


RESEARCH ARTICLE

What makes urban parks good for California quail? Evaluating park suitability, species persistence, and the potential for reintroduction into a large urban national park

Kelly J. Iknayan¹  | Megan M. Wheeler¹  | Samuel M. Safran^{1,2}  |
Jonathan S. Young³ | Erica N. Spotswood¹ 

¹San Francisco Estuary Institute, Richmond, CA, USA

²Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, Minneapolis, MN, USA

³Presidio Trust, San Francisco, CA, USA

Correspondence

Kelly J. Iknayan
Email: kellyi@sfei.org

Funding information

Presidio Trust; National Science Foundation, Grant/Award Number: EF-1638725

Handling Editor: Tien Ming Lee

Abstract

1. Preserving and restoring wildlife in urban areas benefits both urban ecosystems and the well-being of urban residents. While urban wildlife conservation is a rapidly developing field, the majority of conservation research has been performed in wildland areas. Understanding the applicability of wildland science to urban populations and the relative importance of factors limiting species persistence are of critical importance to identifying prescriptive management strategies for restoring wildlife to urban parks.
2. We evaluated how habitat fragmentation, habitat quality and mortality threats influence species occupancy and persistence in urban parks. We chose California quail *Callipepla californica* as a representative species with potential to respond to urban conservation. We used publicly available eBird data to construct occupancy models of quail in urban parks across their native range, and present an application using focal parks interested in exploring quail reintroduction.
3. Urban parks had a 0.23 ± 0.02 probability of quail occupancy, with greater occupancy in larger parks that were less isolated from potential source populations, had higher shrub cover and had lower impervious cover. Less isolated parks had higher colonization rates, while larger parks had lower extinction rates. These results align with findings across urban ecology showing greater biodiversity in larger and more highly connected habitat patches.
4. A case study highlighted that interventions to increase effective park size and improve connectivity would be most influential for two highly urban focal parks, while changes to internal land cover would have a relatively small impact. Low joint extinction probability in the parks (0.010 ± 0.013) indicated reintroduced populations could persist for some time.
5. *Synthesis and applications.* We show how eBird data can be harnessed to evaluate the responsiveness of wildlife to urban parks of variable size, connectivity and habitat quality, highlighting what management actions are most needed. Using California quail as an example, we found park size, park isolation and presence of coyotes are all important drivers of whether quail can colonize and persist in parks. Our results suggest reintroducing quail to parks could be successful

provided parks are large enough to support quail, and management actions are taken to enhance regional connectivity or periodic assisted colonization is used to supplement local populations.

KEYWORDS

California quail, eBird data, ground-dwelling species, urban biodiversity support, urban connectivity, urban park management, urban rewilding, urban wildlife reintroduction

1 | INTRODUCTION

Urban areas have a significant negative impact on biodiversity across the globe (McDonald et al., 2020). Yet, cities are also critical for native biodiversity conservation. Urban parks in particular, whether natural or human-managed, are recognized for their unique contributions to regional and local biodiversity support (Soanes & Lentini, 2019). Promoting and restoring biodiversity in urban parks, including providing support for unique, charismatic and culturally significant wildlife, is a growing priority for municipalities (Aronson et al., 2017). Supporting unique wildlife in urban parks will require a robust understanding of what factors limit priority species in urban contexts—information that is lacking for many species. Conservation research conducted in natural areas does not account for urban conditions, leading to the question of whether scientific knowledge garnered in less disturbed areas is transferable to urban landscapes.

Parks are the nucleus of urban biodiversity, with natural and human-managed greenspaces supporting more species than heavily urbanized areas (Müller et al., 2018). However, not all parks are created equal, and the ability of a park to promote biodiversity is impacted by a variety of factors. Park size and habitat quality are important determinants of biodiversity (Beninde et al., 2015), both independently and synergistically. For example, a small park may not have adequate area to support a species even if habitat restoration increases the amount and quality of suitable habitat. Parks are also influenced by factors beyond their borders: large expanses of impervious surfaces can impede movement and provide little shelter or forage; free-roaming domestic cats *Felis catus* can increase predation; and high traffic volume may increase mortality rates when wildlife move beyond park boundaries (Rodewald & Gehrt, 2014). Urban parks are often isolated from each other and the urban boundary, which can decrease a species' ability to persist in a park over time. For ground-dwelling wildlife in particular, movement across the urban matrix may be difficult (Rondinini & Doncaster, 2002) and stochastic events may lead to eventual loss of the species from an isolated park with little chance of natural recolonization (Soulé et al., 1988).

The presence of wildlife helps support functioning ecosystems and can increase residents' engagement in urban greenspaces (Soulsbury & White, 2016). To this end, managers are increasingly interested in conserving and restoring native wildlife in urban parks (Aronson et al., 2017). For example, natural resource managers in the Presidio of San Francisco, California, the nation's largest urban national park, have reintroduced several species of wildlife after

substantial habitat restoration (Presidio Trust, 2018). Management interventions can include a suite of actions similar to activities in wildland areas, including controlling invasive species, planting new native vegetation and managing vegetation height and structure. However, urban wildlife are subject to different stressors than their rural counterparts, and there is evidence that many species alter their behaviour in urban landscapes, including their wariness of predators and their interactions with conspecifics (Ryan & Partan, 2014). In some cases, habitat preferences can shift because of alterations in diet—for example, in response to human food subsidies—or absence of competitors (Ryan & Partan, 2014). Given these changes, a crucial question is the extent to which scientific information related to habitat preferences, diet, response to predators, corridors and patch size in natural spaces is transferable to urban parks (Alexander et al., 2019).

The California quail *Callipepla californica*, a ground-dwelling bird native to the west coast of North America (Figure 1b), is an ideal candidate for assessing variation in an urban area's ability to support wildlife as they are a broad-ranging species able to persist in some but not all urban environments. Further, quail can grant insight into the importance of urban connectivity, which to date is little understood, particularly for ground-dwelling species (LaPoint et al., 2015). Quail are known to be sensitive to habitat fragmentation driven by urbanization. For example, they have been lost from many native habitat remnants in urban San Diego (Crooks et al., 2004; Soulé et al., 1988) and have recently been extirpated from the Presidio and Golden Gate Park, large urban parks on the San Francisco Peninsula (Figure 1c). Nonetheless, quail do continue to occupy some urban areas within their native range (Crooks et al., 2004; Soulé et al., 1988). Although habitat use by quail in natural areas is reasonably well-quantified, there has been little exploration of their habitat use in urban areas.

We evaluated which attributes of urban parks allow for occupancy and persistence of California quail by using eBird records across the state of California, USA. We expected factors at multiple spatial scales would influence the occupancy and persistence of quail in urban parks, including: (a) local-scale characteristics of parks, (b) larger scale attributes of urban areas surrounding parks and (c) landscape-scale factors related to park connectivity and proximity to the urban edge. We assessed the characteristics of urban parks via measures of habitat fragmentation, habitat quality and mortality threats using single-season and multi-season occupancy models. From research conducted in wildland areas,

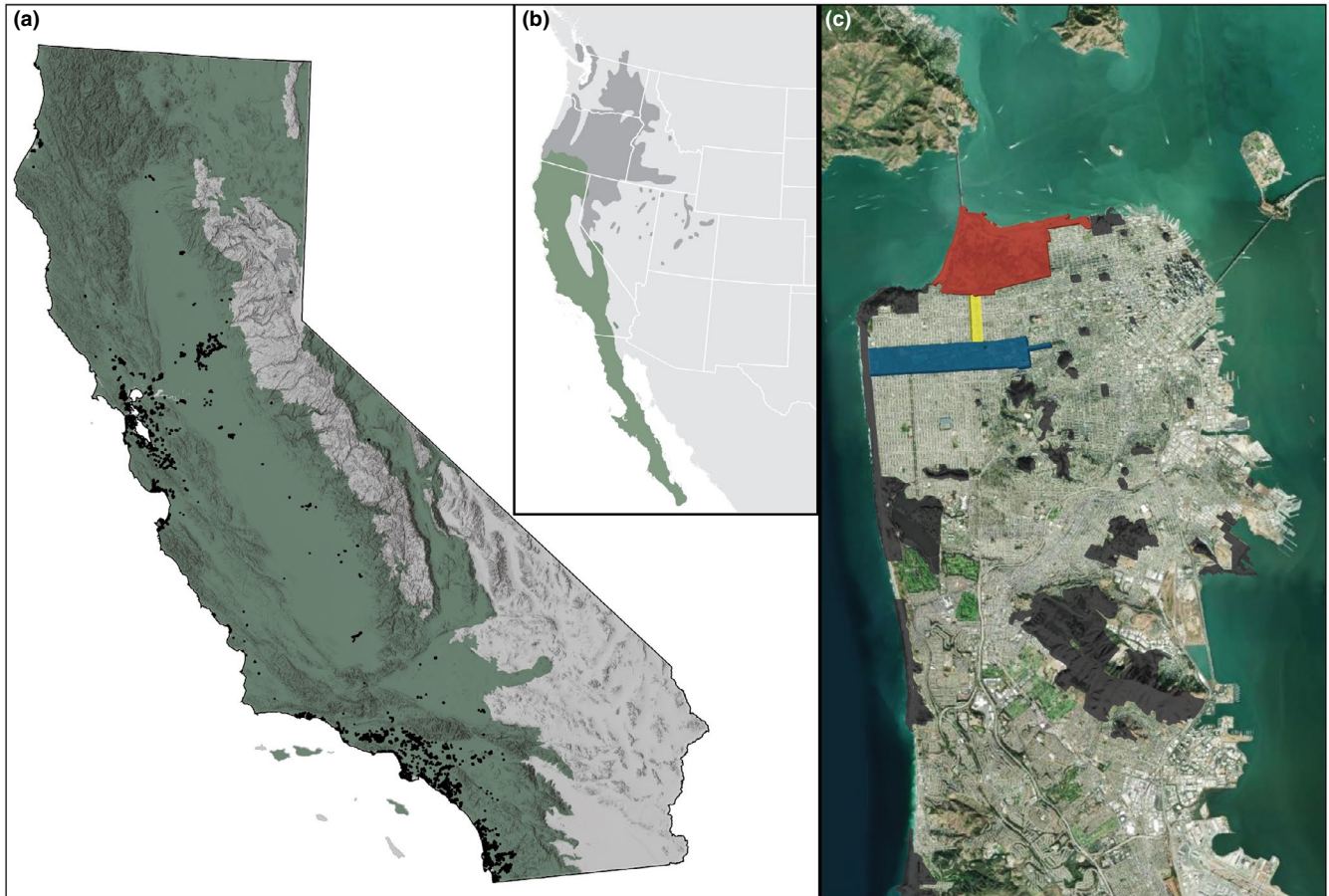


FIGURE 1 Distribution of Californian urban parks (black) within the California quail's range (a). The California quail's North American historic (green) and contemporary range (grey; b; adapted from Leopold 1977). The focal parks used in our case study: the Presidio (red), Golden Gate Park (blue) and Park Presidio Boulevard (yellow) in San Francisco, California, and other urban parks (black; c)

we expected that larger parks with higher habitat quality, lower mortality threats, surrounded by higher quality matrix and more connected to the urban edge would better promote quail. Using a case study of two parks in San Francisco, the Presidio and Golden Gate Park, we show how results can be applied to real-world park management to uncover what management actions, and at which spatial scale, would be needed to support long-term persistence of California quail in urban parks.

To facilitate interpretation by park managers, we focused on variables with clear real-world interpretations.

2 | MATERIALS AND METHODS

2.1 | Study area

We quantified California quail occurrence and persistence in urban parks across the state of California (Figure 1a), which encompasses >90% of the quail's historic native range in the United States (Figure 1b), and we analysed >97% of urbanized area contained therein. California quail are found in arid to Mediterranean climates

primarily in areas with combinations of shrub cover, open habitat for foraging and available water sources (Calkins et al., 2014). We included all parks from the California Protected Areas Database (CPAD, 2019) that were classified as protected open space with at least 15% of land area falling within a US Census-designated Urban Area, excluding parks that are primarily recreation facilities.

2.2 | eBird data

California quail occupancy in urban parks was quantified using citizen science data recorded in eBird (Cornell Lab of Ornithology, 2019). This dataset was filtered to complete checklists using stationary, travelling or area-based search protocols. Data were further filtered following best practices to observations with similar sampling conditions (Strimas-Mackey et al., 2020): duration between 5 min and 5 hr, travel distance <5 km, <10 observers, occurring between 04:30 and 21:00 hr and in parks that were <95% water or wetland. We included checklists from 2010 to 2018, as eBird use increased greatly after 2010, and from April to June when detection frequency was highest. Only parks with ≥3 checklists per year within 10 m of their boundary

were included. To adjust for uneven sampling effort, checklists were randomly subsampled to a maximum of 10 per year.

2.3 | Environmental variables

We quantified relevant environmental characteristics for each park from publicly available data sources—park area, land cover (shrub, wetland and impervious cover), road density, quail avian predator densities and coyote presence (as a proxy for suppressed free-ranging cat populations which likely predate quail, *F. catus*; see Supplemental Information for justification)—and important urban landscape qualities surrounding each park: isolation from natural landscapes and impervious cover in the urban matrix. Park areas were calculated as the proportion of terrestrial land cover from the 2016 National Land Cover Database (NLCD; Homer et al., 2020) multiplied by total park area from CPAD. Per cent shrub and impervious cover within each park was calculated from the NLCD's land cover and imperviousness products respectively. Per cent wetland cover was generated from the California Aquatic Resources Inventory (San Francisco Estuary Institute [SFEI], 2017).

Mortality threats were included as traffic mortality risk, avian predator densities and the presence of coyotes. Road density (m/km² of park area) was calculated by summing road length within each park using the US Census TIGER dataset. An avian predator density index was calculated for known predators (Cooper's hawk *Accipiter cooperii*; sharp-shinned hawk *A. striatus*; northern harrier *Circus hudsonius*; red-tailed hawk *Buteo jamaicensis*; American kestrel *Falco sparverius*; and prairie falcon *F. mexicanus*) and likely predators (i.e. red-shouldered hawks *B. lineatus*) of California quail in urban areas (Calkins et al., 2014). We included all eBird observations (January 2000 to May 2019) of predator species, filtering checklists using best practices. Median abundance for each species was averaged across years, summed across species and divided by park area (predators/km²). Using median abundance reduced the impact of extreme counts, which may occur during seasonal migrations. Coyote presence was estimated from research-grade iNaturalist observations from January 2010 to July 2019 (Global Biodiversity Information Facility database, 2019). iNaturalist does not record associated effort data, so probable absence of coyotes was determined using the number of records as a proxy: ≥ 1 coyote observation determined the presence, ≥ 50 observations in kingdom Animalia without any coyote records determined the absence and, otherwise, coyote presence was considered unknown.

The quality of the urbanized matrix surrounding each park was quantified using the per cent impervious cover from NLCD, in a 400 m buffer around each park. This buffer size was chosen based on the limits to local dispersal for California quail (Calkins et al., 2014). Landscape-level isolation was calculated as either the shortest Euclidean distance to the nearest stream corridor or the shortest overland path to the nearest urban boundary. Urban streams are important corridors for wildlife movement and can connect urban parks to rural and exurban source populations (Carter et al., 2019).

The urban boundary, excluding coastlines, was defined using the US Census urban layer (2018). Stream data were sourced from CalFish (Christy, 2003). For models of temporal occupancy dynamics, we also included spring precipitation, which may impact adult survival and breeding success (Botsford et al., 1988). Total spring precipitation (April to June of each year) was retrieved by county from WestMap (<https://cefa.dri.edu/Westmap/>). For comprehensive descriptions of each environmental variable's derivation, see Appendix S1.

2.4 | Occupancy modelling

To account for uneven detection probabilities inherent in eBird data, we used occupancy modelling, which models the processes of occupancy and detection separately (MacKenzie et al., 2018). Following best practices for analysing eBird data with occupancy approaches (Johnston et al., 2019), we built three separate models. First, to evaluate predictors of California quail occupancy with the broadest sample of parks, we built a single-season model with year-stacking using data from all parks with ≥ 3 eBird checklists in a given year ($n = 1,059$ parks; Table S1). Second, to evaluate the influence of coyotes, we built a single-season occupancy model using the subset of parks for which coyote presence was known ($n = 423$ parks). Finally, to investigate the temporal dynamics of quail in urban parks, we used a multi-season model with the subset of parks containing data in every year from 2010 to 2018 ($n = 102$ parks). Modelling was conducted in R version 3.6.1 (R Core Team, 2019) using the package UNMARKED (version 0.12-3, Fiske & Chandler, 2011).

The single-season occupancy model included predictors for park area, isolation, park shrub cover, park impervious cover, park road density, matrix impervious cover, avian predator density and survey year. Park wetland cover was fit with its quadratic, as we expected intermediate amounts of wetland to be more suitable for California quail. Predictors were standardized, had low correlation (Pearson: < 0.55) and showed no evidence of problematic multicollinearity (VIF < 1.45 ; linear and quadratic terms of wetland cover: VIF < 3.19). Detection covariates were start time, duration, distance travelled and number of observers. The global model had a sufficiently good fit and no evidence for overdispersion (MacKenzie & Bailey, 2004; 1,000 samples; chi-square: $p = 0.26$; $\hat{c} = 1.0$). For model selection, we used the secondary candidate model set approach (Morin et al., 2020), fitting occupancy and detection submodels independently using a null model for non-focal submodels. Relative support for submodels was evaluated using sample size-corrected Akaike's information criterion (AICc; Burnham & Anderson, 2002); models that had a $\Delta\text{AICc} \leq 6$ were carried over into the final model selection stage. To consider the effect of coyote presence on quail occupancy, we ran a global, single-season occupancy model with the subset of parks for which coyote presence was known. This model included all occupancy and detection predictors used in the main single-season model plus the presence or absence of coyotes.

To understand how environmental variables determine the processes of California quail loss and colonization, we also ran a

multi-season occupancy model. In the global model, we used the same set of predictors as above for initial occupancy and detection probability. Colonization and extinction probability were fit using the same covariates as initial occupancy with the addition of annual spring precipitation. The global model had a sufficiently good fit and no evidence for overdispersion (chi-square: $p = 0.1$; 1,000 samples; $\hat{c} = 1.21$). The same secondary candidate set approach was used for model selection.

We performed model-averaging among highly supported models to account for model uncertainty in predictions for both single-season and multi-season models ($\leq 6 \Delta AIC_c$; Richards, 2008), disregarding models with uninformative parameters (Arnold, 2010). Our inferences about parameters and covariate effect sizes (quantified using odds ratios) were derived from only the top performing models from each candidate model set (Jones & Peery, 2019).

2.5 | Case study: San Francisco's Presidio and Golden Gate Parks

The Presidio is a national park in San Francisco 1.5 km north of Golden Gate Park (Figure 1c). A string of small patches along Park Presidio Boulevard connects the two parks and could be managed as a wildlife corridor. Busy roads separate these patches, possibly affecting this function. However, at least one banded California quail is known to have moved between the parks, presumably using this corridor. Quail were once abundant in both parks, but have rapidly declined since the 1990s. Despite goals put forth in the San Francisco Quail Recovery Plan (2004), the last quails were seen in 2006 in the Presidio and in 2018 in the Golden Gate Park. The Presidio has considered reintroducing a quail population but first seeks to understand the underlying factors that determine survival in urban

parks. We explored how changes in environmental variables would affect quail outcomes in these focal parks, including the hypothetical outcome for quail if the parks were functionally connected with a corridor.

3 | RESULTS

3.1 | Urban parks that support quail occupancy

A minority of urban parks across California supported California quail, with an estimated average occupancy probability of 0.230 ± 0.02 . Nearly 40% of parks (37.6%) had a low (<0.10) probability of being occupied by quail. On average, quail that were present at a site during surveys were very likely to be detected at least once ($p^* = 0.940 \pm 0.045$; MacKenzie et al., 2018, p. 126).

Larger parks, less isolated parks and parks with lower impervious cover both within the park and in the local matrix had significantly higher California quail occupancy (Table 1; Figure 2). Additionally, intermediate wetland cover and higher shrub cover within a park were significantly related to higher occupancy. Park area and isolation had the strongest effect on occupancy. For every 0.5 km² increase in park area, there was a 10.9% increase in the odds a park will be occupied. For each kilometre a park is closer to the urban boundary or stream corridor, there was a 23.8% increase in the odds a park will be occupied. Four land cover measures had the next strongest effects on occupancy probability. For every 10% decrease in impervious cover within a park, the odds a park will be occupied nearly doubled (99.0%); equivalent reductions in impervious cover in the matrix increased the odds by 45.1%. Park wetland cover of approximately 25.0% was optimal for a park's occupancy (0.307 probability); however, only parks that were majority wetland showed substantial

TABLE 1 Coefficients of quail occupancy probability from the top single-season model with all parks ($n = 1,059$) and a subset of parks ($n = 423$) with sufficient data on coyote presence. For the park subset, global models were run excluding and including likely coyote presence. '—' indicates variables not included in the top model

	All parks				Park subset, without coyote covariate				Park subset, with coyote covariate			
	Est.	SE	95% CI		Est.	SE	95% CI		Est.	SE	95% CI	
Intercept	-1.21	0.08	-1.37	-1.05	-1.08	0.11	-1.29	-0.86	-1.28	0.13	-1.52	-1.03
Coyote presence	—	—	—	—	—	—	—	—	0.55	0.15	0.25	0.85
Isolation	-0.88	0.11	-1.10	-0.66	-0.74	0.12	-0.96	-0.51	-0.75	0.11	-0.97	-0.53
Park size	0.97	0.17	0.65	1.30	1.33	0.25	0.83	1.82	1.11	0.27	0.57	1.65
Road density	—	—	—	—	0.14	0.08	-0.02	0.30	0.11	0.08	-0.05	0.28
Matrix impervious cover	-0.66	0.06	-0.78	-0.54	-0.56	0.08	-0.73	-0.40	-0.61	0.09	-0.78	-0.44
Park impervious cover	-0.81	0.09	-0.98	-0.64	-1.28	0.13	-1.54	-1.02	-1.22	0.14	-1.48	-0.95
Park shrub cover	0.17	0.05	0.06	0.27	0.15	0.07	0.00	0.29	0.13	0.08	-0.02	0.28
Park wetland cover	0.18	0.09	0.00	0.37	0.28	0.11	0.06	0.50	0.29	0.11	0.07	0.52
Park wetland cover ²	-0.31	0.06	-0.42	-0.20	-0.48	0.08	-0.63	-0.33	-0.46	0.08	-0.62	-0.31
Year	-0.06	0.05	-0.16	0.04	-0.11	0.07	-0.24	0.02	-0.10	0.07	-0.23	0.03
Avian predator density	—	—	—	—	0.03	0.08	-0.12	0.18	0.03	0.08	-0.12	0.18

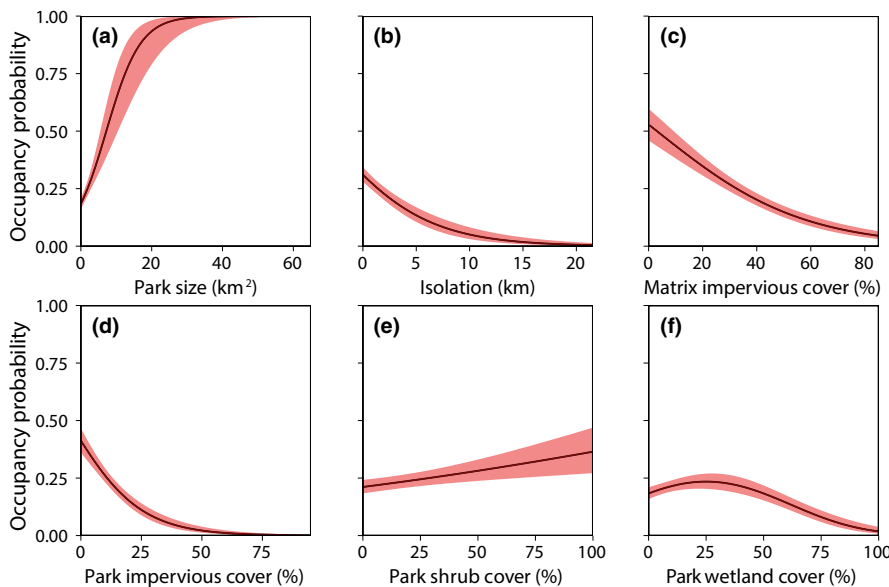


FIGURE 2 Relationship of park characteristics to quail occupancy probability with standard error (shaded). Only informative covariates whose 95% confidence intervals do not overlap zero are plotted (Table 1)

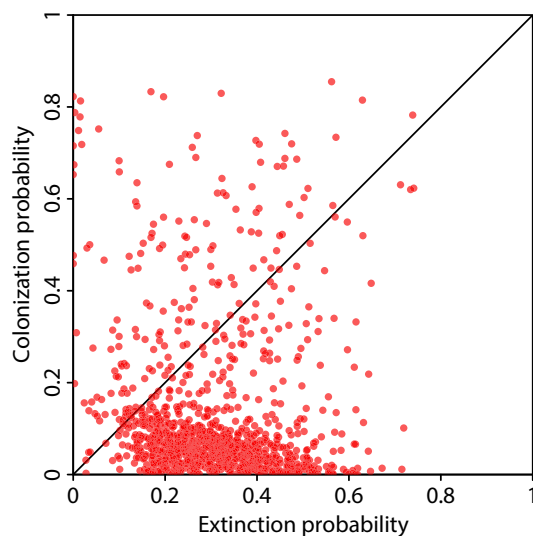


FIGURE 3 Relationship between colonization and extinction probabilities in urban parks

declines in occupancy (Figure 2f). When shrub cover increased by 10% within a park, the odds of being occupied increased by 7.9%. Survey year did not have a significant effect on quail occupancy. Neither park road density nor avian predator density was included in the top models of quail occupancy, indicating these variables do not significantly impact a park's ability to support quail. Values of detection coefficients are reported in Table S4.

The presence of coyotes had a significant positive effect on California quail presence and increased the odds of a park being occupied by 73.3% compared with a park without coyotes (Table 1). The single-season model fit to the park subset where coyote presence or absence was known showed the same significant relationships with other predictors as in the full dataset, except for park shrub cover, whose effect became non-significant. Adding coyotes to the model

did not change the effect of any other predictors (Table 1); however, the addition did improve model fit ($\Delta\text{AICc} = 11.05$).

3.2 | Drivers of quail turnover in urban parks

California quail were more likely to become locally extirpated from parks (0.13 ± 0.04) than they were to colonize unoccupied ones (0.10 ± 0.03). The vast majority of parks (83.9%; Figure 3) had extinction probabilities higher than their probability of being colonized, indicating that quail, if present, will be lost from these parks over the long term. However, over the 9 years evaluated, most parks (81.4%) had a stable trend in occupancy, that is, occupancy probability varied by <0.2 over the course of 2010–2018. Parks with more shrub cover and that were less isolated were significantly more likely to be colonized (Table 2; Figure 4). Parks more than 6.3 km from an urban boundary or stream corridor were unlikely to be colonized (<0.05 probability, Figure 4a). Additionally, colonization events were more likely in years with higher spring precipitation. Quail extirpation was largely driven by park size alone (Table 2; Figure 4d). Quail in parks larger than 5.3 km^2 had <0.05 probability of becoming locally extinct. Quail extirpation was also higher with higher impervious cover in the matrix. Parks with high amounts of shrub cover had higher levels of both colonization and extinction (Figure 4c,f), indicating quail transiently occupy these types of sites. Values of detection coefficients are reported in Table S5.

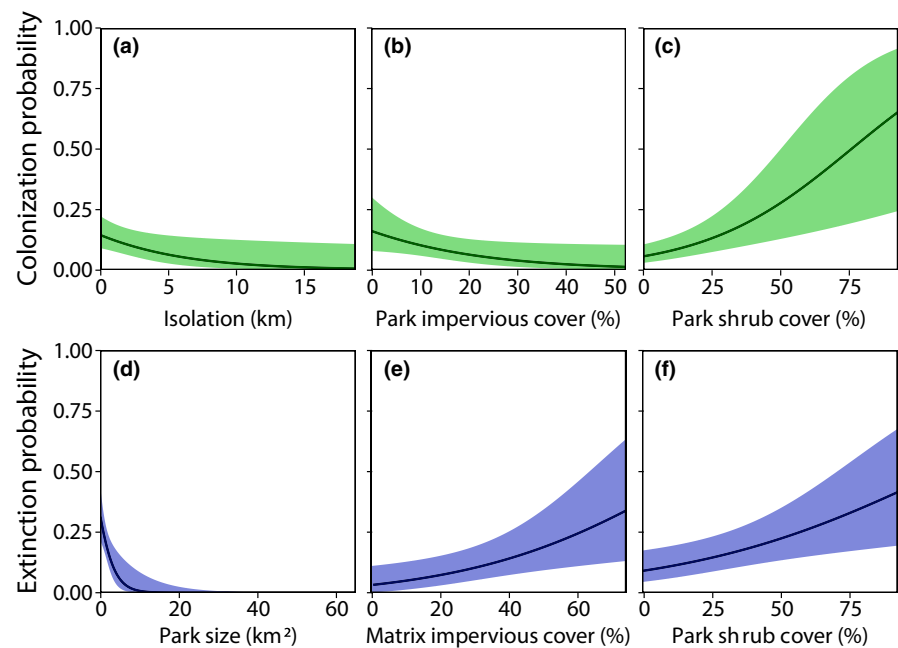
3.3 | Presidio and Golden Gate case study: Effects of potential management

Predicted California quail occupancy was low for both the Presidio (0.014 ± 0.008) and Golden Gate Park (0.006 ± 0.003). Increasing park size or decreasing isolation would have the largest impact on quail occupancy (Figure 2). The Park Presidio Boulevard between the

TABLE 2 Coefficients of initial occupancy, colonization and extinction probabilities for quail in urban parks ($n = 102$) from a multi-season occupancy model. ‘—’ indicates variables not included in the top model

	Initial occupancy				Colonization				Extinction			
	Est.	SE	95% CI		Est.	SE	95% CI		Est.	SE	95% CI	
Intercept	0.04	0.44	-0.83	0.9	-2.22	0.31	-2.83	-1.62	-1.97	0.32	-2.59	-1.35
Park size	—	—	—	—	—	—	—	—	-3.39	1.18	-5.71	-1.07
Park shrub cover	0.75	0.36	0.05	1.46	0.86	0.25	0.37	1.36	0.49	0.18	0.14	0.85
Isolation	—	—	—	—	-0.85	0.40	-1.62	-0.07	—	—	—	—
Park impervious cover	-0.81	0.38	-1.55	-0.07	-0.56	0.28	-1.12	-0.01	—	—	—	—
Matrix impervious cover	-0.58	0.31	-1.18	0.03	—	—	—	—	0.55	0.21	0.13	0.96
Spring precipitation	—	—	—	—	0.48	0.19	0.11	0.85	—	—	—	—
Park wetland cover	-0.17	0.37	-0.89	0.56	-0.17	0.27	-0.7	0.36	—	—	—	—
Park wetland cover ²	-0.75	0.45	-1.64	0.14	-0.22	0.20	-0.62	0.18	—	—	—	—
Road density	—	—	—	—	—	—	—	—	—	—	—	—
Avian predator density	—	—	—	—	—	—	—	—	—	—	—	—

FIGURE 4 Relationship of park characteristics to quail colonization (green) and extinction probability (blue) with standard error (shaded). Only informative covariates whose 95% confidence intervals do not overlap zero are plotted (Table 2)



parks is unlikely to support a population of quail due to its small size (0.0001 ± 0.0001 occupancy probability). However, it could theoretically function as a movement corridor. If the parks were functionally connected, predicted occupancy would increase (0.04 ± 0.02) mainly due to the larger area of the combined parks (Figure 2).

Without a functional corridor, changing park shrub, wetland and impervious cover would have a relatively small impact on California quail occupancy. However, a combination of management strategies could improve the occupancy probability of both parks. For example, decreasing impervious surfaces within the parks by 5% (current values: Presidio = 19.4%, Golden Gate = 10.6%), decreasing impervious

surfaces outside the parks by 10% (current values: Presidio = 27.4%, Golden Gate = 71.4%) and increasing shrub cover within the parks by 10% (current values: Presidio = 4.1%, Golden Gate = 4.3%) would increase the estimated occupancy probability of both parks (Presidio: 0.03 ± 0.016 ; Golden Gate: 0.012 ± 0.005). Combining these changes with a fully functional corridor would increase the occupancy of the joined parks to 0.08 ± 0.04 occupancy probability, doubling the effect of the corridor alone.

Natural colonization of these parks by California quail is unlikely to occur based on our model results. Predicted annual colonization was very low in the Presidio (0.003 ± 0.004), Golden

Gate Park (0.007 ± 0.009) and the hypothetical combined park (0.005 ± 0.008). Predicted extinction was also low in the Presidio (0.028 ± 0.025) and the hypothetical combined park (0.01 ± 0.013). Extinction probabilities in Golden Gate Park (0.2 ± 0.03), however, were an order of magnitude higher than the Presidio, a difference driven largely by differences in park size, the Presidio being 1.5 times larger than Golden Gate Park. Higher predicted extinction than colonization points towards eventual loss of quail without intervention, as was observed over time in these parks. However, functionally connecting the parks would reduce the predicted extinction rate (0.01 ± 0.013) to levels comparable to the predicted colonization rate (0.005 ± 0.008), which would improve the persistence of this species over time.

4 | DISCUSSION

Of the more than a thousand urban parks in our sample, relatively few supported California quail. Quail colonization and occupancy were driven most strongly by park size, park isolation, coyote presence and impervious cover both within the park and in the surrounding matrix. Large parks are most likely to support quail. However, regardless of size, extinction probability increases if the park is isolated from source populations. As a corollary, small, isolated parks are least likely to be able to support quail regardless of local habitat conditions. This work provides a framework for understanding which management interventions may be the most effective given the size, isolation and habitat quality within and around parks.

Park size played an outsized role in determining quail persistence, while isolation by distance and habitat quality (i.e. shrub cover and impervious cover) determined the likelihood of colonization. These relationships are consistent with general ecological theory of how species reach and persist in isolated habitats, which has its foundations in insular biogeography and metapopulation ecology (Hanski, 1998; MacArthur & Wilson, 2001), as well as empirical studies of the impact of habitat fragmentation (Prugh et al., 2008). Further, these trends are consistent with research at a smaller scale documenting local extirpation of quail from fragmented chaparral remnants in urbanized San Diego (Crooks et al., 2004; Soulé et al., 1988) indicating a transferability of findings across scales for urban quail. Although urban park size and species diversity are consistently positively related, other large-scale studies have found minimal effects of isolation (Nielsen et al., 2014). Our results suggest isolation is potentially important for at least a subset of species even if it has limited effects on overall diversity.

The response of California quail in urban parks was consistent with responses to habitat in natural areas, indicating transferability of knowledge across the wildland–urban spectrum. In natural areas, quail inhabit areas that are a mix of shrubby and open habitat (~50% shrub cover, Koford, 1987). In urban areas, parks with very high shrub cover, particularly those smaller in size, may be acting as ecological traps or stepping stone habitat for quail as they were less likely to remain consistently occupied over time (Figure 4c,g;

Table 2). Higher levels of colonization with increasing shrub cover indicates the importance of escape and roosting cover for immigrating quail, but concomitant high levels of extinction indicates a trade-off with the need for open areas for foraging and nesting. Importance of habitat quality is also demonstrated by the relationship between occupancy and impervious and wetland cover, where at higher levels, these cover types supplant suitable habitat for quail (Figure 2c,f; Table 2). Although variables describing fragmentation and urban effects were more influential for quail occupancy than were habitat quality variables, park design to support quail should still consider these characteristics.

Wildland and urban California quail appear to diverge in their exposure to predation threat. Avian predator density in urban parks was not an important predictor of quail occupancy, whereas, in the wild, avian predation is assumed to be the main source of mortality for quail (Calkins et al., 2014). We expected mesopredators to be an important source of predation in urban areas, given higher densities of free-roaming cats (Lepczyk et al., 2004) and their increased likelihood of taking avian prey compared with their rural counterparts (Kauhala et al., 2015). The presence of coyotes may suppress free-ranging cat populations (Gehrt et al., 2013), and we found the presence of coyotes substantially increased the likelihood of a park being occupied by quail—an increase of 73.3%—potentially because of mesopredator release. In other urban areas, coyote presence is related to decreased mesopredator densities and increased presence of chaparral avian species, including quail (Crooks & Soulé, 1999). The direct impacts of mesopredator pressure and quail mortality in urban parks warrants further study, but correlative evidence from findings, here and elsewhere, support this being an important limiter for urban quail.

Higher extinction rates relative to colonization implies California quail in urban parks are relict populations carrying an extinction debt from the urbanization process (Crooks et al., 2001; Kuussaari et al., 2009). On average, urban parks were more likely to lose quail (0.13 ± 0.04 extinction probability) than be colonized by immigrating quail (0.10 ± 0.03). When multi-season model results were projected to all 1,059 parks, extinction probability was greater than colonization for most parks (83.9%), which indicates, quail likely will be eventually lost from these parks, if they have not been already. The low colonization probability across parks (Figure 3) means local populations are unlikely to be rescued by recolonization. Such extinction debt often goes unnoticed, posing a problem for conservation, but once recognized, can inform where intervention needs to take place (Kuussaari et al., 2009). For example, our case study of Golden Gate Park and the Presidio in San Francisco indicated that increasing the effective size of urban parks, through provision of an effective corridor, could reduce extinction rates (0.01 ± 0.013) to be comparable with colonization rates (0.005 ± 0.008). Although natural colonization remains improbable, low extinction rates indicate a translocated population would persist for some time. Further, achievable habitat restoration within the park—through a 5% reduction of impervious surfaces, 10% increase in shrub cover and improvement in urban matrix permeability (10% reduction of impervious surfaces)—greatly

increases the parks' occupancy probability (prior to restoration: Presidio 0.014 ± 0.008 , Golden Gate 0.006 ± 0.003 ; after hypothetical habitat restoration and functional connection: 0.08 ± 0.04).

Connectivity is likely important to wildlife in urban areas given the patchy mosaic of open space present in most cities; however, knowledge of connectivity in urban landscapes remains limited (LaPoint et al., 2015). Connectivity appears to be important for small, ground-dwelling species in urban environments (Rondinini & Doncaster, 2002), and California quails' inability to reach urban parks is an important factor limiting persistence in our study. The creation of wildlife corridors has been promoted as the most effective way to reverse the impacts of fragmentation in urban environments (Soulé et al., 1988); however, it remains a question whether quail would utilize or survive in a corridor. The observations of quails in remnant habitat strips as narrow as 10 m (Soulé et al., 1988) and the regular occurrence of daily movements >1.6 km (Calkins et al., 2014) make corridor use feasible in terms of quail mobility; however, actual utilization and mortality will need to be validated by further study. As an urban-sensitive, ground-dwelling species of least concern with appropriate body size for existing movement tracking technology, quail could be an ideal candidate for evaluating urban corridor use. Further, a functional corridor for quail would likely benefit other dispersal-limited species.

Assisted recolonization is one strategy for returning California quail to urban parks to overcome low natural colonization rates, particularly where improvements in conditions have occurred since extirpation. California quail have been successfully introduced for hunting across the globe, from Germany to Australia, demonstrating the potential for successful translocation. To improve conditions for quail, park managers should do everything possible to increase the park's effective size, whether it be improving matrix quality around the park or functionally linking habitat patches, as increasing the absolute area of parks may not be feasible. Improving the habitat quality of a park through removal of impervious surfaces and increases in shrub cover will also better support quail. Promoting the presence of coyotes or controlling free-ranging cats will likely have a substantial positive impact on a park's ability to support quail. For the Presidio, enhancements have improved park quality for quail since extirpation. Habitat restoration has increased the park's overall shrub cover >0.40 km², coyotes returned to the park in 2003 and an under-construction habitat bridge over a busy highway will increase intra-park connectivity and habitat area by 14 acres. Opportunities also exist to enhance the connection between the Presidio and Golden Gate Park along Park Presidio Boulevard or through residential and park areas along the coast. Increasing shrub cover—which is associated with increased richness of urban-sensitive chaparral species, including quail, in habitat strips (Bolger et al., 2001)—will likely improve the quality of the connection. If reintroduced to the Presidio, quail are likely to persist for some time giving the park's low extinction probability (0.028 ± 0.025). Joint reintroduction of quail to both the Presidio and Golden Gate Park would likely bolster the persistence of quail in both parks, given their proximity and size.

Using eBird data allowed us to evaluate park management for species conservation across a broad range of urban parks without targeted data collection efforts. The eBird dataset is particularly well-suited to the study of urban parks, where observations are often concentrated (Callaghan et al., 2017). While the accuracy of individual observations within this citizen science dataset is likely lower than in a standardized survey, aggregating observations for the easily identified California quail provides a dataset suitable for making occupancy comparisons across the entire state of California. Further parsing occupancy trends into the components of colonization and extinction provided a more nuanced view into the drivers of quail population turnover. These insights enabled us to provide actionable guidance to local land and wildlife managers who are poised to support this iconic California species.

ACKNOWLEDGEMENTS

This research was performed with support from the Presidio Trust and the NSF (EF-1638725; NSF 18-102). M. Tingley, L. Stringer, colleagues at SFEI and two anonymous reviewers provided valuable assistance in the development of this manuscript.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

AUTHORS' CONTRIBUTIONS

E.N.S., S.M.S., J.S.Y. and M.M.W. conceived the ideas and designed the methodology; S.M.S., M.M.W. and K.J.I. analysed the data; K.J.I. led the writing of the manuscript. All authors contributed to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.6078/D1KD93> (Iknayan et al., 2021).

ORCID

Kelly J. Iknayan  <https://orcid.org/0000-0002-3327-2235>

Megan M. Wheeler  <https://orcid.org/0000-0001-5220-9648>

Samuel M. Safran  <https://orcid.org/0000-0003-0742-2321>

Erica N. Spotswood  <https://orcid.org/0000-0002-7787-7180>

REFERENCES

- Alexander, J., Ehlers Smith, D. A., Ehlers Smith, Y. C., & Downs, C. T. (2019). Drivers of fine-scale avian functional diversity with changing land use: An assessment of the effects of eco-estate housing development and management. *Landscape Ecology*, 34(3), 537–549. <https://doi.org/10.1007/s10980-019-00786-y>
- Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's information criterion. *The Journal of Wildlife Management*, 74(6), 1175–1178. <https://doi.org/10.1111/j.1937-2817.2010.tb01236.x>
- Aronson, M. F., Lepczyk, C. A., Evans, K. L., Goddard, M. A., Lerman, S. B., MacIvor, J. S., Nilon, C. H., & Vargo, T. (2017). Biodiversity in the city: Key challenges for urban green space management. *Frontiers in Ecology and the Environment*, 15(4), 189–196. <https://doi.org/10.1002/fee.1480>

- Beninde, J., Veith, M., & Hochkirch, A. (2015). Biodiversity in cities needs space: A meta-analysis of factors determining intra-urban biodiversity variation. *Ecology Letters*, 18(6), 581–592. <https://doi.org/10.1111/ele.12427>
- Bolger, D. T., Scott, T. A., & Rotenberry, J. T. (2001). Use of corridor-like landscape structures by bird and small mammal species. *Biological Conservation*, 102(2), 213–224. [https://doi.org/10.1016/S0006-3207\(01\)00028-3](https://doi.org/10.1016/S0006-3207(01)00028-3)
- Botsford, L. W., Wainwright, T. C., Smith, J. T., Mastrup, S., & Lott, D. F. (1988). Population dynamics of California quail related to meteorological conditions. *The Journal of Wildlife Management*, 52(3), 469–477. <https://doi.org/10.2307/3801593>
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multi-model inference: A practical information-theoretic approach* (2nd ed.). Springer.
- Calkins, J. D., Gee, J. M., Hagelin, J. C., & Lott, D. F. (2014). California Quail (*Callipepla californica*), version 2.0. In A. F. Poole (Ed.), *The Birds of North America Online*. Cornell Lab of Ornithology. <https://birdsna.org/Species-Account/bna/species/calqua/>
- Callaghan, C. T., Lyons, M. B., Martin, J. M., Major, R. E., & Kingsford, R. T. (2017). Assessing the reliability of avian biodiversity measures of urban greenspaces using eBird citizen science data. *Avian Conservation and Ecology*, 12(2), 12. <https://doi.org/10.5751/ACE-01104-120212>
- Carter, N., Cooke, R., White, J. G., Whisson, D. A., Isaac, B., & Bradsworth, N. (2019). Joining the dots: How does an apex predator move through an urbanizing landscape? *Global Ecology and Conservation*, 17, e00532. <https://doi.org/10.1016/j.gecco.2019.e00532>
- Christy, T. (2003). *CalHydro: Statewide 1:100k routed hydrography for California in Shapefile Format* (2003.6). <https://www.calfish.org/ProgramsData/ReferenceLayersHydrography/CaliforniaHydrography.aspx>
- Cornell Lab of Ornithology. (2019). *EBird basic dataset. Version: EBD_relMay-2019*.
- CPAD. (2019). *California Protected Areas Database (CPAD)*. www.calandis.org
- Crooks, K. R., & Soulé, M. E. (1999). Mesopredator release and avifaunal extinctions in a fragmented system. *Nature*, 400(6744), 563–566. <https://doi.org/10.1038/23028>
- Crooks, K. R., Suarez, A. V., & Bolger, D. T. (2004). Avian assemblages along a gradient of urbanization in a highly fragmented landscape. *Biological Conservation*, 115(3), 451–462. [https://doi.org/10.1016/S0006-3207\(03\)00162-9](https://doi.org/10.1016/S0006-3207(03)00162-9)
- Crooks, K. R., Suarez, A. V., Bolger, D. T., & Soulé, M. E. (2001). Extinction and colonization of birds on habitat islands. *Conservation Biology*, 15(1), 159–172. <https://doi.org/10.1111/j.1523-1739.2001.99379.x>
- Fiske, I., & Chandler, R. (2011). unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software*, 43(10). <https://doi.org/10.18637/jss.v043.i10>
- Gehrt, S. D., Wilson, E. C., Brown, J. L., & Anchor, C. (2013). Population ecology of free-roaming cats and interference competition by coyotes in urban parks. *PLoS ONE*, 8(9), e75718. <https://doi.org/10.1371/journal.pone.0075718>
- Global Biodiversity Information Facility. (2019). *GBIF occurrence download*. <https://doi.org/10.15468/dl.d7hpyh>
- Hanski, I. (1998). Metapopulation dynamics. *Nature*, 396(6706), 41–49. <https://doi.org/10.1038/23876>
- Homer, C., Dewitz, J., Jin, S., Xian, G., Costello, C., Danielson, P., Gass, L., Funk, M., Wickham, J., Stehman, S., Auch, R., & Riitters, K. (2020). Conterminous United States land cover change patterns 2001–2016 from the 2016 National Land Cover Database. *ISPRS Journal of Photogrammetry and Remote Sensing*, 162, 184–199. <https://doi.org/10.1016/j.isprsjprs.2020.02.019>
- Iknayan, K. J., Wheeler, M. M., Safran, S. M., Young, J. S., & Spotswood, E. N. (2021). Data from: What makes urban parks good for California quail? Evaluating park suitability, species persistence, and the potential for reintroduction into a large urban national park. *Dryad Digital Repository*, <https://doi.org/10.6078/D1KD93>
- Johnston, A., Hochachka, W. M., Strimas-Mackey, M. E., Ruiz Gutierrez, V., Robinson, O. J., Miller, E. T., Auer, T., Kelling, S. T., & Fink, D. (2021). Analytical guidelines to increase the value of community science data: An example using eBird data to estimate species distributions. *Diversity and Distributions*, 27(7), 1265–1277. <https://doi.org/10.1111/ddi.13271>
- Jones, G. M., & Peery, M. Z. (2019). Phantom interactions: Use odds ratios or risk misinterpreting occupancy models. *The Condor*, 121(1), duy007. <https://doi.org/10.1093/condor/duy007>
- Kauhala, K., Talvitie, K., & Vuorisalo, T. (2015). Free-ranging house cats in urban and rural areas in the north: Useful rodent killers or harmful bird predators? *Journal of Vertebrate Biology*, 64(1), 45–55. <https://doi.org/10.25225/fozo.v64.i1.a6.2015>
- Koford, E. J. (1987). *Variations in California quail productivity in relation to precipitation in Baja California Norte*. University of California, Davis.
- Kuussaari, M., Bommarco, R., Heikkinen, R. K., Helm, A., Krauss, J., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Rodà, F., Stefanescu, C., Teder, T., Zobel, M., & Steffan-Dewenter, I. (2009). Extinction debt: A challenge for biodiversity conservation. *Trends in Ecology & Evolution*, 24(10), 564–571. <https://doi.org/10.1016/j.tree.2009.04.011>
- LaPoint, S., Balkenhol, N., Hale, J., Sadler, J., & van der Ree, R. (2015). Ecological connectivity research in urban areas. *Functional Ecology*, 29(7), 868–878. <https://doi.org/10.1111/1365-2435.12489>
- Lepczyk, C. A., Mertig, A. G., & Liu, J. (2004). Landowners and cat predation across rural-to-urban landscapes. *Biological Conservation*, 115(2), 191–201. [https://doi.org/10.1016/S0006-3207\(03\)00107-1](https://doi.org/10.1016/S0006-3207(03)00107-1)
- MacArthur, R. H., & Wilson, E. O. (2001). *The theory of island biogeography*. Princeton University Press.
- MacKenzie, D. I., & Bailey, L. L. (2004). Assessing the fit of site-occupancy models. *Journal of Agricultural, Biological, and Environmental Statistics*, 9(3), 300–318. <https://doi.org/10.1198/108571104X3361>
- MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Bailey, L. L., & Hines, J. E. (2018). *Occupancy estimation and modeling: Inferring patterns and dynamics of species occurrence* (2nd ed.). Academic Press.
- McDonald, R. I., Mansur, A. V., Ascensão, F., Colbert, M., Crossman, K., Elmqvist, T., Gonzalez, A., Güneralp, B., Haase, D., Hamann, M., Hillel, O., Huang, K., Kahnt, B., Maddox, D., Pacheco, A., Pereira, H. M., Seto, K. C., Simkin, R., Walsh, B., ... Ziter, C. (2020). Research gaps in knowledge of the impact of urban growth on biodiversity. *Nature Sustainability*, 3(1), 16–24. <https://doi.org/10.1038/s41893-019-0436-6>
- Morin, D. J., Yackulic, C. B., Diffendorfer, J. E., Lesmeister, D. B., Nielsen, C. K., Reid, J., & Schaubert, E. M. (2020). Is your ad hoc model selection strategy affecting your multimodel inference? *Ecosphere*, 11(1), e02997. <https://doi.org/10.1002/ecs2.2997>
- Müller, A., Bøcher, P. K., Fischer, C., & Svenning, J.-C. (2018). 'Wild' in the city context: Do relative wild areas offer opportunities for urban biodiversity? *Landscape and Urban Planning*, 170, 256–265. <https://doi.org/10.1016/j.landurbplan.2017.09.027>
- Nielsen, A. B., van den Bosch, M., Maruthaveeran, S., & van den Bosch, C. K. (2014). Species richness in urban parks and its drivers: A review of empirical evidence. *Urban Ecosystems*, 17(1), 305–327. <https://doi.org/10.1007/s11252-013-0316-1>
- Presidio Trust. (2018, April 3). *Presidio trust releases first native species into mountain lake* [Press release]. <https://www.presidio.gov/presidio-trust/press/presidio-trust-releases-first-native-species-mount-lake>
- Prugh, L. R., Hodges, K. E., Sinclair, A. R. E., & Brashares, J. S. (2008). Effect of habitat area and isolation on fragmented animal populations. *Proceedings of the National Academy of Sciences of the United*

- States of America*, 105(52), 20770–20775. <https://doi.org/10.1073/pnas.0806080105>
- R Core Team (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Richards, S. A. (2008). Dealing with overdispersed count data in applied ecology: Overdispersed count data. *Journal of Applied Ecology*, 45(1), 218–227. <https://doi.org/10.1111/j.1365-2664.2007.01377.x>
- Rodewald, A., & Gehrt, S. (2014). Wildlife population dynamics in urban landscapes. In R. A. McCleery, C. E. Moorman, & M. N. Peterson (Eds.), *Urban wildlife* (pp. 117–147). Springer US. https://doi.org/10.1007/978-1-4899-7500-3_8
- Rondinini, C., & Doncaster, C. P. (2002). Roads as barriers to movement for hedgehogs. *Functional Ecology*, 16(4), 504–509. <https://doi.org/10.1046/j.1365-2435.2002.00651.x>
- Ryan, A. M., & Partan, S. R. (2014). Urban wildlife behavior. In R. A. McCleery, C. E. Moorman, & M. N. Peterson (Eds.), *Urban wildlife conservation: Theory and practice* (pp. 149–173). Springer US. https://doi.org/10.1007/978-1-4899-7500-3_9
- San Francisco Estuary Institute (SFEI). (2017). *California Aquatic Resource Inventory (CARI) version 0.3*. <https://www.sfei.org/data/california-aquatic-resource-inventory-cari-version-03-gis-data>
- Soanes, K., & Lentini, P. E. (2019). When cities are the last chance for saving species. *Frontiers in Ecology and the Environment*, 17(4), 225–231. <https://doi.org/10.1002/fee.2032>
- Soulé, M. E., Bolger, D. T., Alberts, A. C., Wrights, J., Soric, M., & Hill, S. (1988). Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conservation Biology*, 2(1), 75–92. <https://doi.org/10.1111/j.1523-1739.1988.tb00337.x>
- Soulsbury, C. D., & White, P. C. L. (2016). Human–wildlife interactions in urban areas: A review of conflicts, benefits and opportunities. *Wildlife Research*, 42(7), 541–553. <https://doi.org/10.1071/WR14229>
- Strimas-Mackey, M., Hochachka, W. M., Ruiz-Gutierrez, V., Robinson, O. J., Miller, E. T., Auer, T., Kelling, S., Fink, D., & Johnston, A. (2020). *Best practices for using eBird data v1.0*. Cornell Lab of Ornithology. <https://cornelllabofornithology.github.io/ebird-best-practices/>
- The Quail Recovery Task Force. (2004). *Quail recovery plan for the city of San Francisco*. <https://www.biodiversitylibrary.org/item/150918>
- US Census Bureau. (2018). *TIGER/Line shapefiles (machine-readable data files)*. https://www2.census.gov/geo/pdfs/maps-data/data/tiger/tgrshp2018/TGRSHP2018_TechDoc.pdf

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Iknayan, K. J., Wheeler, M. M., Safran, S. M., Young, J. S., & Spotswood, E. N. (2021). What makes urban parks good for California quail? Evaluating park suitability, species persistence, and the potential for reintroduction into a large urban national park. *Journal of Applied Ecology*, 00, 1–11. <https://doi.org/10.1111/1365-2664.14045>