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Release strategies and ecological factors influence mitigation translocation outcomes for burrowing owls: a comparative evaluation

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Abstract

Mitigation translocations are increasing and if they are to fulfill their regulatory intent, the application of best-practice principles to release strategy and monitoring is required. With an investment of 3 years, we engaged with stakeholders, including developers, to improve outcomes from mitigation translocations of an at-risk species, the western burrowing owl *Athene cunicularia hypugaea* (BUOW). We evaluated the consequences of two primary translocation methods, displacement (i.e. exclusion from burrow) and translocation, against control owls, using a suite of success metrics focused on dispersal, survival and reproduction. We also tested the provision of visual and acoustic conspecific cues to dampen dispersal away from release sites. Within the displaced group, BUOW settled closer to the origin site if burrows were available nearby. Although translocated BUOW dispersed farther from the release site than displaced BUOW, this difference disappeared when conspecific cues were present. BUOW were 20 times more likely to settle at the release site when conspecifics or their cues were present. Translocating animals over longer distances (>17.5 km) reduced the incidence of BUOW returning to the origin site. When avoiding direct impacts to BUOW is not feasible, a determination of the most beneficial translocation method must be made, driven by site-specific conditions and the feasibility of implementing best management practices. The known costs of translocation to survival may be offset by long-term advantages such as the establishment of breeding populations inside protected areas. Mitigation translocations can benefit from carefully devised and tested hypotheses to determine what works and what does not; we advocate the increased use of evidence in mitigation translocation to guide management decisions and policies.

Introduction

When applied to a protected species impacted by land development projects, the term ‘mitigation’ describes attempts to offset habitat losses and/or impacts to individuals occupying the habitat, and often includes translocation of animals out of harm’s way (Germano *et al.*, 2015). Although development impacts both individuals and their habitat, regulatory mitigation requirements may address one but not the other. In the United States, regulations allow mitigation to be defined as the minimization of harmful effects on individuals (40 C.F.R. §1508.20, 2012). This has created a class of projects designed primarily to translocate individuals away from the development site, with little or no effort to address habitat loss or enhance species conservation, hereafter referred to as mitigation translocations (*sensu* Germano *et al.*, 2015). This action, in avoiding the immediate death of the individual and meeting regulatory requirements, may seem sufficient. However, this definition of mitigation conflicts with the public responsibilities of regulatory agencies and intent of legislation, in that salvaging of individuals does not necessarily meet the objective of fully mitigating contributions to population decline and further endangerment. There are established guidelines for conducting translocations and reintroductions that focus on longer-term outcomes for populations and species viability (IUCN, 2013). Mitigation translocations likely far exceed ‘conservation translocations’ in number, yet fail to incorporate many best practices developed in translocation biology, including clearly stated objectives and learning how these can be met through strategic monitoring and adaptive management (Germano *et al.*, 2015; Sullivan, Nowak & Kwiatkowski, 2015; Bradley *et al.*, 2021). Many mitigation translocations are small and isolated projects, with limited opportunities for conducting robust experimental trials of potential methodological improvements. Seeking out those situations where many mitigation translocations are occurring can identify opportunities for leveraging a research effort to improve tactics for the species, make mitigation more effective for conservation, and potentially generate new knowledge in the field of translocation biology.

Given the current frequency of mitigation translocations and calls for scrutiny from the conservation community, workable templates are needed for improving the efficacy of mitigation translocations. With an investment of 3 years, we engaged with stakeholders, including developers, to improve outcomes from mitigation translocations of an at-risk species, the western burrowing owl *Athene cunicularia hypugaea* (BUOW). The species has declined steadily throughout North America including southern California, a hotspot of intensive land development for urban, exurban and energy uses. This decline has led to listing at the state level as a Species of Special Concern (Gervais, Rosenberg & Comrack, 2008). Although BUOW can adapt to a variety of disturbed and developed grassland sites, the presence of BUOW in development areas results in conflicts between conservation and economic activity (Klute *et al.*, 2003). While regulatory agencies prefer a strategy of avoiding direct impacts, BUOW are increasingly the subject of mitigation actions.

Displacement – excluding owls from their burrows, collapsing the burrows, and forcing owls to relocate without human assistance – is the primary approved method by regulatory agencies in California, and is used throughout their range. The process is sometimes referred to as 'passive relocation', but is closer to an eviction. Because BUOW rely on fossorial mammals to create burrows required for nesting and refuge (Poulin *et al.*, 2011), limited burrow availability may influence displacement outcomes. If there are other burrows available nearby (within about 650 m of the home burrow), the owl can resettle without losing its established home range (Haug & Oliphant, 1990; Gervais, Rosenberg & Anthony, 2003), presuming enough foraging habitat remains. Short-distance burrow displacements are associated with high survival rates (Trulio, 1995). By contrast, translocation involves capturing owls, moving them offsite into an acclimatization enclosure, then releasing them after a holding period (Trulio, 1995; Smith & Belthoff, 2001; Mitchell *et al.*, 2011). However, post-release effects, including transient elevated mortality rates due to the novel environment or long-distance movements away from the release site, are to be expected (Sarrazin & Legendre, 2000; Letty, Marchandeau & Aubineau, 2007; Stamps & Swaisgood, 2007; Tavecchia *et al.*, 2009; Harrington *et al.*, 2013; Armstrong *et al.*, 2017; Bertolero, Pretus & Oro, 2018). Translocation may have an advantage over displacement because it provides an opportunity to establish animals in areas protected from additional future development impacts, especially if prospects for future development lead to serial evictions that further compromise survival. Thus, when deciding between these two methods (translocation vs. displacement), conservation practitioners and regulatory agencies must consider the pros and cons of each approach, informed by evidence about their comparative efficacy across different contexts.

Across hundreds of case studies, one of the most frequently encountered obstacles facing successful animal translocations is dispersal away from release sites (Berger-Tal, Blumstein & Swaisgood, 2020). Longer dispersal movements following release have been shown to increase risk exposure and mortality rates of several species (Stamps & Swaisgood, 2007; Le Gouar, Mihoub & Sarrazin, 2012; Shier & Swaisgood, 2012) and finding ways to limit this behavior has become a top research priority (Armstrong & Seddon, 2008; Greggor *et al.*, 2016). Among the many tactics used to improve conservation outcomes, one approach to reducing post-release dispersal is to hold animals in acclimatization enclosures at the release site (Mitchell *et al.*, 2011; Batson *et al.*, 2015). However, this method alone does not always yield success, and in some cases can have negative effects on desired outcomes (Parker *et al.*, 2012; Richardson *et al.*, 2015; Moehrenschlager & Lloyd, 2016). Factors such as species traits and release context influence whether delayed release is beneficial (Moseby, Hill & Lavery, 2014). The nuances between acclimatization and dispersal have led translocation practitioners to trial a number of other techniques, often more closely tied to species behavior and biology (Swaisgood & Ruiz-Miranda, 2019).

To address concerns that BUOW would disperse away from release sites after acclimatization, we tested the efficacy of using conspecific cues to increase settlement. Conspecific cues are a promising tool to facilitate settlement during natural dispersal (Reed & Dobson, 1993), or to encourage translocated animals to settle near the release site (Swaisgood, 2010; Le Gouar *et al.*, 2012). Reviews of conservation interventions for bird species by Conservation Evidence (https://www.conservationevidence.com) indicate that both visual (decoy) and acoustic (vocalizations) are 'likely to be beneficial' for attracting birds to settle in safe areas. For example, 20 out of 24 migratory songbird species were attracted to settle in response to song playbacks (Ahlering *et al.*, 2010). However, results have been mixed and vary across species and context, and so must be tested for each potential application (Putman & Blumstein, 2019). We hypothesized that the presence of conspecifics would be an important factor governing settlement decisions of the semi-colonial BUOW.

We sought to capitalize on ongoing mitigation translocations as an opportunity to test the efficacy of alternative tactics and to advance evidence-based conservation. The relative efficacy of displacement vs. translocation has not been evaluated previously for BUOW. Displacement is known to occur in mitigation for other species, or at least to occur indirectly when construction destroys nesting habitat or dens, forcing animals to relocate. However, these actions are rarely studied and published. We believe our work addressing this issue in BUOW will have value for understanding the relative merits of these interventions for other species. In addition, to the best of our knowledge conspecific cues have not been trialed to reduce post-release dispersal. Specifically, our primary objectives were to:

- Compare dispersal, survival and reproduction for displaced owls able to retain an existing home range versus translocated owls required to establish a new home range.
- Evaluate whether experimental placement of conspecific cues or presence of conspecifics reduces post-translocation dispersal from the release area or impacts survival and reproduction.

To generate additional management insights, we also sought to:

- Determine whether post-displacement and post-translocation dispersal distances predict survival and reproduction.
- Determine how burrow availability influences dispersal and survival of displaced owls.

We engaged closely with ongoing mitigation-driven projects, using a question-driven approach, a consistent protocol, extensive post-release monitoring, and GPS tracking of owl movements. This research took place in the context of intensive development and mitigation activities. These data and results have great relevance for regulatory agencies, environmental consultants and other practitioners across the species' range, and provide a useful model for making mitigation translocations for other species more effective.

Materials and methods

From January 2017 to August 2018, we studied mitigation impacts on BUOW across four regions of southern California (western San Diego County, western Riverside/San Bernardino Counties, Imperial County and Coachella Valley, Fig. 1). Mitigation-impacted BUOW were either displaced or translocated. For some release sites, owls were present (reinforcement) and for others owls were absent (reintroduction; details in Supporting Information Data S2). BUOW displacement and translocation took place outside of the breeding season, as state regulatory requirements do not permit these activities during the breeding season.

Displacements

For *displacements*, we installed one-way doors at burrow entrances and left them in place for a minimum of 48 h to exclude owls from re-entry, then collapsed burrows after confirming the owls had exited. We installed artificial burrows when required by the regulatory agencies. Herein, we differentiate between two displacement outcomes: (1) settlement with retention of the established home range, and (2) loss of the established home range and dispersal.

Translocations

For *translocations*, we captured and transported owls to release sites (methodological details for translocation protocols are presented in Supporting Information Data S1). Translocated owls were held on-site for an acclimatization period of 30 days in temporary field enclosures including an artificial burrow (release burrow). Acclimatization is currently considered a best practice based on evidence indicating positive effects on outcomes for owls reared in human care (Mitchell *et al.*, 2011). However, systematic tests of acclimatization for wild-translocated BUOW appear to be lacking. We chose to acclimatize translocated BUOW in part to ensure they were present at the release site long enough to perceive the conspecific cues we provided (see below).

Burrows occupied by BUOW typically have an abundance of whitewash and vocalizing owls. These behavioral cues may signal habitat suitability to conspecifics. To examine the impact of conspecific cues on settlement, survival, and reproduction of translocated owls, we assigned the following treatments: (1) *natural* whitewash and auditory cues from existing resident owls (Fig. 2a); (2) *artificial* visual and auditory conspecific cues; and (3) *no* resident owls present or artificial cues deployed. We determined the presence of resident owls from site visits (Supporting Information Data S2). Artificial visual cues consisted of simulated whitewash (non-toxic latex paint, Fig. 2b) placed around artificial burrow entrances. Acoustic cues consisted of timed playbacks of pre-recorded vocalizations (Fig. 2c; Supporting Information Data S2) deployed near acclimatization enclosures 1 week prior to and 1 week following owl release. While territorial calls are not expected to attract settlement immediately adjacent to the speaker, they can encourage settlement in a variety of territorial avian species (Ahlering *et al.*, 2010).

Controls

We captured resident owls in areas adjacent to pre-displacement burrows and translocation release sites as *controls*. The control BUOW did not experience the disruption of either burrow exclusion or translocation, and represented the fitness and survival of BUOW with an established burrow and home range in the sites where BUOW were intended to settle after displacement or translocation.

Post-release monitoring

For all groups, we captured, banded and fitted owls with GPS satellite telemetry units (Biotrack PinPoint Argos Solar, Wareham, UK) using a backpack-style harness (Supporting Information Data S3). We translocated 47 BUOW and fitted 20 with transmitters. To maintain data independence, one individual per translocated pair ($n = 15$) received a GPS transmitter. We also included 19 displaced and 15 control BUOW in the study (Table 1). Four additional telemetry units deployed on two control and two displaced BUOW failed within a month of deployment. While sample sizes depended on existing permitted development projects, we made efforts to evenly distribute study owls by region and translocation type (Supporting Information Data S4).

We programmed GPS transmitters (Fig. 2d–e) to collect locations three times/24 h, and we used camera traps and visual surveys to monitor burrow occupancy, owl survival, nesting and productivity for a minimum of 1 year following

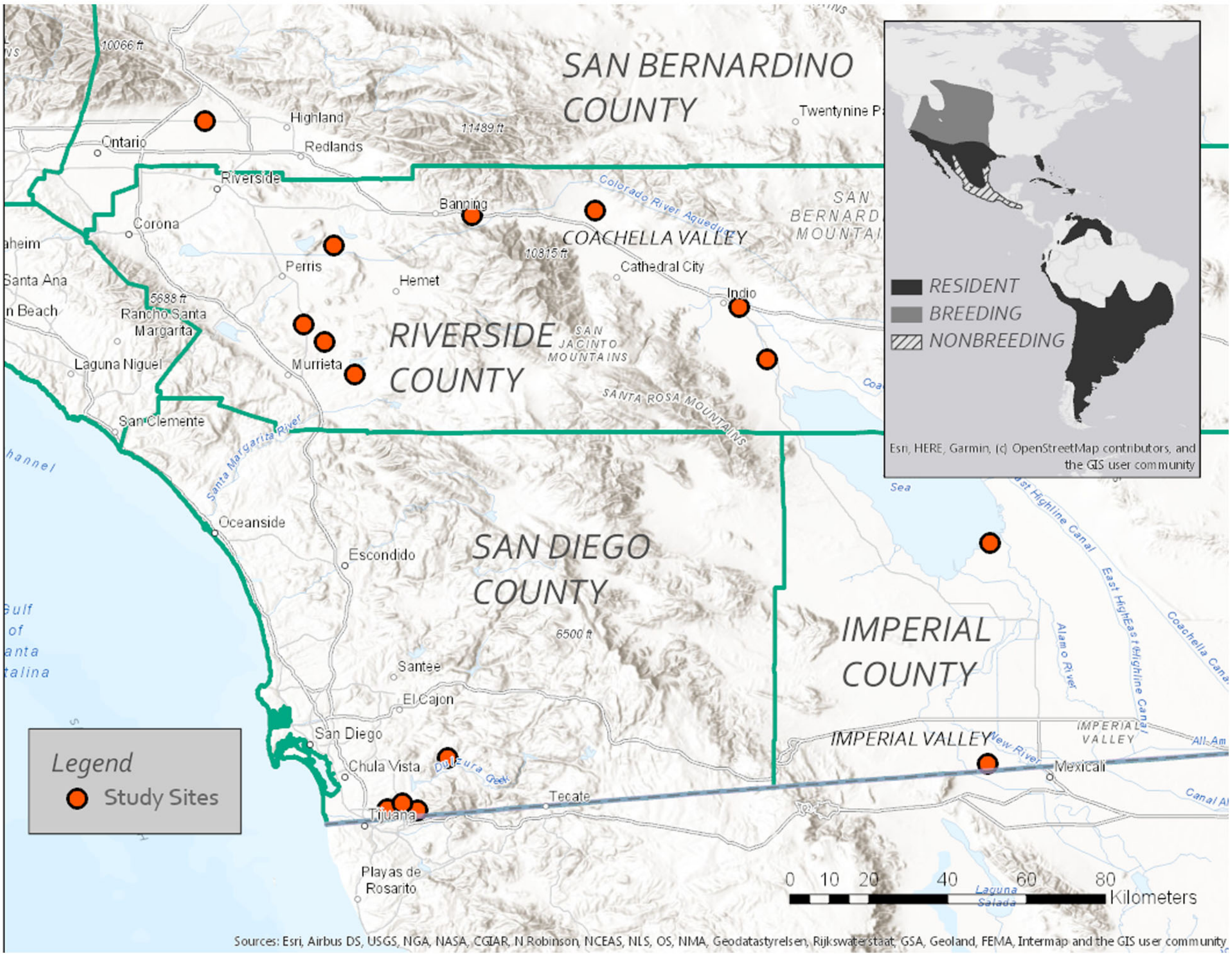

Figure 1 All project sites were located in the resident region of burrowing owl distribution (CAL FIRE, 2007; BirdLife International, 2018; Esri, 2020*a*,*b*).

displacement or translocation or until transmitter failure or mortality. We conducted field observations monthly during the non-breeding season (September–February) and weekly during the breeding season (March–August). As burrow availability is likely to be an important determinant of habitat quality, settlement decisions and survival, we evaluated natural burrow availability within 100 m of all origin burrows, release burrows and settlement burrows (Supporting Information Data S1). All translocated BUOW had access to artificial burrows and most also had natural burrows nearby, but regulatory agencies do not require artificial burrows for displaced BUOW (details in Supporting Information Data S1). Thus, our analysis of burrow availability was only possible for displaced BUOW.

Data analysis

Unless otherwise specified, we conducted analysis of variance or mixed effects models in JMP® Version 14 software (1989–2019; SAS Institute Inc., Cary, NC, USA). We excluded BUOW with unknown dispersal and survival status for specific variables from those analyses.

Dispersal and settlement

We defined settlement (Yes/No) as remaining within 650 m of the pre-displacement or translocation release burrow, or approximately one BUOW home range (Haug & Oliphant, 1990; Gervais, Rosenberg & Anthony, 2003; Swaisgood *et al.*, 2015), for a minimum of 30 days of occupation. For displaced owls, movement of >650 m will remove them from familiar territory, so movements of this distance are more likely to influence fitness. We used recursive partitioning with the LogWorth splitting criterion to assess drivers of settlement. We measured dispersal distance as the total distance traveled between pre-displacement or translocation release and settlement burrows, and applied a $\log(n + 1)$ transformation to dispersal distance. For translocated owls, we also measured translocation distance between the origin and release burrows as a predictor variable.

Reproduction

To evaluate treatment effects on BUOW reproduction, we selected reproductive variables *a priori*. We categorized

Figure 2 Types of conspecific cues utilized in the study: natural cues from resident owls (a), artificial visual (b) and acoustic (c) cues. GPS telemetry units deployed on burrowing owls (d,e).

individuals as breeding/not breeding, using typical breeding behaviors: territorial vocalization, copulation, and burrow decoration. We measured reproductive success (Yes/No) as survival of at least one chick to fledgling stage (21 days post-emergence), and inferred maximum number of chicks from the greatest number of post-emergent chicks observed simultaneously. We defined productivity as the number of chicks reaching fledgling stage.

Survival

We modeled daily survival in Rmark with the Nest Survival module (Laake, 2013), which can be applied to telemetry data with staggered entry and unequal sampling intervals (Rotella, 2019). We determined mortality dates using telemetry, camera trap and site visit information. We right-censored data for BUOW with unknown fates due to transmitter failure and/or mortality. The model interval was 918 days (25 January 2017–1 August 2019). We used the Delta method to estimate standard error (Powell, 2007) and examined explanatory relationships with translocation type and covariates (settlement within 650 m, dispersal distance, translocation distance, conspecific cues, available burrows and region) using Akaike's information criteria corrected for small sample size (AICc) (Burnham & Anderson, 2004) in R 3.5.3 (R Core Team, 2019).

Results

Settlement and dispersal

Among the two mitigation groups (displacement and translocation) and the control group, most BUOW dispersal distances were shorter than the radius of a home range (650 m). Eight BUOW (two displaced without nearby burrows, five translocated without cues, one with cues) dispersed farther (median = 4846 m, maximum = 40.7 km; Supporting Information Figure S1). The two mitigation groups (displacement and translocation) and the control group differed with regard to settlement patterns. The

Table 1 Number of burrowing owls in the study by treatment group and location. Owls excluded from the study due to transmitter failure are not reported in this table

Group	Location	BUOW (n)	Total
Displacement	Total		19
	Western Riverside	2	
	Coachella Valley	3	
	Imperial Valley	5	
	San Diego	9	
Translocation w/cues	Total		11
	Western Riverside	2	
	Imperial Valley	3	
	San Diego	6	
Translocation no cues	Total		9
	Western Riverside	5	
	Coachella Valley	4	
Resident control	Total		15
	Western Riverside	3	
	Coachella Valley	3	
	Imperial Valley	8	
	San Diego	1	
Study total			54

percentage of translocated and displaced BUOW settling within 650 m was similar, but lower than control BUOW (Fig. 3a). Control BUOW exhibited the shortest dispersal distances, followed by displaced BUOW, while translocated BUOW dispersed the longest distances (n = 48, $P < 0.01$, $R^2 = 0.33$, Fig. 3b). For the displaced group, the availability of burrow resources influenced dispersal distance. Although low and unbalanced sample sizes did not allow for statistical comparison, BUOW appeared to settle closer to the origin site if burrows were available nearby (Fig. 3b). When burrows were available, BUOW resettled only 162.0 ± 53.5 m from their pre-displacement burrow, essentially remaining within their home range (n = 13). By contrast, when no burrows were available, BUOW left their home range and settled in new burrows an average distance of 3222.0 ± 678.0 m from their pre-displacement burrow (n = 2).

Our conspecific cue treatments for the translocation group significantly influenced whether BUOW dispersed beyond 650 m of the release burrow. Exploratory analysis showed no significant differences between artificial cues and natural cues, so the cue treatments were aggregated for analysis. Translocated BUOW were 20 times more likely to settle within 650 m of the release site when cues were present (n = 20, P = 0.02, $R^2 = 0.30$, Fig. 3a). In addition, the farthest dispersal distances occurred when cues were absent, and the shortest dispersal distances were associated with the use of conspecific cues (n = 19, $P < 0.01$, $R^2 = 0.35$, Fig. 3b). Translocation distance (ranging between 5.5 and 61.7 km) was also a strongly significant predictor of settlement (n = 20, $P < 0.01$, $R^2 = 0.72$). Recursive partitioning created a decision tree with presence of cues as the primary driver of this effect, but translocation distance had a secondary effect. When cues were present, settlement was 100% (n = 6) for translocation distances >17.5 km compared to 80% settlement (n = 5) for translocation distances <17.5 km.

Reproduction

The dataset for reproduction is smaller than for measures of dispersal and survival and limited to those owls with known burrows accessible for monitoring, rendering statistical power too low to detect anything but very large effects. We first compared reproductive outcomes for the two mitigation groups (displacement and translocation) against the control group. Breeding attempts were equally likely among the two mitigation groups and the control group (n = 32, P = 0.36, $R^2 = 0.13$, Fig. 3c). Of the subset of breeding BUOW, there were no differences in reproductive success (n = 30, P = 0.63, $R^2 = 0.03$, Fig. 3d), maximum number of chicks (n = 30, P = 0.70, $R^2 < 0.01$, Fig. 3e) or productivity (n = 30, P = 0.70, $R^2 < 0.01$, Fig. 3f) due to mitigation or control status.

We found that owls settling within 650 m of the pre-displacement burrow or translocation release site were more likely to attempt breeding (n = 32, $P < 0.01$, $R^2 = 0.55$). Of the five BUOW that dispersed >650 m, 60% attempted to breed, whereas 92% of owls settling within 650 m (n = 27) did so. However, caution is warranted due to the unequal and small sample sizes.

We examined all explanatory relationships between effects of cue treatment on reproduction and found them to be non-significant; however, this dataset does not have the statistical power to detect potential treatment effects on reproduction (n = 1–5 per group).

Survival

With time, the number of unknown fates increased, reaching 70% by the end of the study period (Supporting Information Figure S2). After 12 months, 41% of the displaced group, 26% of the translocation group and 33% of the control group had unknown fates. We therefore truncated our survival analysis at 6 months when unknown fates were <30%. Increasing uncertainty is reflected in increasing confidence intervals around survival estimates.

After 1 month, survival of displaced BUOW was 99.4 (95.7, 99.9)%, similar to survival of controls at 98.3 (93.5, 99.6)%. Survival after translocation was also high at 91.4 (85.0, 95.1)%. Examination of 95% confidence intervals for overlap indicated that by 6 months, survival of translocated BUOW [58.2 (37.6, 74.1)%] was lower than for displaced BUOW [96.3 (76.8, 99.5)%] and control BUOW [90.4 (66.9, 97.5)%]. AICc values were consistent with the presence of a treatment effect (for the treatment model, AICc weight = 0.99 and AICc = 173.3 compared to AICc = 183.9 for the intercept-only model, Supporting Information Table S1).

Model comparison did not distinguish between single-factor models for survival regressed on region, settlement within 650 m, and dispersal distance for all treatment groups. Within the translocation group, we tested whether

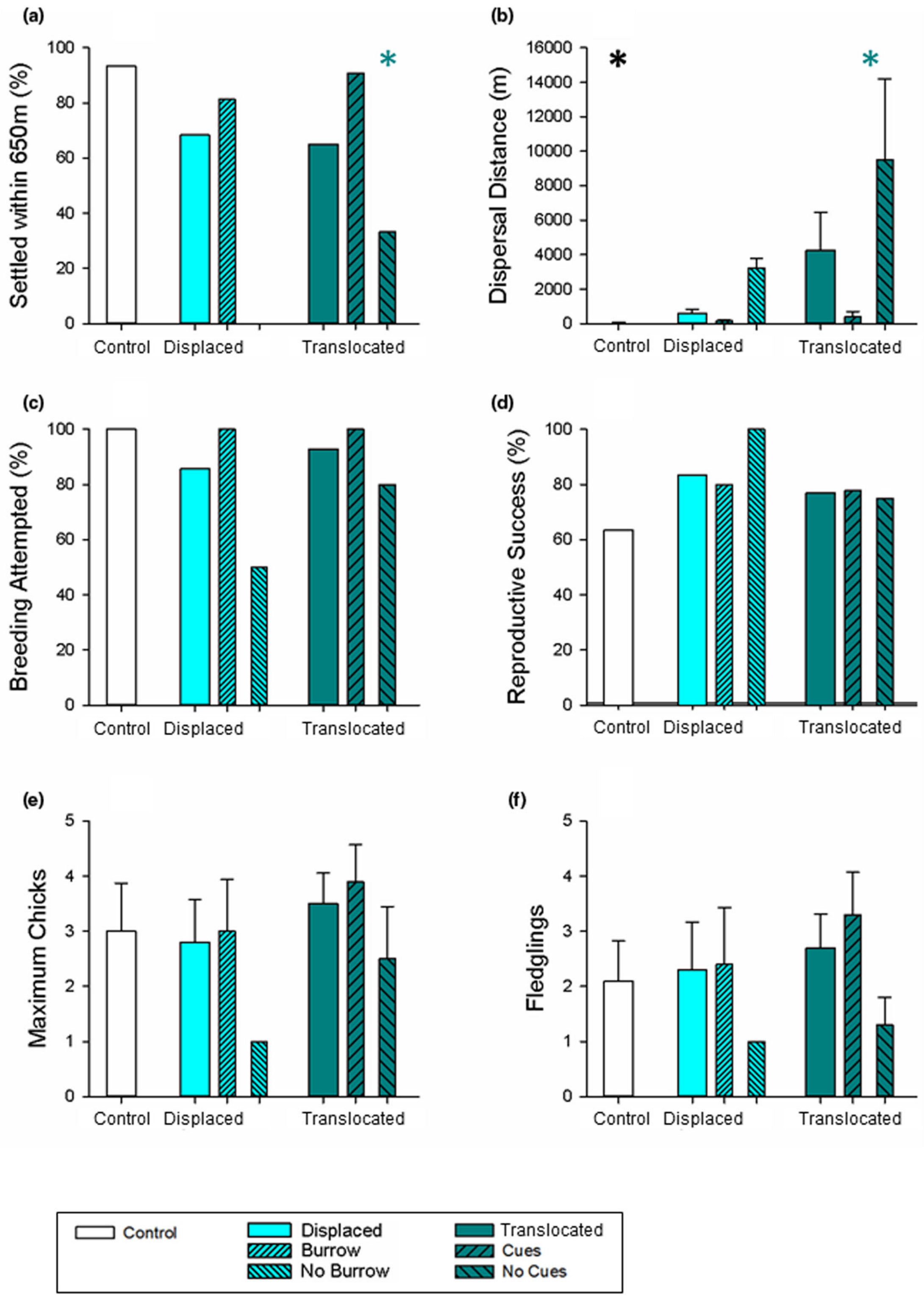

Figure 3 Influence of translocation method, conspecific cues and burrow availability on dispersal and reproduction. Burrowing owls with unknown settlement locations >650 m (n = 3) are included in the settlement status rate (a), but excluded from distance calculations (b). Measures of reproduction (c–f) include the first year after translocation for owls that were displaced or translocated, with controls. Significant differences are marked with an asterisk.

conspecific cues impacted survival. The model with conspecific cues was not more parsimonious (ΔAICc = 1.20, AICc weight = 0.35, for the model with cues compared to intercept-only, Supporting Information Table S1). Finally, model comparison did not distinguish between survival of displaced BUOW with and without available burrows (ΔAICc = 0.18, AICc weight = 0.48 for the model without burrows compared to burrows available). Although the adjusted mean 6-month survival rate of BUOW displaced with burrows available nearby was much higher (100%, $n = 16$) relative to displaced BUOW forced to disperse to a new home range (73.9%, $n = 3$), the results are compromised by unequal and small sample sizes.

Discussion

With mitigation- and conservation-driven translocations on the rise (Seddon *et al.*, 2014; Germano *et al.*, 2015), it is imperative that we develop the necessary tools to ensure that we are not simply moving animals out of harm's way only to have them suffer low survival and reproduction after translocation. Mitigation translocations in particular often focus on minimizing damage to individuals rather than contributing to species recovery, and rarely document a net positive benefit to species persistence (Germano *et al.*, 2015). Consistent with this status quo, nearly all BUOW mitigation translocations and displacements currently occur with little or no experimentation and typically only a maximum of 1 month of post-translocation site monitoring. By contrast, conservation translocations often incorporate experimentation with protocols, effective monitoring, and additional support in the form of supplemental feeding and restocking. Mitigation translocations have been critiqued for shortcomings including poor implementation, lack of documentation, failure to apply scientific principles and poor outcomes (Dechant *et al.*, 1999; Germano *et al.*, 2015; Sullivan *et al.*, 2015).

We sought to bring a conservation-focused mindset to mitigation translocations to assist agencies to approximate the goals of regulatory frameworks and policies they enforce, that is, to develop best practices for mitigation translocations that contribute to species viability. Coupling experimental trials with adequate monitoring across ongoing mitigation projects was a major step towards developing more successful strategies for the future (Seddon, Armstrong & Maloney, 2007; Armstrong & Seddon, 2008). Investing in this approach enabled us to detect failures, recognize improvements, and improve conservation outcomes for an active class of mitigation translocations (Germano *et al.*, 2015). A growing body of literature is developing a biologically and ecologically based toolbox that can improve translocation outcomes if considered during design and implementation (Seddon, Strauss & Innes, 2012; Batson *et al.*, 2015; Jachowski *et al.*, 2016). In this study, we have attempted to apply best practices from conservation translocations to improve the efficacy of BUOW mitigation translocations (Bradley *et al.*, 2021). We encourage the regulatory community to now use these updated best practices for this class of mitigation translocations.

Displacement

For displaced individuals, settlement decisions have cascading effects. Dispersal movements following translocation have been shown across species to increase risk exposure and mortality rates (Stamps & Swaisgood, 2007; Le Gouar *et al.*, 2012; Shier & Swaisgood, 2012). Longer dispersal distances when burrows were unavailable suggest an advantage for BUOW that are able to quickly locate and select a new burrow. This supports the existing strategy of installing nearby artificial burrows or ensuring the presence of available natural burrows (Trulio, 1995). High survival rates were associated with retention of an established home range. In practice, displacements represent a continuum from ideal to poor conditions that our study attempted to represent in the projects we sampled. However, the majority of displaced BUOW included in this study ($n = 16$) came from two large projects with relatively ideal conditions. For one, the site remained undeveloped 6 months after burrow exclusion leaving foraging habitat unchanged; for both, ample burrow availability supported short dispersal distances. For both projects, the BUOW settled within their home ranges and did not lose foraging habitat during the course of the study. Most displacements included in our study thus likely represent best-case scenarios. Smaller projects conducted under less ideal, though commonly encountered conditions, were underrepresented in our sample ($n = 3$). These conditions included intensive surrounding urban development, limited foraging habitat, and few or no burrows available nearby, presenting higher risks for displaced BUOW. The survival estimates, while not robust enough for significance testing, suggest higher mortality under these circumstances.

The importance of burrow availability to displaced BUOW highlights the importance of considering refuge when evaluating habitat in species conservation programs. Although this aspect of habitat quality has previously not received the attention it merits, refuges have featured more prominently in conservation in recent years. This is especially true for species reliant on burrows and cavities (Cockle, Martin & Wesolowski, 2011; Manning *et al.*, 2013; Wei *et al.*, 2019), and translocation success can be influenced by availability of burrows in desert tortoise (Nafus *et al.*, 2017), the provision of artificial dens in European wild rabbits *Oryctolagus cuniculus* (Cabezas & Moreno, 2007) and the availability of soils suitable for burrowing in California ground squirrels *Otospermophilus beecheyi* (Swaisgood *et al.*, 2019). Not only can refuges directly affect survival and reproduction by affording protection from inclement weather and predators, but they may also reduce costs incurred when lack of refuges at the mitigation site motivates animals to disperse, looking for a more suitable site.

Translocation

As expected, translocated BUOW experienced greater mortality compared to displaced BUOW that retained their home range (Stamps & Swaisgood, 2007; Harrington *et al.*, 2013).

Post-translocation dispersal, which can cause lost foraging opportunities, delayed breeding, and increase exposure to predators (Swaisgood & Ruiz-Miranda, 2019), must be limited to achieve population establishment (Berger-Tal *et al.*, 2020). In this case, dampening dispersal may have facilitated breeding, as indicated by the inverse relationship between dispersal distance and breeding attempts. In contrast to many mitigation translocations, our study tracked reproductive outcomes among treatment groups and controls; the trends, although non-significant, suggest a lack of reproductive penalty to translocation.

Although translocated BUOW dispersed farther on average than displaced BUOW, this difference disappeared when conspecific cues were present to dampen dispersal. The presence of conspecifics can be used as a behavioral shortcut for identification of suitable habitat, and numerous species are known to use the presence of conspecifics when making settlement decisions (Stamps, 1988). Given the semi-colonial nature of BUOW (Poulin *et al.*, 2011), our findings of improved settlement when conspecific cues were present is perhaps unsurprising. The strength of the effect for both settlement and dispersal distance underscores the importance of conspecific attraction relative to more traditional measures of habitat quality (Campomizzi *et al.*, 2008). Biologically, both artificial and natural cues of conspecifics worked equally well and appear to be powerful attractants for BUOW, leading us to recommend the use of conspecific cues whenever BUOW are released into suitable but unoccupied habitat.

Conclusions and management implications

While impact avoidance and habitat preservation should always be the preferred conservation measure, on-the-ground realities mean that mitigation translocation of BUOW and other wildlife are sometimes unavoidable solutions to conflict with human land-use (Germano *et al.*, 2015). When avoidance measures are not feasible, practitioners must determine whether displacement or translocation should be used. This decision should be driven by site-specific conditions and the feasibility of implementing best management practices (IUCN, 2013). To aid in these decisions, we created flowchart tools designed for use by managers and regulatory agencies. The first focuses on identifying whether a mitigation project is a candidate for successful displacement, or whether translocation would be more beneficial, and the second guides managers through the planning process for translocation (Supporting Information Figures S3 and S4). The creation of a pathway for evidence-based decision-making supports managers seeking to implement actions that prioritize species recovery. More broadly, we advocate that researchers in the field of translocation biology, and conservation in general, strive to develop tools like these that break down barriers between science and management, and ensure lessons are incorporated into management decisions and policy (Walsh *et al.*, 2019; Greggor *et al.*, 2021).

Our findings indicate that the presence of conspecifics (or conspecific cues) at translocation release sites are vital; without them, most BUOW will disperse, potentially compromising their survival and conservation goals associated with establishing a population at the site. We encourage the consideration of conspecific cues in translocation biology: cues can be relatively easy to deploy and have a high likelihood of successfully encouraging settlement for the right species in the right context (https://www.conservationevidence.com). For reintroductions –translocations to sites where the species has been extirpated (IUCN, 2013) – this tool may play a vital role in re-establishing species in unoccupied but suitable habitat. A less frequent but significant problem facing some translocations is the tendency of some animals to 'home' back to the origin site (Stamps & Swaisgood, 2007; Germano & Bishop, 2009; Le Gouar *et al.*, 2012; Hinderle *et al.*, 2015). While cue deployment increased settlement, we additionally found higher settlement rates associated with translocation distances >17.5 km. Translocation practitioners working with species that may have such a homing tendency should be mindful that one simple solution may be to translocate them over longer distances, taking into consideration species vagility.

Our findings also highlight the importance of careful selection of displacement sites, ensuring that sufficient natural burrows are available in the vicinity or, if not, installing artificial ones with a long-term management plan in place. This finding parallels the documented importance of habitat quality in translocation outcomes (Wolf, Garland & Griffith, 1998), especially the need to consider refuge availability, an idea increasingly recognized in conservation generally (Manning *et al.*, 2013) though less often explicitly addressed in conservation translocations. On the regulatory side, mandating more careful planning ahead of mitigation translocations would increase the clarity of the regulatory objectives and improve the probability that objectives are met, including their contribution to species or habitat conservation where relevant.

Even if there is a survival penalty associated with translocation, it is important for managers and regulatory agencies to consider that translocation may achieve conservation goals better than displacement. The long-term value of translocation exceeds that of displacement when there are plausible projections of increasing future threats on the unprotected landscape around displacement sites. As the pace of development continues without any apparent de-escalation, wildlife such as BUOW experience 'serial eviction' as one habitat patch after another is lost to infrastructure expansion. Under these circumstances, it may be wise to consider translocation to protected areas that can manage these threats, conduct restoration activities to enhance habitat suitability, and include extra management support following release. Further experimentation with predator control and supplemental feeding protocols may provide further improvements in outcomes. As indicated by our results, the lack of a reproductive penalty associated with translocation further supports its consideration when conservation goals prioritize establishing or bolstering populations in protected areas. A protected area network is often available for these purposes and many of these may lack (viable) populations of key wildlife species (Swaisgood *et al.*, 2019). Although not specifically tested in our study, it is essential that managers of protected areas at selected release sites be committed to managing habitat to maintain or improve quality.

Increasingly, such forward-looking considerations will replace traditional approaches that simply evaluate current on-the-ground circumstances. This trend is already observed in the use of climate change forecasts in selecting release sites that will sustain species under future conditions (Thomas, 2011) but – especially in highly urbanized and other areas subject to intense increasing development pressure – we also need to consider the likelihood of emerging additional anthropogenic impacts that decrease habitat suitability in the future. In fact, a meta-analysis of avian species translocation to protected areas revealed higher survival probabilities (Skikne *et al*., 2020) plausibly because unprotected sites are exposed to more anthropogenic disturbance. Risk assessment is a critical component of translocation planning (IUCN, 2013) and the likelihood of future impacts leading to serial evictions should occupy a more prominent role in such planning during the Anthropocene. This problem is especially relevant for mitigation translocations, which are inherently supply-driven, meaning they are motivated by a source of animals for translocation; by contrast, conservation translocations are demand-driven in that the release site is typically selected because the species has been extirpated or requires supplementation (Germano *et al*., 2015). Thus, mitigation translocations could be most useful to advancing species conservation if the supply of individuals is used more strategically to re-establish populations in areas where there is demand, for example protected areas lacking the species. One of the more general implications of our work with BUOW mitigation translocations is that this class of translocations requires more thoughtful scrutiny in selecting release sites that support continued species recovery; too often, they succumb to a short-term vision of salvaging individual animals in the path of development.

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Data availability statement

Data is provided in Supporting Information.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Histogram of dispersal distances for all BUOW in the study.

Figure S2. Number of uncertain fates by month of study (n = 54).

Figure S3. Flowchart tool designed for use by managers and regulatory agencies to identify whether a BUOW mitigation project is a candidate for successful displacement, or whether translocation would be more beneficial.

Figure S4. Flowchart tool designed for use by managers and regulatory agencies to guide managers through the planning process for translocation.

Table S1. AICc values and model weights from survival analysis.

Data S1. Translocation protocol details.

Data S2. Artificial cue treatment protocol details.

Data S3. GPS telemetry protocol and transmitter performance.

Data S4. Distribution and composition of study owls.

Data S5. Dispersal, settlement, and reproduction dataset.

Data S6. Survival analysis dataset.