Research Article

Long-Term Population Dynamics of a Managed Burrowing Owl Colony

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ABSTRACT We analyzed the population dynamics of a burrowing owl (*Athene cunicularia*) colony at Mineta San Jose International Airport in San Jose, California, USA from 1990–2007. This colony was managed by using artificial burrows to reduce the occurrence of nesting owls along runways and within major airport improvement projects during the study period. We estimated annual reproduction in natural and artificial burrows and age-specific survival rates with mark–recapture techniques, and we estimated the relative contribution of these vital rates to population dynamics using a life table response experiment. The breeding colony showed 2 distinct periods of change: high population growth from 7 nesting pairs in 1991 to 40 pairs in 2002 and population decline to 17 pairs in 2007. Reproduction was highly variable: annual nesting success (pairs that raised ≥1 young) averaged 79% and ranged from 36% to 100%, whereas fecundity averaged 3.36 juveniles/pair and ranged from 1.43 juveniles/pair to 4.54 juveniles/pair. We estimated annual adult survival at 0.710 during the period of colony increase from 1996 to 2001 and 0.465 during decline from 2002 to 2007, but there was no change in annual survival of juveniles between the 2 time periods. Long-term population growth rate (λ) estimated from average vital rates was $\lambda_a = 1.072$ with $\lambda_i = 1.288$ during colony increase and $\lambda_d = 0.921$ ($\Delta\lambda = 0.368$) during decline. A life table response experiment showed that change in adult survival rate during increasing and declining phases explained more than twice the variation in growth rate than other vital rates. Our findings suggest that management and conservation of declining burrowing owl populations should address factors that influence adult survival. © 2011 The Wildlife Society.

KEY WORDS airport, *Athene cunicularia*, burrowing owl, California, demography, life table response experiment, mark recapture, population dynamics, survival.

Populations of many imperiled wildlife species vary through time, showing periods of growth and decline. Although variable, population and demographic performance of a species are necessary to evaluate a population's conservation status (Caswell 2001, Morris and Doak 2002), to identify factors limiting growth (Emlen and Pikitch 1989), and to understand relationships between habitat characteristics and population performance (Van Horne 1983, Garshelis 2000). Unfortunately, few wildlife studies are conducted for the length of time necessary to separate long-term trends from transient population dynamics and identify the influence of changes to key vital rates (Calder 1984, Wiens 1984, Durant et al. 2007). Thus, many studies provide only partial understanding of the forces influencing population dynamics over time. Similar challenges exist for management, where we seldom have the detailed, long-term monitoring data necessary to evaluate the effectiveness of management efforts (Dennis et al. 1991, DeSante and Rosenberg 1998). These problems are especially evident for small, isolated popula-

tions that exhibit temporal population fluctuations. In these cases, long-term population and demographic studies are needed to evaluate the variability in population performance, the contribution of different vital rates to population change, and the efficacy of management efforts.

Many populations of western burrowing owls (*Athene cunicularia hypugaea*) have declined in recent years (James and Espie 1997, Holroyd et al. 2001, Klute et al. 2003), and the owl's existence in isolated colonies exemplifies the challenges of conserving species with only short-term and local demographic data. Burrowing owl declines have been attributed to a variety of factors including habitat loss and conversion, loss of burrows due to control of burrowing mammals, and exposure to pesticides (James and Espie 1997, Klute et al. 2003). Long-term demographic and population-level information is needed to better understand why some burrowing owl populations have declined and to manage the factors that can contribute to population growth (DeSante and Rosenberg 1998, Holroyd et al. 2001).

Several studies have evaluated the demographic mechanisms of burrowing owl population dynamics. Haug et al. (1993) documented considerable annual variation in burrowing owl demographic rates, especially reproduction, which

should be expected given the burrowing owl's reproductive strategy (Lack 1968, Newton 1979). Age-specific survival rates have also been well documented (Haug et al. 1993), but analyses of survival rates over long time periods (i.e., >5 yr) or during phases of population change are less common. James et al. (1997) examined the parameters of a declining burrowing owl population over 6 years (1986–1992) in Saskatchewan, Canada and implicated nest predation, which caused complete nesting failures, as a primary causal factor. In a 4-year (1997–2000) study of a burrowing owl population in central California, USA, Gervais et al. (2006) found that a 1-year population increase was largely attributable to fecundity, whereas adult survival, and to a lesser extent juvenile survival, contributed to a 1-year population decline. Johnson (1997) analyzed the population dynamics of a small owl colony in Davis, California over a 10-year period (1981–1991) and suggested that stochastic environmental events, annual variation in reproduction and survival, and perhaps a regional trend of population decline contributed to an accelerated rate of decline in the study colony. Rosenberg and Haley (2004) reported high annual variation in reproduction during a 4-year (1997–2000) study of burrowing owl population dynamics in the Imperial Valley, California, where the density of owl pairs was relatively constant. Although these studies provide robust vital rate estimates for comparison, it is unclear to what extent changes in vital rates contributed to population change.

We studied the demography of a burrowing owl colony that occurred entirely within the managed vegetated areas on Norman Y. Mineta San Jose International Airport (SJC) in San Jose, California. Beginning in 1991, the SJC burrowing owl colony increased, which contrasted with the species' trend in the greater San Francisco Bay, California area where the burrowing owl population was estimated to have declined >50% from the mid-1980s to the early 1990s (DeSante et al. 1997, DeSante et al. 2007, Townsend and Lenihan 2007). The initial growth of the SJC colony was followed by a marked period of decline from 2002 to 2007, which coincided with continued decline in the local burrowing owl population in the south San Francisco Bay area (Wilkerson and Siegel 2010).

Burrowing owls are frequent residents on airports throughout their North American range (Haug et al. 1993, Mealey 1997, Trulio 1997, Barclay 2007). In fact, one of the early studies of burrowing owl biology was conducted by Thomsen (1971) on the Oakland, California airport 50 km from our study site. Regular mowing of airfield infields maintains short herbaceous vegetation conditions favored by burrowing owls (Haug et al. 1993), and secure perimeter fences keep airfields largely free of disturbance from humans and mammalian predators. Furthermore, in highly developed urban areas, airports are often attractive because they function as unintentional habitat islands in a matrix of otherwise unfavorable habitat (Barclay 2007). However, bird strikes by aircraft are an important safety issue on airports and there is concern that maintaining a resident species like the burrowing owl on airports might increase bird strikes (Federal Aviation Administration [FAA] 2004, 2006).

We estimated key demographic parameters (i.e., reproduction and survival) of the SJC burrowing owl colony during 2 distinct periods of population growth and decline. We had complete demographic data for several years of increase and decline, which met the recommendation by Wiens (1984) that a long-term study should span the periodicity of change. We used capture–recapture statistical techniques (White and Burnham 1999) to model recapture probability, survival, and other parameters, therefore enabling more accurate estimates of juvenile and adult survival over a long 12-year time period. Our objectives were to: 1) evaluate annual differences in reproduction of burrowing owls nesting in natural burrows and artificial burrows, 2) estimate juvenile and adult survival rates and determine temporal trends in these rates, 3) evaluate the effects of fecundity and survival on observed population change using a life table response experiment (LTRE; Caswell 1996), which can be useful for identifying management efforts to affect the most important vital rates, and 4) assess the effectiveness of managing burrowing owls on airports, including the implications for aviation safety.

STUDY AREA

The SJC airport was located in San Jose, California, 15 km from the south end of the San Francisco Bay. The airport occupied approximately 400 ha but contained only about 134 ha of vegetated area amidst paved surfaces (runways, taxiways, and aircraft parking ramps). The 42 vegetated areas between runways and taxiways (i.e., infields) supported mixtures of annual herbaceous plant species characteristic of the California annual grassland series (Sawyer and Keeler-Wolf 1995). Infields were mowed regularly during the spring and summer to maintain the vegetation <30 cm tall. California ground squirrels (*Spermophilus beecheyi*) were limited in numbers and distribution and occurred primarily in the northwest corner of the airfield where soils were more friable than in the south and east infields where the soils were more compacted. Ground squirrels were controlled (but not eliminated) every few years with diphacinone-treated bait and with broadcast zinc phosphide–treated grain bait in the fall of 2006. The airport was surrounded by an urban matrix of light industry, commercial development, urban streets, and highways (Buchanan 1997).

METHODS

We constructed artificial burrows using commercially available plastic irrigation valve boxes and 10-cm flexible plastic pipe described by Barclay (2008). We installed artificial burrows completely underground in burrowing owl management areas in infields adjacent to perimeter taxiways or off the ends of runways (Barclay 2007). We first installed 2 artificial burrows in 1990 after which we installed variable numbers annually in fall or winter to mitigate the closure of natural burrows or to replace artificial burrows that were in airport construction areas.

To study burrowing owl use of artificial burrows and to estimate survival rates, we banded all juvenile owls raised by pairs nesting in artificial burrows on the airport beginning in 1996 (Barclay 2007). We captured nestlings from 14 May to

1 August by hand inside artificial burrows after removing the lid of the nest chamber (Barclay 2008). We used a modified rubber garden hose to coax older nestlings out of artificial burrow tunnels. We also banded adult owls opportunistically captured while banding nestlings or when doing artificial burrow maintenance. We banded owls with a U.S. Geological Survey number 4 aluminum leg band on one leg and a blue aluminum band with a unique alphanumeric code (Acraft Sign and Nameplate Company, Edmonton, Alberta, Canada) on the other leg.

From January 1990 through December 2007 we counted burrowing owls during biweekly wildlife point counts at 6 locations and during travel among point-count locations on the airfield. The surveys served as a means of resighting marked owls and estimating total population size each year. We conducted 6-min point counts mostly in the morning, under favorable weather conditions for viewing birds (we postponed monitoring sessions during steady rain). We conducted bi-weekly point counts to comply with Federal Aviation Regulations (FAR Part 139) regarding wildlife hazard monitoring on airports serving air carriers. We recorded the age class of each owl (juvenile or adult) by plumage (Haug et al. 1993, Priest 1997) using age category conventions for banding (U.S. Fish and Wildlife Service 1991). We recorded gender of adult owls if we could reliably determine it based on plumage or behavior (Haug et al. 1993). We recorded whether each owl was banded, the color band number if we could read it, and whether the owl occupied a natural or artificial burrow. We also located and identified burrowing owls during the capture period, 14 May to 1 August, and recorded resightings of live owls and recoveries of dead owls during the non-capture period (2 Aug–13 May). Recoveries consisted of carcasses of dead owls found by JHB on the airport or reported by airport personnel and bands found at artificial burrows during banding or burrow maintenance. Encounters of banded owls included dead owls found off the airport reported to the Bird Banding Laboratory or JHB by the public and resightings of live owls off the airport by JHB and other local burrowing owl researchers (e.g., Trulio 1997, Trulio and Chromczak 2007).

We recorded locations of prospective nesting pairs, and band identity if known, beginning in March each year. We conducted bi-weekly monitoring and focused nesting owl censuses of occupied burrows from May through July (i.e., the nesting season) to determine reproductive status. We inferred nesting at burrows where we observed a pair of adult burrowing owls on >1 occasion during the early portion of the nesting cycle (Garcia and Conway 2009). We adjusted the frequency of nesting surveys during the nesting season until we obtained definitive information about the nesting status of each previously recorded pair (Steenhof and Newton 2007). We considered a nest successful if we observed ≥1 juvenile owl (2–4 weeks old) outside the burrow entrance (Garcia and Conway 2009). We assessed differences in annual (1990–2007) nesting success of pairs in artificial versus natural burrows with a paired *t*-test ($\alpha = 0.05$). We considered a pair unsuccessful if one or both adults abandoned an occupied burrow during the nest-

ing season or if we observed no juveniles at the burrow entrance through July. We could not directly compare reproduction of pairs nesting in artificial versus natural burrows because we measured true reproduction of pairs nesting in artificial burrows by opening artificial burrow nest boxes, whereas we estimated minimum reproduction for pairs in natural burrows using above-ground counts of juveniles. Estimates from the latter method may be biased low because an entire brood may not be seen above ground simultaneously (Gorman et al. 2003). In a study comparing detection probability of juveniles in 21 artificial burrow nests in California, Gorman et al. (2003) found that juvenile counts based on above-ground observation were 23% lower than true juvenile numbers. Although the actual bias of our count methods is not known, we applied a 23% adjustment factor to natural burrow juvenile counts as an approximation. We used a paired *t*-test to determine if annual reproduction varied by burrow type.

We obtained wildlife strike reports (FAA Form 5200-7) from SJC personnel each year (1990–2007) and reviewed them for accuracy of species identification if feathers were included. We assigned strike reports into 4 categories: hawk, owl, other bird, and unknown bird. We compiled all owl strike reports into one category because some strike reports stated the species was barn owl (*Tyto alba*) when burrowing owl feathers were included with the report and some strike reports gave the species as burrowing owl when barn owl feathers were included. Strike reports were filled out by airport personnel after runway inspections (several times a day) for all birds found dead or injured regardless of whether there was evidence that the bird was struck by an aircraft. Pilots also file strike reports when they believe they have struck a bird. We used a Pearson's correlation to determine the relationship between annual burrowing owl population size (adults and juveniles) and the number of owl strike reports. We emphasize that strike reports are only an index of bird strikes and we have no measure of actual bird strikes.

We estimated survival for juvenile (0–1 yr old) and adult (>1 yr old) burrowing owls using the Barker model (Barker 1997, 1999; Barker et al. 2004) within Program MARK (Version 4.3; White and Burnham 1999). The Barker model can accommodate multiple data types including live recaptures, live resightings, and dead recoveries from data collected during capture periods as well as between capture periods. Compared with the Cormack–Jolly–Seber model (CJS; Cormack 1964, Jolly 1965, Seber 1965), which only uses data from the capture period, the Barker model can improve accuracy of survival estimates by including additional data sources (i.e., recoveries and resightings outside the study area) and by modeling site fidelity, which helps separate the effects of mortality from permanent emigration (Lebreton et al. 1992). Because animals can be found dead or resighted alive outside the study area, the Barker model estimates true survival rates rather than apparent survival, which confounds mortality with emigration. The biological focus of our analysis was on age-specific survival, so we ignored the other nuisance parameters of the Barker model (i.e., those related to fidelity) that aid in its estimation.

Parameters estimated in the Barker model include: probability of survival (S_i), probability of capture (p_i), probability of dead recovery (r_i), probability of live resighting (R_i), probability of live resighting of birds that died within the annual period (R_i'), site fidelity (F_i), and temporary emigration (F_i').

We collected all data types (i.e., recaptures, live resightings, and dead recoveries) during the capture period (14 May–1 Aug) and we recorded resightings of live owls and recoveries of dead owls during the non-capture period. In the case of encounters of dead owls or band recoveries found during the capture period, we assigned the death of the bird to the previous non-capture period so that encounter histories for those animals would not incorrectly show survival through the capture period. Encounter histories spanned 12 years, beginning in 1996 when we began banding. We included resightings of live owls and recoveries of dead owls that occurred off the study area in the model and were thus accounted for explicitly. Considering that owls at SJC were highly observable and we conducted a complete census annually, these dispersal events supported our use of the Barker model.

We tested a set of 18 candidate models (Table 1) to estimate survival for juveniles (S_j) and adults (S_a). Burrowing owls demonstrate adult behavior, including breeding, at the end of their first year (Haug et al. 1993), suggesting that a 2-stage model would represent the most important variation in survival. Additionally, previous studies have found stage-structured survival rates in burrowing owls (Thomsen 1971, James et al. 1997, Johnson 1997, Lutz and Plumpton 1997, Gervais et al. 2006). For both juveniles and adults, we modeled survival as constant through time (c), annually variable (t), and as a 2-period time trend (T; Table 1). The 2 time periods included the years of observed population increase (T_i, 1996–2001), followed by the years of observed population decline (T_d, 2002–2007; Fig. 1). We modeled recapture rate (p) as constant with time and as a 2-stage model to account for possible differences in recapture rates between juveniles and adults. We modeled the other
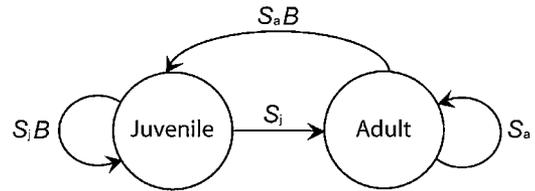

Figure 1. Two-stage life cycle diagram for post-breeding census of female burrowing owls at San Jose International Airport, California, USA, 1990–2007. We show vital rates for each arc. S_a is adult survival, S_j is juvenile survival, and B is fecundity. We show juveniles to be reproductive because they reproduce at the end of their first year.

nuisance parameters (r, R, R', F, and F') as constant with age and time.

We compared candidate models using Akaike's Information Criterion (AIC; Akaike 1973) corrected for small sample size (AIC$_c$; Burnham and Anderson 2002). Akaike's Information Criterion is an information-theoretic, model selection approach that balances model fit with the number of model parameters (Burnham and Anderson 2002). We ranked the 18 models according to ΔAIC$_c$, calculated for each model, i, as the difference between its AIC$_c$ value and the best-fit model (Burnham and Anderson 2002). We considered models with ΔAIC$_c \leq 2$ to have strong support and models with ΔAIC$_c > 10$ to have minimal support (Burnham and Anderson 2002). We also calculated AIC$_c$ weights (w_i) for each candidate model in order to evaluate its relative support from the data.

Of the 679 owls banded, we identified 92 as males or females when we re-sighted them as adults. We used the least parameterized Barker model $[S(a2 - c/c)p(.)r(.)R(.)R'(.)F(.)F'(.)]$ and a subset of the data including individuals of known sex, to determine the effect of sex on stage-structured survival. To assess goodness-of-fit, we used the median $\hat{c}$ procedure in Program MARK. The value $\hat{c}$ is an estimate of model overdispersion (lack of fit), which in turn, can affect model selection (Burnham and Anderson 2002).

Table 1. Parameter combinations modeled with the Barker model. We determined the effect of time on burrowing owl survival as an annual effect (t), a trend with survival calculated for 2 time periods (T; 1996–2001 and 2002–2007), and constant with time (c), at San Jose International Airport, California, USA.

Model description	Model name
Basic Barker model	$S(.) \, p(.) \, r(.) \, R(.) \, R'(.) \, F(.) \, F'(.)$
Survival—2-stage: juveniles constant, adults constant	$S\,(a2 - c/c)$
Survival—2-stage: 2-period time effect on juveniles, adults constant	$S\,(a2 - T/c)$
Survival—2-stage: juveniles constant, 2-period time effect on adults	$S\,(a2 - c/T)$
Survival—2-stage: 2-period time effect on juveniles and adults	$S\,(a2 - T/T)$
Survival—2-stage: annual time effect on juveniles, adults constant	$S\,(a2 - t/c)$
Survival—2-stage: juveniles constant, annual time effect on adults	$S\,(a2 - c/t)$
Survival—2-stage: annual time effect on juveniles and adults	$S\,(a2 - t/t)$
Survival—2-stage: 2-period time effect on juveniles, annual time effect on adults	$S\,(a2 - T/t)$
Survival—2-stage: annual time effect on juveniles, two-period time effect on adults	$S\,(a2 - t/T)$
Recapture—no age effect: constant through time (all years)	$p(.)$
Recapture—2-stage: juvenile and adults, no time effects	$p(a2 - c/c)$
Recovery: constant	$r(.)$
Resighting: constant	$R(.)$
Resighting': constant	$R'(.)$
Fidelity: constant	$F(.)$
Return parameter: constant	$F'(.)$
(9 Survival) × (2 Recapture) × (1 Recovery) × (1 Resighting) × (1 Fidelity) × (1 Return) × (1 Resighting') = 18 models	

We used model averaging within MARK to estimate S_j and S_a from comparable models that included 2-period trend analysis (T) of survival. To calculate an average demographic response for subsequent LTRE analysis (see below), we also estimated time-invariant juvenile survival by averaging the 6 models for which we held juvenile survival constant. We followed the same method to estimate time-invariant adult survival.

We estimated population trends by calculating the annual realized population growth rate (λ_r) as N_{t+1}/N_t, with N = total adult and juvenile owls observed during the capture period and t = year, and we calculated average $\overline{\lambda}_r$ as a geometric mean for the years 1991–2007. We also used stage-based matrix population models to estimate the long-term population growth rate (Lefkovitch 1965, Caswell 2001) for the time period 1996–2007 (λ_a). We used a 2-stage life-cycle model based on a post-breeding census of females (Fig. 1). The basic form of the population projection matrix, $\mathbf{A}$, was:

$$\mathbf{A} = \begin{bmatrix} S_j B & S_a B \\ S_j & S_a \end{bmatrix}$$

where the 4 matrix elements were composed of vital rate estimates including B (female young per breeding female), S_a, and S_j. We assumed fecundity rates of juvenile (at the end of their first year) and adult females were the same. We estimated λ_a as the dominant eigenvalue of the matrix (Caswell 2001) and determined the sensitivity of λ_a to small perturbations in each of the matrix elements using the equation:

$$s_{ij} = \frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_j}{\sum_{k=1}^{s} v_k w_k}$$

where s_{ij} is sensitivity of the matrix element, w_j is the jth element of the dominant right eigenvector, and v_i is the ith element of the dominant left eigenvector. However, sensitivities calculated in this way represent whole matrix elements (a_{ij}), not vital rates, which are often more relevant to understanding how changes in population growth may be partitioned by demographic rate. To calculate the sensitivity of λ to lower-level vital rates, we used the chain rule for differentiation (Caswell 2001). We calculated sensitivity of each of the k vital rates, r (S_a, S_j, and B) as:

$$s_{r_k} = \sum_{i=1}^{s} \sum_{j=1}^{s} \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial r_k} = \sum_{i=1}^{s} \sum_{j=1}^{s} s_{ij} \frac{\partial a_{ij}}{\partial r_k}$$

We also calculated elasticity of λ for each vital rate using:

$$E_{r_k} = \frac{r_k}{\lambda} \frac{\partial \lambda}{\partial r_k}$$

We conducted a LTRE analysis to assess the relative importance of demographic rates in explaining the observed change in population growth rate during the increasing and declining phases of study (Caswell 1996, 2001). When λ varies due to experimental manipulation or when comparing groups (or time periods), a LTRE can be used to calculate the proportional change in λ attributable to vital-rate differences between groups. Unlike sensitivity analysis, LTRE accounts for the observed magnitude of change in each vital rate. Thus, vital rates with high sensitivities but low variation may be less important to population growth rate than less sensitive but highly variable vital rates (Mills and Lindberg 2002).

The 1996–2007 matrix ($\mathbf{A}_{96-07}$) served as our average projection matrix and provided the vital rate sensitivities necessary for the LTRE. Using the methods described above, we used stage-based matrix population models to calculate λ for the periods of population increase (λ_i: 1996–2001) and decrease (λ_d: 2002–2007). To parameterize the period-specific projection matrices $\mathbf{A}_i$ and $\mathbf{A}_d$, we estimated demographic rates (S_a, S_j, and B) separately for the 2 time periods. We calculated the change in λ between the 2 time periods by $\Delta\lambda = \lambda_i - \lambda_d$, which is also approximated by:

$$\approx \sum_k (r_{k_i} - r_{k_d}) \times s_{r_k}$$

where $(r_{k_i} - r_{k_d})$ is the difference in vital rate k between the increasing period and the declining period, and s_{r_k} is the sensitivity of that vital rate as calculated from the average matrix ($\mathbf{A}_{96-07}$). For each vital rate, we divided the $[(r_{k_i} - r_{k_d}) \times s_{r_k}]$ term by the estimated change in λ to calculate the percent LTRE contribution, or the amount of change in λ attributable to that vital rate.

RESULTS

We recorded 342 pairs of adult burrowing owls during the breeding seasons (Mar–Jul) from 1990 to 2007 (Fig. 2, Appendix). The annual breeding population at SJC increased from a low of 7 pairs in 1991 to a high of 40 pairs in 2002 (Fig. 2). Expressed as total burrowing owls (adults and juveniles) observed during the breeding season, the colony increased by an average of 4.8% per year ($\overline{\lambda}_r = 1.048$; Fig. 3). There was considerable variability in the observed annual population growth rate during the study period, especially in the early years when the population was small (Fig. 3).
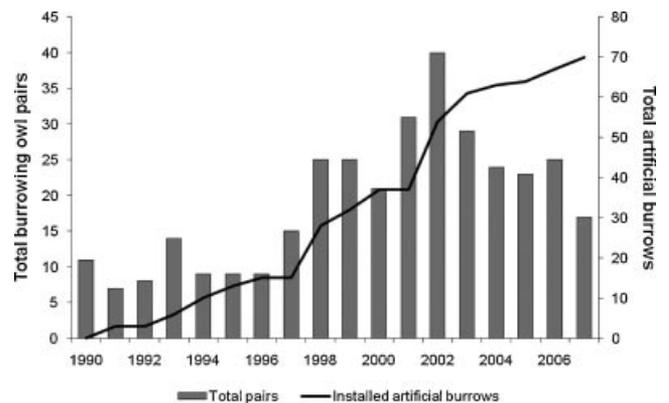

Figure 2. Annual census (1990–2007) of adult burrowing owl pairs at San Jose International Airport, California, USA, and annual availability of artificial burrows.
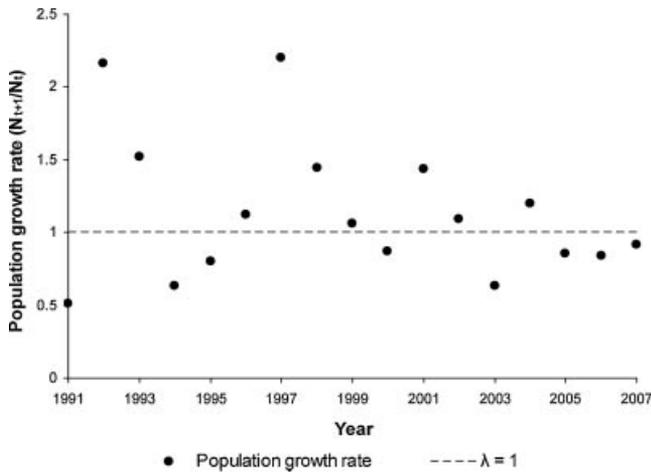
Figure 3. Annual (1991–2007) realized population growth rate (λ_r) of all burrowing owls (adults and juveniles) at San Jose International Airport, California, USA. Dashed line represents stable population growth for reference.

Figure 5. Annual (1990–2007) nesting success of burrowing owl pairs in artificial burrows (AB) and natural burrows (NB) at San Jose International Airport, California, USA. We considered a nest to be successful if we observed ≥1 2–4-week-old juvenile outside the burrow entrance. Dashed lines represent average nesting success in artificial and natural burrows.

Recruitment of juvenile and adult owls from artificial and natural burrows also varied (Fig. 4). Population size showed a clear increasing trend from 1990 to 2002 and a declining trend from 2002 to 2007 (Figs. 2 and 4). We found no correlation between annual strike reports of owls ($\bar{x} = 5.4$, SD = 5.7, range = 0–22 strike reports per year, including some barn owls) and annual burrowing owl population size (Pearson correlation = 0.185; $P = 0.477$).

From 1990 to 2007, 274 breeding pairs produced ≥1 young for an average nesting success rate of 79% (SD = 0.156; Fig. 5). Nesting success in natural burrows varied considerably from a low of 36% in 1990 to highs of 100% in 1992, 1996, and 1999 (Fig. 5). Average nesting success was 87% (95% CI = 0.807–0.935) in artificial burrows ($N = 189$ pairs) compared to 76% (95% CI = 0.662–0.848) in natural burrows ($N = 153$ pairs), and a paired t-test across all 17 years showed the 11% difference was marginally significant ($P = 0.07$; Fig. 5).

Reproduction averaged 3.36 juveniles/pair (SD = 0.982), but it was highly variable, ranging from 1.43 juveniles/pair in 1991 to >4 juveniles/pair in 6 other years (Fig. 6). Pairs nesting in artificial burrows produced an average of
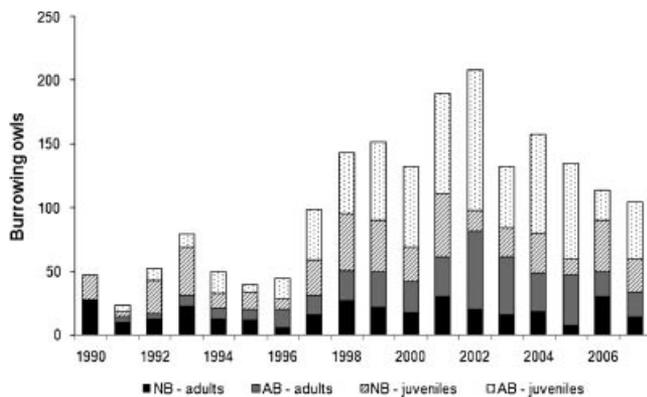

Figure 4. Annual (1990–2007) numbers of adult and juvenile burrowing owls in artificial (AB) and natural burrows (NB) at San Jose International Airport, California, USA.
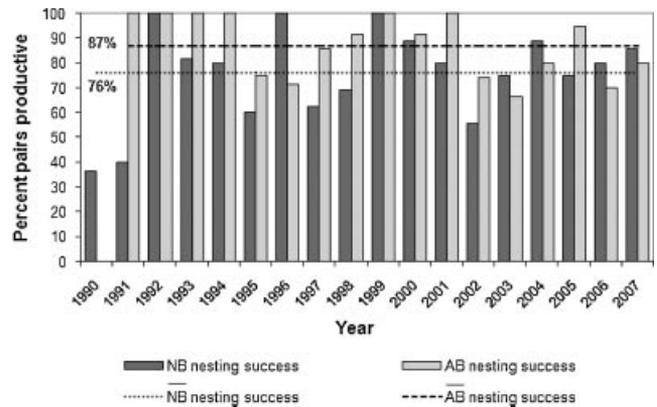
3.80 juveniles/pair (SD = 1.234) compared to an estimated 3.03 juveniles/pair (SD = 0.892) in natural burrows. With natural-burrow counts adjusted by 23%, reproduction of adults in artificial and natural burrows was not different (paired t-test, $P = 0.646$).

At SJC 55% of all nesting pairs used artificial burrows and 45% used natural burrows. The annual proportion of pairs occupying natural burrows ranged from 100% in 1990 (when no artificial burrows were present) to 17% in 2005 (Figs. 2 and 4). Pairs of owls occupied artificial burrows at 33% of their availability over the study period (189 pair occupancy-years out of 578 artificial burrow-years, Fig. 2). Of the 111 burrows installed during 18 years, 82 (74%) were occupied by a pair at least once during a nesting season, and these artificial burrows were occupied an average of 48% (SD = 0.272) of the years they were available. Of 79 artificial burrows available ≥3 years, 23 (29%) were occupied by nesting pairs ≥3 years. The first artificial burrow installed in 1990 was occupied 14 of 15 years (93% occupancy).

We banded 679 burrowing owls comprised of 656 nestlings and 23 adults from 14 May to 1 August. The median $\hat{c}$ procedure showed adequate model fit for the most parameterized Barker model and no evidence of overdispersion ($\hat{c} = 1.093$, SE = 0.003). There was no support for inclusion of sex effects on juvenile or adult survival in the least parameterized Barker model ($\Delta AIC_c = 1.91$), probably due to a low sample size of individuals of known sex; therefore we excluded sex as a factor in all subsequent models.

The 3 top-ranked models with $\Delta AIC_c < 2$ showed stage-structured survival and time period–dependent (T) survival for adults (Table 2). The best-fit model estimated juvenile survival as constant over the 12-year time period ($S_j = 0.262$, SE = 0.024) and adult survival as higher during the time of population increase (1996–2001; $S_{a_i} = 0.708$, SE = 0.055) and lower during population decline ($S_{a_i} = 0.460$, SE = 0.040). In our final estimation of these rates, we averaged estimates across all models weighted by their model support, which yielded similar final estimates (Table 3).
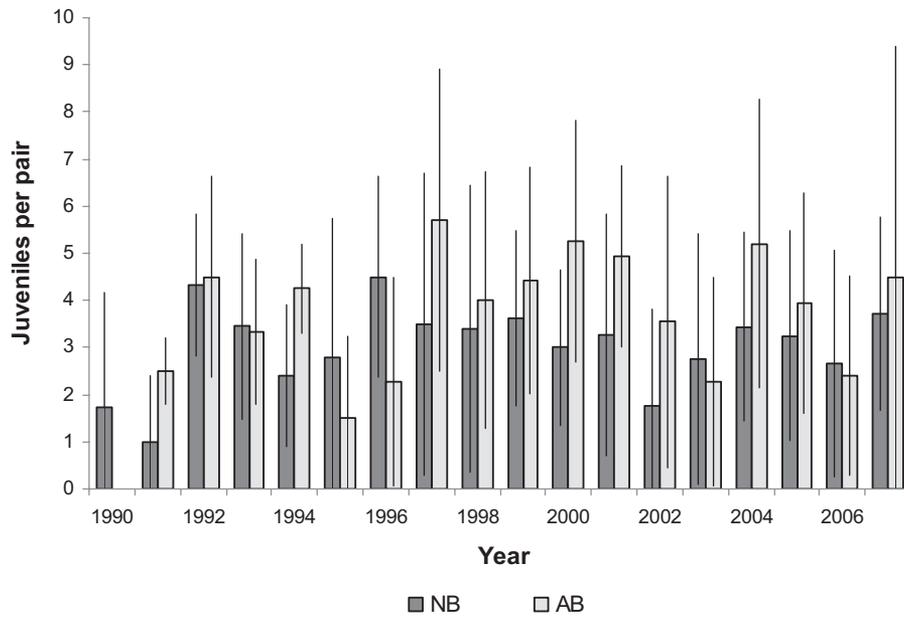
Figure 6. Annual (1990–2007) reproduction (juveniles per pair [SD]) of burrowing owls in artificial burrows (AB) and natural burrows (NB) at San Jose International Airport, California, USA. We used above-ground observations to estimate reproduction in natural burrows, whereas we based reproduction in artificial burrows on counts of nestlings inside nest chambers.

Long-term population growth rate (λ_a) estimated from average vital rates was 1.072, which was within 3% of the annual realized population growth rate. Long-term population growth rate calculated with vital rates from the increasing period was much higher ($\lambda_i = 1.288$) than population growth rate based on vital rates from the population decline ($\lambda_d = 0.921$; $\Delta\lambda = 0.368$). Sensitivity of λ_a to juvenile survival was twice as great as sensitivity to adult survival and sensitivity of λ_a to fecundity was low (Fig. 7). Elasticities of all 3 vital rates were approximately 0.50. Elasticities of vital rates do not necessarily sum to 1 as do elasticities of matrix elements (Caswell 2001).

Despite high sensitivity of λ to juvenile survival, the LTRE analysis revealed that adult survival was the major LTRE contributor (Fig. 7), explaining more than twice the variation in λ than the other vital rates. The higher contribution of adult survival was attributable to the large magnitude of change in estimated adult survival between the 2 time periods (Table 3). Although λ was highly sensitive to juvenile survival (Fig. 7), low variation (Table 3) tempered its effect. The weak influence of fecundity on annual population growth was further substantiated by regression analysis that showed a weak relationship between annual growth of the adult population and reproduction the previous year (juveniles per

Table 2. Models of survival probability (*S*) for burrowing owls at San Jose International Airport, California, USA, 1996-2007 ($n = 679$). All models estimated survival separately for juveniles (0–1 yr) and adults (>1 yr), indicated by the nomenclature, *S* (a2-juvenile/adult). We modeled survival as constant with time (*c*), as a function of time period (*T*; 1996–2001 and 2002–2007), or as an annual time effect (*t*). We listed models by Akaike Information Criterion (AIC$_c$) and show only models with AIC weights (w_i) > 0.05.

Model	ΔAIC$_c$	AIC$_c$	w_i	K	Deviance
S (a2 − *c/T*) *p*(a2 − *c/c*) *r*(.) *R*(.) *R'*(.) *F*(.) *F'*(.)	0.000	2,357.3	0.338	10	677.6
S (a2 − *T/T*) *p*(a2 − *c/c*) *r*(.) *R*(.) *R'*(.) *F*(.) *F'*(.)	1.388	2,358.7	0.169	11	676.9
S (a2 − *c/T*) *p*(.) *r*(.) *R*(.) *R'*(.) *F*(.) *F'*(.)	1.434	2,358.7	0.165	9	681.0
S (a2 − *T/T*) *p*(.) *r*(.) *R*(.) *R'*(.) *F*(.) *F'*(.)	2.751	2,360.0	0.085	10	680.3
S (a2 − *c/t*) *p*(a2 − *c/c*) *r*(.) *R*(.) *R'*(.) *F*(.) *F'*(.)	2.953	2,360.3	0.077	20	659.9
S (a2 − *c/t*) *p*(.) *r*(.) *R*(.) *R'*(.) *F*(.) *F'*(.)	3.754	2,361.1	0.052	19	662.8

Table 3. Model-averaged survival estimates for juveniles and survival and fecundity estimates for adult burrowing owls at San Jose International Airport, California, USA, 1996–2007. T_i and T_d correspond to periods of population increase and decline, respectively. We calculated model-averaged survival estimates for 3 time periods for use in a life table response experiment analysis, although model selection showed strong support for a 2 time-period time effect on adults and no time effect on juveniles.

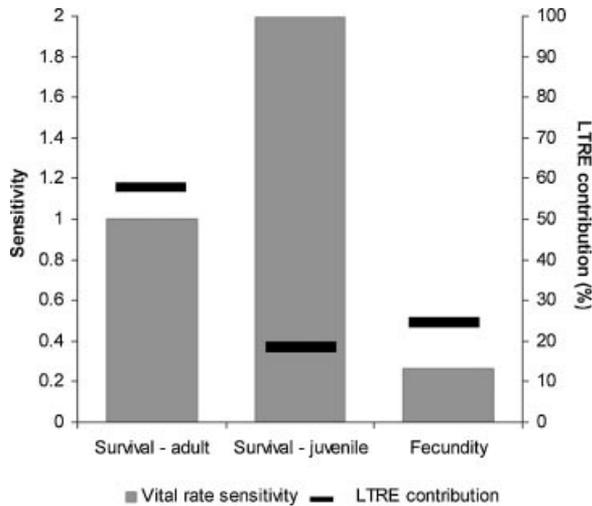|	Juvenile		Adult			
Time period	Survival	95%CI	Survival	95%CI	Fecundity	95%CI
T_i: 1996–2001	0.278	0.216–0.349	0.710	0.590–0.807	2.19	1.59–2.79
T_d: 2002–2007	0.241	0.186–0.306	0.465	0.387–0.545	1.80	1.17–2.43
1996–2007	0.258	0.214–0.309	0.545	0.479–0.610	1.99	1.62–2.37

Figure 7. Life table response experiment (LTRE) showing sensitivity and percent contribution of vital rates (1996–2007) to population change in the burrowing owl population at San Jose International Airport, California, USA.
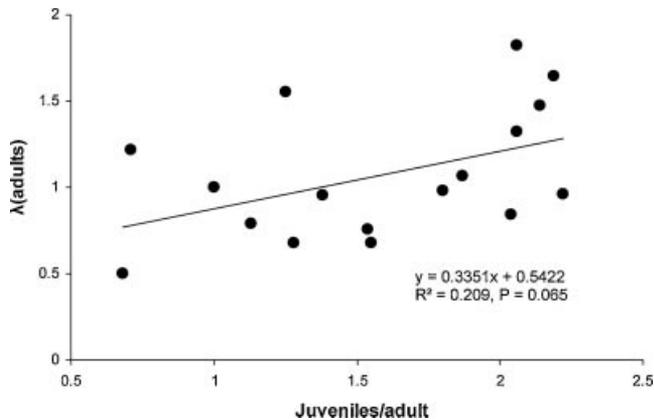

Figure 8. Annual (1991–2007) realized growth rate of the adult burrowing owl population (λ = adults$_{t+1}$/adults$_t$) and annual reproduction (juveniles per adult in year t, 1990–2006) of burrowing owls at San Jose International Airport, California, USA. Linear regression showed that annual reproduction explained little of the variation in annual adult population growth rate.

adult; R^2 = 0.209, P = 0.065, Fig. 8). Fecundity had low sensitivity and varied little between the increasing and declining phases (Table 3).

DISCUSSION

The long-term nature of the demographic and population-level monitoring in our study provides a unique glimpse at the factors influencing the dynamics of this population over time, especially because annual censuses of adult owls in our study area showed 2 distinct periods of population growth: one of marked increase from 1996 to 2001 and another of decline from 2002 to 2007 (Fig. 2). Reproduction (i.e., nesting success and fecundity) by burrowing owls at SJC was highly variable (Figs. 5 and 6), and the variation we recorded fell within the wide ranges reported in other studies. Average nesting success of 0.79 at SJC was in the upper half of values reported from 10 other studies where nesting

success averaged 0.69 (median 0.71) in a range from a low of 0.45 (3 yr, Mealey 1997) to a high of 1.0 (2 yr, 15 pairs, Martin 1973). The effect of burrow type on nesting success was marginally significant (P = 0.07), suggesting that nesting success of owls in artificial burrows was comparable to that of owls in natural burrows. The 33% occupancy rate we observed was similar to the 35% occupancy rate Smith et al. (2005) reported for 23 artificial burrows installed within 200 m of natural burrows in Washington, but less than the 55% occupancy of artificial burrows in Idaho reported by Belthoff and Smith (2003).

Average fecundity of 3.36 juveniles/pair (SD = 0.982) at SJC was also above the average (non-weighted) fecundity of 3.10 juveniles/pair from 15 other studies, where it ranged from 2.0 juveniles/pair (Ronan 2002) to 4.9 juveniles/pair (or nest; Martin 1973, see summaries in Haug et al. 1993, Klute et al. 2003). Average annual juvenile survival of 0.258 at SJC was within the range of 0.120–0.307 that Gervais et al. (2006) reported during 4 years (1997–2000) in a burrowing owl colony in central California. Annual adult survival of 0.545 also fell within the range of adult survival from 0.294 to 0.575 that Gervais et al. (2006) reported. Although vital rates we estimated were within the ranges from studies elsewhere, our study is the first to identify significantly different adult survival rates corresponding with periods of population increase and decline (Table 3). However, the dynamics of the resident burrowing owl population at SJC may not be representative of the dynamics of migratory populations where natal and breeding dispersal can confound accurate estimates of survival rates (e.g., James et al. 1997, Lutz and Plumpton 1997).

No studies have reported a distinct multi-year period of increase similar to what we observed (Fig. 2), so we are unable to compare vital rates coincident with growth in other increasing populations. Poulin et al. (2001) and Poulin (2003) reported a direct relationship between fecundity and population increase and a delayed (1 yr) numerical response by burrowing owls to a 1-year meadow vole (*Microtus pennsylvanicus*) irruption in an otherwise declining owl population in Saskatchewan. At SJC we initially suspected that management of this population with the construction of artificial burrows may have contributed to positive growth by increasing nest burrow availability and enabling higher fecundity of owls nesting in artificial burrows; however, reproduction of owls nesting in artificial and natural burrows was equivocal and population growth showed no strong correlation with fecundity (Fig. 8).

The decline of the SJC colony since 2002 was qualitatively similar to declines reported in some other burrowing owl populations in western North America (e.g., James et al. 1997, Johnson 1997, Wellicome et al. 1997). James et al. (1997) suggested that increased nest predation and reduced recruitment was responsible for declines observed during a 6-year study of an owl population in Saskatchewan. In that study estimated adult survival, based on resightings of banded adults, increased while the observed annual numbers of pairs declined. In another study to investigate the influence of enhanced reproduction on population change, Wellicome

et al. (1997) reported that supplemental feeding during the nesting cycle and modified artificial burrow entrances to reduce nest predation increased the number of young raised and initially lessened the rate of annual population decline. However, these experimental management activities did not reverse the long-term decline of their study population in Saskatchewan.

Our most important finding was the survival analysis showing that adult survival changed significantly between the increasing and declining phases and the LTRE indicating that adult survival contributed to >50% of the variation in λ. Gervais et al. (2006) also concluded that lower adult and juvenile apparent survival in a burrowing owl population in the Central Valley of California had a greater effect on population growth than did lower fecundity. Gervais et al. (2006) concluded that increased fecundity contributed more to positive population growth during years of greater California vole (*Microtus californicus*) abundance.

The natural history of the burrowing owl including the short lifespan, large clutch size, asynchronous hatching, and high reproductive potential suggests a reproductive strategy that evolved to take advantage of favorable breeding conditions, especially irruptive abundance of small mammal and insect prey (Poulin 2003). Population change in species with these life-history characteristics is generally more sensitive to reproduction than survival (Emlen and Pikitch 1989, Gervais and Rosenberg 1999). The results of our LTRE and the analysis of population change by Gervais et al. (2006) show that λ is theoretically most sensitive to changes in juvenile survival (Fig. 7). However, we found no evidence that this vital rate changed between the increasing and declining population phases of our study (Table 3), thus juvenile survival did not influence the change we observed in population growth. Furthermore, results of supplemental feeding experiments (Wellicome et al. 1997) and numerical response of burrowing owls to prey irruption (Poulin et al. 2001, Poulin 2003, Gervais et al. 2006) suggest that short-term transient population growth can be sensitive to fecundity and juvenile survival, especially positive changes in response to increased prey abundance. In our study, these short-term responses appeared to have been outweighed by the greater contribution of changes in adult survival rates that influenced change at the population level. These results suggest that reductions in adult burrowing owl survival may also contribute to longer-term declining trends.

Estimating demographic rates and analyses using population models have added much to our understanding of wildlife population dynamics (Caswell 2001, Morris and Doak 2002). The ability to use sensitivity and elasticity analyses to evaluate the influence of changes to specific vital rates has been particularly useful because it can often suggest management actions that can enhance key demographic rates to which λ is most sensitive (Crouse et al. 1987). But, as our study shows, large changes to vital rates of low sensitivity (adult survival in this case) can be substantial enough to contribute to population decline. A more striking pattern occurred with the decline of peregrine falcons (*Falco peregrinus*). As a longer-lived and less fecund raptor than

burrowing owls, peregrine falcon population growth is less sensitive to reproductive rates and more sensitive to changes in adult survival rates (Emlen and Pikitch 1989, Wootton and Bell 1992). Yet, it was a profound decline in reproduction caused by organochlorine pesticide–induced eggshell thinning (Peakall 1976, Peakall and Kiff 1979) and widespread nesting failure that caused the historic, global declines of peregrine falcon populations (Hickey 1969).

Caswell (2000) has argued that sensitivity analyses (i.e., prospective analyses) are most appropriate to guide management efforts and that LTRE (i.e., retrospective analyses) only identify the factors that have been important for populations in the past. However, we suspect that long-term studies such as ours will allow researchers and managers alike to better understand how empirical patterns of vital-rate change influence population dynamics, especially the vital rates that contribute to increase and those that influence decline. Despite their retrospective nature, we suggest that such long-term monitoring and modeling will allow managers to better identify on-the-ground actions that can improve key vital rates identified by such analyses. For burrowing owls on SJC, it appears that management directed towards enhancing adult survival might be most effective at enhancing population growth. Our findings suggest that management such as supplemental feeding (Wellicome 1997, Wellicome et al. 1997), or augmenting reproduction through fostering (Barclay 1987)—both actions directed towards increasing fecundity—may not be effective at reversing decline and bringing about long-term population stability.

The LTRE suggests that the proximate cause of the change in the SJC owl colony was change in adult owl survival. However, despite our long-term study of this population the ultimate cause of lower adult survival during the period of decline is unclear. Factors that could have contributed to lower adult survival rates include increased predation, lower over-winter survival, or emigration. Although we have no estimates of the incidence of predation on burrowing owls on SJC, long-term wildlife monitoring data (biweekly, 1990–2007; J. H. Barclay, Albion Environmental, unpublished data) suggested no conspicuous changes in the predator community on the airport where mammalian predators such as red foxes (*Vulpes fulva*), striped skunks (*Mephitis mephitis*), and feral dogs and cats were rare. Avian predators typically increased during spring and fall migration, but there have been no conspicuous long-term increases in raptor abundance or persistence observed during airport bird monitoring (J. H. Barclay, unpublished data). However, we cannot rule out predation having contributed to lower adult survival rates in recent years.

Burrowing owl habitat on the airport was affected beginning in 2000 and continued intermittently through 2006 in the form of temporary habitat disturbance associated with airport improvement projects (e.g., lengthening and resurfacing runways). Together these projects caused temporary disturbance in the form of vegetation and topsoil removal and compaction in approximately 79 ha (59%) of infield area and permanent habitat loss from increased paved area totaling about 10 ha (7.5%) of infields. Temporary habitat dis-

turbance lasted only a few months after which mixed herbaceous vegetation typical of the airport's infields was restored. Small mammal populations are sensitive to changes in aboveground plant structure and biomass caused by fire and grazing (Cook 1959, Grant et al. 1982). Removal of vegetation and topsoil in the airport improvement project areas was thorough and eliminated the vegetation and soil media used by litter-dwelling and burrow-dwelling small mammals (Grant and Birney 1979, Grant et al. 1982). Adult burrowing owl over-winter survival could have been affected by project-related changes to the plant and animal communities on the airfield. If effects on the prey base had influenced adult survival we would have expected to see an effect on juvenile owl survival as well, yet we found none (Table 3).

We received information about encounters off the airport of 12 (1.7%) burrowing owls banded as nestlings at SJC and the most distant of these was an owl observed nesting at Moffett Federal Airfield 12 km from SJC. None of the 12 banded owls that dispersed from SJC represented dispersal of an owl banded as an adult or seen as an adult at SJC and later encountered off the airport. These records suggest emigration was not common. Johnson (1997) also reported a low dispersal rate (2 of 87 owls or 2.3%) from an owl colony in Davis, California. We observed 4 owls on SJC that were banded off the airport and the most distant was an owl banded as a nestling approximately 7 km away.

Although some emigration from our study population occurred, we think dispersal contributed little to the population decline we observed. Burrowing owls in resident and migratory populations exhibit high site fidelity (Haug et al. 1993). Several studies including those of resident burrowing owls in California (Rosenberg and Haley 2004, Gervais et al. 2006, Rosier et al. 2006) show that juveniles disperse farther and more frequently than adults. Our limited dispersal data are consistent with the notion that dispersal is more common in juveniles than adults. Rosenberg and Haley (2004) estimated probability of emigration of adult burrowing owls in the Imperial Valley as <0.04. Thus, if dispersal differed greatly between increasing and decreasing phases of our study, we would expect it to influence estimates of juvenile survival, not adult survival, as we found. Finally, we note that burrowing owls were intensively monitored in other colonies in the Santa Clara Valley (Trulio 1997, Trulio and Chromczak 2007) and >800 owls were banded during our study period at other locations in the Santa Clara Valley (Harman and Barclay 2007). Given such intense banding and monitoring, we would have expected more observations of immigrants and emigrants if dispersal was more common than suggested by 12 reported encounters.

MANAGEMENT IMPLICATIONS

Artificial burrows were an effective management tool at SJC that facilitated managing the spatial occurrence of nesting owls and mitigating owl strikes by minimizing the occurrence of nesting owls along the edges of runways. Their use provided nesting opportunities comparable to natural burrows, allowing managers to offset the effects of intentionally closing burrows near runways and in construction areas. Each year 10–20% of artificial burrows at SJC required minor maintenance to clear their entrances. This rate of artificial burrow closure fell within the range of 0–33% ($\bar{x} = 17\%$) of natural burrows that Holmes et al. (2003) reported were closed due to natural processes (i.e., erosion). Some burrows at SJC were made unavailable by valley pocket gophers (*Thomomys bottae*) that filled the tunnels with soil. Our finding that annual strike reports of owls (including some barn owls) were not correlated with the annual burrowing owl population size suggests that burrowing owls can be maintained on airports without compromising aviation safety. This was likely facilitated by preventing owls from nesting along runway edges, where owls hunting from low perches would be exposed to aircraft moving nearby at high speed. These findings suggest that it is possible to maintain regional burrowing owl numbers by careful management in isolated habitat patches surrounded by intense development. Given limited resources, we suggest managers focus on accurately estimating annual adult owl populations rather than devoting time to estimating reproduction, which shows high annual variation and is difficult to accurately estimate. Future research should address management opportunities to enhance adult survival.

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Appendix. Burrowing owl reproduction in natural and artificial burrows at San Jose International Airport, California, USA, 1990–2007.

Burrow type	Adults	Pairs	Productive pairs	Percent productive	Juv	Mean juv/pair	SD	Mean juv/adult	SD
Natural burrows	325	153	115	75	459	3.03	0.89	1.41	0.43
Artificial burrows	386	189	159	84	735	3.80	1.24	1.90	0.63