The Case for Quail Reintroduction, Section 2: Viability

Articulating the benefits, outcomes, and long-term strategy for a sustainable reintroduction plan for California Quail in the Presidio

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Section II:
Reintroduced Quail Population Viability

One way to evaluate the potential success of a reintroduced population is to simulate expected population viability through time. Population viability analysis (PVA) is a widely-used tool for species management and conservation due to the focus on the factors that limit a population's persistence and growth. In the context of species reintroductions, PVA can model the impacts of initial release strategies as well as management strategies following reintroduction. Here we evaluate the likely persistence of a reintroduced California quail population to the Presidio under a range of conditions.

Model Approach

To select our approach we did a systematic review of the population viability literature for reintroduced or translocated populations to understand the current state of analytical approaches. We searched Web of Science through the end of 2021 using the following search terms: (reintroduc* OR re-introduc* OR translocat*) AND (population model* OR population viability*). We built upon an existing search covering literature prior to 2010 by Armstrong and Reynolds (2012). We filtered the results to papers where data were modeled to predict the viability of an existing or potential translocated or reintroduced population. This resulted in 116 papers. Before 2010, about half of the papers used specialized PVA software (e.g., RAMAS, Riskman, Vortex), with Vortex being the most popular. The remaining papers used custom-coded approaches in other software such as Matlab, Microsoft Excel, SAS, and R. After 2010, Vortex became the dominant method used for all such analyses (>70%).

We chose Vortex 10 (Lacy and Pollak 2017) because it is the most commonly used software for modeling population viability. Vortex is an individual-based simulation model that allows for the investigation of demographic and genetic processes and management decisions. PVA models in Vortex are easily updatable when new information from monitoring changes the estimation of population parameters. We used a population viability analysis to compare different scenarios and test the sensitivity of different population parameters. All models run in Vortex were run with the same basic model specifications for number of iterations, timesteps, and the duration of each timestep (Table 2.1).

Table 2.1. Simulation Specifications. Model specifications that were held constant across models.

Model Specification	Value
Number of iterations	1000
Number of timesteps	100
Duration of each timestep (in days)	365
Extinction definition	Only individuals of one sex remain

Population Parameters

A comprehensive literature review was conducted to establish parameter ranges. We searched the Web of Science with the following search term: ("California quail" OR "Californian valley quail" OR "Valley quail" OR "*Lophortyx californicus*" OR "*Callipepla californica*") AND ("brood*" OR "clutch*" OR "fecundity" OR "nest*" OR "survival*" OR "reproduction"). We extracted demographic parameters from the resulting literature. For demographic parameters that were sufficiently well known from the literature, values were held constant over all models (Table 2): breeding system, age of first reproduction, maximum lifespan, maximum age of reproduction, sex ratio at birth, and proportion of males in the breeding pool.

Initial age and sex structure of translocated population

We assumed that the age structure of the reintroduced population would match that of a stable population assuming baseline demographic values (Tables 2 and 4). The recommended age and sex distribution for a translocated population of 50 individuals (Table 3) would contain more females (*n* = 29) than males (*n* = 21), and more first-year (i.e., juvenile, *n* = 32) birds than adults (i.e, after first year, *n* = 28). However, the number of individuals in each category would change if the initial population size changes.

Catastrophes

A catastrophe is any one-year decrease in population size of 50% or greater (Reed et al. 2003). Because information on the frequency of and impact of catastrophes for California quail is lacking, we assumed catastrophes occur on similar levels to other wildlife populations (Reed et al. 2003), which for quail would be a 4.9% chance of occurring in any year.

Table 2.2. Basic demographic parameters. Demographic parameters that were held constant across models.

Model parameter	Value	Citations	Explanation
Initial population age distribution	Stable distribution		This assumes that the ages of translocated individuals will create a stable initial population based on established demographic parameters.
Breeding system	Monogamous	Calkins 2007	Limited evidence of double brooding; short-term monogamy (within an annual cycle) is appropriate for modeling.
Age of first reproduction	1 year	Calkins et al. 2014	Quail are reproductively mature in their first spring and are independent of parental care by three months, at covey formation.
Maximum lifespan, maximum age of reproduction	6 years	Raitt and Genelly 1964	Longest measured life span in a wild population.
Sex ratio at birth	50%	Lewin 1963	Though direct observation of sex ratios at hatching has not occurred, early summer trapping data indicates that sex ratios are equal at hatching, i.e., 50/50
Male breeding pool	100%	Calkins et al. 2014	No evidence in scientific literature for males being fully excluded from the breeding pool due to dominance structure.
Local catastrophe probability per year	4.90%	Millar and Zammuto 1983; Reed et al. 2003	Assumes catastrophes occuring on similar levels to other wildlife populations: 14.7% per generation. A generation is considered as three times the mean age at sexual maturity for females of the species. Thus, generation time was estimated for quail to be 3 years.
Density-dependent reproduction	False	Savage 1974; Barclay and Bergerud 1975; Botsford and Brittnacher 1992; Calkins et al. 2014	Data to parameterize density dependence is not available for quail. Studies have found populations with neutral, negative, and positive relationships between population density and reproductive success.

Density Dependence

There is mixed evidence on whether California quail populations are subject to density-dependent reproduction. Populations with negative density dependence (i.e., as populations approach carrying capacity reproductive success declines), positive density dependence (i.e., as population density increases reproductive success increases), and no density dependence (i.e., no apparent relationship between reproductive success and density) have been reported (Savage 1974; Barclay and Bergerud 1975; Botsford and Brittnacher 1992; Calkins et al. 2014). For this reason, along with sufficient data for parameterizing density dependence models being absent from the scientific literature, density dependence was not modeled as part of this work.

Table 2.3. Stable age distribution. The age distribution of a hypothetical translocated population of 50 individuals that would result in a stable population assuming baseline demographic values (Tables 2 and 4).

Age	Females	Males
1st year	19	13
2nd year	7	5
3rd year	2	2
4th year	1	1

Genetic Diversity and Population Supplementation

Inbreeding depression is the reduced survival or reproductive output of the offspring of two closely related individuals. Inbreeding depression is generally understood to be caused by the increased likelihood that inbred offspring will carry two copies of harmful recessive genes. Small populations are more prone to inbreeding depression because they tend to have lower genetic diversity and individuals are more likely to mate with a close relative simply by chance. An isolated reintroduced population of quail in the Presidio will be subject to inbreeding depression for the same reasons.

To evaluate the potential impacts of inbreeding depression on a reintroduced population, we selected literature-based values of genetic diversity. Two parameters are used to model inbreeding depression: lethal equivalents (i.e., a form of a gene that is lethal if an individual carries two of the same copy) and the percent of total genetic load (i.e., percent of lethal equivalents) that are due to recessive alleles. Because these values have not been studied in California quail, we used values from two other quail species for our models. In Japanese quail, individuals have 3.4 lethal equivalents per individual (Sittmann et al. 1966; Ralls et al. 1988) and the estimate of genetic load from highly deleterious recessive alleles in 3 populations of Montezuma quail was 0.93% (Mathur and DeWoody 2021). A conservation genomics project that includes California quail is in progress (https://www.ccgproject.org/), and species-specific genetic values will be available upon its completion which in the future can be incorporated into models. Assuming the same baseline scenario demographic parameters above (Tables 2 and 4), a baseline population with inbreeding depression was simulated. We were able to find a level of supplementation that counteracted the impacts of inbreeding depression (see Results and Recommendations). For the remainder of our modeling, we assumed that a reintroduction program would have sufficient supplementation to mitigate inbreeding and excluded the impacts of inbreeding from our models.

Sensitivity Testing

For demographic values where there is more uncertainty from the scientific literature, we tested a range of values to understand how sensitive the model was to each choice of value. We performed two approaches to sensitivity analysis: (i) perturbation analysis and (ii) a relative sensitivity approach. For the perturbation approach, we examined a range of potential values (Table 4) varying one value at a time (i.e., single-factor testing). For the relative sensitivity analysis, we varied parameters ± 10% of their baseline value (Table 4) and compared the resultant growth rates relative to the growth rate of the baseline value. Parameters that show sensitivities > 1 or < -1 had a disproportionate effect on the population growth rate (Table 5; Cooper et al. 2002).

Table 2.4. Sensitivity Test Ranges for Baseline Demographic Parameters.

Model Parameter	Baseline Value (SD)	Sensitivity Test Range		Citations
		Min	Max	
Initial population size	50	25	200	
Percent of females breeding	62.7% (29.8%)	0	100	Williams 1967*
Number of offspring per female	10.4 (2.0)	0	12	Anthony 1970*
Female mortality: 1st year	69.8 (10%)	0	100	Williams 1965†
Female mortality: >1st year	54.5 (10%)	0	100	Williams 1965
Male mortality: 1st year	79.5 (10%)	0	100	Williams 1965†
Male mortality: >1st year	46.2 (10%)	0	100	Williams 1965
Carrying capacity	214	0	1500	Emlen 1939‡

* Percent females breeding is the probability that a given adult female will successfully raise ≥1 young in a given year. Average brood size at 15 weeks (post-fledging) for females that have successfully raised ≥1 young in a given year.
† Survival from approximately 15 weeks of age through the first spring.
‡ The lowest reported population density in a wild population (0.345 birds/ha).

Results and Recommendations

Supplementation to Counteract Inbreeding Depression

Without supplementation, in the face of inbreeding depression an isolated reintroduced population of California quail will decrease in size over time to eventual extinction. Within 50 years, 75% of simulated populations without supplementation become extinct and within 100 years, all simulated populations become extinct (Figure 1). However, low levels of supplementation appear to counter the effects of inbreeding depression.

In absence of unassisted immigration from wild populations, inbreeding depression can be offset by periodically supplementing the population with translocated individuals from other populations. We assessed the minimum number of supplemented individuals needed to stabilize population loss. We considered supplementation effective if extinction risk was less than 5% in every year modeled (i.e., above the black dashed line in Figure 1). This threshold is met if 5 individuals per sex are supplemented every five years. This finding is bolstered by evidence that wild populations of California quail receive approximately 5.5 immigrants per sex per generation in North American populations (Zink et al. 1987). If a network of connected California quail populations is established in San Francisco, immigration and emigration between populations could replace or reduce the need for supplementation for preserving population genetics.

We also assessed the frequency of supplementation by comparing supplementation of (i) 5 individuals per sex every ten years and (ii) 10 individuals per sex every ten years (Figure 2). Supplementation of 5 individuals per sex every five years results in the most stable population size and lowest annual risk of extinction. However, if more risk is tolerated (<10% extinction risk in any year modeled), then 10 individuals per sex every ten years is also an acceptable approach. Population supplementation will also buffer the slow decline of a small population regardless of whether inbreeding depression is impacting the population (Figure 2, gray line).

Figure 2.1. The impacts of increasing the number of supplemented individuals to a reintroduced population. Baseline model is a population with baseline demographic parameters (Tables 2 and 4), including the influence of inbreeding depression. Supplementation was increased by 1 individual per sex supplemented every five years. Extinction risk of 5% is represented by the dashed line. Every simulated population will be 100% extant the year it is supplemented, minimally, this is due to the introduced individuals. Only populations with >5 individuals per sex supplemented every five years always have <5% extinction risk.

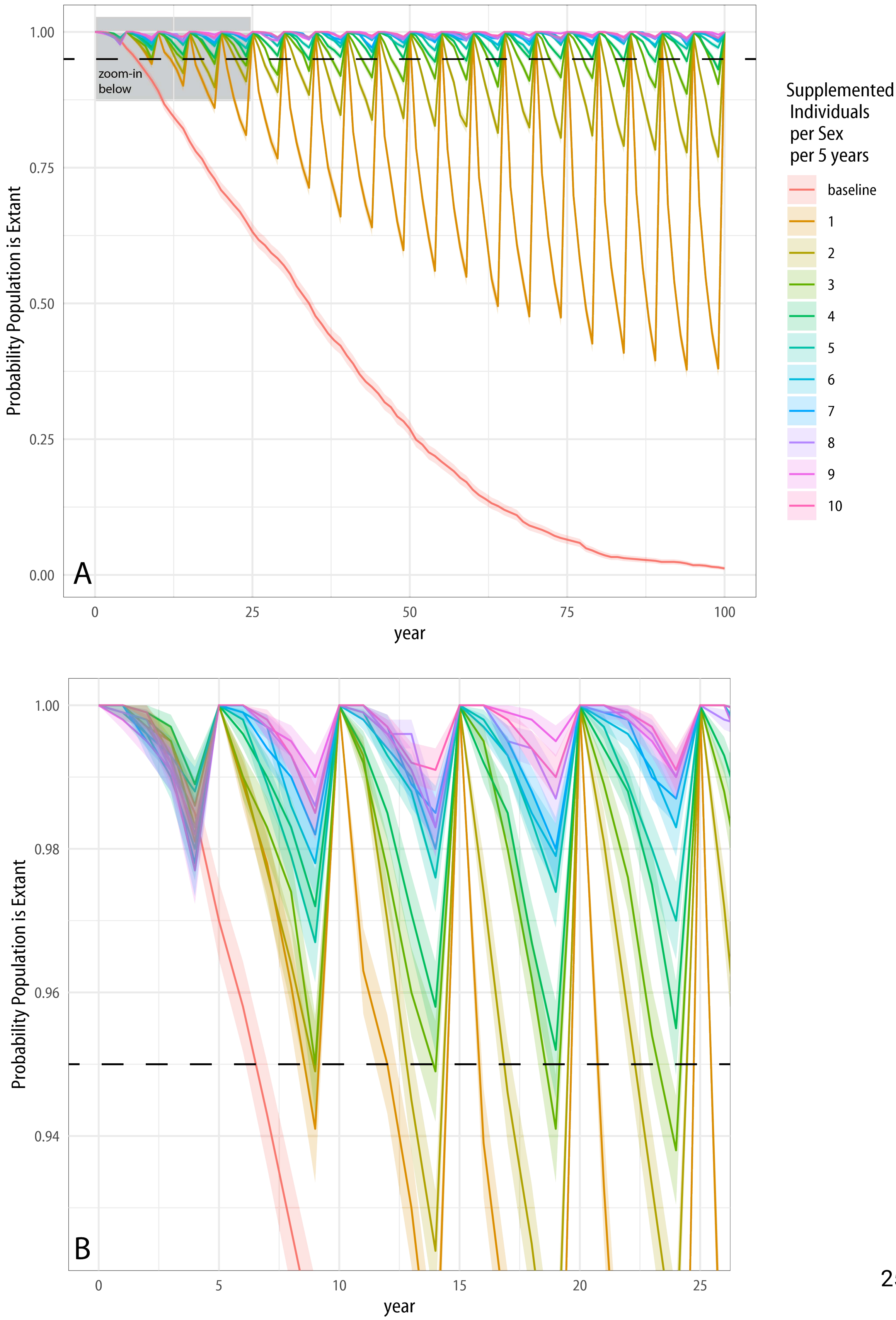
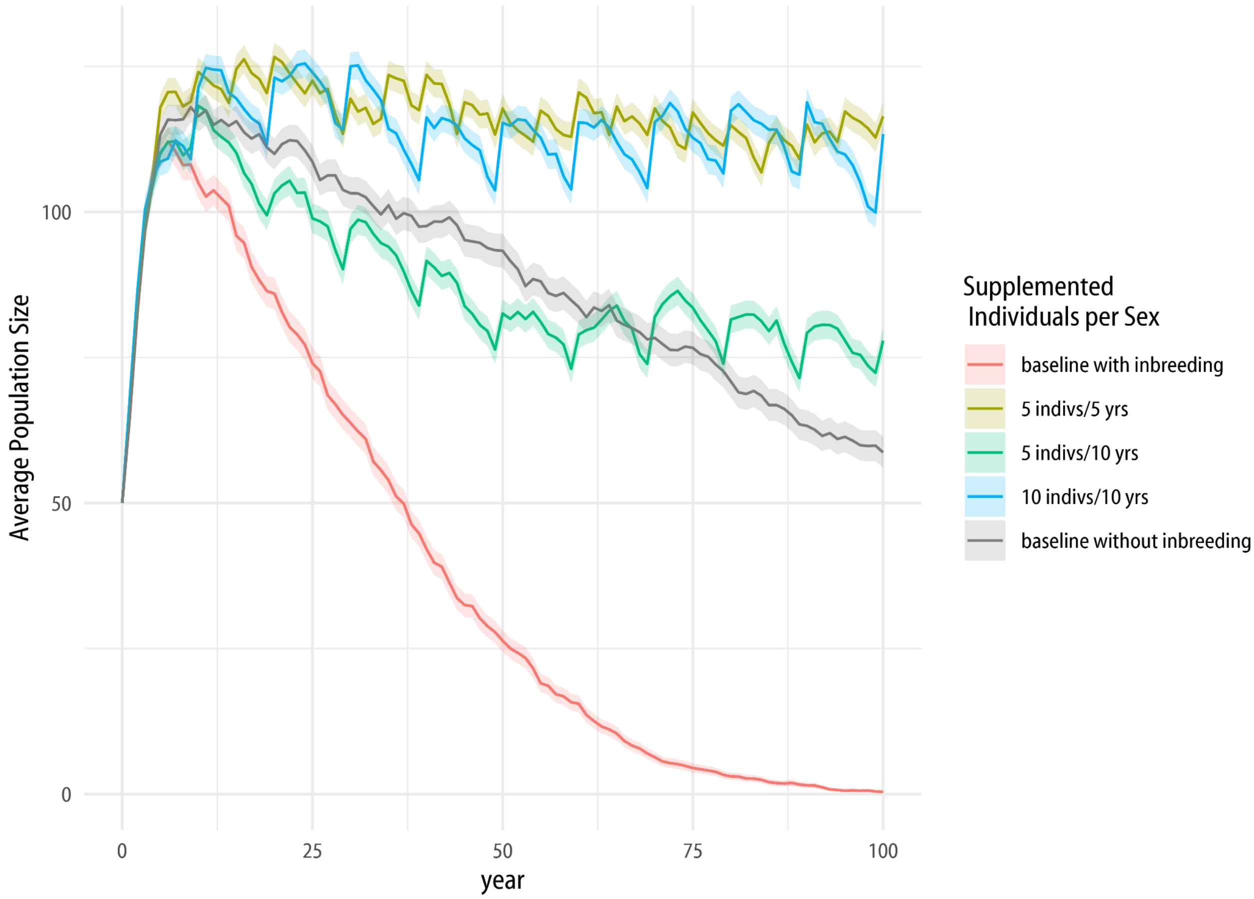


Figure 2. The impacts of altering the frequency of population supplementation from five to ten years for populations experiencing inbreeding depression.



Thresholds and Importance of Different Demographic Parameters

If a population reintroduced into the Presidio has the same demographic parameters as those reported in the scientific literature, that population is very likely to persist, particularly if regular, low levels of supplementation occurs (extinction risk <5%).

However, demographic parameters in a reintroduced population of quail to the Presidio will need to be monitored to establish the population's specific values and to understand the population's trajectory. The sensitivity analysis elucidates which demographic parameters are of the greatest concern if they vary from baseline literature values. Table 2.5 lists (i) the baseline values extracted from the scientific literature, (ii) the values of those parameters that would lead to practically guaranteed extinction of a population (the 'extinction threshold'), and (iii) the change point value beyond which the probability of extinction rapidly increases (illustrated in Figure 2.3). Table 2.5 is ordered by the parameter importance to the population's outcome, from most important to least. If post-reintroduction monitoring reveals demographic parameters close to or beyond the extinction threshold values presented in Table 2.5, it is likely the population will not persist if the threats related to those values are not remedied.

Three key findings resulted from our sensitivity analysis:

1. **Increases in first-year mortality in both males and females are most likely to impact the persistence of a reintroduced population.** The threshold across which population persistence sharply declined occurs above 80% for males and 70% for females, which is relatively close to the values reported in the scientific literature: 79.5% and 69.8% respectively (Figure 2.3G and 2.3E).

2. **Decreases in reproductive success will impact population persistence, but to a lesser extent.** The probability of population extinction increases as the average number of young per successfully breeding female drops below 8.5 and as the percentage of successfully breeding females drops below 60%. However, the impacts of incremental changes in either value are relatively gradual (Figure 2.3D and 2.3C).

3. **Adult mortality in a reintroduced population could be substantially higher before it would impact population persistence.** In a reintroduced population, mortality of adult males could be substantially (8.8%) higher than seen in other studies before it has noticeable impacts on population size and persistence. Mortality above 55% would start to impact size and persistence, however, change in both as mortality increases are somewhat gradual (Figure 2.3H). Similarly, 5.5% higher adult female mortality could occur in a reintroduced population compared to reported levels before substantial impacts occurred (Table 2.5). Increases in adult female mortality also have a gradual impact on population size and persistence (Figure 2.3F).

Figure 2.3. Quail Perturbation Sensitivity Analysis. Demonstrates the change in the probability of extinction (left size) and population size (right side) that occurs when each demographic parameter is varied one at a time.

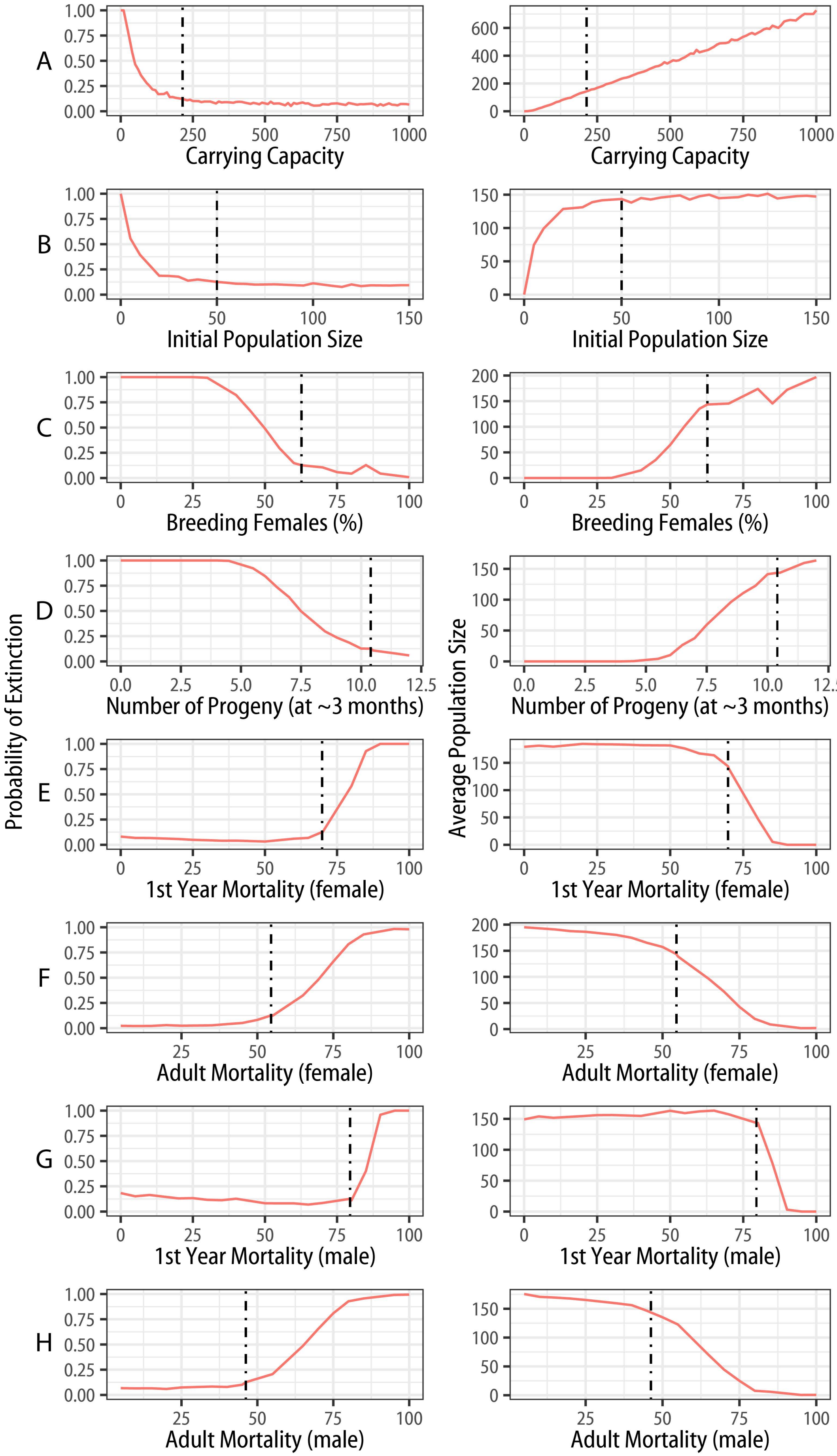


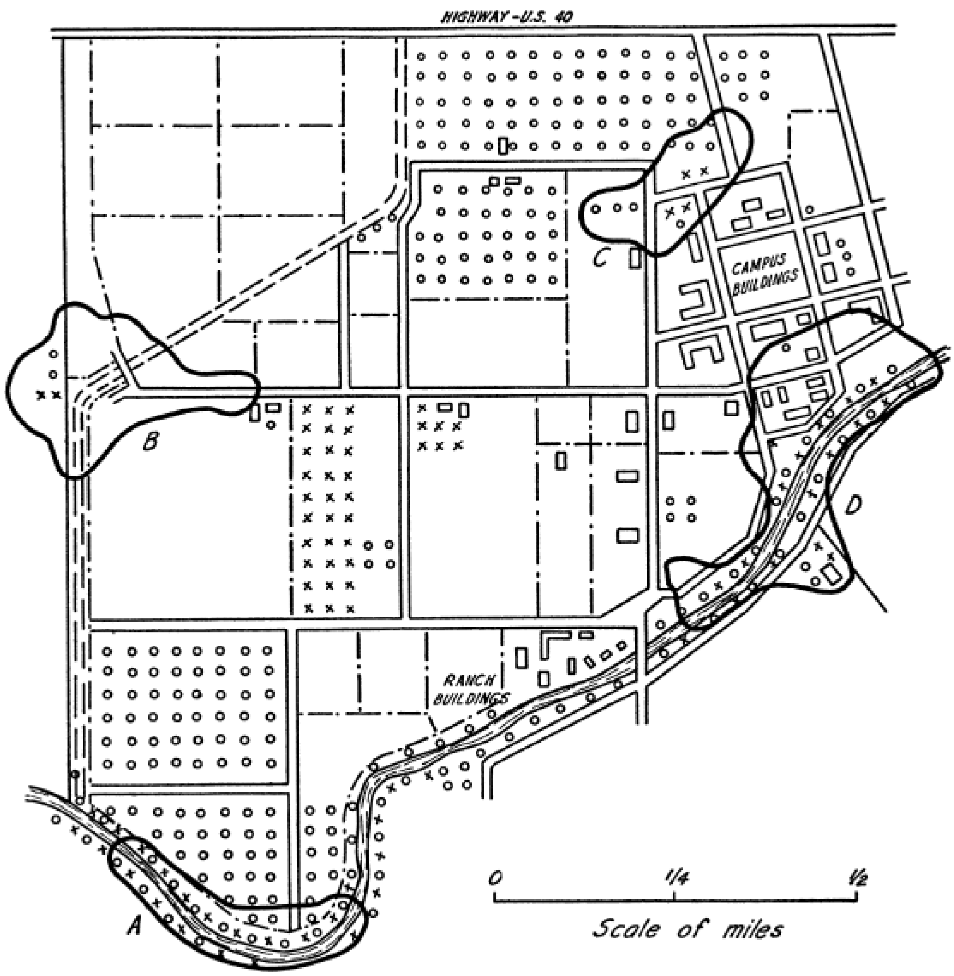
Table 2.5. Results from Sensitivity Analysis. Presented are the baseline values extracted from the scientific literature, extinction thresholds (the values of those parameters that would lead to practically guaranteed extinction of a population), and the extinction probability change point (value beyond which the probability of extinction rapidly increases, illustrated in Figure 2.3). Table is ordered by the parameter importance to the population's outcome, from most important to least.

Demographic Parameter	Baseline Value	Relative Importance	Parameter Rank	Extinction Threshold	Extinction Probability Change Point
1st Year Mortality (male)	79.5	-5.48	1	>85%	80%
1st Year Mortality (female)	69.8	-4.31	2	>85%	70%
Number of Progeny (at ~3 months)	10.4	2.84	3	<5.5	8.5
Breeding Females (%)	62.7	2.18	4	<40%	60%
Adult Mortality (female)	54.5	-1.93	5	>90%	60%
Adult Mortality (male)	46.2	-0.6	6	>80%	55%

Carrying Capacity

Ideally the Presidio would have a carrying capacity of ≥270 quails to achieve <10% extinction risk during the first 50 years post-establishment. Simulated populations were not strongly impacted by varying values for carrying capacity once carrying capacity surpassed 170 individuals (Figure 2.3A). It seems likely that the Presidio could support quail populations in these numbers, 270 is only slightly above the lowest reported population density in a wild population, 0.345 birds/ha which would result in approximately 214 birds in the Presidio. The reported density of 0.345 birds/ha was estimated across both occupied and unoccupied areas of UC Davis's campus and adjacent fields (Figure 2.4; Emlen 1939). Other reported population densities range from 0.753 birds/ha (Barclay and Bergerud 1975) to a high of 12 birds/ha on a private hunting range (Leopold 1977).

Figure 2.4. Distribution of the lowest density California quail population reported in the literature (0.345 birds/ha) on the UC Davis Campus (Emlen 1939).



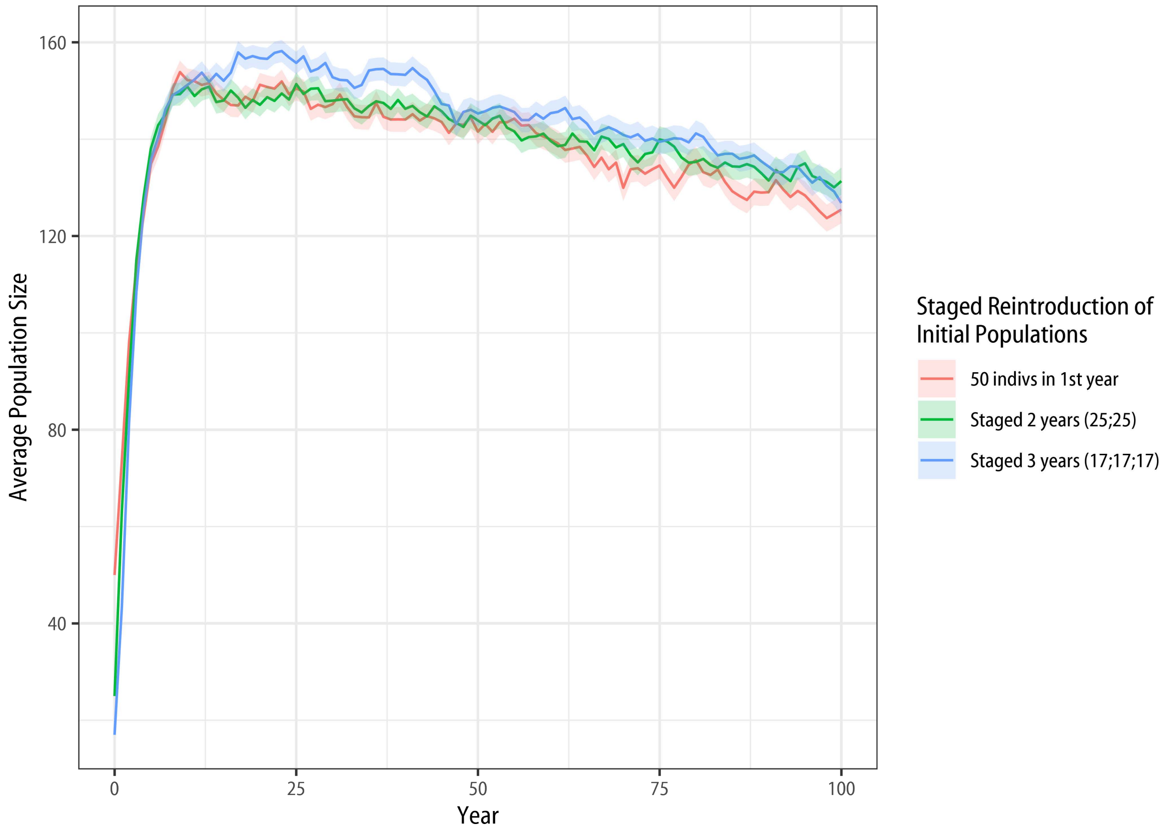
Initial Population Size

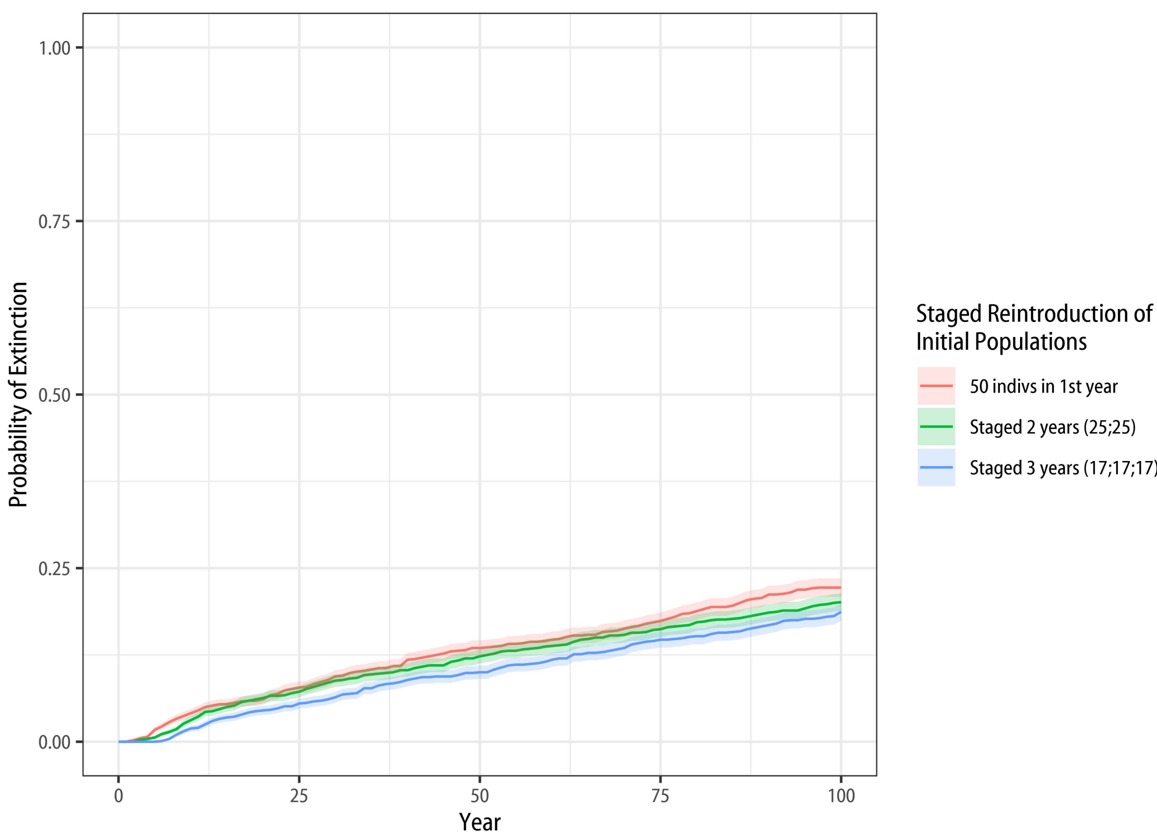
An initial population of a minimum ≥ 50 individuals is recommended as above this number extinction risk of the population stabilizes with increasing numbers of individuals introduced. An absolute minimum of 20 individuals should be considered in any reintroduction attempt, as below that number, extinction risk increases rapidly (Figure 2.3B).

Staging of Initial Population Reintroduction

Staging the introduction of the initial population over two or three years appears to have minimal impact on the eventual size and persistence of the reintroduced population. We evaluated introducing all individuals in one year and evenly spreading the introduction over two years (25 individuals per year) and three years (17 individuals per year). Population growth, size, and extinction risk were similar across all three scenarios (Figure 2.5).

Figure 2.5. Effects of staging initial reintroduction across multiple years. Scenarios included introducing all individuals in one year and evenly spreading the introduction over two years (25 individuals per year) and three years (17 individuals per year).





General Recommendations for Reintroduction

Supplemental Feeding

Supplemental feeding can help maintain higher densities of California quail and keep coveys anchored to one location (Leopold 1977). Supplemental feeding through the broadcast spreading of feed is commonly used in translocations of other quail species, particularly, northern bobwhite and scaled quail (Terhune et al. 2006; Henson et al. 2012), and was used in the recent introduction of California quail to Texas (Rushing et al. 2022). For northern bobwhite, broadcast supplemental feeding can significantly increase survival and reduce home range sizes (Sisson et al. 2017). However, we anticipate the broadcast spreading of feed will not be practical in the Presidio.

Another option for supplemental feeding is through the use of free-standing feeders. The use of feeders by other quail species is highly variable (Henson et al. 2012; Rollins et al. 2017). Free-standing feeders in the Presidio could be trialed. If installed, they should be coupled with video surveillance to evaluate quail use and use by non-target species, such as raccoons.

Artificial Water Sources

Guzzlers (i.e., artificial water sources) have been widely installed across the western United States to promote wildlife and game species (Rosenstock et al. 1999). However, guzzler use and effectiveness for supporting quail populations have been understudied, particularly outside of desert and other arid regions (Rosenstock et al. 1999). California quail will likely use guzzlers if available (Williams and Koenig 1980). For example, California quail were one of the most frequent visitors of guzzlers in a study in an oak woodland in Hastings, California (Williams and Koenig 1980). However, they potentially do not require drinking water for survival outside of periods of heat and drought (Leopold 1977; Calkins et al. 2014). A potential downside to guzzlers is that they can both attract predators and may expose quail to greater predation risk by causing quail to aggregate in one location (Rosenstock et al. 1999). We recommend that guzzlers be piloted in the same fashion as supplemental feeding to monitor their use by quail and non-target predators (see (Rollins et al. 2017) for a potential approach.

Introduction of Wild-reared versus Captive-reared Individuals

Wild-reared quail are recommended for reintroduced populations over captively-reared individuals. Captive-reared galliforms have much lower survival and reproduction rates and have higher mortality than wild birds (Sokos et al. 2008). Further, the offspring of captive-reared individuals also tend to have lower survival and reproduction rates than offspring reared by wild birds (Sokos et al. 2008).

Soft versus Hard Releases

Translocated individuals can be released directly, without any additional support (a hard release), or gradually acclimated to a new location (a soft release), often through release into an enclosure with food and shelter. Increasing site fidelity through reducing post-release dispersal is one of the main purposes of soft releases, however, a comparison of the effectiveness of the two techniques has seldom been studied (Resende et al. 2021). Even though study has been limited, soft releases appear to have positive impacts on translocation success. In a cross-taxonomic meta-analysis, Resende et al. (2021) found soft releases increased the success of translocation programs by 77%. However, this finding was mostly driven by reptilian translocations, and a comparison of techniques has only been studied in a limited number of 90bird species (n = 3; Resende et al. 2021). For New World quail, a single comparative study indicates that soft releases have a positive impact on adult survival when compared to hard releases (Ruzicka et al. 2017). Though formal study of the technique is limited, we recommend using a soft-release method given the available evidence.

Specially-designed release boxes can also help keep adults and their chicks together post-translocation (Meyerpeter et al. 2021). It should be noted that soft-release pens can attract predators, including raccoons which can spend extended periods of time trying to break into pens (Keiter and Ruzicka 2020). This could increase the stress levels of translocated birds. Monitoring for predator visits to release pens should be done, and if occurring, mitigation should take place.

Marking of Reintroduced Individuals

Reintroduced individuals should be tagged with active-tracking devices, such as VHF or digital trackers (Rushing et al. 2022) or GPS trackers (telemetrysolutions.com). As many individuals in the reintroduced population should be marked with active-tracking technology as budgetary constraints allow. Reintroduction experts should be consulted for tracker type and attachment method as the field is rapidly changing.

All reintroduced individuals should be marked with uniquely identifiable bands that are observable at a distance, such as through unique combinations of plastic color bands (North American Banding Council 2001). This will allow for the long-term identification of reintroduced individuals, including by citizen scientists. Color banding is a widely used method, and color banding does not appear to affect the survival or predation of birds (Cresswell et al. 2007; Sharpe et al. 2009; Fair et al. 2010; Roche et al. 2010)

Post-reintroduction Needs

Monitoring of Reintroduced Population

It is essential that post-release monitoring of the reintroduced quail population occur to determine the ultimate outcome of the Presidio's reintroduction program, as well as adaptively manage the program during reintroductions. Post-release monitoring should last at least 3 to 5 years (World Pheasant Association and IUCN/SSC Re-introduction Specialist Group 2009).

Monitoring should include data collection on reproduction, survival, site fidelity and dispersal, and habitat use. Table 2.6 presents different parameters to be monitored along with survey methods and statistical approaches to parameter estimation once monitoring is complete. Additional methods for quail surveys can be found in Rollins et al. (2005) and Overton et al. (Overton et al. 2020). Mortality type and frequency should be noted whenever possible including from incidental recoveries. Once demographic parameters have been sufficiently monitored to allow for estimation, lower levels of monitoring can be instituted.

Table 2.6. Survey methods and statistical approaches to demographic parameter estimation.

Survey Type	Survival	Site Fidelity & Dispersal	Habitat Use	Population Size and Density Index	Reproductive Success
Observation data from tracked quail (short-term) and resighting of uniquely marked individuals (long-term), with associated spatial locations.	Mark-Recapture (Buckland 1982; Gilroy et al. 2012)	Spatial relationship of locations	Resource Selection Functions (Boyce and McDonald 1999)		
Autumn population counts: Covey Counts (Rollins et al. 2005; Rusk et al. 2007) or Active Call-Counts using playback (Overton et al. 2020)	Integrated Population Models (Riecke et al. 2019)			Simple statistics	
Post-nesting Covey Counts (Rollins et al. 2005; Rusk et al. 2007)					Simple statistics
Nest monitoring†					Logistic exposure, etc. (Shaffer 2004)

† Nest monitoring can be done through many methods, such as regular visitation by field workers, nest cameras (Hereward et al. 2021), or temperature loggers (Hartman and Oring 2006). Advances in nest camera and temperature logger technologies mean these methods can be very cost-effective (Hartman and Oring 2006; Hereward et al. 2021).

Iterative Updates of Models from Monitoring

Anytime a new demographic parameter is estimated (or re-estimated) from monitoring data gathered on the reintroduced population the PVA models presented here should be rerun and the trajectory of the reintroduction program should be reevaluated. Vortex models are easily updatable, so new data can be readily incorporated.

Conclusion

Population viability analyses show that reintroduction of California quail into the Presidio is feasible. The recent introduction of California quail to Texas, which saw high rates of survival post-release (up to 92.5% at six weeks post-release; Rushing et al. 2022) also lends support to reintroduction feasibility. Our PVA analyses provide guidance for a quail reintroduction plan including the age and sex distribution, size, and timing of initial reintroductions and approaches to mitigate the impacts of inbreeding depression on – at least at the onset – a small and isolated population of quail. We further provide guidance on practical aspects of a reintroduction plan: supplemental feeding, choice of wild-reared versus captive-raised birds, soft versus hard releases, marking of individuals, and monitoring and population parameter estimation approaches.

Reintroduction of quail into the Presidio has significant potential to advance the science around urban ecology and conservation in multifaceted ways. However, reintroduction is difficult, expensive, and requires a long-term commitment and the Presidio Trust should be prepared for unexpected complications and the potential for an unsuccessful reintroduction program, including the political backlash that may come with a lack of success. Regardless of success, a reintroduction program offers the unique opportunity to understand the importance of different stressors in urban areas for quail species and develop approaches for addressing stressors.

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