found in the translocation control plots. Repeated sampling through time showed that these proportions were stable, indicating that the initial burrowing sets the pattern for years to come. Once a burrow is established, the squirrels continue digging in the immediate vicinity, creating a burrow complex.

Table 2. Generalized linear model repeated measures results from burrowing activity, measured as apron area, sampled during 2011-2014 (n=6). The data were square root transformed. Analysis includes time points for year 1 post-translocation, year 2 pre- and post-supplemental translocation, and year 3 spring timepoint. All interactions were modeled.

<table>
<thead>
<tr>
<th>Treatment Effect</th>
<th>df</th>
<th>ΔR²</th>
<th>F</th>
<th>P</th>
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<tr>
<td><strong>Between Subjects</strong></td>
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<td></td>
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<td>0.92</td>
<td>105.0</td>
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<tr>
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<td>Error</td>
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<tr>
<td>Error</td>
<td>30</td>
<td>0.33</td>
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Inferential analysis of the apron area of disturbed ground surrounding squirrel burrows also shows substantive effects of squirrel and vegetation treatments, as well as time effects (Table 2). The repeated measures model confirms the highly significant interaction of squirrel translocation and vegetation treatment ($R^2 = 0.36, F_{2,10}=19.3, p<0.01$, Table 2). The interaction between vegetation and squirrel treatments indicates that both mowing and squirrel translocation are needed to stimulate squirrel burrowing activity.

The analysis also indicates a significant interaction ($R^2 = 0.29, F_{3,15}=11.9, p<0.01$) between time and squirrel translocation. The time variable represents the repeated annual fall and spring measurements conducted in each subplot since the initiation of the experiment. The variable incorporates both variation across year and across seasons, treating the passage of time as a linear, nonhierarchical effect. Thus the interaction includes such patterns as the staggered initiation of plots in 2011 and 2012, and the seasonal timing of translocations.

The significant patterns in ground surface disturbance in the repeated measures analysis are depicted in Figure 4. Ground disturbance increased across time points from year 1 to year 3. Overall ground disturbance was highest in squirrel translocation plots that received both mowing and augering.
Discussion

Effects of experimental vegetation management and squirrel treatments on ecosystem engineering activity

Our results showed that the combination of vegetation management and squirrel translocation supports higher levels of squirrel activity than the use of either strategy alone. The mowing treatment was associated with a reduction of vegetation density, but the long-term effects of this reduction were not significant. The secondary goal of the mowing treatment—reduction in non-native plant cover and increased native plant cover—was also not achieved. The mowing treatment was scheduled to occur at the end of the growing season for exotic grasses, but before
the growing season for many native plant species peaked, so it was possible for the mowing treatment to shift competitive dominance in favor of natives if a sufficient seed and forb bank remained in the soils. Exotic annual grass communities in California exhibit stability and successful restoration efforts generally require seeding of native species (Seabloom et al. 2003b, Stromberg et al. 2007), so it is unsurprising that a relatively simple treatment by mowing did not alter the composition of the plant community. Thus, the persistent effects on vegetation structure desired in order to create more suitable habitat for ground squirrels and burrowing owls were limited.

Despite the lack of strong persistent effects of mowing, this experimental treatment had large effects on squirrel activity. Within the squirrel release plots, mowed areas had large numbers of burrows, whereas few squirrel burrows were located in the unmowed control treatments. Apparently, the conditions produced by mowing encouraged squirrels to colonize treated areas. However, this was only the case at translocation release plots: when no squirrels were released, few squirrel burrows were found in the mowed plots.

It is worth noting that vegetation density across all plots was also relatively low in spring 2014 due to drought effects on growing conditions. The density analysis showed that the drought was likely limiting negative effects of grass density on squirrel activity more strongly than the experimental effects from vegetation treatment. This (relatively) positive effect of drought must be evaluated along with probable negative impacts on squirrel food supply, reduced reproductive success, and increased predation pressure.
Squirrel effects on vegetation structure

The evidence that the digging and foraging activities of squirrels can also influence vegetation structure has been qualitative to date. Squirrels cut and trample grass and forb stems during their normal foraging activity, and qualitative observations of a lower and more open vegetation community with squirrel activity have been published (Evans and Holdenried 1943, Fitch 1948, Lenihan 2007). For owls, low vegetation makes detection of predators and prey easier and they appear to have a preference for this vegetation structure (Green and Anthony 1989, Clayton and Schmutz 1999). The extensive spatial extent of communities dominated by tall and dense exotic annual grass and forb species increases the importance of the feedback effect of squirrel activity on vegetation structure.

We hypothesized that if squirrel density was sufficiently high in the vegetation treatment plots, their foraging activities would sustain the effects of the mowing treatment, helping to maintain a more open habitat structure. Our transects were designed to capture large-scale plot-level effects, but we detected no effect of squirrels on vegetation structure at this scale. However, squirrels had obvious effects at smaller spatial scales on vegetation in the immediate vicinity of the burrow, creating open ground and thinned grass cover around burrows from digging and foraging activities. These effects increased with time after the burrow was established. We can conclude that squirrels do have a substantive impact on the microhabitat around burrows and that with time a squirrel colony at historical densities may have larger, plot-level impacts on vegetation structure.
Conspecific cues of habitat suitability

Naturally dispersing animals can use the presence of conspecifics, or cues associated with conspecifics, to guide habitat selection. According to theory, individuals copy the habitat selection decisions of others because the presence of conspecifics is a reliable cue of habitat quality that reduces search costs (Stamps 1988, Valone 2007). It has been hypothesized, and in some cases demonstrated, that the presence of conspecific cues will enhance settlement for animals reintroduced into areas currently unoccupied by conspecifics (Swaisgood 2010). Thus, the use of cues indicating the presence of conspecifics might be a powerful tool to encourage settlement by translocated animals. Failure to settle at the release site is a major problem in translocations and is associated with high mortality (Stamps and Swaisgood 2007). In translocations of ecosystem engineers such as ours, failure to settle at the release site would result in failure to meet desired site management goals.

Our experimental use of augering to assist squirrels with rapid burrow establishment was a fortuitous and unintended test of the conspecific cueing hypothesis. This management action was designed to create starter burrows for squirrels to use, reasoning that this would aid in squirrel retention and predator evasion. Our findings, however, indicate that while augering supported increased squirrel retention (as evidenced by a greater number of burrows in augered treatments than mow-only treatments), squirrel burrows were not directly associated with the auger holes. There was no evidence of additional digging in the auger holes, and no clusters of burrows around them. A plausible explanation for this unexpected finding is that squirrels perceived the augered sites as evidence that conspecifics previously occupied the site, and chose to establish their own burrows nearby. An alternate explanation is that squirrels used the presence of

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heterospecific fossorial animals as an indicator of suitable soils for burrow excavation (Parejo et al. 2005).

Habitat copying has been documented in a wide variety of taxa, but only limited evidence has been found in mammals (Valone 2007). Our work with translocated squirrels indicates that habitat copying may be an important mechanism guiding habitat selection in mammalian species. It is plausible that habitat copying is more prevalent when animals have less knowledge about the environment (Valone 2007) or need to make habitat selection decisions rapidly to reduce dispersal costs (Stamps 1988). Both of these conditions are likely to be met in translocation programs. Thus, we recommend that managers and researchers explore the use of conspecific cues to facilitate settlement and translocation success.

*Reintroduction of an ecosystem engineer*

An important outcome of this project was the finding that squirrel translocation can successfully create more numerous burrow complexes than artificial burrow installations, currently the focus of most burrowing owl management. Our translocated squirrels created nearly 1000 burrows, an achievement that would be difficult and expensive to replicate with artificial burrows. Artificial burrows, with their simple configurations of one or two entrances and one chamber, cannot match the complexity of natural burrows, and also have the added expense of human maintenance costs in perpetuity (VanVuren and Ordenana 2012). Moreover, patterns of burrow usage by breeding owls indicates that a family of owls needs multiple burrows in the vicinity, as chicks are moved between several burrows, and fledglings disperse to burrows in the vicinity of the natal burrow before they initiate end-of-season migration (Davies and Restani 2006).
There are other reasons to broaden management focus to include fossorial (burrowing) mammal interactions. The decline of fossorial mammals has been implicated as a key factor in declining burrowing owl populations in the Great Plains of the U.S. (Kotliar et al. 1999, Desmond et al. 2000, Smith and Lomolino 2004), Argentina (Machicote et al. 2004) and southern California (Lincer and Bloom 2003). In addition to the benefits of burrow creation, owls benefit from a suite of indirect interactions with fossorial mammals, including effects on prey availability (Lenihan 2007). The presence of ground squirrels likely also provides some protection from predators, because ground squirrels spend significant energy on vigilance, and squirrels and owls share many of the same predators. Ground squirrels use antipredator vocalizations and visual displays to maintain an early warning system for predator detection and deterrence (Owings and Hennessy 1984, Loughry and McDonough 1988, Swaisgood et al. 1999) and owls may benefit from “eavesdropping” on these signals. Such heterospecific eavesdropping is not uncommon and confers important fitness benefits (Schmidt et al. 2010). Antipredator calls may aid in predator evasion and periods with no alarm calls may signal safety, enabling eavesdroppers to focus on foraging instead of vigilance. Burrowing owls living in association with black-tailed prairie dogs appear to benefit from these effects, as they experience lower predation levels (Desmond et al. 2000). Thus, squirrels have important benefits for burrowing owls beyond the provision of burrows for nesting.

The presence of squirrels also supports a wider community. Squirrel burrows are utilized by many reptiles, rabbits, and invertebrates such as tarantulas and burrow-specialist beetles (Schiffman 2007). Sites with ground squirrel colonies have quantitatively greater diversity levels of reptiles, amphibians, insects and birds than sites where squirrels are absent (Lenihan 2007). There is ample historical evidence that digging and foraging disturbances by ground squirrels
have physical effects on soil structure, temperature, nutrient levels, and vegetation composition patterns (Schiffman 2007). These interactions suggest that California ground squirrels should be considered an ecosystem engineer in California grasslands (Byers et al. 2006, Jones et al. 2010). At a minimum, ground squirrels are a key species in these ecosystems.

*Implications for conservation and management*

Given the mounting evidence showing that California ground squirrels (and other burrowing mammals elsewhere) play a key role in engineering grassland ecosystems (Reichman and Seabloom 2002, James and Eldridge 2007), it is surprising how little attention this species has received in conservation planning and policy. Squirrels were historically, and still are widely perceived as pests that damage crops and need to be controlled (Marsh 1998). Squirrels have been targeted by control efforts and have been eradicated in many locations (Lenihan 2007). Continuing eradication efforts keep ground squirrels at 10-20% of historic population levels (Marsh 1998). While it may not be possible to increase ground squirrel activity at large scales, it is realistic to return them to targeted, protected reserve lands as a key component of restoring more functional grasslands.

The theoretical best-case scenario of an intrinsically self-sustaining ecosystem after reintroduction of the ecosystem engineer (Byers et al. 2006) was not realistic due to established exotic seedbanks at all of our sites. Therefore our restoration goals were that reintroduction of the ecosystem engineer would shift the site to a more sustainable hybrid state (Hobbs et al. 2009). It is now evident that a realistic hybrid state would consist of dominant exotic grass cover, active human management of grass structure, burrowing squirrels, and breeding owls. The potential stability of this hybrid ecosystem is uncertain but will be influenced by abiotic and biotic indirect effects of the ecosystem engineer (Byers et al. 2006). For example, possible
undesired biotic effects include increased exotic grass growth on abandoned burrows from increased nutrient levels and soil temperature (Schiffman 2007).

We anticipate that the primary usage of this management protocol will be the creation of burrow nesting habitat for burrowing owls on protected, targeted sites. Managers might best leverage the findings of this experiment by identifying target sites where owl occupancy is desired, and where either component of vegetation management and squirrel presence is already in place. Since both were necessary for significant burrow habitat creation, managers could seek opportunities to create the combination in locations where, for example, vegetation density is already kept low by grazing or other disturbance, or in locations with an existing squirrel population. Adding vegetation management to a site with a small population of resident squirrels may increase the size of the colony and squirrel activity levels.

This work was done as part of an ongoing active conservation effort, and was designed as part of an adaptive management framework (Sabine et al. 2004, Nichols and Williams 2006). The experimental design allowed us to test various management alternatives against one another (for example, translocating squirrels vs. natural squirrel colonization and different forms of habitat management). The results indicate clear lessons learned, and inform both future management actions and future research questions to further refine management protocols. Clearly our results show that active squirrel translocation was needed at the restoration sites where we worked, but different starting conditions regarding the proximity and abundance of squirrel populations may be more conducive to natural squirrel colonization provided vegetation management creates favorable habitat. Future work can test this hypothesis and explore the potential for this more cost-effective solution to ecosystem engineer recruitment in some prescribed circumstances. Our results also indicate to managers that ongoing vegetation management is likely required to retain
a more open habitat structure, but alternatives to mowing, for example grazing and fire, may be evaluated with regard to efficacy for squirrel establishment. Our study also did not rule out an ecosystem engineering role for squirrels on vegetation management. Future work could explore whether larger number of squirrels established for longer periods of time help maintain more open habitat or alter the competitive balance in the plant community in favor of native grasses and forbs. Our intriguing results from augering indicate that the role of conspecific attraction should be explored more rigorously in California ground squirrels and whether cue manipulation might assist with colonization by this ecosystem engineer. Finally, the long-term goal of re-establishing burrowing owls to these restored habitats is the next and most important goal to validate our approach to restoration.

Acknowledgements

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CHAPTER 2.
A Bayesian model framework to consolidate disparate field data
and support credible estimates of key vital rates

Abstract

Managers are often in the position of needing to make decisions in the absence of good
information. Field measurements are difficult and costly to acquire, and so it is desirable to
maximize the value of existing data. We describe an approach that characterizes the variability in
available data sources and allows us to make precise and robust estimates of demographic
parameters. We utilize a statistical framework that enables generalization across a range of
studies to estimate four key life history parameters of Western Burrowing Owl (Athene
cunicularia hypugaea): adult and juvenile mortality, nest success, and nest productivity. After a
literature search for available published estimates, we generated estimates of the mean and
variance of each vital rate with an intercept-only model. Jackknife analysis of the estimators of
mean and variance indicated that Bayesian Markov Chain Monte Carlo estimation was superior
to maximum likelihood estimation. Jackknifed estimates of credible intervals for each vital rate
confirmed the stability of the estimates. In this suite of vital rates the estimate of juvenile
mortality of Burrowing Owls was least well-resolved. While our specific goal is to provide
improved estimates of burrowing owl vital rates, this approach is broadly applicable to
synthesizing the findings of field studies, linking demographic estimates to simulation models,
and informing management decisions.

Introduction

When development pressure and species habitat needs collide, good conservation decisions that
avoid making situations worse are crucial. Managers are often in the position of needing to make
decisions in the absence of good information, and face the challenge of moving forward when it is not possible to wait for additional data. Since field measurements are often costly and difficult to acquire, it is desirable to leverage the value of all existing data. In conservation, data are often sparse, existing analyses may be varied in approach and rigor, and efforts to model projected impacts on populations of conservation concern are susceptible to the uncertainties introduced by poorly estimated parameters (Conroy et al. 1995). We offer an approach to integrate and evaluate the uncertainty in available data sources, in order to draw the most robust demographic estimates possible from them.

The integration of information from multiple datasets requires overcoming numerous biological and statistical challenges. Often there are no data-defined estimates of vital rates for targeted populations. Using information from similar species or populations is likely to be effective only if uncertainty is low (Beissinger and Westphal 1998). Quantitative uncertainty comes from small sample sizes, reflected by greater standard errors (Beissinger and Westphal 1998, Clark 2005). When data are available, they typically were collected using different methodologies in multiple locations and years, such that accounting for the effects from these factors becomes a major issue. Further, utilizing mean values reported in the literature requires the inclusion of sample size and variance estimates or else results in the error of modeling published sample means as single data points (Thorson et al. 2014).

In addition to the challenges posed by quantitative uncertainty, a separate set of challenges arises from the underlying variability of vital rates. For population viability analysis and more complex models that incorporate stochasticity, one to two generations of data are recommended to capture a representative range of variability from the target population (Beissinger et al. 2006). Vital rate
estimates are limited by weak or absent estimates of variability when these conditions cannot be met. For species with longer life cycles, short-term datasets underestimate variability.

The selection of a statistical model and associated estimation methods also have an effect on variance estimates. Mixed effects models are an excellent tool for clustered data because they pool information about variance across clusters in order to improve prediction for all the clusters, including future ones (Gelman and Hill 2007). Mixed effects models are suitable when the goal is to make predictions for existing clusters, but may underestimate variance with overly precise confidence intervals when making predictions for new populations (Clark 2003). When models are fit using maximum likelihood estimation (MLE), the quality of the variance estimates decreases when sample size is small or models are complex. Using Markov Chain Monte Carlo (MCMC) methods can improve on MLE model estimates, especially the variance estimates for varying effects (McElreath 2011).

Thorson et al. (2014) used a multispecies approach to assess the quality of life history data of fishes from a large marine database. However, for most species, large sample sizes, such as those used by Thorson, are not available. In this study, we conduct single-species parameter estimation utilizing relatively small numbers of separate studies. Using a suite of computationally sophisticated tools, we develop an approach for producing robust vital rate estimates that captures the variability across populations and overcomes the constraints of methodological differences and small sample sizes. The driving motivation for this work was a need for high quality parameter estimates for use as inputs to a stochastic simulation model. The analytical approach that we developed treats the uncertainty and variability in the available field data in a way that is compatible with the ultimate intended use of the parameter estimates.
Application to Western Burrowing Owl

The Western Burrowing Owl (*Athene cunicularia hypugaea*) is a species of management concern for which a relatively large number of published studies on species autecology are available from research groups across the United States and Canada (Table 3). These prior research efforts have focused on habitat selection, impacts of human disturbance, estimates of adult and juvenile mortality, as well as nest success and productivity, but the information is unconsolidated and highly variable. The existing studies are limited in their ability to generalize about key vital rates or life history traits of burrowing owls due to the wide regional range of study locations, obligate associations with several different fossorial mammals, and habitat variability. The main habitat of the burrowing owl is grasslands where fossorial mammals are found, but several multi-year population studies have been conducted in disturbed sites such as airports, agricultural lands, and suburban developments (Barclay et al. 2011, Millsap 2002, Rosenberg and Haley 2004). Some studies focus on owls in natural burrows, but others include artificial burrows; the installation of artificial burrows in presumed owl habitat is the most frequently used management approach and data collection can be easier with artificial burrows (Barclay et al. 2011, Rosenberg and Haley 2004, Todd et al. 2003). Thus, while considerable information exists on aspects of the life history of this species, it is not clear how best (or even if it is possible) to use this information in a collective manner to derive robust and reliable estimates of key vital rates to assist in population modeling and conservation planning. This was a central goal of our study.
### Table 3. Data summary from literature.

| Study ID | Study | Site | Habitat | Fossorial Mammal | Burrow Type | Method | Year | Juvenile Mortality n | Juv. Mortality n | Adult Mortality n | Nest Success n | Nest Success SE | Nest Success n | Nest Success SE | Nest Success n | Nest Success SE | Nest Success n | Nest Success SE | Nest Success n | Nest Success SE | Nest Success n | Nest Success SE | Nest Success n | Nest Success SE | Nest Success n | Nest Success SE |
|----------|-------|------|---------|-----------------|-------------|--------|------|----------------------|-----------------|------------------|---------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|
| A        | Barclay et al 2011 | California | Airport | CA ground squirrel | Both | Observations | 1990-2007 | 0.74 | 656 | 0.46 | 23 | 0.79 | 342 |
| B        | Berardelli et al 2010 | New Mexico | Urban/Grassland Pasture | Rock squirrel | Both | Observations | 2000-01 | 0.74 | 144 | 3.47 | 0.21 | 106 |
| C        | Clayton & Schmutz 1997 | Alberta | NA | NA | NA | Radiotelemetry | 1995-1996 | 0.53 | 46 | 0.43 | 30 |
| D        | Conway et al 2006 | Washington | Urban/Agriculture Grassland | Badger, marmot, ground squirrel | Natural | Observations | 2000-2004 | 0.46 | 1088 | 3.15 | 0.13 | 500 |
| E        | Davies & Restani 2006 | North Dakota | Grassland | Prairie dogs | Natural | Radiotelemetry | 2003-4 | 0.45 | 40 |
| F        | Green & Anthony 1989 | Oregon | Grassland/Shrubland | Badger | Natural | Observations | 1980-1 | 0.53 | 139 |
| G        | Grabe & Savidge 2007 | South Dakota | Grassland | Prairie dogs | Natural | Observations | 1999-2000 | 0.76 | 274 | 3.5 | 207 |
| H        | Holm & Plamton 1999 | Oregon | Grassland | Badger | Natural | Observations | 1995-1997 | 0.57 | 99 |
| I        | Lantz & Conway 2009 | Wyoming | Grassland | Prairie dogs | Natural | Observations | 2003-4 | 0.71 | 77 |
| K        | Lutz & Plamton 1999 | Colorado | Grassland | Prairie dogs | Natural | Banding, Observations | 1990-1994 | 0.82 | 167 |
| L        | Millsap & Bear 2000 | Florida | Suburban | Owls | Natural | Banding, Observations | 1987-90 | 0.7 | 736 | 2.9 | 0.1 | 512 |
| M        | Millsap 2002 | Florida | Suburban | Owls | Natural | Banding, Observations | 1987-1991 | 0.7 | 310 | 0.33 | 271 |
| N        | Restani et al 2001 | Montana | Grassland | Prairie dogs | Natural | Observations | 1998 | 0.92 | 13 |
| O        | Rosenberg & Haley 2004 | Imperial County, CA | Agricultural | CA ground squirrel | Both | Banding, Observations | 1997-2000 | 0.36 | 295 | 0.79 | 78 | 3.09 | 62 |
| P        | Rosenberg & Plamton 2007 | California | Urban/Agriculture/Grassland/Fragmented | CA ground squirrel | Natural | Radiotelemetry | 1997-2003 | 0.62 | 419 | 3.38 | 0.43 | 297 |
| Q        | Thomsen 1971 | California | Airport | CA ground squirrel | Natural | Banding, Observations | 1965-6 | 0.27 | 71 | 0.19 | 21 | 0.54 | 24 | 4.4 | 13 |
| R        | Todd 2001 | Saskatchewan | Pasture | Richardson’s ground squirrel | Most | Observations | 1998-2000 | 0.55 | 64 | 12 | 106 | 0.21 | 106 | 0.13 | 106 |
| S        | Todd et al 2003 | Saskatchewan | Pasture | Richardson’s ground squirrel | Most | Observations | 1998-2000 | 0.55 | 64 | 12 | 106 | 0.21 | 106 | 0.13 | 106 |
Bayesian elements of analysis

We utilize a statistical framework that enables generalization across the range of studies in order to estimate four life history parameters of the western burrowing owl: adult mortality, juvenile mortality, nest success, and nest productivity. While our focus is on the parameters for which we currently have the most and highest quality data, we use a Bayesian framework and a prior to posterior philosophy for the natural structure it provides for updating estimates in the future as additional data becomes available. We report variability in the form of credible intervals calculated from sampling the posterior distribution, and treat data and model parameters as random variables, rather than attempting to estimate an unknown true and fixed value (Ellison 2004). Our intent is not to develop a “novel” framework but rather to formally address an existing problem with a suite of analytical techniques chosen for their ability to characterize uncertainty in sparse datasets.

While the specific purpose of our work is to provide a deeper understanding of several key vital rates of burrowing owls, our approach also has general utility in offering a path forward to link the results of field studies and modeling when field data are sparse. Ultimately, conservation and management projects need to be supported in a synthetic way by all three legs of the ecological toolkit – empirical field studies, statistical analyses, and simulation modeling. A rigorous conceptual framework that integrates all three approaches is one in which biological data are fit into a statistical framework to create a coherent description of the center and spread of the variables in question. The statistical description is then used to parameterize a model that addresses questions about relationships among variables, or makes predictions based on different management scenarios. The estimation of vital rates is necessary and important, but is not sufficient to answer research questions without being imbedded in this larger framework. The
estimation process is usually perceived as the middle step in a directional workflow, as a transition between field data and inference often guided by simulation models. We emphasize the importance of connecting the results of modeling backwards to estimation and field data collection. In this way, the process of modeling can guide data collection and analysis in an integrated way that improves the overall utility of all three approaches over time.

Methods

We searched the literature for all field studies of western burrowing owl that reported estimates for juvenile mortality, adult mortality, nest success, or nest productivity. Studies were included regardless of methodology as long as both parameter estimates and sample size were reported. For the mortality estimates, this included studies that reported field observations from banded birds, and observations from radiotelemetry. Estimates of mortality that used a mark-resight methodology were also included (Millsap 2002, Barclay et al. 2011). The sample size for juveniles was taken as the number of juveniles banded. The same rule was used for adult mortality. Specific resight numbers were not published, so we made the assumption that the number of banded juveniles resighted as adults was relatively small. In migratory populations, adult return rates range 14-19%, while only roughly 5% of juveniles return as adults (Lutz and Plumpton 1999). The data we utilized for adult and juvenile mortality were raw counts of surviving owls, which we fit to beta-binomial models. When raw data and adjusted mortality estimates (through methods such as Cormack-Jolly-Seber) were both provided, we utilized the data as presented (Todd et al. 2003, Davies and Restani 2006). Juvenile mortality estimates represent a time interval from hatching to migration at the end of the breeding season. The adult mortality interval was annual survival for three studies (Millsap 2002, Rosenberg and Haley
2004, Barclay et al. 2011), and breeding season mortality for two studies (Thomsen 1971, Clayton and Schmutz 1997).

The minimum criteria for nest success was defined as the emergence of at least one chick 14-28 days old from the burrow of a breeding pair (Rosenberg et al. 2007, Barclay et al. 2011). Four studies (Green and Anthony 1989, Millsap and Bear 2000, Lantz and Conway 2009, Berardelli et al. 2010) required at least one juvenile fledged from the nest at approximately 40 days old as a measure of nest success. Nest success estimates came from field observations for all studies. Nest productivity was reported in the literature either for successful nests only, or for all nests included in the sample, whether successful or not. Our analysis utilized the successful nest only values, to exclude the redundant information of zero fledges from unsuccessful nests. For most studies the value reported for productivity represents the count of chicks fledged per nest, but Rosenberg and Haley (2004) defined productivity as the maximum number of 14-21 day chicks observed aboveground during multiple timed observation periods.

Another dimension of variability came from whether studies reported different breeding seasons as separate samples, or pooled data from multiple breeding seasons. To maintain consistency across all studies, we aggregated all reported annual samples to create one estimate per study. The variability among studies, which encompasses at least 5 major dimensions of variability (fossorial mammal, geographic region, burrow type, habitat, and methodology), dwarfs the variability within studies arising from annual variation. This approach was also justified in terms of the intended analysis. The objectives of this study were to acquire an estimate of the overall mean, along with an estimate of among-study variance for each parameter. We decided that resolving variability related to an annual sample effect nested within study was not a high priority and was not strongly aligned with the main goals for this effort.
Statistical Methods

The parameter for nest productivity was estimated with the following Poisson gamma mixture model,

(Eq 1) \[ x_{ij} \sim \text{Poisson}(\lambda_i) \]
\[ \lambda_i \sim \text{Gamma}(\alpha, \beta), \]

where \( x_{ij} \) refers to the productivity of the \( j \)th nest in the \( i \)th study. Within this model there were multiple levels of variability, and it was necessary to use simplifying assumptions to achieve a tractable model. The primary focus was again on among-sample variability. The parameter estimates for nest success, juvenile mortality, and adult mortality were estimated with the following beta-binomial mixture model,

(Eq 2) \[ x_i \sim \text{Binomial}(n_i, p_i) \]
\[ p_i \sim \text{Beta}(\alpha, \beta) \]

where \( x_i \) refers to the total number of events (i.e. nest successes or mortality events) within the \( i \)th study. The beta distribution constrained the estimates between 0 and 1, which was an important component of the realism of these estimates. For the \( \alpha \) and \( \beta \) hyperparameters in all models we used a relatively uninformative Gamma(0.001, 0.001) hyperprior.

As we took a Bayesian approach, we first calculated the posterior distribution of all parameters, and then sampled from these distributions with the use of Gibbs sampling. When the posterior distribution was only known up to a constant of proportionality, we used the Metropolis Hastings algorithm to sample from the posterior distribution. For each model, we ran the Gibbs sampler for 5000 iterations, of which the first 1000 iterations were discarded as the burn-in period. The remaining 4000 iterations comprised the posterior distribution and were used to create 95% credible intervals and posterior means. All model procedures were conducted in the base package.
To enable comparison of the Markov Chain Monte Carlo (MCMC) and maximum likelihood estimation (MLE) modeling approaches, maximum likelihood parameter estimation was also conducted using the same beta binomial model structure. The estimates were created using the mle2 method from the bbmle package version 1.0.17. Plots were created using the rethinking package version 1.47.

The two approaches were compared with unbiased jackknife estimators of mean and variance for nest success and juvenile mortality (Williams et al. 2002). Each jackknife iteration contributes a pseudovalue to the calculations, calculated by:

(Eq 3) \[ \hat{\theta}_i = n\hat{\theta} - (n - 1)\hat{\theta}_{-i} \]

where \( \hat{\theta} \) is the model estimate for nest success or juvenile mortality, respectively. The mean estimator is calculated using:

(Eq 4) \[ \bar{\hat{\theta}} = \sum_{i=1}^{n} \frac{\hat{\theta}_i}{n} \]

The variance estimator then follows as:

(Eq 5) \[ \text{var}(\hat{\theta}) = \sum_{i=1}^{n} \frac{(\hat{\theta}_i - \bar{\hat{\theta}})^2}{n - 1} \]

We conducted a second, separate jackknife procedure to verify the stability of the MCMC estimates for each parameter. In this procedure we re-estimated the distribution parameters \( \alpha \) and \( \beta \) with MCMC while excluding each study iteratively. The credible intervals for each jackknife
iteration were calculated to illustrate the consistency of the MCMC mean estimate and overlap of the intervals.

The standard deviation estimates came from the mathematical properties of the beta and gamma distributions and are based on $\alpha$ and $\beta$ estimates from MCMC for each parameter (Evans et al. 1993). The variance of a beta distribution with known $\alpha$ and $\beta$ is given as:

(Eq 6) \[ \sigma^2 = \frac{\alpha \beta}{(\alpha + \beta)^2 \times (\alpha + \beta + 1)} \]

The variance of a gamma distribution with known $\alpha$ and $\beta$ is given as:

(Eq 7) \[ \sigma^2 = \frac{\alpha}{\beta^2} \]

**Results**

*Comparison of modeling approaches*

In order to evaluate the relative strength of the estimates of mean and variance for the suite of four variables, we first compared the MCMC and MLE modeling approaches. Graphically, MLE shows a wider spread in variance and lower density peaks for both juvenile mortality and nest success of burrowing owls (Figure 5). MCMC exhibits higher density peaks and narrower spread in variance. The credible intervals for both variables are wider with MLE than with MCMC.

The jackknife estimators of mean and variance, which represent the accuracy and precision achieved by each model approach, verify the visual patterns (Table 2). The estimated means from the jackknife procedure fall closer to the full-dataset mean for MCMC compared to MLE. Juvenile mortality shows a gain in precision of the variance estimate of 28%, and the estimator of nest success variance shows a gain in precision of 7% from using MCMC instead of MLE. These estimators converge to the theoretical mean and variance of the estimator as sample size
increases. The mismatch between the mean estimates from the full dataset and from the jackknife estimator is the result of small sample size.

The central tendency in the jackknifed models was consistent, indicating that these estimates are robust, although based on a relatively small number of field samples.

**Figure 5.** Simulated posterior distributions for juvenile mortality rate (smaller dataset, greater variability) and nest success rate (larger dataset, lower variability), showing the higher degree of precision achieved with Markov Chain Monte Carlo. The solid line represents the mean distribution and dashed lines represent the upper and lower bounds containing 95% of the density at each possible mortality level.
Table 4. Jackknife estimators of mean and variance.

<table>
<thead>
<tr>
<th></th>
<th>Juvenile Mortality</th>
<th>Nest Success</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>Variance</td>
</tr>
<tr>
<td>MCMC</td>
<td>0.504</td>
<td>0.068</td>
</tr>
<tr>
<td>MLE</td>
<td>0.534</td>
<td>0.087</td>
</tr>
</tbody>
</table>

MCMC parameter estimates

While the parameter estimates for juvenile mortality show a central tendency of the mean near a mortality estimate of 45% across the jackknife iterations, the coefficient of variation (0.47) indicated greater variability in this estimate than for any other variable we examined. The range of the credible interval (26-64% mortality) suggests that this variable is not highly resolved.

Methodological differences are pronounced in this set of studies. The lowest reported mortality in the set was likely biased low because individuals were presumed alive unless a carcass was located (Thomsen 1971). The estimates based on radio-telemetry were higher (range: 45-55%), in part due to better ability to locate evidence of mortality events, including discarded radio-transmitters with predator damage. Radio-telemetry methodologies are accurate, but often limited to small sample sizes. The two large-sample mark-resight studies reported the highest estimates: 70 and 74%, respectively (Millsap 2002, Barclay et al. 2011). These high estimates are consistent with biological expectations of high mortality during the juvenile period, and the large sample sizes are more robust to inference. Resightings in this method help to parse out mortality from dispersal events, although low resighting rates for juvenile burrowing owls could limit estimates. In this case the current estimate of 45% for juvenile mortality may be pulled down by the lower mortality values from the rest of the study set.
The estimate of 35% adult mortality is consistent with the biological expectation of lower adult mortality for this species relative to juvenile mortality. The estimate of adult mortality was also resolved with higher precision, indicated by a coefficient of variation (0.09) one-fifth that of the CV for juvenile mortality. The credible interval (30-40%) also contains a narrower range of mortality values than the juvenile estimate. The set of studies is smaller than that for juvenile mortality, but includes two large-sample mark-resight studies. The lowest reported mortality in the set came from the same banding study that reported the lowest estimate for juveniles, again likely due to the difficulty of locating positive evidence of mortality without tracking equipment (Thomsen 1971).

Compared to the CV for juvenile mortality, the CV values for both nest success and productivity of successful nests were relatively low. The estimated means of 67% nest success and productivity of 3.3 fledglings/successful nest are in line with the reported values in Table 1. More studies reported nest success (14 studies) than reported juvenile mortality, adult mortality, or productivity.

**Table 5.** Parameter estimates with standard deviation and 95% credible interval derived from the posterior distribution of the MCMC procedure.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Mean ± SD</th>
<th>CV</th>
<th>95% credible interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>Juvenile mortality</td>
<td>0.45 ± 0.21</td>
<td>0.47</td>
<td>0.257 – 0.637</td>
</tr>
<tr>
<td>Adult mortality</td>
<td>0.35 ± 0.03</td>
<td>0.09</td>
<td>0.295 – 0.401</td>
</tr>
<tr>
<td>Nest success</td>
<td>0.67 ± 0.02</td>
<td>0.03</td>
<td>0.609 – 0.733</td>
</tr>
<tr>
<td>Productivity</td>
<td>3.3 ± 0.32</td>
<td>0.10</td>
<td>3.0 – 3.6</td>
</tr>
</tbody>
</table>
Stability assessment

The stability of the MCMC estimates were assessed through a separate and more stringent jackknife procedure conducted for each of the four variables. For juvenile mortality, the jackknife iteration excluding study R (Todd 2001) shows the influence of one unusual mortality measurement, in which one sample of 12 birds equipped with radio-transmitters experienced no mortality during the breeding season. Without the data point the point estimate would be 14% higher and the credible interval would be 20% narrower. Also note the upwards influence of the two large-sample mark-resight studies, A and M, on the mean (Barclay et al. 2011, Millsap 2002).

Conversely, for adult mortality, the jackknife iteration excluding study O (Rosenberg and Haley 2004) shows that the credible interval would be 64% wider in the absence of this large-sample study. The study is influential because it was conducted in an agricultural site with a large resident population, and individuals yielded high probability of resighting. However, all of the jackknifed credible intervals were wider than for the CI representing the full set of studies, indicating that each study contributed to the precision of this parameter estimate.

Credible intervals were very narrow for the estimate of nest success, indicating a high degree of confidence in the estimated parameter value (Figure 6). Across the models, there is a strong pattern of stability in the estimates and high degree of overlap in credible intervals. This suggests that in cases where information on nest success is required, values in the range of the credible interval may be used with confidence.

The consistency in credible intervals for productivity also indicates stability in the estimated parameter value. For this parameter there were four large sample studies available, reporting
mean productivities of 2.9, 3.15, 3.38, and 3.5 respectively (Conway et al. 2006, Millsap and Bear 2000, Rosenberg et al. 2007, Griebel and Savidge 2007).

**Figure 6.** Mean parameter estimates and 95% credible intervals for the models including all studies (left panels) and for each jackknife iteration from MCMC. Each jackknife model is labeled with the Study ID for the one study excluded from the model.
Discussion

In conservation, monitoring and management decisions are made with limited data. In order to maximize our understanding of a species or ecosystem, conservation biologists often apply complex statistical procedures and develop analytical or simulation models of the system. These computational approaches synthesize data from field studies, provide measures of vital rates, and make predictions about system dynamics. Our work on burrowing owls uses all three approaches to provide managers with the best possible set of predictions and/or recommendations.

Markov Chain Monte Carlo estimates were more precise than maximum likelihood estimates of the mean and variance for the suite of four burrowing owl vital rates. This precision provides better data for our purpose of parameterizing a simulation model of owl population dynamics. The overall and jackknifed estimates of juvenile mortality were least well-resolved, indicating the need for more field studies on this aspect of burrowing owl life history. These results demonstrate how robust statistical analysis both feeds back to the empirical estimates derived from field studies and leads forward into the simulation model. We explore the insights from the statistical analysis as an integrated step towards the parameterization of a stochastic model with credible variance estimates representing variability across multiple populations. We also emphasize that interconnections between the three approaches can support an iterative process of overall improvement in methods and results over time.

Biological field studies

Biological field studies provide insight into the life history of the study species, and verify that statistical analyses and modeling are being conducted at appropriate spatial and temporal scales, and that all necessary factors have been taken into account. Without being able to evaluate model
predictions and findings against patterns observed in an existing biological system, there is no assurance that the model is appropriate for meeting management and conservation goals and objectives. For example, the estimates of nest success produced by this analysis seem surprisingly invariant, assuming that nest success is driven by differences in predation and resource levels (Martin and Li 1992, Paton 1994, Wesolowski and Tomialojc 2005). The productivity estimates also appear to display a high degree of precision across studies (Table 3). However, inclusion of potential driving factors might reveal associations with these vital rates within the range of variation of individual studies, for example the observational evidence that owls fledge more young in years with high vertebrate prey populations, when high quality and amount of food supports the survival of more nestlings (York et al. 2002, Gervais et al. 2006).

Undoubtedly differences in nest success and productivity are occurring at smaller microhabitat scales, although we found a strong central tendency in the among-study analysis. Gradients of each variable are likely captured within individual studies, masking the potential for higher rates of nesting success and productivity. In order for field data to be analyzed appropriately, the field methods must be reported with enough detail about the rules followed during data collection. For example, life history theory for burrowing owls and cavity nesters suggests that nest failure is affected by resource availability and nest predation, but productivity from successful nests is driven mainly by prey availability (Martin and Li 1992, Gervais et al. 2006). In the burrowing owl literature, productivity values are inconsistently reported both for the entire set of nests, including zero values from failed nests, and for the subset of successful nests only. If the details of the data structure were not taken into account in the analysis, we would risk confounding the processes of nest predation and prey availability. The result would be estimates with biased means and overestimated variance.
**Statistical analyses**

One of the core purposes of statistics is the estimation of variance, and the ability to identify poor estimates resulting from small sample size or inconsistent field methods. However, the choice of statistical model structure influences the variance estimates. In this case the analytical objective of estimating the measure of center across variable datasets drove the choice of an intercept-only model. The obvious candidates for alternative model structures would include subsets of the factors shown in Table 1. While estimating the effect size due to different locations, fossorial mammals, habitats, or methods was not a driving goal of this analysis, future efforts could seek to address research questions about how to generalize mechanisms or correlations across multiple studies.

Comparing the conceptual treatment of variance by the two approaches, mixed effects models partition stochastic variability around different factor levels. Although mixed effects models control underestimation of variance by pooling variance, rather than fully partitioning it to each separate varying effect, models with independent variables still produce compressed confidence intervals around the intercept. However, our goal for the next phase of modeling owl populations was to parameterize a stochastic model with credible variance estimates representing variability across multiple populations and so this treatment of variance was not well aligned with our primary goals. The intercept-only model incorporated more overall variability among studies into the variance estimate, leading to wider credible intervals around the mean estimate, and was more appropriate for our specific objectives. However, we acknowledge the mixed effects approach is critical for making population-level predictions for specific times, places, habitat associations, or methodologies, and also leverages sparse population-level data more efficiently than other model structures.
The comparison of estimation methods (MLE vs MCMC) enabled both validation and comparison of the model fit produced by each method. Both methods produced generally similar distributions each for juvenile mortality and nest success, validating each other. However with MCMC, concentrated peaks around the mean and narrower credible intervals indicated more precise estimates. The comparison increased our level of confidence in the MCMC parameter estimates.

The jackknife procedure evaluated the effect of the study-specific effects inherent in the data by testing the influence of each study on the stability of the parameter estimates. The most critical measure of sample size in these data was the number of studies, rather than the number of data points from each study, or the number of annual samples within each study. However, each cluster of non-independent data points within study included different sample sizes for the number of data points and annual samples, complicating calculations of effective sample size and the relative influence of each study. The jackknife procedure identified the relatively poor precision for juvenile mortality and verified that the other parameter estimates were very stable across studies.

We also used the statistical analyses to examine the estimated means for bias arising from methodological issues. One of the outcomes from this study is that in many cases it may not be necessary to expend additional effort in measuring nest success for the purposes of model parameterization. However, it is important to caution that these estimates appear to be relatively high, and the issue of overestimating nest success has been documented in the literature (Johnson 1979). Many field estimates are assumed to be biased high because of the difficulty of detecting nests at the very beginning of the egg-laying period, which leads to low detection of nests that fail early. Early detection is difficult since nests are often camouflaged, but the problem is
especially difficult with underground nests. Therefore, the potential for lower mean nest success should not be ignored.

While best scientific practice might appear to suggest conducting separate analyses by methodology, we intentionally avoid filtering out studies unless the intended application would be constrained to a particular geographic region, methodology, or other factor level. We based the estimate of the global mean for each vital rate on as many field measurements as possible to guard against underestimating variability. This approach is justified since our objective was to generalize across the available information.

**Modeling**

To this point, we have described two of the three legs that underlie the conceptual framework of our analyses – synthesis and evaluation of multiple field estimates of key vital rates, and rigorous statistical analysis to estimate the central tendency and variability of those estimates, including an assessment of any potential differential influence of specific studies. We are now poised to complete the third phase of modeling the data relative to other factors in the study system. We fully recognize that until we do so, we lack assurance that we have correctly identified the most influential factors. Sensitivity and elasticity analyses will help to verify that field data collection is focused on the factors that influence population outcomes the most (Benton and Grant 1999). In the burrowing owl model, until an elasticity analysis is conducted, it will not be clear whether additional field measurements of juvenile mortality are necessary, even though the credible intervals indicated that juvenile mortality is the least well resolved of this set of variables. If the elasticity analysis shows that juvenile mortality is an important driver of population growth, this would indicate the study set needs to be updated with at least one additional large-sample study. Quantifying the influence of juvenile mortality is a priority because adult mortality is considered
by many to be the primary driver of burrowing owl population persistence (Barclay et al. 2011). Since different suites of factors are involved whether the conservation objective is to manage for adult or juvenile survival, settling this issue is an important next step in addressing the burrowing owl population declines observed in the past 15 years (Sheffield 1997, Desmond et al. 2000, Poulin et al. 2005). In this way the expected results of modeling will guide the improvement of the statistical parameter estimates and prioritization of field work.

Conclusions

The analytical framework presented here both consolidates fundamental species information gleaned from painstaking and expensive field efforts, and addresses the uncertainty in life history parameter estimates. Accounting for uncertainty in modeling is critical because it has the potential to affect numerous types of analyses. When the goal is to identify the most influential vital rates supporting population growth, uncertainty about parameters can affect elasticity measures (Heppell et al. 2000). Overly wide estimates of variability in replicated model runs can produce such a wide range of outcomes that meaningful conclusions are precluded (Beissinger et al. 2006). When management and conservation decisions are based on model output, there is the potential for the model to lead to poor decision-making (Burgman et al. 2005).

Gathering and utilizing field data is a primary activity in ecology, but ecologists also need options for drawing conclusions beyond the data-driven constraints of specific studies, years, methods, or other factors. We demonstrate that formalizing the analysis across studies can produce specific insights into the influence of such constraints. The use of an intercept-only model and a Bayesian framework also loosened the constraints of inference from field data in an appropriate and goal-driven way.
This study demonstrates that the results of these statistical analyses could guide additional field data collection. While the analysis feeds into the next step of simulation modeling, the expected results of modeling could also guide the improvement of statistical parameter estimation. Due to the interconnections between the three approaches and the potential for supporting an iterative process of overall improvement in methods and results over time, two best practices are suggested: first, we should look for opportunities for strengthening working relationships and communication between field biologists, statisticians, and modelers. Second, projects should be designed at the outset to incorporate iterative rounds of data collection, statistical analysis, and modeling, rather than delaying simulation modeling until after a “full” understanding of the study system is achieved.

The payoff we seek from an approach focused on producing credible estimates of species-level variance is an improved ability to create management models designed to facilitate decision making even in the context of great uncertainty. Grappling with uncertainty is necessary because it is used so frequently as an argument against conservation and management action (Beissinger et al. 2006).

Acknowledgements

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References


CHAPTER 3.
An agent-based model to link habitat selection rules and population dynamics of a declining species and an ecosystem engineer

Abstract
The Western Burrowing Owl (*Athene cunicularia hypugaea*) is one of a number of avian species for which declining populations have prompted preemptive management ahead of potential listing by state and federal agencies. We developed, parameterized, and evaluated the stability of an agent based model of burrowing owls that uses explicitly defined individual behavior to examine the relationship between owl settlement decisions and the habitat quality consequences for reproduction and population growth. In an analysis of model sensitivity, juvenile mortality consistently was the most influential input parameter, followed by adult owl mortality and squirrel mortality. Uncertainty in results due to model stochasticity was small, verifying the reliability of the model. Observations of density-dependent owl population growth were a further indicator that the model produces biologically realistic population-level emergent behavior. We utilized the model to conduct a factorial experiment comparing the relative influences of owl density and a gradient of landscape proportions of low vs. high habitat qualities, which showed that initial owl density is also an influential driver of population persistence. The model currently enables qualitative consideration of the proximate mechanisms behind population decline, including the factors that attract owls to disturbed edge habitats.

Introduction
The Western Burrowing Owl (*Athene cunicularia hypugaea*) is one of a number of avian species for which declining populations have prompted concern and preemptive management ahead of potential listing by state and federal agencies (Sheffield 1997, Desmond et al. 2000, Poulin et al. 2005). The factors that are likely driving the decline of burrowing owl populations in southern
California are habitat losses due to urban development and changes in habitat composition and structure of native grasslands (D’ Antonio et al. 2007, Gervais et al. 2008). Because burrowing owls are obligate breeders in burrows generally created by fossorial mammals, reductions in California of the distribution and abundance of the California Ground Squirrel (*Otospermophilus beecheyi*) by 80-90% have reduced potential habitat even further (Marsh 1998, Lenihan 2007). However, even when the ultimate causes are known, the proximal mechanisms of species decline are frequently less certain. Current and ongoing changes to habitat composition and structure, such as increases in ground cover and heavy thatch from exotic annual grass species like wild oat (*Avena fatua*) and brome (*Bromus diandrus, Bromus madritensis*), suggest that decreases in habitat quality as well as quantity may play a key role (D’ Antonio et al. 2007). However, defining and measuring habitat quality is difficult and imprecise. Our approach is to use the term “quality” more generally as an overall measure of positive and negative effects of habitat (food resources, predation, etc.) rather than in the narrower sense of the nutritional value of a food source (Maher and Lott 2000). The impact of deteriorating habitat quality is therefore inferred indirectly from metrics such as survivorship, reproduction, and fitness, although when a focal population declines due to low habitat quality, the mechanisms driving the decline still need to be identified.

To examine the proximal mechanisms of burrowing owl declines, we developed an agent based model (ABM) focused on the interaction of habitat quality and habitat selection decisions by individuals. Habitat quality and habitat selection are sometimes conflated- for example, some metapopulation models assume individuals make optimal habitat selection decisions based on perfect knowledge of habitat quality (Kristan 2003). However, in real situations individuals make
decisions using readily discernable, rather than perfect, information about factors such as apparent prey availability, resource availability, and levels of competitors, predators, and physiological stress (Battin 2004, Morin 2011). Decisions based on incomplete or misleading information can lead to the presence of owls in non-optimal habitats. In these cases, the quality of habitat will influence whether owl populations are able to persist over time. The mechanistic design of agent-based models make them an ideal framework for separating habitat selection and habitat quality.

Managers will be better equipped to ameliorate the effects of habitat fragmentation and species invasions if the consequences of burrowing owl habitat selection are better understood. For example, a proportion of burrowing owl individuals appear to make maladaptive habitat selection choices. Across the species range, some individuals choose to breed in anthropogenically altered habitats such as airports, agricultural fields, and roadsides (Thomsen 1971, Plumpton and Lutz 1993, Millsap and Bear 2000), which tend to be highly disturbed and insecure. The cue that draws owls to these sites is uncertain, but even when a cue suggesting good habitat quality is present, the habitat may have undergone such rapid change that owl habitat selection has not been able to adapt quickly enough to the negative effects of the selected habitat. In this case, owls may be settling in an ecological trap, and settlement will eventually lead to population extinction (Battin 2004). Previous studies have considered airports, agricultural fields, and urban areas as traps for other avian species (Best 1986, Kershner and Bollinger 1996, Boal and Mannan 1999).
Currently there is a gap between the results of habitat survey field studies and the development of management plans for declining populations. Most habitat selection studies for burrowing owls have focused on correlations at small spatial scales between the presence or absence of owls and physical habitat structure, in order to define the types of habitat preferred by owls (Belthoff and King 2002, Poulin et al. 2005, Moulton et al. 2006, DeSante et al. 2007, Lantz et al. 2007). Whether the habitats where owls choose to breed are actually associated with positive or negative effects on their population demographics is unknown. A better understanding of the seemingly maladaptive habitat choices of the owls that choose to occupy human-altered habitat could contribute to the understanding of burrowing owl population declines. Better understanding could lead in turn to better chances of successful habitat restoration and more efficient allocation of management resources.

We use the agent based model to predict owl population outcomes based on modeled habitat selection rules in order to relate habitat management and restoration activities to the persistence of burrowing owl populations. The ABM framework is an appropriate way to address fundamental management questions about owls that are not feasibly addressed through field methods, because it is designed to simulate the adaptive behavior of multiple individuals in a mechanistic framework. During the model run, patterns at larger scales emerge that (1) are not imposed from variable parameterization, (2) are not easily predictable by individual behavior, and (3) have larger-scale properties than individuals (Grimm and Railsback 2005). One of the main strengths of ABM are their ability to explore cross-scale linkages between individuals and populations (Grimm and Railsback 2005).
While the primary purpose of this model is to predict the population consequences of habitat selection behavior by owls, a secondary purpose is to evaluate the reliability of predictions based on the current understanding of owl demography. Quantifying the relative influence of juvenile mortality is a priority. While the current understanding is that adult mortality is the most important driver of burrowing owl population persistence (Barclay et al. 2011), other analyses have indicated that there is a high degree of uncertainty about the influence of juvenile mortality (Hennessy et al., in prep). The resolution of this question is important because different management strategies are employed to minimize losses of adults compared to juveniles. A sensitivity analysis is needed to verify the relative influence of these two drivers and to clarify whether additional field measurements of juvenile mortality are necessary (Benton and Grant 1999).

We parameterize the model using estimates of demographic rates based on the available field data (Hennessy et al., in prep). We evaluate model stability through an exploration of uncertainty about demographic rates, and consider the relative influence of demographic rates with a sensitivity analysis. We conduct a factorial experiment to examine potential interactions of owl density, habitat area, and habitat quality. Together these approaches add to the current understanding of the relationship between owl settlement decisions and habitat quality consequences for reproduction and population growth.

**Methods**

We report model structure following the Overview, Design, Details (ODD) format (Grimm et al. 2006, Grimm et al. 2010). We report the full ODD in Appendix A, and provide a brief synopsis in this section (Figure 7). The model was developed in the Java-based software platform MASON (Luke 2011). Once the initial simulation environment was created, hierarchical routines
and subroutines were developed, coded, and evaluated as separate modules to simplify model development and facilitate debugging (Topping et al. 2010).

**Figure 7.** Compact overview of model components. The model agents are squirrels, owls, and burrows.

**Model Objectives**

The primary purpose of this model is to predict the population consequences of habitat selection behavior by squirrels and owls. The secondary purpose is to evaluate the reliability of predictions based on current understanding of owl demography, while identifying areas of critical uncertainty. The model will produce predictions of population change (lambda) and projected species spatial distribution across varying simulated configurations of core habitat surrounded by edges (Amano 2012). In the model, the successful fledging of chicks from nests supports positive
lambda rates. Breeding success is a key event from which learning effects emerge, as the parent owls return to the breeding grounds the following season with a memory of breeding success associated with the breeding burrow.

**Model Description**

In this stochastic and spatially defined model, dispersing owls move randomly through areas of variable and explicitly defined burrow availability and habitat quality. The complexity of the burrowing owl life cycle is represented by differences in dispersal and habitat selection rules based on the age, sex, and nesting experience of individual owls, so that individuals accumulate a unique history of habitat selection decisions, breeding outcomes and dispersal.

Both habitat selection and habitat quality are explicitly modeled, with habitat selection including mate-finding behavior. The probability of selecting habitat is set by the user for habitat interior and edge areas. Differences in habitat quality are expressed by setting the parameters for adult and juvenile mortality. Juvenile survival to reproductive age, and adult survival to subsequent breeding seasons will be greater in high quality habitat. Based on empirical and theoretical evidence that habitat selection is a hierarchical and scale dependent process (George and Zack 2001), the owl habitat selection rule has four components: a requirement for a burrow with space available, a preference when a potential mate is already settled in the burrow, and a probabilistic chance of settling in the burrow alone. The settling probability is modified by a logistic closing time rule based on the length of the breeding season so that as the breeding season progresses, owls become more willing to accept less ideal habitat.

Model owls are able to sense changes in their conditions and react to stochastic events such as nest depredation or burrow destruction. Owls have awareness about nearby owls and burrows
Modeled owls will remember whether they nested successfully in the previous year. Although burrowing owls are not strongly philopatric (Lutz and Plumpton 1999), a proportion of owls do return to previously utilized breeding burrows, and so the model incorporates the concept of win-stay-lose-switch and priority effects. These properties contribute to emergent patterns from individual adaptive behavior (Grimm and Railsback 2005).

**Initialization**

Initialized rates include breeding season adult, fledgling, and juvenile mortality for owls, and year-round adult and juvenile mortality for squirrels (Table 6). The user also sets nonbreeding mortality, stochastic burrow destruction rate, post-predation adult dispersal probability, and the size of the surrounding area for which owls can sense conditions. Initial squirrel and owl density is input by the user. Both squirrels and owls are created according to a 1:1 sex ratio, and are initialized with a suite of variables that track location and status at each time step.
Table 6. Parameter values used in demographic stochasticity runs.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>mean</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Spatial/temporal</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>simulated breeding seasons</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>landscape height and width</td>
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<td></td>
</tr>
<tr>
<td>border width</td>
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<td></td>
</tr>
<tr>
<td><strong>Owls</strong></td>
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<td></td>
</tr>
<tr>
<td>initial number of adults</td>
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<td></td>
</tr>
<tr>
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</tr>
<tr>
<td>adult mortality- interior</td>
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<td>juvenile/fledged mortality- border</td>
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The model has a temporal resolution of one day per time step, and runs for a user-defined number of years, with each year represented by 360 days in order to simplify calculations. The model focuses on the owl breeding season, which lasts 150 days in the model (equivalent to April 1-Sept 1). The nonbreeding season is represented by the departure of all owls from burrows for the remainder of the model run, accounting for migration in migratory populations and
regional movement in non-migratory populations. The spatial model extent represents a landscape defined by the number of potential squirrel territories. Each grid represents a female squirrel territory of approximately 0.24 ha, or a radius of ~27 m around the burrow (Evans and Holdenried 1943). Grid spaces are aggregated into patches that have an edge and an interior. For each grid space, parameters for probability of owl habitat selection, bare cover, soil texture, degree of uncertainty about habitat quality, and owl clutch size are each specified as a mean and standard deviation. Grid spaces also have modifiable occupancy functions for both squirrels and owls that apply a nonlinear relationship to the owl selection probability and/or bare ground cover and soil texture (for squirrel occupancy). A single burrow in the grid space represents a burrow complex with multiple developed entrances.

_Runtime_

The processes of dispersal, habitat selection, reproduction, and mortality are explicitly modeled for both squirrels and owls. In each step, unsettled squirrels move, then make a habitat selection decision. Squirrel habitat selection is based on a habitat selection function supported by data (Wisinski et al. 2013). When squirrels select habitat, they dig a burrow complex and settle in it. The creation of burrows by squirrels is modeled explicitly for burrow location, use, and availability. Female squirrels nest on day 60. Juveniles fledge at day 150. Stochastic mortality occurs for adults and juveniles. Burrows are removed through two separate processes: stochastic destruction at a constant rate, and deterioration through disuse. Burrows are considered deteriorated when they have been unoccupied by either squirrels or owls for 6 months.

Owls are scheduled to arrive on the breeding grounds on day 90. Owls that were successful in the previous breeding season arrive first and return to the location of the previous years’ burrow. If
the burrow still exists and is unoccupied, they settle. Unsuccessful or inexperienced owls arrive next and land randomly on the breeding ground.

The habitat selection function is hierarchical (Figure 8). If there is a burrow for the owl and a potential mate, the owl always settles. In the absence of a potential mate, the probability of settlement is modified according to a logistic function that is defined by midpoint and slope parameters set by the user (Table 6). Setting the midpoint parameter for later in the season and a high slope parameter results in a greater degree of choosiness in habitat selection by owls.

**Previously successful owls**

- Priority arrival on breeding ground
  - **N** Previous year’s burrow with space?
    - **N** Remains not settled
    - **Y** Settles. Evicts all squirrels in burrow.
  - **Y** Settles. Evicts all squirrels in burrow.

**All other owls**

- Random movement
  - **N** Burrow with space?
    - **Y** Potential mate present?
      - **Y** Occupancy probability function with logistic closing time rule
      - **N** Remains not settled
    - **N** Settles. Evicts all squirrels in burrow.
  - **Y** Occupancy probability function with logistic closing time rule

**Figure 8.** Comparison of habitat selection rules for owls with previous year breeding success and all other owls, including owls that were unsuccessful breeders or juveniles in the previous year.
If settling, the owl evicts any squirrels in the burrow. If the owl has a mate in the burrow, they nest, and lay eggs. After an incubation period of 28 days, eggs hatch. Stochastic mortality occurs for eggs and juveniles. Nesting adults who lose eggs or juveniles may disperse based on a post-predation dispersal probability, and eggs and juveniles remaining in the nest after dispersal of both adults die. Juveniles who survive 40 days fledge. Adults that fledge chicks from the nest are considered successful for the breeding season. At the end of the breeding season, any unfledged eggs and juveniles die, and all fledglings are considered adults. The owls leave the breeding ground, and stochastic owl nonbreeding mortality occurs. Breeding- and nonbreeding-season mortality levels are defined separately. Mortality is the only process occurring during the nonbreeding season.

*Sensitivity Analyses*

To examine the sensitivity of population growth, expressed as year over year population change (λ, lambda), we first conducted an elasticity analysis based on 1 percent variation in each input parameter to estimate the proportional contribution of each parameter to lambda (Table 6). However, the effect on lambda was indistinguishable relative to model stochasticity. We then conducted 200 runs of the model that concurrently sampled all input parameters randomly according to their known distributions. If distribution was unknown we sampled from a normal distribution derived from the input value and a standard deviation set at 10% of the input value. The initial density was held constant at 0.15 owl/ha for all runs. Sensitivity strength was evaluated with Spearman rank correlation values (r) for the correlation of lambda with the input values for each parameter.
Model stability

An uncertainty analysis is the primary analysis used to assess the compounding effects of variability in multiple parameters as well as uncertainty from the sample size of model runs (Pacala et al. 1996, Smith and Heath 2001). We undertook two analyses. First, we conducted 200 runs using baseline values with all parameters held constant at their mean values (Table 6). Variation in lambda in these runs represent baseline model stochasticity due to model structure. In the second set of validation analyses, we ran 200 model iterations wherein we concurrently sampled from the distributions of all input parameters (described above) to identify combinations of variables producing extreme outcomes.

Scenario analyses

We evaluated hypotheses about population dynamics under different habitat conditions in an experimental framework (Grimm and Railsback 2005). We conducted a three-way factorial experiment to distinguish the effect on lambda of squirrels in habitat edges if the edges offer less space for owls and/or lower quality habitat for owls. For these simulations edge habitat quality was linked to juvenile and fledgling owl mortality by assigning daily mortality rates to four levels of habitat quality. The levels of habitat quality represent a qualitative gradient from low to high (0.25, 0.45, 0.65, 0.85). The full scale of habitat quality (seasonal mortality) ranges from 0 (lowest possible quality/highest mortality) to 1 (highest quality/lowest mortality). Core owl habitat area was assigned a constant, high habitat quality value of 0.85 through all simulation runs. Daily mortality rates were derived by dividing the 95% credible interval of juvenile mortality into a gradient of four equivalent intervals. The portion of overall habitat area contained in the edges was tested at three levels (10%, 50%, and 90% of total habitat area). Two levels of initial owl density were evaluated (0.02 owl/ha and 0.15 owl/ha). Effect sizes of
different factor combinations were compared in terms of lambda (Grimm et al. 1999). The influence of owl density on lambda was further evaluated by varying density over a wide range in values, while holding all other parameters constant.

Results
Sensitivity analysis
In the sensitivity analysis, juvenile mortality consistently was the most influential input parameter. Since juvenile mortality is not well resolved from field estimates, the estimate of variability was drawn from a beta distribution, which exhibited heavy tails from a relatively large proportion of extreme values (Hennessy et al., in press). Because the tails of the estimated distribution were not biologically realistic, we constrained juvenile mortality by the endpoints of the 95% credible interval (0.25-0.65), converted into daily rates (0.0042-0.0153). According to the model structure, juveniles born at the beginning of the breeding season are subjected to higher overall mortality (maximum 150 days, 47% survival to end of breeding season) than juveniles born closer to the end of the breeding season (minimum 68 days, 71% survival). Therefore the daily rates are based on 68 days to the end of the breeding season, corresponding to a conservative estimate of model sensitivity to juvenile mortality. Of the three parameters with Spearman rank correlation values above 0.1, juvenile owl mortality (-0.71) was more strongly correlated with lambda than adult owl mortality (-0.29) (Figure 9). Lambda was also negatively correlated with adult squirrel mortality (-0.15).

These correlations influence lambda over the course of multi-year simulations. Variation in juvenile and adult owl mortality is associated with an increased range of lambda values in the 5th year, with high mortality values associated with high lambda, and low mortality values associated with low lambda. In contrast, the correlation of adult squirrel mortality and lambda is
weak enough that high and low mortality levels are associated with overlapping lambda values (Figure 9).
Figure 9. Simulation trace graphs and correlation diagrams for the three parameters most strongly correlated with output lambda (juvenile owl mortality, adult owl mortality, and adult squirrel mortality). Low input values for each of the input parameters are coded green and high input values are coded in red.
Model stability

When parameters were held constant at their mean values over 200 runs, variability was low (741 ± 57 owls) (mean ± SD) with a mean annualized lambda of 0.945 (Figure 10). The low variability in these 200 runs, since the input values were identical, represents the fundamental degree of demographic stochasticity from model structure. This stochasticity results from events in the model with a random component, such as whether individuals are able to find a burrow and a mate, based on initial random placement in the landscape and a random movement rule. Other sources include biological processes that are modeled with a probabilistic rate, such as mortality and adult abandonment after nest predation. When all input parameters were sampled randomly according to their known distributions among 200 runs of the model, we observed large variability in owl population size by the end of five years. The average number of owls after 5 years was 951 ± 1047 owls with a mean annualized lambda value of 1.04 in the fifth year. The difference in means (951 vs. 741) reflects the influence of the parameter distributions. Therefore the top panel reflects the degree of uncertainty stemming from the model, while the bottom panel reflects uncertainty about the true value of the parameters. Only 5% of the variance stems from demographic stochasticity, while 95% results from parameterization. By demonstrating that parameter variability is much more influential than model structure, we verify the model is sensitive to input parameters in a biologically and statistically realistic way.
Figure 10. Baseline stochasticity resulting from model structure was measured by holding all parameters constant at their mean values over 200 runs (top). The input parameters for these 200 runs were identical. Projection of owl population size after five years given the uncertainty about input parameters (bottom). Variability was measured by concurrently sampling all input parameters randomly according to their known or assumed distributions (n=200).
Scenario analysis

The factorial experiment showed a three-way interaction of owl density, edge area, and edge habitat quality ($R^2=0.97$, $F_{6,216}=14.1$, $p<0.01$), with annualized lambda in the fifth (final) year of the simulation as the response variable.

When owl density was considered separately and varied over a wide range in values, owl density exhibited density-dependent behavior (Figure 11). The rate of population change was greater for very low owl densities, as very small populations approached extinction more rapidly than populations at intermediate densities. Populations increased at higher owl densities, suggesting that reproduction was more successful above a threshold of owl density.
Figure 11. Relative change in owl population size during 5 year simulations, expressed as overall lambda. Initial owl densities represent a gradient from medium owl density (1.5 owl/ha) to very low (0.02 owl/ha) (10 simulation runs per density level).

Similarly, in the factorial experiment, low density populations decreased towards extinction, and effects of habitat quality and edge area were seen only at higher owl densities. Comparison of the habitat factors when owl density was high showed that when the edge habitat quality was the same as the interior, different proportions of habitat area in the edge produced similar lambda values. When the edge habitat quality was lower than interior habitat quality, greater proportions of habitat area in the edge had a negative effect on lambda (Figure 12).
Figure 12. Interaction of edge habitat area and quality at high owl density (10 simulations per parameter combination). End of season mean and standard errors are shown for each of five simulation years. Only the high owl density level is visualized since no differences were found at low owl density.
Discussion

Our results show that the uncertainty due to model stochasticity is small relative to the effects of varying the input parameters. This finding verifies the model by determining that the results are reliable and not due to unintended interactions resulting from model structure. The finding of density-dependent owl population growth (discussed below) was a further indicator that the model produces biologically realistic population-level emergent behavior as intended.

The uncertainty analysis demonstrated that a range of lambda values (year to year population changes) resulted from varying the input parameters. This variation in lambda shows that management could have beneficial effects on population persistence. The sensitivity analysis indicates that juvenile mortality is an influential driver of population growth, in addition to adult owl mortality. Since juvenile mortality is currently parameterized with sparse data, these results require further quantitative evaluation. The simulations in this study are perhaps most appropriately used to identify influential variables and interactions rather than to identify specific target values, as would be needed to set restoration goals. Before the model could be used in this way, additional data on juvenile mortality would be required.

The model does provide valuable insight into the proximate mechanisms behind observed declines in owl populations. The factorial evaluation of owl density, habitat quality (as linked to juvenile mortality), and the proportion of high to low quality habitat indicated that owl density is the most influential driver of population persistence. Model runs that varied owl density alone achieved positive lambda, which correspond to population numbers that are either stabilized or growing. Combinations with a greater proportion of high quality habitat also produced positive lambda rates. The persistence of declining populations could be supported by managing the areas
they occupy for habitat quality in terms of juvenile survival (limiting predation and ensuring adequate food supply).

In considering the drivers behind owl population change, the observed density-dependent behavior suggests that ability to find mates is a major driver. Model structure explicitly incorporated individual mate-finding behavior, while other potential drivers, such as predation and food supply, were implicitly assumed within the juvenile and adult mortality parameters. These parameters were held constant across the range of densities modeled in Figure 11. Therefore the model appeared to show Allee effects at low owl densities, in which reproductive rates drop in response to low population density (Greene and Stamps 2001). It is important to note that the modeled densities represent the low end of owl population density, not precluding the possibility of negative density dependence at very high densities. Since owls are linked so strongly to burrow availability, owl population could (theoretically) outgrow burrow supply, with a concomitant decrease in population growth rate.

One of the benefits of the ABM model structure is that the imposed focus on mechanism itself can produce insights during model development. When coding the habitat selection rule, we realized that habitat selection for burrowing owls is hierarchical. Since owls have an obligate need for a burrow, the consideration of additional habitat selection cues (vegetation height, perch availability) only matters when there is a burrow available. Owls won’t settle into high quality habitat without a burrow, and conversely, burrows in low-quality sites may still attract owls to settle. The hierarchical habitat selection creates the possibility that owls could be attracted to low-quality habitat, even though settlement results in high juvenile and/or adult mortality. As a result, the selection rule is one component of the model that produces insight into potential ecological trap effects on burrowing owls.
The scientific understanding of traps is incomplete, but evidence suggests they can have large impacts, and complicate efforts to conserve animal populations (Battin 2004). In ecological traps true habitat quality and the cues used to select habitats are mismatched, so that individuals “prefer” low-quality habitat, and choose to occupy it over higher quality habitat. The eventual outcome of settlement in an ecological trap is local population extinction, and potentially decreased regional population growth rates (Battin 2004). Some of the concern about this species has arisen from observations of owls in frequently disturbed locations with low vegetation, such as airports and golf courses, after studies reported an association between owl occupancy and low vegetation height (MacCracken et al. 1985, Green and Anthony 1989, Rosenberg et al. 2007).

The insight from using a mechanistic model structure is that trap effects for owls may be more likely to result from burrow availability than vegetation or other habitat components. It is more important to link owl management to factors such as squirrel density and squirrel habitat preferences over variables that may influence settlement decisions. Management actions that improve habitat without burrow creation will not result in owl settlement. These results do not describe the potential influence of disturbed sites, however, and the overall effects of these habitats on burrowing owls are still unknown. There is even the potential that these areas could provide good quality habitat for juveniles though increased prey availability and/or decreased predation rates (Millsap and Bear 2000). However, they may also provide low quality habitat, and we found that populations declined when a greater proportion of the owl population settled
in burrows located in low-quality habitat, as modeled with a greater proportion of low-quality edge habitat on the landscape (Figure 12).

At this stage in model development, several directions exist for further work. During our exploration of model behavior it became clear that there is a temporal component to burrow availability that appears to be critical to determining burrow supply during the owl breeding season. In the model, burrow availability is highest after juvenile squirrels fledge, and as mortality reduces the squirrel population through the fall and winter seasons, unoccupied burrows degrade. As a result of the mechanistic rules determining burrow supply, the number of burrows is at its lowest when owls return to breed, which likely influences lambda through the amount and timing of owl reproduction. This points to a need to better understand and qualify the dynamics of burrow availability and turnover in the field.

The spatial behavior of the model also needs to be evaluated, as patterns form due to owls following clusters of squirrels to good squirrel habitat. Through the range and accuracy of awareness that owls have about their surroundings, owls locate and occupy clusters of burrows, creating a supply of potential mates that attracts additional owls. If edges concurrently offer good-quality squirrel habitat and poor-quality owl habitat, clusters of squirrels and owls form in the ecotone region between edge and border. Therefore the influence of squirrel habitat quality should be examined further. Model analysis indicates that squirrel mortality is one of the parameters most strongly correlated with owl population change, and these findings should be extended to the influence of the amount and quality of squirrel habitat on owl populations.
This study shows that due to the high impact of juvenile mortality on owl population change, it is important for researchers to continue making field observations of mortality rates. It is also important for conservation managers to develop practices that minimize juvenile owl mortality. When the model is parameterized with the best estimates possible from field data, it produces a declining mean lambda over the course of multiyear simulations. One of the two primary explanations for a declining lambda is that one or more input parameters may be underestimated by this parameterization. However the biological interpretation, that populations are in fact decreasing under current mortality rates, would be consistent with recent field observations of widespread decline across many populations.

Even though limited to qualitative observations with the current level of parameterization, the model is already producing useful information about the degree of uncertainty in parameterization and insights into the mechanism of owl habitat selection. In addition to these findings, the value of agent based models lies in the link between individual behavior and population-level change. Including individual behavior in the model reveals interactions not captured by analytical models. In this case, using a mechanistic model structure led to consideration of the potential for Allee effects in addition to the more obvious factors of predation and food supply through mortality levels. We anticipate that this agent based model will also enable a more comprehensive analysis of the impact of squirrel habitat selection on owl population change in the near future.

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Appendix A. Overview, Design, Details (ODD) Protocol

1.1 Purpose

The primary purpose of this model is to predict the population consequences of habitat selection behavior by squirrels and owls. The secondary purpose is to evaluate the reliability of predictions based on current understanding of owl demography, while identifying areas of critical uncertainty. The model will produce predictions of population change (lambda) and projected species spatial distribution across varying simulated configurations of core habitat surrounded by edges.

1.2 Process overview and scheduling

During model runs, the processes occur in discrete daily time steps. Individual agents step in a fixed order, and updating happens asynchronously during the step. Owls, squirrels, burrows, and the observer have step methods. The last day of the simulation is scheduled for the final day of the last breeding season.

Squirrels are scheduled for every day of the simulation. In each step, the process of movement occurs, then habitat selection followed by settlement and burrow creation. Female squirrels then check to see if it is time to nest. If it is nesting, juveniles are born on day (step) 60, and fledged on day 150. The process of daily stochastic mortality occurs last.

Owls are scheduled to arrive on breeding ground on day 90 to start the breeding season. Owls who were successful breeders in the previous season return first to the previous year’s nest site and have priority in habitat selection. Unsuccessful owls follow and land at a random place on the breeding ground. From day 90 to day 240 the owl schedules itself for the next day, and then conducts breeding season behavior. In each step, the order of processes is: unsettled owl
movement, adult mortality, and habitat selection. Settling owls evict squirrels from their selected burrow. Then owls conduct a nesting check to see if they are settled in a burrow with a partner and are ready to breed. If so, female owls lay eggs. Next adult owls conduct a nest predation check and if predation has occurred there is a probabilistic chance of dispersal, representing nest abandonment. Eggs check to see if they have reached the end of the incubation period of 28 days, and if so the eggs become juveniles. Both juveniles and eggs are subject to daily mortality, and if both adults have dispersed after nest predation, eggs and juveniles remaining in the nest die. If juveniles survive the juvenile period of 40 days, they fledge. Fledglings are subjected to daily mortality. On the last day of the breeding season, day 240, stochastic owl nonbreeding mortality occurs, then remaining eggs and juveniles die, and fledglings become adults. On the first day of the nonbreeding season, day 241, the owl schedules itself for the next breeding season, and leaves the breeding ground.

The creation of burrows by squirrels is modeled explicitly for burrow location, use, and availability. During the burrow step method, the list of squirrels and owls occupying each burrow is updated, as is the counter for number of days a burrow has been unoccupied. Burrows are stochastically destroyed at a constant rate. Finally, burrows unoccupied for 6 months are removed from the population of burrows. On day 241, the predation status of each burrow is reset for the next breeding season.

1.3 Design concepts

In the model, dispersing owls move randomly through areas of variable and explicitly defined burrow availability and habitat quality. The complexity of the burrowing owl life cycle is represented by differences in dispersal and habitat selection rules based on the age, sex, and
nesting experience of individual owls, so that individuals accumulate a unique history of habitat selection decisions, breeding outcomes and dispersal. The model includes owl breeding and nonbreeding seasons, but focuses on the details of the breeding season. The only nonbreeding season process included explicitly in the model is mortality. During the nonbreeding season, owls leave the breeding grounds, accounting for both migration in migratory populations and regional movement in non-migratory populations.

Habitat selection decisions by owls are constrained by presence of required resources (burrows and mates), probability of selection, and by owls’ ability to accurately perceive habitat quality. The hierarchical habitat selection function has four components: available burrow space, whether a potential mate has already settled in the burrow, a probabilistic habitat selection function, and a logistic “closing time” rule based on the length of the breeding season: as the breeding season progresses, owls become more willing to accept lower quality habitat.

Both habitat selection and habitat quality are explicitly and separately modeled. The probability of selecting a given habitat can be isolated relative to the probability of mortality in that habitat. The two can be linked by assigning selection probabilities to a range of quality (mortality) values. When linked, individuals are more likely to select high quality habitats and less likely to select low-quality habitats. The impact of variation in habitat quality is expressed in terms of survivorship and reproduction, which ties the functions to the biological principle of fitness.

1.4 Emergence

In the model, owl population change (lambda) emerges from individual habitat selection decisions through the factors of habitat selection, habitat quality, and population density. The model enables the input of configurations of edge and interior habitat that vary the number of
core habitat patches, width of edge habitat, and difference in habitat quality between the core and edge areas. With the ability to test different scenarios of edge and interior habitat, spatial patterns of settled and nesting owls emerge. By separating the habitat selection rule from actual habitat quality, the model enables emergent population change and spatial patterns from scenarios where selection cues and habitat quality are either aligned or mismatched.

1.5 Adaptation

As the breeding season progresses, owls become more willing to accept less ideal habitat. The probability of settlement is set for each grid space, but is modified according to a logistic function that is defined by midpoint and slope parameters set by the user. Setting the midpoint parameter for later in the season and a high slope parameter results in a greater degree of choosiness in habitat selection by owls.

1.6 Objectives

The objective of the model is productivity, the number of juveniles who become fledglings during a breeding season. Breeding success is the core objective from which learning effects emerge, as the parent owls return to the breeding grounds the following season with a memory of breeding success associated with the breeding burrow.

1.7 Learning

Owls that successfully fledge young return to breeding grounds at the beginning of the next breeding season, with habitat selection priority over owls who were previously unsuccessful. The habitat selection rule for owls with a memory of success is modified by removing the probabilistic component for settling into an empty burrow. Therefore the owl settles in the same
location as the previous year as long as the burrow has not been destroyed. Learning from breeding success affects both the habitat settlement decision of the successful owl, and on owls in the vicinity who detect the successful settled owl as a potential mate.

1.8 Prediction

The degree and accuracy of prediction is variable, depending on how the user sets mortality rates. When the range of mortality rates are linked to the habitat quality scale, then owls are able to predict the effect of high or low quality habitat on their own survival and reproduction. The accuracy of prediction may be reduced by increasing the value of the information uncertainty parameter.

1.9 Sensing

Both owls and squirrels have the ability to sense their surroundings. For owls, unsettled owls evaluate their probability of settling in each grid space, and sense the presence of burrows, squirrels, and other owls in the habitat surrounding their current location, to a spatial distance specified by the user. After settlement, nesting adults sense the loss of single chicks when nest predation occurs and respond with probabilistic nest abandonment. Juveniles in turn sense when both nesting adults have abandoned the nest; juveniles cannot survive without parental care and die in response. Settled owls also sense stochastic burrow destruction and react by dispersing. For squirrels, the ability to sense is limited to sensing stochastic burrow destruction and habitat quality through a function soil texture and bare ground.
1.10 Interaction

Settling owls evict all squirrels currently in the burrow, but the competition for burrow space is unidirectional: squirrels never outcompete owls for an existing burrow. Unsettled owls compete with other owls for space in burrows; during each step, whichever owl senses a potential mate and settles, or probabilistically chooses to settle first in an available burrow gets the burrow space.

1.11 Collectives

The fate of eggs and juveniles is determined by nest. The probabilistic process of post-predation adult dispersal results in the death of all remaining eggs and juveniles if both adults abandon the nest.

1.12 Stochasticity

All of the processes for squirrel habitat selection, owl habitat selection in the absence of a potential mate already in the burrow, all daily owl and squirrel mortality rates, owl nonbreeding season mortality, nest predation, adult dispersal, and burrow destruction occur stochastically. Stochasticity is used to model realistic variability in two situations: a) for processes not modelled explicitly, such as predation; and b) to cause processes such as mortality to occur at a specified rate. For the stochastic process of post-predation adult dispersal from the nest, with each chick lost, the nesting adult owls consider dispersal. The loss of multiple chicks leads to a higher probability that parent owls abandon the nest.
1.13 Observer

The observer reports data at the end of each simulated year (one breeding season plus one nonbreeding season) and at the end of the simulation. Each report from the observer provides counts of the current number of owls, squirrels, and burrows, number of successfully breeding owls who survived to return the following year, number of owls who settled or nested, number of eggs laid, number of eggs surviving to juvenile stage, number of juveniles surviving to fledgling stage, number of fledglings surviving to adult stage. Mortality events are reported as number of mortality events for eggs plus juveniles, fledglings, breeding adults, and nonbreeding adults. Number of egg and juvenile deaths after nest abandonment is also counted. The observer reports the number of squirrels that settled, nested, juveniles born, and juveniles surviving to fledgling stage. Juvenile and adult squirrel mortality is reported as well as the number of squirrels evicted by owls. The number of owls and squirrels lost to the population by moving off the modeled landscape is also reported.

2.0 Initialization

Owls are initialized at the simulation start for sex, dispersal probability, and owl regional awareness distance and by variables that track location and status at each time step (lifestage, whether settled, nesting, bred, fledged, whether dispersed after nest predation, whether still alive, and memory of current and previous breeding success). When owls are initialized, the number of owls is input by the user. Owls are created according to a 1:1 sex ratio, and are initialized as live, unsettled adults who have not yet nested or bred. Dispersal status is set to undispersed, and owls have no memory of previous breeding success. Squirrels are similarly defined by one fixed parameter (sex) and several variables representing status (location, lifestage, whether settled,
nesting, fledged, evicted, and whether still alive). The number of squirrels set by the user is also created with a 1:1 sex ratio, and squirrels are initialized as unsettled adults that are not nesting, fledglings, evicted by owls, or dead.

The user determines the height and width of the overall landscape in grid spaces. The configuration of interior and border patches is determined by specifying the height and width of each patch and width of borders. For each grid space, parameters for habitat selection probability, bare cover, soil texture, degree of uncertainty about habitat selection probability and owl clutch size are each specified as a mean and standard deviation. Separate values for interior and border habitat can be input for each parameter. The rate of stochastic burrow destruction, which is held constant across core and edge patches, is also initialized, as is the number of breeding seasons to simulate.

Mortality rates vary by edge and interior and by lifestage: egg/juvenile, fledgling, and adult. The owl nonbreeding mortality rate for adults represents seasonal mortality from the end of one breeding season to the beginning of the next. The owl breeding season mortality rate is applied to each individual as a daily rate derived from the seasonal rate. The mortality rate for eggs and juveniles represents nest predation. Squirrels have separate mortality rates for adults and juveniles.

3.0 Submodels: owl habitat selection

Owls are scheduled to arrive on the breeding grounds on day 90. Owls that were successful in the previous breeding season arrive first and return to the location of the previous years’ burrow. If the burrow still exists and is unoccupied, they settle. Unsuccessful or inexperienced owls arrive next and land randomly on the breeding ground.
The habitat selection function is hierarchical. If there is a burrow for the owl and a potential mate, the owl always settles. In the absence of a potential mate, the probability of settlement is modified according to a logistic function that is defined by midpoint and slope parameters set by the user. Setting the midpoint parameter for later in the season and a high slope parameter results in a greater degree of choosiness in habitat selection by owls.