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Impacts of Passive Relocation on the Survival, Dispersal, and Reproduction of Burrowing Owls (*Athene cunicularia*) in Southcentral Arizona

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ABSTRACT.—Land development in the southwestern USA has caused intensive landscape change and created conflicts with Burrowing Owls (*Athene cunicularia*), which rely on underground burrows and occupy sites often attractive for development. Passive relocation is a mitigation method for owls on development sites that involves excluding owls from their burrows followed by collapsing and filling those burrows to prevent reuse. We worked with developers in Phoenix, Arizona, to locate owls, and we evaluated how passive relocation and other factors influenced their survival, dispersal, and reproduction. From 2021 to 2022, we used radiotelemetry to monitor 25 resident (control) owls and 14 passively relocated owls. Known-fate models indicated higher annual survival for control owls (0.65, 85% confidence interval [CI] = 0.44, 0.87) than for passively relocated owls (0.43, 85% CI = 0.16, 0.70); however, 85% CIs for all regression coefficients bounded zero, suggesting insufficient evidence to confirm the potential effects of evaluated factors. Displaced owls dispersed farther than control owls ($\bar{x}$ = 450.73 m vs. 121.21 m), though most owls remained within their home ranges. For every one SD increase in the percentage of agriculture within 200 m of a nest, the odds of owl nest success increased by a factor of 2.51 (85% CI = 1.04, 6.01) and expected productivity increased by a factor of 1.62 (85% CI = 1.04, 2.51). The effectiveness of passive relocation relied on the availability of habitat and burrows within owl home ranges and communication with developers. Limitations related to coordination with developers, project scales, and burrow availability before displacement necessitate further investigation.

KEY WORDS: *agricultural habitat*; *demography*; *land development*; *mitigation*; *movement*; *wildlife conflict*.

IMPACTOS DE LA RELOCALIZACIÓN PASIVA SOBRE LA SUPERVIVENCIA, DISPERSIÓN Y REPRODUCCIÓN DE *ATHENE CUNICULARIA* EN EL CENTRO-SUR DE ARIZONA

RESUMEN.—El desarrollo urbano en el suroeste de EE.UU. ha causado cambios intensivos en el paisaje y generado conflictos con *Athene cunicularia*, que depende de madrigueras subterráneas y ocupa sitios frecuentemente atractivos para la promoción inmobiliaria. La relocalización pasiva es un método de mitigación para búhos en sitios de desarrollo que consiste en excluir a los búhos de sus madrigueras y posteriormente colapsar y rellenar dichas madrigueras para evitar su reutilización. Trabajamos con inmobiliarios en Phoenix, Arizona, para localizar búhos y evaluamos cómo la relocalización pasiva y otros

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factores influyeron sobre su supervivencia, dispersión y reproducción. Entre 2021 y 2022 utilizamos radiotelemetría para monitorear 25 búhos residentes (control) y 14 búhos relocalizados pasivamente. Los modelos de destino conocido indicaron una supervivencia anual mayor para los búhos control (0.65, intervalo de confianza [IC] del 85% = 0.44, 0.87) que para los búhos relocalizados pasivamente (0.43, IC del 85% = 0.16, 0.70); sin embargo, los IC del 85% para todos los coeficientes de regresión incluyeron el cero, lo que sugiere evidencia insuficiente para confirmar los posibles efectos de los factores evaluados. Los búhos desplazados se dispersaron más lejos que los búhos control ($\bar{x}$ = 450.73 m vs. 121.21 m), aunque la mayoría permaneció dentro de sus áreas de campeo. Por cada incremento de una desviación estándar en el porcentaje de agricultura dentro de los 200 m alrededor de un nido, las probabilidades de éxito del nido aumentaron en un factor de 2.51 (IC del 85% = 1.04, 6.01) y la productividad esperada aumentó en un factor de 1.62 (IC del 85% = 1.04, 2.51). La efectividad de la relocalización pasiva dependió de la disponibilidad de hábitat y madrigueras dentro de las áreas de campeo de los búhos y de la comunicación con los promotores. Las limitaciones relacionadas con la coordinación con los promotores, la escala de los proyectos y la disponibilidad de madrigueras antes del desplazamiento requieren mayor investigación.

[Traducción del equipo editorial]

INTRODUCTION

Increases in anthropogenic landscapes have intensified the loss of biological diversity and accelerated declines in species populations worldwide (McKinney 2002, Morelli et al. 2016, Powers and Jetz 2019). Urban expansion is associated with wildlife exposure to disease and chemicals, the loss and degradation of habitat, and increased risk of predation and competition (Brearley et al. 2013, La Sorte et al. 2018). Additionally, declines in species richness have occurred in relation to the intensity of urbanization (Marzluff 2001, McKinney 2008, Fidino et al. 2021). Wildlife species that persist in these altered environments are influenced by human population density, intensity and type of land use, and vulnerability to mortality threats. For example, the application of agricultural insecticides can cause chronic sublethal effects on avian species (Goulson 2013), illustrated by migratory species experiencing declines in fat stores and extended migratory stopovers after being exposed to neonicotinoids (Eng et al. 2019). Increased land fragmentation changes competitive interactions among native species. For example, interference competition reduced reproductive rates among Eurasian Goshawks (*Astur gentilis*) that nested densely in forests that were highly fragmented by urbanization (Natsukawa et al. 2019). Urban expansion leads to further encroachment into natural areas, directly impacting local wildlife.

The Burrowing Owl (*Athene cunicularia*; hereafter owl) is a native species that occurs across much of North, Central, and South America and appears to adapt to anthropogenic environments. In some regions, these owls may occupy urban and agricultural landscapes at a higher density than in native grassland and shrubland habitats (Millsap and Bear 2000). Irrigation drains and canals associated with agricultural fields in Imperial Valley, California, supported some of the highest reported densities of owls (DeSante et al. 2004). Living in a human-developed landscape can come at a cost for these owls, however. In Florida, owl nest density declined once urban land development exceeded a threshold of 60% areal coverage (Millsap and Bear 2000). In New Mexico, the survival of juvenile owls in anthropogenic landscapes varied with land use; owls in agricultural areas had higher survival than those in urban areas and greenspace (Griffin et al. 2017). Moreover, occupying larger territories surrounded by open space can increase nest success for urban owls (Berardelli et al. 2010). There remains a need for further assessments of owl survival and reproduction across a gradient of anthropogenic habitats.

Owls have a broad distribution and occupy a variety of habitat types and land uses in western North America; however, their populations are declining and ranges are contracting (Klute et al. 2003, Macías-Duarte and Conway 2015). Declines are attributed to several factors, including the effects of climate change, loss of habitat due to conversion of native grassland to urban land uses, pesticide exposure, and extirpation of native fossorial animals on which these owls depend (Desmond et al. 2000, Gervais et al. 2000, Macías-Duarte and Conway 2015, Porro et al. 2020). Expansion of human populations and agricultural land leads to loss of native habitat and increasing conflicts between development activities and owl conservation, which is a particularly acute issue in the southwestern USA (Berardelli et al. 2010; Griffin et al. 2017; Doublet et al. 2023a, 2023b).

This owl species is endangered in Canada, under special protection in Mexico, and considered a U.S. Fish and Wildlife Service species of conservation concern in several states across the western USA. In addition, owls were recently petitioned for candidacy as an endangered species in compliance with the California Endangered Species Act, emphasizing the urgent need to improve current mitigation efforts in the state (California Department of Fish and Wildlife 2024). This status amalgam has resulted in varied regulatory protections (Klute et al. 2003) and, as a result, mitigation methods that address the effects of land development vary across the species' North American range.

Passive relocation, also termed displacement, is a common mitigation method specifically for owls (Trulio 1995, Hennessy et al. 2022). Passive relocation involves excluding a non-breeding owl from its burrow(s) and collapsing and filling the burrow(s) to preclude reuse, and assumes the owl will relocate independently. Passive relocation is listed as a management strategy by state wildlife agencies in Arizona, California, and Florida. The states' guidelines include the recommendation that artificial burrows are to be installed in advance of passive relocation within 100 m of the burrow to be collapsed, provided that suitable habitat will exist on-site after development activities are completed (Arizona Game and Fish Department 2007, California Department of Fish and Game 2012, Florida Fish and Wildlife Conservation Commission 2013). However, installing artificial burrows within this short distance is often not feasible with large development projects. Further, although passive relocation is a common management practice, few studies have monitored the outcomes of such methods (Trulio 1995, Hennessy et al. 2022).

We aimed to assess the impacts of passive relocation, when used as a mitigation response to land development, on owls in Phoenix, Arizona, particularly with respect to survival, dispersal, and reproduction. We defined dispersal as movements following displacement for passively relocated owls and following transmitter attachment for control owls. Leading up to this study, Phoenix and the surrounding suburbs were experiencing rapid urban development, and owls were in direct conflict with these activities. We hypothesized that owl survival was influenced by movement, sex, and surrounding habitat. Displaced owls are more likely to survive if they can remain within their individual core use areas, as long-distance dispersal can increase the risk of mortality (Catlin and Rosenberg 2006, Hennessy et al. 2022). Because passively relocated owls were likely to disperse greater distances than owls that were not evicted from their burrows (controls), we predicted that displaced owls would have lower survival rates than control owls. We also predicted that female owls would make longer movements and experience lower survival rates compared to males, as females tend to disperse farther than males after nest failure (Catlin et al. 2005, Riding and Belthoff 2018). Agricultural land provides refuge and burrow availability for owls; therefore, we predicted that more agriculture and less development around burrows would positively influence survival (Millsap 2002, Rosenberg and Haley 2004, Griffin et al. 2017).

Finally, we hypothesized that owl reproduction would be influenced by 1) passive relocation, 2) the amount of agriculture around a nest, and 3) nest initiation date. We predicted that the challenges associated with displacement (i.e., securing a new burrow and sometimes a mate) would lead to lower nest success and productivity for passively relocated owls during the breeding season following displacement, compared to control owls. We predicted that nest success and productivity would be higher at nests near larger areas of agricultural land, as this land-use type supports prey and burrow availability around nests (DeSante et al. 2004, Rosenberg and Haley 2004, Moulton et al. 2006). We predicted that nest success and productivity would be higher at nests with earlier initiation dates, as nest establishment early in the breeding season increases brood sizes and the number of fledglings (Griebel and Savidge 2007).

METHODS

Study Area. We conducted this study in and around the greater metropolitan area of Phoenix, Arizona, within Maricopa County (two subareas with center points at 33°22′12″N, 112°35′1″W and 33°25′47″N, 112°11′43″W) and Pinal County (one subarea centered at 33°10′8″N, 111°31′7″W; Fig. 1). Elevation in the study area ranged from 200 to 600 m. This area was historically Sonoran Desert scrubland dominated by creosote bush (*Larrea tridentata*) and interspersed with shrubs such as palo verde (*Parkinsonia* spp., Robinett et al. 2005); however, much of the area was converted to other land uses prior to this study, including a mosaic of commercial, residential, and agricultural spaces. Irrigated agricultural land included crops such as alfalfa (*Medicago sativa*), cotton (*Gossypium hirsutum*), wheat (*Triticum aestivum*), barley (*Hordeum vulgare*), and corn (*Zea mays;* Lahmers and Eden 2018). During the study period, the mean annual minimum and maximum temperatures were 14°C and 36°C, respectively; the overall mean annual temperatures were 23°C in 2021 and 24°C in 2022; and mean annual precipitation varied between 18 cm in 2021

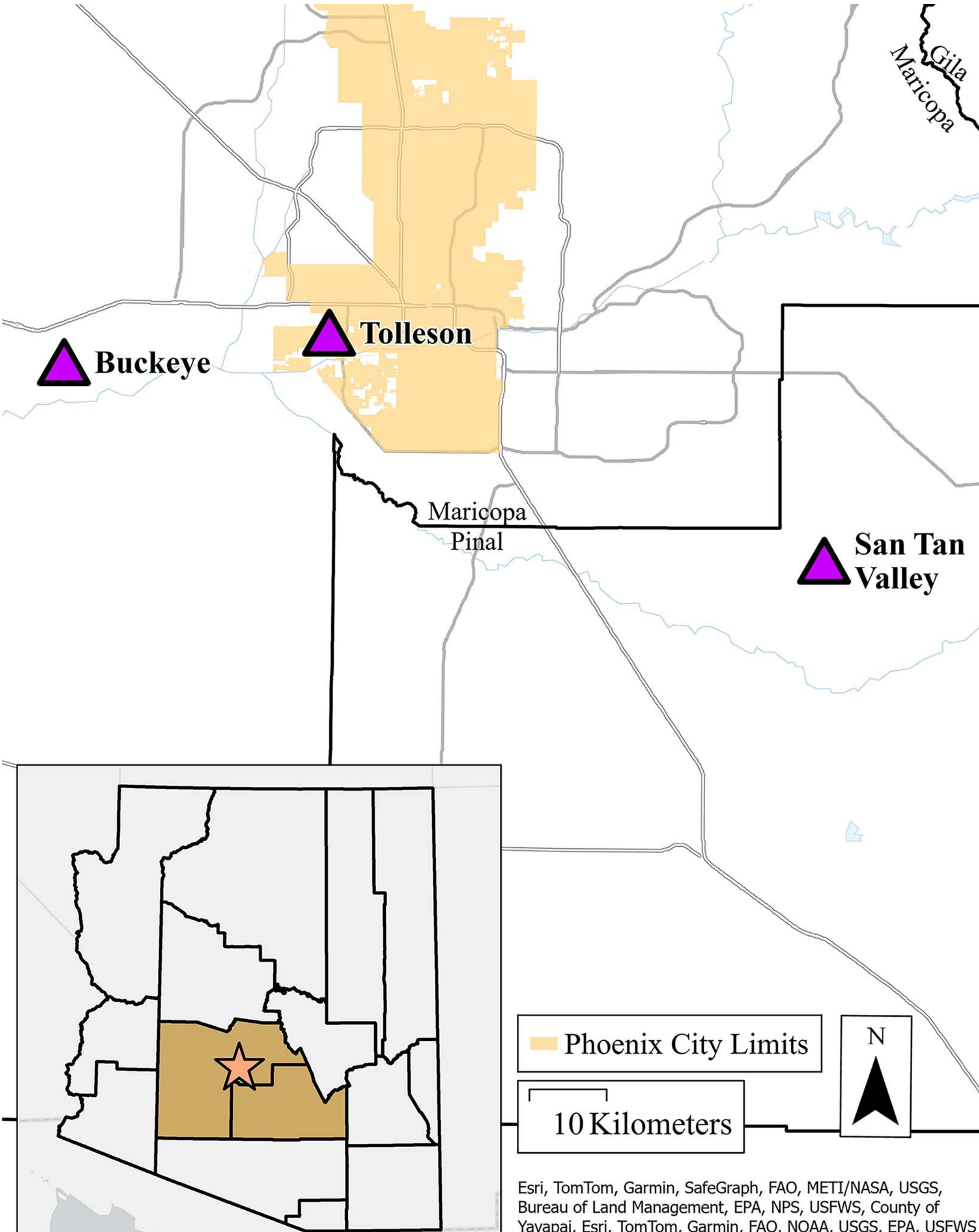

Figure 1. Study sites in southcentral Arizona, USA, where owls were tracked in 2021–2022 to evaluate the effects of passive relocation.

and 15 cm in 2022 (National Weather Service 2022). From 2000–2014, urban areas increased more than four-fold and impervious surfaces tripled in the Phoenix metropolitan area (Wang et al. 2016). A large owl population occurs in Phoenix that has often come into conflict with urban expansion (Doublet et al. 2023a, 2023b).

Development Sites. To locate development sites for the passive relocation of owls, we worked jointly with the Arizona Game and Fish Department, Audubon Southwest, and Wild At Heart to contact developers for information on ongoing or future development projects. We also identified future development sites with the assistance of the planning and development departments of Pinal and Maricopa Counties. Pinal County offered an online GIS map that documented parcels zoned for development with zone type and case numbers for reference. Similarly, Maricopa County provided an online GIS map that included information on building permits with their status and issue dates. In addition, we used Google Earth imagery to identify large, active development sites. After identifying development sites through these various resources, we attempted to determine and contact developers or landowners to obtain permission to conduct owl surveys.

Owl Surveys. We conducted field research from September 2021 through the end of the subsequent breeding season in July 2022. From September 2021 to February 2022, we conducted driving surveys within Pinal and Maricopa Counties to locate owls for passive relocation and to serve as controls. We surveyed at speeds below 20 km/hr in the morning (civil twilight to 4 hr after sunrise) and evening (2 hr before sunset to civil twilight), when the ambient temperature was <30°C and winds were <20 km/hr (i.e., conditions when the probability of detecting owls was expected to be highest; Conway and Simon 2003; Latif et al. 2012; Doublet et al. 2023a, 2023b). All driving surveys included stopping every 0.8 km, exiting the vehicle, and scanning the area with 8 × 42 binoculars in arcs of up to 360°, depending on visual obstruction from anthropogenic structures. We examined burrows to identify evidence of activity (i.e., whitewash, pellets, decoration, prey remains; Desmond et al. 2000, Berardelli et al. 2010). If we did not see an owl at a suitable burrow, we conducted a second survey of the site approximately 1 wk after the first visit.

When we were granted permission to survey a development site for opportunities to passively relocate owls, we conducted driving surveys along on-site roads, including secondary dirt roads. When site access was not yet granted, we conducted driving surveys along surrounding public roads. For control owls, we conducted driving surveys within 3 km of accessible passive relocation sites (Doublet et al. 2023a, 2023b). This included areas where owls were most likely to be encountered with sparse vegetation or bare ground, often including areas along agricultural irrigation canals (Beebe et al. 2014). We selected control owls that were not on the site undergoing development, a minimum of 100 m from the outer edge of the development site (range = 100–1800 m), and on areas with at least 50% cover of agriculture within 200 m of the used burrow. During all driving surveys, we also noted any other sites with zoning or development signage to gather further information and contact the developer.

Survival and Dispersal. We primarily targeted owls observed as pairs for passive relocation, but also opportunistically trapped single adults if they occupied sites undergoing development. All control owls were pairs or single inhabitants within 3 km of study sites with passively relocated owls. Some control owls were near developed sites but were not excluded from their burrows. We used 15 × 15 × 45 cm one-way box traps to capture owls (Conway and Garcia 2005) for the purpose of radio-marking, and we checked traps every hour to ensure owl safety. We included call-playback during the breeding season to trap males (Haug and Didiuk 1993, Conway and Simon 2003).

We used radiotelemetry to track the movements and survival of study owls. We fitted owls with 3.3-g very high frequency (VHF) transmitters (Holohil, Ontario, Canada) attached with backpack-style harnesses. We deployed transmitters only on owls weighing a minimum of 120 g to maintain total attachment weight (transmitter and harness) below 3% of body mass, as recommended by the U.S. Geological Survey (USGS) Bird Banding Lab (Patuxent, MD, USA). Other studies have reported no significant impacts on the survival of juvenile owls outfitted with a similar transmitter/harness design (Todd et al. 2003, Davies and Restani 2006). We set the VHF pulse rate to 20 pulses/min and the pulse width to 12 ms to have a lifespan of 12–13 mo. We also placed a USGS aluminum band and a unique combination of three plastic color bands (Avinet Research Supplies, Portland, ME, USA) on each study owl. Owls do not display sexual size dimorphism (Pyle 2008); therefore, we determined sex by behavior and confirmed our observations genetically by collecting a small blood sample (Griffin et al. 2017, Doublet et al. 2023b). We obtained blood samples from the wing brachial vein using a

26-gauge needle and capillary tube, and transferred the samples to collection cards. We collected <75 μL of blood from each owl, well below the accepted guideline of 1% of the bird's body mass in a single collection event (USGS Bird Banding Lab, Patuxent, MD, USA). The DNA Diagnostic Center processed all blood samples (DDC Veterinary Diagnostic Lab, Fairfield, OH, USA).

Our experimental design involved displacing owls before the breeding season, as displacing nesting owls is generally prohibited by state and federal regulations. After attaching transmitters to owls that we expected to passively relocate, we allowed 5–7 d for acclimation to the transmitter before displacing owls from their burrows. After this time, we put one-way excluder doors (Clark and Plumpton 2005) at the focal burrow(s) and all other suitable burrows within 100 m to prevent owl settlement to nearby burrows. We allowed 1–2 d for the owl(s) to leave the burrow, then used a camera peeper probe specifically designed for owl burrows to confirm there were no owls inside, and then collapsed the burrows and filled them in following established protocols (California Department of Fish and Game 2012).

We monitored the survival and movements of owls that either remained on-site or left the study area from the time of transmitter attachment to either the end of the study period or upon owl death or transmitter failure. To monitor radio-marked owls, we used a vehicle-mounted, omni-directional antenna (Model LM150, Pulse Larsen Antennas, San Diego, CA, USA) or a hand-held H-type Yagi directional antenna connected to a radio receiver (Model R1000, Communications Specialists, Inc., Orange, CA, USA). For the first 2 mo following transmitter attachment, we monitored passively relocated owls intensively (located at least 2–3 times per wk) to document movements; after 2 mo, we tracked them weekly. We monitored control owls weekly after transmitter attachment. If we did not detect a signal from an individual owl, we conducted driving surveys in each cardinal direction away from the owl's last known location. These surveys incorporated a vehicle-mounted antenna and extended to a maximum distance of 8 km throughout the study period, as most displaced owl movements in California occurred within this range (Hennessy et al. 2022). The antenna had a range of approximately 1 km (Doublet et al. 2023b). The loss of a transmitter signal for the remainder of the study period indicated an owl might have dispersed beyond our monitoring range, died, or its transmitter failed. We examined the remains of dead owls to determine the cause of death. At the end of the study period, we attempted to trap all owls to remove their transmitters and color bands.

Reproduction. During the breeding season (February–July 2022), we monitored all tagged owls to collect data on nest initiation, success, and productivity. We used a camera peeper probe to check burrow contents. We defined nest initiation as a minimum of one egg laid in a burrow. Based on previous methods to calculate the nest initiation date, we backdated ~31 d or 73 d from the hatch date or fledge date, respectively, depending on accessibility to each nest (Garcia and Conway 2009, Lantz and Conway 2009, Porro et al. 2020). We considered a nest successful if at least one juvenile was alive at 35 d of age, which is 1 wk before fledging and when a juvenile is not capable of flight but is active above ground (Davis 2012, Doublet et al. 2023a). If we observed eggs, but juveniles did not emerge from their burrow, or if the emerged juveniles did not survive to 35 d, we classified the nest as failed. When juveniles were 35–42 d old, we conducted three, 30-min periods of observation at dawn and dusk to count the maximum number of visible juveniles, which we defined as productivity (Davis 2012, Doublet et al. 2023a). We observed some study owls pairing with owls that we did not capture. We assigned a nest as a passive relocation nest if at least one individual in the pair was passively relocated. A control nest included a pair of control owls or a control owl and an owl that we did not capture.

Land Use. We collected data on land use at the burrows where study owls were captured and where they initiated nests. We obtained land-use data by creating a GIS database that included four variables: the percentages and areas of agriculture and of development around each location. We originally intended to document land uses within a 650-m radius around each burrow, as 80–95% of owl movements are within this range (Haug and Oliphant 1990, Gervais et al. 2003, Rosenberg and Haley 2004, Swaisgood et al. 2015). However, due to the clustered nature of owl nests, there was substantial overlap within the 650-m buffers among individuals. Therefore, we reduced the buffer to 200 m to account for the territoriality of male owls in urban and agricultural landscapes (Berardelli et al. 2010). We used ArcGIS Pro 3.0.2 (Esri, Redlands, CA, USA) to visually determine habitat based on 2022 Landsat 7 Enhanced Thematic Mapper Plus imagery (30-m spatial resolution) obtained from the USGS EarthExplorer (USGS 2022).

Statistical Analyses. *Survival.* We used package *RMark* in R 4.2.1 (R Core Team 2022) to create known-fate models to estimate survival (S) of owls (White and Burnham 1999, Laake 2013). Known-fate models are typically used with data from radio-marked individuals, where sampling (p) and reporting (r) probabilities are set to 1. We coded encounter histories in the live-dead (LD) format, with each pair of values serving as a sampling occasion (White and Burnham 1999, Cooch and White 2021). We coded encounters for each interval in the first position (unknown fate/not tagged = 0, alive/tagged = 1) and the second position (alive = 0, dead = 1; Supplemental Material Table S1). We created weekly encounter histories for known-fate data to estimate survival over 35 wk. We censored owls that went missing after the interval in which they were last encountered. We used the percentage and area of agriculture and development within 200 m of the burrows where each study owl was captured as possible covariates in our analyses. To assess collinearity between continuous variables, we used Pearson's correlation coefficient. We retained the percentage of agriculture within 200 m around each burrow, but excluded all other potential land-use predictors due to high collinearity ($|r| > 0.65$) with this variable. Thus, we developed *a priori* univariate and multivariate models based on the following covariates: relocation status (i.e., passively relocated or control), sex, and percentage of agriculture within 200 m of an owl's initial burrow.

We evaluated our candidate models (Table 1) using Akaike information criterion corrected for small sample sizes (AIC_c) and Akaike weights (w_i; Burnham and Anderson 2002). We considered models within $\Delta AIC_c \leq 2$ to be competitive (Burnham and Anderson 2002). To account for model uncertainty, we model-averaged all candidate models using the *model.avg* function from the R package *MuMIn* (Bartoń 2023), and we reported the conditional model-averaged parameter estimates. We considered parameters to be important predictors of survival if their model-averaged 85% confidence intervals (CIs) did not overlap zero (Arnold 2010). We set the other covariates in the models to their mean values and predicted model-averaged weekly survival estimates for both passively relocated owls and control owls. To derive annual survival estimates for passively relocated owls and control owls, we exponentiated model-averaged weekly survival estimates to the power of 52, which corresponded to the number of weeks in a year. We used the delta method to calculate the standard error of survival estimates (Powell 2007).

Dispersal. We defined site fidelity as an individual owl moving up to 650 m from the original burrow and therefore remaining within its core use area (Haug and Oliphant 1990, Gervais et al. 2003, Rosenberg and Haley 2004, Swaisgood et al. 2015). For each individual, we measured the straight-line distance (m) from the original burrow to every consecutive dispersal location and calculated the average of the movements in ArcGIS Pro. We used the Wilcoxon rank sum U-test with the R package *stats* to assess differences in median dispersal distances of passively relocated owls and control owls, as well as between males and females. We excluded one potential passive-relocation owl from the analyses because development activities caused burrow collapse and mortality before the owl was displaced from its burrow.

Reproduction. We used generalized linear models with a binomial error distribution for nest success and a Poisson error distribution for productivity to examine differences between nests of passively relocated and control owls. We developed *a priori* univariate and multivariate models to assess the effects on nest success and productivity of passive relocation, nest initiation date, and percentage of agriculture within 200 m of nest burrows. We excluded the percentage and area of development within 200 m and area of agriculture within 200 m of each burrow due to collinearity. We standardized all numerical covariates to have a mean of 0 and a variance of 1. To examine model fit for the two model sets

Table 1. Known-fate model selection results examining the effects of passive relocation, sex, and agriculture on survival (S) of owls in Maricopa and Pinal Counties, Arizona, USA, from 2021 to 2022.

Model Parameters[a]	K[b]	AIC_c[c]	ΔAIC_c	w_i[d]	Deviance
S(Status)	2	89.62	0.00	0.26	36.36
S(.)	1	89.98	0.36	0.22	38.73
S(Sex + Status)	3	91.28	1.66	0.11	85.25
S(Agriculture + Status)	3	91.59	1.97	0.10	85.56
S(Sex * Status)	4	91.76	2.14	0.09	83.71
S(Agriculture)	2	91.80	2.18	0.09	87.79
S(Sex)	2	91.89	2.27	0.08	87.87
S(Agriculture * Status)	4	93.57	3.95	0.04	85.51
S(Global)	6	95.51	5.89	0.01	83.39

[a] Model notation: (.) = null model, Status = control and passively relocated owls, Sex = male and female, Agriculture = percentage of agriculture within 200 m of original burrow, Global = model including all main effects and selected interactions (Sex * Status; and Agriculture * Status).
[b] Number of model parameters.
[c] Akaike information criterion value, corrected for small sample sizes.
[d] Akaike model weight.

separately, we conducted a goodness-of-fit test and calculated an overdispersion parameter ($\hat{c}$). To estimate $\hat{c}$ for each model set, we used the goodness-of-fit chi-square statistic and degrees of freedom from the global model that contained all main effects (Burnham and Anderson 2002). When $\hat{c}$ was above 1, we used AIC scores corrected for overdispersion and small sample size (quasi AICc [$QAIC_c$]) for model selection (Burnham and Anderson 2002). Additionally, we used $\hat{c}$ to adjust SEs and CIs for overdispersion. To account for model uncertainty, we model-averaged all candidate models using the *model.avg* function from the R package *MuMIn* (Bartoń 2023) and reported the conditional model-averaged parameter estimates. If the model-averaged 85% CIs for regression coefficients did not bound zero, we considered the predictor variables to be important predictors of nest success and productivity. To calculate the odds ratio for nest success and to estimate productivity, we exponentiated the model-averaged regression coefficients derived from the nest success and productivity models, respectively.

RESULTS

Development Sites. Our outreach effort to developers resulted in contacting 35 companies, including home builders, commercial and residential real estate agencies, and land brokers. We obtained information from five companies, while the other 30 were unresponsive. We located and surveyed 106 development sites either on-site or via public roads, and detected owls at 20% of those sites. We observed most owls on sites where construction activity had yet to be initiated. Of the 21 development sites with owls detected, we received permission to work on five sites to passively relocate owls away from development.

Survival. We monitored 39 owls with telemetry over 35 wk, including 25 control owls (12 males and 13 females) and 14 passively relocated owls (nine males and five females). Among control owls, 20 survived, we recovered three dead, and two had unknown fates (i.e., were last encountered within 4 mo of transmitter attachment). Among passively relocated owls, seven survived, we recovered five dead, and two had unknown fates. For passively relocated owls, five of the dead recoveries or last encounters occurred within 3 mo of burrow collapse and two dead recoveries occurred within 6 mo of burrow collapse. Of the three control owls that we recovered dead, one was likely depredated by a raptor, another likely drowned under cracked concrete inside a flooded irrigation canal, and we could not determine a cause of death for the third owl. Of the five passively relocated owls that we recovered dead, one died due to burrow collapse during construction activities, two were likely depredated by raptors, and we could not determine a cause of death for the remaining two. We ultimately recovered 84% of the deployed transmitters.

Our survival analyses resulted in four known-fate models with $\Delta AIC_c \leq 2$, including the null model, which together accounted for 69% of the model set weights (Table 1). The top model included relocation status (i.e., passively relocated or control), which was present in all competitive models other than the null model. The other two competitive models included the additive effects of relocation status and either sex or the percentage of agriculture around initial burrows. The model-averaged 85% CIs for relocation status, sex, and percentage of agriculture overlapped zero, indicating little evidence for the effect of each covariate on survival (Table 2). The model-averaged estimate of annual survival for control owls was nominally higher (0.65, 85% CI = 0.44, 0.87) than for passively relocated owls (0.43, 85% CI = 0.16, 0.70; Fig. 2).

Dispersal. Most study owls remained within 650 m of their original burrows, thus exhibiting site fidelity; however, proportionately fewer relocated owls showed this pattern. We observed site fidelity in 23 of 25 control owls (92%) and 8 of 14 passively relocated owls (57%). Individual dispersal distances varied significantly between control and passively relocated owls (U-test = 46, $P < 0.001$) but not between males and females (U-test = 179, $P = 1.0$). Though most study owls did not disperse beyond their core use areas (Fig. 3), passively relocated owls averaged longer individual dispersal distances ($\bar{x}$ = 450.73 m, SE = 115.93) than control owls ($\bar{x}$ = 121.21 m, SE = 46.81; Fig. 4).

Reproduction. The 30 owls (22 control and eight passively relocated individuals) monitored during the breeding season initiated 19 nests, including 12 control nests and seven passive relocation nests. We observed a higher proportion of pair-bond shifts among passively relocated owls compared to control owls; nevertheless, all study owls with known fates through the breeding season attempted breeding. Of the 11 pairs of control owls that were pair-bonded at capture, three separated. Mate loss occurred due to mortality for two of those pairs. The three pairs of passively relocated owls separated following displacement; one separation was due to mate mortality associated with development (i.e., the same individual excluded from the dispersal analyses). The two

Table 2. Conditional model-averaged regression coefficients and 85% confidence intervals (CIs) for final known-fate models evaluating survival of passively relocated (and control) owls from 2021 to 2022 in Phoenix, Arizona, USA.

Model Parameters[a]	Estimate	SE	Lower CI	Upper CI
Intercept	4.78	0.81	3.61	5.94
Status (Relocated)[b]	−1.28	0.96	−2.67	0.11
Sex (Female)[b]	0.07	1.02	−1.39	1.54
Agriculture	0.27	1.22	−1.48	2.02
Sex (Female) * Status (Relocated)	1.85	1.54	−0.36	4.07
Agriculture * Status (Relocated)	0.48	2.28	−2.81	3.78

[a] Status = control and passively relocated owls, Sex = male and female, Agriculture = percentage of agriculture within 200 m of burrow.
[b] Reference category for categorical variables.

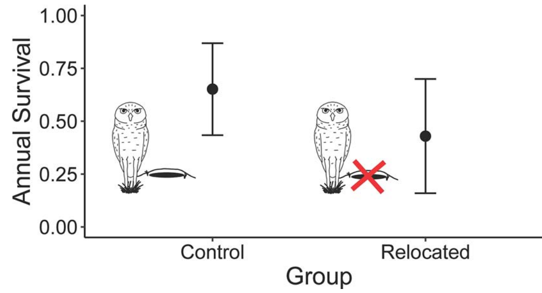

Figure 2. Model-averaged estimates from final known-fate models evaluating survival of control and passively relocated owls from 2021 to 2022 in Phoenix, Arizona, USA. Error bars reflect 85% confidence intervals.

passively relocated owls that were single individuals at capture subsequently mated and attempted breeding.

Mean nest initiation dates in 2022 were 2 April (SE = 2.53) for the control nests and 16 April (SE = 13.70) for the passive relocation nests. Nest success was 75% for control nests and 57% for passive relocation nests. Productivity averaged 2.33 fledglings/nest (SE = 0.58) for control nests and 1.43 fledglings/nest (SE = 0.69) for passive relocation nests.

The goodness-of-fit test results showed no strong evidence of overdispersion for both the nest success model ($\chi^2 = 3.55$, df = 3, $P = 0.308$, $\hat{c} = 1.26$) and the productivity model ($\chi^2 = 7.53$, df = 3, $P = 0.057$, $\hat{c} = 1.18$). Both the nest success and productivity analyses resulted in two competitive models: the null model and the model with percentage of agriculture within 200 m of nest burrows (Table 3). The model-averaged 85% CIs for the positive effect of agriculture, adjusted for overdispersion, did not overlap zero for either nest success or productivity, indicating influential effects (Table 4). For every one SD increase in the percentage of agriculture within 200 m of a nest, the odds of nest success increased by a factor of 2.51 (85% CI = 1.04, 6.01), and the expected productivity increased by a factor of 1.62 (85% CI = 1.04, 2.51).

DISCUSSION

This study examined the effects of passive relocation as a mitigation method influencing the demographic rates of owls. The predominance of agricultural lands (including those surrounding development sites) and small sample size affected our ability to detect differences in survival between passively relocated and control owls. Nevertheless, although not a strongly significant effect, passively relocated owls had lower survival than control owls, which may represent a biologically meaningful effect. In California, Hennessy et al. (2022) observed a similar pattern: limited support for differences in individual survival and nest success, but similar lower survival estimates for passively relocated owls compared to control owls. Future research could integrate datasets from multiple studies in a meta-analysis to more rigorously evaluate whether survival rates differ between the two groups. We used known-fate models to estimate survival. These models assume that all dead or missing owls are recovered. Violation of this assumption can bias estimates upward and make survival comparable between passively relocated and control owls. However, our reporting rate of 84% suggests limited potential for biased survival estimates.

We found that the amount of agriculture surrounding nests positively influenced nest success and productivity independent of the relocation status of the owls. Other studies similarly demonstrated that owl habitat selection and juvenile post-fledging survival were positively associated with agriculture (Moulton et al. 2006, Beebe et al. 2014, Griffin et al. 2017). We also think that agricultural land influenced survival by providing nearby burrow availability that affected owls' decisions to remain nearby or disperse. Most owls in this study were surrounded by agricultural land, which provided ample roosting burrows along irrigation canals.

In this study, most passively relocated owls remained within their individual home ranges, similar to the finding of Hennessy et al. (2022), who

Figure 3. Movements of four owls tracked using radiotelemetry in Phoenix, Arizona, USA, from 2021 to 2022. (A) Passively relocated owl; average distance to confirmed displacement points 342 m. (B) Passively relocated owl; average distance 456 m. (C) Control owl; single distance 72 m. (D) Control owl; single distance 96 m.

attributed this pattern to proximal habitat and burrow availability. Daily survival estimates for passively relocated owls reported by Hennessy et al. (2022; 0.96, 95% CI = 0.77, 1.00) were similar to this study (0.98, 85% CI = 0.97, 0.99). These results indicate that habitat conducive to burrow availability increases site fidelity and therefore decreases mortality risk.

Dispersal distances of displaced owls may be indicative of habitat quality and burrow availability nearby. The larger dispersal distances, up to 3900 m, observed by Hennessy et al. (2022) were attributed to sites surrounded by intensive development that were not conducive to owl settlement. In another California study (Nguyen and Gardner 2017), researchers passively relocated fewer owls than expected because fewer development projects were initiated, allowing surrounding high-quality habitat to persist. That study reported similar dispersal distances for relocated and control owls, but the distances were also larger (1600 m) than observed in our study. Shorter dispersal distances in our study suggested greater availability of sufficient, nearby settlement habitat.

We observed behaviors that increased mortality risk among displaced owls as they adjusted to the loss of their burrows. These behaviors included multiple short-distance movements to new roost locations, often within the development site, that included use of human-made structures as refugia, such as storm drains on busy roads, open maintenance holes, and discarded corrugated tubing. This may have contributed to the predation of two owls by raptors. Some of these displaced owls moved to a natural burrow before the breeding season; others remained on the development site for longer but

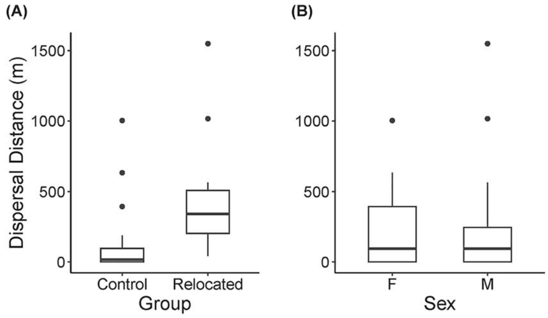

Figure 4. Average dispersal distances (m) of owls tracked using radiotelemetry in Phoenix, Arizona, USA, from 2021 to 2022. (A) Control and passively relocated owl dispersal. (B) Female and male owl dispersal.

moved to a natural burrow at the start of the breeding season. One of the latter owls died.

We found working with developers to passively relocate owls to be challenging. Owls are protected under the Migratory Bird Treaty Act (MBTA) and the Arizona Game and Fish Department lists management recommendations to protect them (Arizona Game and Fish Department 2007). However, developers in Arizona are not required to survey for owls and appeared reluctant to respond to our inquiries. While we were able to locate owls on development sites, we often could not connect with the developer or land management company to include those owls in our passive relocation efforts. Consequently, passively relocated and control owls were sampled unevenly, and future studies should prioritize large development projects to increase the likelihood of monitoring adequate sample sizes of both groups. Variations in development timelines can limit efforts to experimentally examine passive relocation. Studies in Florida (N. Jennings pers. comm.) and California (C. Wisinski pers. comm.) reported experiencing difficulties with development timelines, resulting in lower sample sizes and delays in development activities throughout the study period. These challenges complicated efforts to quantify the effect of mitigation techniques to achieve owl management objectives in areas experiencing intensive development. The highly variable nature of development timelines further complicated the ability to conduct research on active development sites. We observed future development sites where owls were present, but no development activity was initiated during our study period. If owls are displaced in advance of development activity and have surrounding habitat available for settlement, our results suggest that they may remain on-site. Alternatively, owls that are not passively relocated beforehand may be displaced by the onset of development activity, as evidenced by fewer owls on sites with more advanced

Table 3. Model selection results for generalized linear models examining the effects of passive relocation, nest initiation date, and percentage of agriculture on nest success (with binomial error) and productivity (with Poisson error) of owls in Maricopa and Pinal Counties, Arizona, USA, in 2022.

Response Variable	Model Parameters[a]	K[b]	$QAIC_c$[c]	$\Delta QAIC_c$	w_i[d]	Deviance
Nest Success	Null model	2	24.78	0.00	0.44	23.70
	Agriculture	3	25.57	0.80	0.29	20.59
	Status	3	27.53	2.75	0.11	23.06
	NID	3	28.02	3.24	0.09	23.68
	Status + Agriculture	4	29.09	4.32	0.05	20.29
	Status + NID	4	31.27	6.49	0.02	23.04
	Global	5	33.37	8.59	<0.01	20.15
Productivity	Null model	2	43.61	0.00	0.37	41.01
	Agriculture	3	43.69	0.08	0.35	34.35
	Status	3	45.96	2.35	0.11	39.11
	NID	3	46.79	3.18	0.08	40.86
	Status + Agriculture	4	47.03	3.42	0.07	33.48
	Status + NID	4	49.72	6.11	0.02	39.11
	Global	5	51.42	7.81	<0.01	33.48

[a] Variable notation: Status = control and passively relocated owls, Agriculture = percentage of agriculture within 200 m of burrow, NID = nest initiation date, and Global = model including all main effects.
[b] Number of model parameters.
[c] $QAIC_c$ = Quasi Akaike information criterion value, corrected for small sample sizes.
[d] Akaike model weight.

Table 4. Conditional model-averaged coefficients and 85% confidence intervals (CIs) for final generalized linear models, adjusted for overdispersion, evaluating covariate effects on nest success and productivity of owls in Phoenix, Arizona, USA in 2022.

Response Variable	Model Parameter[a]	Estimate	SE	Lower CI	Upper CI
Nest Success	Intercept	0.87	0.59	−0.02	1.76
	Agriculture	0.92	0.58	0.04	1.79
	Status (Relocated)[b]	−0.76	1.13	−2.46	0.95
	NID	−0.03	0.55	−0.87	0.81
Productivity	Intercept	0.68	0.26	0.29	1.07
	Agriculture	0.48	0.29	0.04	0.92
	Status (Relocated)	−0.44	0.53	−1.23	0.36
	NID	−0.05	0.25	−0.43	0.33

[a] Variable notation: Status = control and passively relocated owls, Agriculture = percentage of agriculture within 200 m of burrow, NID = nest initiation date.
[b] Reference category for categorical variable.

development. Such owls may experience increased mortality risk as observed with three owls in this study.

Management Implications. This study elucidates the challenges associated with appropriately implementing and evaluating passive relocation and identifies several factors that may influence the outcomes of this management method. To support the long-term persistence of owl populations, all possible conservation efforts should be pursued, such as protecting existing habitat and natural burrow availability. Passive relocation is a management alternative to habitat preservation, but several factors should be examined if this method is being considered for owls found on development sites. These include the scale of proposed development projects, distance to nearby agricultural land or native habitat for owls to occupy, availability of burrows at nearby suitable sites, and timing of passive relocation activities in relation to development stage. Large development projects that extend beyond an owl's core use area (i.e., within 650 m) create a greater risk for reduced survival of passively relocated owls as this may necessitate longer distance movements (Hennessy et al. 2022). Importantly, there should be consideration of the effects of cumulative development—especially prevalent in the greater Phoenix area—that could further increase dispersal distances and depress survival rates.

This study illustrates the positive association between owl reproductive rates and agricultural land. Therefore, with increasing pressures to limit water usage for agricultural use across the southwest (Rushforth et al. 2022), the importance of agricultural land for supporting owls should be highlighted in mitigation efforts. Current efforts by states such as Arizona and California seek to set aside land (Burrowing Owl Management Areas) for nesting habitat (Arizona Game and Fish Department 2007, California Department of Fish and Game 2012), which should include agricultural land. Available natural burrows in nearby habitat should be evaluated prior to displacing owls, and artificial burrows should be installed and maintained as long-term burrows for owls to occupy if the availability of suitable natural burrows is limited. The timing of displacement depends on whether a population includes migratory individuals, non-migratory individuals, or both. If passive relocation is considered, displacement should occur during the non-breeding season after migrants have left the area, as migratory individuals will naturally disperse from a site. Avoidance should include the period between territory establishment and juvenile dependence. In southcentral Arizona, the relocation period has been identified as October through mid-February (Doublet et al. 2023a). The timing of displacement must be dependent on development timelines; owls should be passively relocated no earlier than 1 mo before initiation of development but prior to any on-site activity. The MBTA protects nest burrows during the breeding season across the species' range. Therefore, any occupied nests should be reported to the U.S. Fish and Wildlife Service and Arizona Game and Fish Department during development project planning to prevent MBTA violations. Appropriate passive relocation of owls includes exclusion from burrows and confirming (e.g., using a scoping camera) that the burrows are empty before collapse. Establishing clear guidelines and strengthening existing permitting requirements related to surveying and managing owls at development sites will improve conditions for owls.

Additionally, these measures may provide more opportunities to examine and improve passive relocation as a mitigation strategy.

SUPPLEMENTAL MATERIAL (available online). Table S1. Example encounter histories from a subset of monitoring data (4 wk) for control and passively relocated owls in southcentral Arizona from 2021–2022 for the known-fate survival analyses in RMark, adapted from Cooch and White (2021).

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