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Capturing pests and releasing ecosystem engineers: translocation of common but diminished species to re-establish ecological roles

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Abstract

Translocation of abundant but declining ecologically important species for re-establishing more sustainable ecosystem function is a neglected but promising form of conservation intervention. Here, we developed a translocation program in which we capture pests and release ecosystem engineers, by relocating California ground squirrels *Otospermophilus beecheyi* from areas where they are unwanted to conserved lands where they can perform ecosystem services such as burrowing and vegetation alteration. We accomplished this using an experimental approach in which some factors were measured or experimentally manipulated, while others were held constant. We translocated 707 squirrels and examined survival and movement patterns as a function of several translocation tactics and ecological factors. We released squirrels at 9 different plots with varying ecological contexts and at each plot experimentally manipulated post-release habitat using mowing, mowing plus the use of augers to establish starter burrows, and controls that remained unmanipulated. The most influential variables affecting short-term survival, dispersal, and long-term persistence were factors relating to soils and vegetation structure. Translocated squirrels had higher initial survival on plots where dense exotic grasses were experimentally altered, greater dispersal when released at sites with less friable clay soils, and improved long-term persistence at sites characterized by more friable soils associated with metavolcanic than alluvial geological layers. Squirrel persistence was also improved when translocations supplemented previous translocation sites than during initial translocations to sites containing no resident squirrels. Our results demonstrate how California ground squirrels can be successfully translocated as part of a larger objective to favorably alter ecological function in novel grassland ecosystems dominated by non-native vegetation. In broader context, our study highlights the importance of testing release strategies, and examining habitat variables and restoration techniques more closely when selecting release sites to improve translocation outcomes.

Introduction

Translocation – the deliberate human-mediated movement of organisms on the landscape – has become a conservation tool adopted to address a variety of conservation problems including re-establishment of extirpated populations, supplementation or genetic rescue of small, isolated populations, and increasingly for environmental mitigation (Germano *et al*., 2015), as well as more forward-looking applications such as assisted colonization to mitigate climate-mediated and other anthropogenic changes in habitat suitability (Seddon & Armstrong, 2016) and rewilding (Pettorelli *et al*., 2018). Although the science of translocation biology has advanced more rapidly in recent decades, there remain several gaps in approaches taken in this developing field (Armstrong & Seddon, 2008; Taylor *et al*., 2017). There have been repeated calls for more careful application of scientific principles, with a goal of reducing uncertainty about alternative management actions. Yet, a recent literature review found that over the past two decades there has been no increase in the proportion of translocation studies that directly test alternative management actions (Taylor *et al*., 2017). Undoubtedly, one of the primary obstacles to such an approach is that most translocations are conducted with highly regulated at-risk species and inherently involve small sample sizes which effectively preclude assigning a sufficient number of individuals to varying experimental treatments. In translocation biology the remaining questions most needed to improve outcomes relate to devising better tactics, or "techniques capable of influencing post-release individual performance or population persistence" (Batson *et al*., 2015).

An emerging application of translocation is to reverse defaunation processes operating on more common species (Seddon *et al*., 2014). Maintenance of ecological systems may require more than prevention of species extinction: individuals of certain species may need to be present in sufficient numbers to perform ecological roles (Gaston, 2010). In contrast to most wildlife species, the use of translocation to restore more common species in plants is routine, and offers beneficial lessons for animal translocations (Watson & Watson, 2015). These efforts at plant restoration more often involve the use of *a priori* experiments to test the effects of alternative management actions (Antonsen & Olsson, 2005). The more conservative approach adopted by practitioners of animal translocation may stem from a more profound risk aversion that characterizes much of the thinking surrounding conservation intervention in many circles (Meek *et al*., 2015). Regardless of the reasons, routine translocation of common animal species is rarely countenanced (Watson & Watson, 2015).

Developing translocation programs for ecologically important common species experiencing defaunation has many potential benefits for conservation (Watson & Watson, 2015). In addition to restoring ecosystem services, translocation of common species offers opportunities to advance knowledge in translocation biology more rigorously and can serve as a "probe" to better understand the habitat requirements for ecologically important species. Habitat suitability for the target species has been implicated as one of the most important variables governing translocation outcomes across taxa (Griffith *et al*., 1989). Evaluating suitable habitat for species that are persecuted by humans or experiencing decline is particularly problematic in the Anthropocene, as current occupancy may not accurately reflect suitable habitat (Cianfrani *et al*., 2010). Following judicious planning and expert consultation, release of individuals into putative suitable habitat can confirm or reject prevailing opinion regarding the factors governing habitat suitability, and do so in a more experimental fashion than possible in presence–absence surveys.

Here, we develop a translocation program for a common but diminished ecologically important species of the grassland ecosystem of the western United States, the California ground squirrel (*Otospermophilus beecheyi*; CAGS). CAGS appear to play an important role in engineering grassland ecosystems, yet little attention is given to this species in conservation planning and policy (Hennessy *et al*., 2016; Hennessy *et al*., 2018). Research has shown that CAGS colonies have greater diversity of reptiles, amphibians, insects and birds than sites where squirrels are absent (Lenihan, 2007), indicating CAGS ecosystem role meet criteria for keystone species designation (Delibes-Mateos *et al*., 2011). Similarly, colonies of black-tailed prairie dog *Cynomys ludovicianus* are associated with higher plant and animal diversity (Kotliar, Baker & Whicker, 1999). Thus, our study species exerts disproportionate influences on ecosystem function that can be used to advance ecosystem conservation (Byers *et al*., 2006).

Unfortunately, like many other burrowing small mammals, CAGS are also among those keystone species persecuted as pests and characterized by unrealized conservation potential (Delibes-Mateos *et al*., 2011; Davidson, Detling & Brown, 2012). Despite significant positive impacts on grassland ecosystems and species of conservation concern, such as the burrowing owl *Athene cunicularia hypugaea*, CAGS are rarely included in conservation management plans and almost no research has been conducted to examine how CAGS can be managed for conservation benefit. In fact, they are commonly viewed as a "pest" species and "...eradication campaigns have poisoned California ground squirrels by foot, horse, vehicles, and aircraft using a variety of chemical toxicants..., anticoagulants..., and burrow fumigants" (Lenihan, 2007). These continued efforts at eradication keep ground squirrels far below their historical carrying capacity (Marsh, 1987) in numbers too low to adequately perform their role as ecosystem engineer.

Whereas CAGS are relatively common in locations where they are not needed or wanted – such as farmland, rangeland, and picnic grounds – they are often absent from or present in low numbers in conserved land (Hennessy *et al*., 2016, 2018). To the extent that CAGS can be successfully managed in California's grassland, their recovery may contribute to the maintenance of one of the world's most endangered temperate ecosystems containing approximately 90% of California's at-risk species (Barry, Larson & George, 2006). Due to their suitability for grazing, agriculture, and housing developments, grasslands are among the most favored ecosystems for human use and are vulnerable to invasion by exotic plants. In California, many native bunch grass systems have been invaded by Mediterranean annual grasses (D'Antonio *et al*., 2010).

Where ground squirrels are absent and their ecosystem engineering role needed, translocation to re-establish squirrel populations is a potentially useful conservation tool. Historically, however, translocations of ground squirrels have been ineffective. Salmon & Marsh (1981) noted "Our experience has been California ground squirrels released into an area will rarely stay." In one translocation study, 83% of ground squirrels translocated using a hard release without acclimation immediately abandoned the release site (Van Vuren *et al*., 1997). As part of a larger study, we evaluated ecosystem engineering effects at sites where CAGS were translocated and compared them to matched-pair control sites where no squirrels were translocated but the same habitat modifications were conducted. These findings clearly indicated that waiting for CAGS to disperse and colonize habitat naturally was ineffective and that under most circumstances active translocation will be required to re-establish CAGS on conserved lands (Hennessy *et al*., 2016).

To develop improved strategies for translocation, we designed a scientifically robust translocation program for CAGS with the goal of informing management decisions by testing salient *a priori* hypotheses and incorporating best practices developed for conservation translocations (IUCN, 2013). We followed an experimental approach wherein some factors were held constant while others were systematically manipulated or quantified to capture lessons learned for future management decisions (Nichols & Armstrong, 2012). We incorporated and attempted to inform standard guidelines for translocation (IUCN, 2013), with a focus on measurement and manipulation of variables in the post-release environment. Taking advantage of the large sample size made possible by working with a more common species, we were able to address and test many strategies recommended in the IUCN (2013) guidelines, among other sources (e.g., Batson *et al*., 2015). These include efforts to optimize release group composition, release of larger numbers of individuals across multiple locations and time periods, and utilization of several different monitoring metrics to ensure that lessons learned are captured to guide interventions and future translocations.

We tested several tactics (*sensu* Batson *et al*., 2015) commonly employed in translocations, including experimental manipulation of putative factors influencing habitat suitability, selection of release sites that vary in potential habitat suitability (soil characteristics), effects of source site where translocated animals were captured, the presence of conspecifics at the release site from earlier translocations, and the role of intrinsic factors such as sex and weight. Specifically, our experiment used mowing to reduce nonnative grass cover and augering to provide starter burrows.

Materials and methods

Subjects and study sites

From 2011 to 2013 we translocated 707 CAGS. We captured squirrels in baited Tomahawk traps, marked them for individual identification with aluminum ear tags and implanted radio-frequency identification (RFID) tags (8.4 mm; Biomark Inc., Boise, ID, USA). We also marked their pelage with a unique 2-digit number/letter combination with Nyanzol dye for identification at a distance.

We sourced squirrels from three sites in southern San Diego County (Figure S1), with the majority of squirrels translocated from Naval Base Coronado ("Navy"; 32°44′57.7″N, 116°29′37.9″W). The Rancho Jamul Ecological Reserve ("Jamul") – owned and managed by California Department of Fish and Wildlife – served as the second source population (32°40′44.1″N, 116°51′17.4″W), and the third was a privately-owned ranch in Pine Valley (32°44′57.7″N, 116°29′37.9″W).

We translocated squirrels to one of nine 0.79-ha plots across three release sites (Figure S1): (1) Jamul, (2) San Diego National Wildlife Refuge ("Sweetwater"; 32°41′41.0″N, 116°58′03.0″W), and (3) Lone Star Mitigation Site ("Otay"), a 25.2-ha open-space easement in Otay Mesa (32°34′43.3″N, 116°57′59.8″W). All three release sites contained predominantly non-native grassland habitat (primarily *Avena barbata* and *Bromus diandrus*; see Hennessy *et al*., 2016) but were designated as protected areas set aside for the preservation of native plants and animals. Further, these sites were selected for habitat management for re-establishment/recovery of burrowing owls *Athene cunicularia hypugaea* and other native wildlife, and squirrels were viewed as a necessary component of habitat enhancement. As part of an environmental selection tactic (Batson *et al*., 2015), we selected sites that varied in characteristic soils (clay, no clay) and underlying geological formation that may influence burrowing activity.

The experimental design for plot establishment is described in detail in Hennessy *et al*. (2016). In summary, we selected sites with an existing plant community of native or exotic grassland and excluded sites with very high clay and cobble content. We established 9 circular plots 100 m in diameter to receive translocated squirrels. Because non-native vegetation present at all sites was judged to be unsuitable for squirrels due to dense, tall structure, each plot was divided into three sections to receive different habitat enhancement experimental treatments (Figure S2): (1) mowing to a height of 7.5–15 cm and dethatching; (2) mowing, dethatching, and soil decompaction via augering holes to serve as "starter burrows" (hole 0.3 m deep angled 45°, 20 holes evenly distributed across each section) to encourage more rapid establishment of burrow systems; and (3) a control which remained unmanipulated. These manipulations address pre-release resource augmentation tactics (Batson *et al*., 2015) to create and test the effects of more favored open habitat. In an additional (untested) predator refuge tactic, in 2012 and 2013 we added additional cover to each section of each plot to provide escape from predators. Each section of each plot received two small brush piles, a large brush pile with a stump, and a log. Some tactics, such as predator refuge, were employed for all subjects, and not tested, in the interest of optimizing translocation outcomes.

Translocation protocol

Following removal from source sites, we housed squirrels in a temperature-controlled holding facility at Jamul for 7–10 days. We then transferred squirrels to acclimation cages with below- and aboveground components at the release plots for a 1-week acclimation period. Acclimation – where animals are confined during a holding period at the release site – is an important tactic used to allow animals to adjust to local conditions, and has been shown to dampen dispersal in some species. Although results are mixed (Moehrenschlager & Lloyd, 2016), it is considered a best practice until proven otherwise. Acclimation cages consisted of an underground chamber (30 cm diameter by 30 cm height, made of concrete form tubes) 90 cm below the surface and connected to an above-ground retention cage (hardware cloth, 90 × 90 × 30 cm) via 2 m long sections of 10 cm irrigation tubing.

Plots where squirrels successfully established (6 of 9) were supplemented the following year, whereas those with no establishment were subsequently removed from further study. We released an average of 48 squirrels per plot during the initial translocations (range 27–59) in June and 44 squirrels for the supplemental translocations (range 34–50) in August of the following year (details of translocated squirrels and translocation sites in Table S2). These translocations resulted in local population density on plots of fewer than 75 squirrels/ha, which falls below densities typical in other populations (Boellstorff & Owings, 1995) but also anticipated high mortality rates for this prey species during establishment. Squirrels were provisioned with apples, yams and rodent pellets for 3 months after release. Because social familiarity in a release cohort can dampen dispersal and increase translocation success in other rodent species (Shier, 2006; Shier & Swaisgood, 2012), we also incorporated a social composition tactic into the release protocol. In 2012 and 2013 we conducted pre-translocation observations on marked squirrels to determine above-ground social associations and burrow co-habitation. Affiliated squirrels (neighbors) were housed together in the pre-release holding facility and later placed either in the same or adjacent acclimation cages.

Post-release monitoring

To determine short-term survivorship and movement patterns, we radio tracked 102 subjects for 4 months after translocation. Ground squirrels were collared with VHF transmitters and tracked using R-1000 telemetry receivers (Communications Specialists Inc., Orange, CA, USA) and Yagi antennas daily for the first 30 days, then three times per week until collars were recovered.

We evaluated longer term squirrel persistence at release sites after the first breeding season in March the following year, approximately 12 months after an initial translocation or 9 months after supplemental translocation. We used the same trapping and marking protocols as described above. Fifty-five tomahawk traps were placed along three transect lines overlaying the plots in an asterisk pattern (Figure S2).

All aspects of this study were approved by the Institutional Animal Care and Use Committee of San Diego Zoo Global (IACUC approval numbers: 11-017 and 12-002).

Statistical analyses

We used linear regression models to evaluate the influence of ten biotic and abiotic factors on survival and movement for radio-collared squirrels. The factors included sex, weight, source location, release site, translocation type (initial/supplemental), treatment (mowing/augering/control), geology (geological formation), soil (presence of clay in the soil), year, and plot (Table S1). All were categorical variables except for weight, which was rescaled to one standard deviation (standardized). Plot was nested within soil, geology and site. We extracted parent geological material (alluvial deposits, metavolcanic rock) and soil layer for each of the plots in ArcGIS 10 with a georeferenced geology layer available from SanDAG (http://www.sandag.org). We applied survival analysis to model the number of days a collared squirrel was known to be alive. Squirrels were right-censored if we did not record predation or remove their collar at the end of the telemetry period (e.g., lost transmitter signal, or squirrel remained underground and collar was not retrieved).

We used nominal logistic regression models to evaluate the effects of the ten factors described above on recapture of individual squirrels during trapping surveys. We also used generalized linear models to evaluate two additional spatial movement parameters. Settlement distance was the Euclidean distance between a squirrel's release burrow and its settlement location, determined as the burrow system where the squirrel remained for more than 7 days. The second parameter, averaged movement, was calculated as the sum of all linear distances between tracked locations divided by the number of GPS locations recorded from the VHF tracking.

We used an information theoretic approach by evaluating the corrected Akaike information criterion (AIC_c) for all possible models. We used model averaging across all candidate models to calculate weighted parameter estimates with 85% confidence intervals and to determine the relative importance of influential parameters. Candidate models were those within two AIC_c units of the model with the lowest AIC_c (Burnham & Anderson, 2004). We calculated odds ratios (ORs) using 85% confidence intervals to examine the relative risk to survival for each retained parameter.

Results

Survivorship and movement of radio-collared squirrels

Descriptive data on squirrel translocation outcomes are provided in Table S3. The candidate set of models predicting survival indicate that experimental treatment (Fig. 1) and sex were the most plausible explanatory factors predicting survival, with Treatment occurring in 10 of the candidate set of 12 models and sex occurring in 7 (Table 1). Other factors contributing to model performance include – in descending order of relative importance – soil, geology, translocation type, weight, and source. Squirrels released in the mowed [OR = 1.82 (1.12, 2.95)] or augered [OR = 1.96 (1.28, 3.00)] treatments were nearly twice as likely to survive than those in the control treatments. Squirrel survival rates begin to diverge between the control treatment and the mow and mow/auger treatments after about 1 month, with survival for control-released squirrels falling below 20% within 3 months post-release (Fig. 1). Survival did not differ between the mow and mow/auger treatments. The odds of male squirrels surviving to 90 days were 1.5 times greater than for females [OR = 1.51 (1.03, 2.22)]. For the remaining influential but non-significant variables survival was higher for squirrels released at sites with no clay, with metavolcanic rock, in supplemental translocations, and for heavier squirrels (Table 1).

Soil type figured prominently in the candidate model sets for settlement distance (Table 1) and was the only variable with a CI for weighted parameter estimate that did not contain zero (Table 1). Squirrels settled at greater distances from their release location on plots with clay soils (Fig. 2). There was some support for sex, weight, and the interaction of sex × weight (females that weighed less settled farther from the release cage), translocation type, and geology, but soil was five to six times more likely.

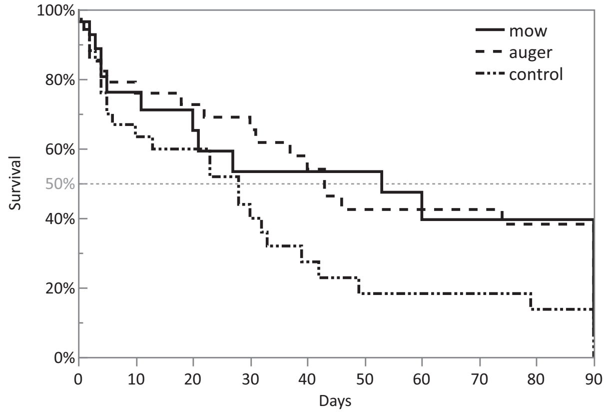

Figure 1 Kaplan–Meier plot for proportion of squirrels surviving to 90 days by treatment for all 3 years (N_{mow} = 28, N_{auger} = 34, $N_{control}$ = 34, N_{total} = 96).

Sex, year, and to a much lesser extent, translocation type were the only variables included in the candidate set of models influencing average movement (Table 1), and the weighted parameter estimate CI's excluded zero only for sex and year. Females averaged greater movement than males (Mean ± SE: $\bar{X}_{female} = 46.6 \pm 11.1$, $\bar{X}_{male} = 28.3 \pm 9.3$) and collared squirrels moved more in 2011 than subsequent years ($\bar{X}_{2011} = 72.0 \pm 18.0$, $\bar{X}_{2012} = 18.5 \pm 4.3$, $\bar{X}_{2013} = 13.7 \pm 5.5$). Although squirrels appeared to move more during initial translocations than supplemental ones (Fig. 2), this result was not significant. Similarly, treatment and geology did not influence average movement. We also examined the relationship between movement and mortality in a separate analysis and found no relationship between survival and linear distance to settlement (Pearson $r = -0.095$, $P = 0.51$) or average movement ($r = -0.098$, $P = 0.34$).

Long-term persistence at release site as measured by trapping data

Our models indicate that by the spring following release – nearly 1 year later – geology, sex, and translocation type were included as influential variables in almost all of the candidate set of models (Table 2). Although release Site and Year also have explanatory power determining whether a translocated squirrel was recaptured, geology, sex and translocation type were 4–5.5 times more likely (Table 2). Squirrels released at sites with metavolcanic rock were more likely to persist than squirrels released on alluvial deposits (Fig. 3), a finding largely driven by the failure of females to persist on alluvial deposits (geology × sex interaction). The odds of capturing translocated squirrels increased twofold from initial to supplemental Translocation type [OR = 2.1, (1.3, 3.4); Fig. 3].

Discussion

By incorporating best-practice protocols into a translocation program for a common but diminished and ecologically important species, we have improved upon past translocation attempts which met with poor success (Salmon & Marsh, 1981; Van Vuren *et al*., 1997). Furthermore, we have been able to manipulate and measure key management variables that provide empirical feedback regarding what tactics work best. In addition to learning which intrinsic variables that are (sex) or are not (weight) important for translocation outcomes in CAGS, we have confirmed that vegetation structure and soil characteristics are the most important components driving habitat suitability for CAGS, as implicated in presence–absence surveys (Ordeñana, Van Vuren & Draper, 2012; Hennessy *et al*., 2018). Our statistical models reveal that of the 10 variables analyzed, only variables relating to soil quality and vegetation were consistently included in the top models.

Our experimental vegetation treatments had significant effects on short-term survival during the initial weeks following release. In fact, vegetation treatment received the highest model support in our survival analysis for radio-tracked squirrels, with squirrels released into control treatments experiencing lower survival than those released into mowed or mowed and augered sites, indicating that efforts to reduce vegetation height and create a more open habitat increases translocation success, at least in the short term, and confirms research demonstrating that CAGS are more likely to be found in grasslands with less vegetation cover (Ordeñana *et al*., 2012; Hennessy *et al*., 2018). CAGS and other native wildlife evolved in a more open grassland habitat than found in the denser stands of non-native grasses that dominate most disturbed grasslands in California today (Barry *et al*., 2006; Hennessy *et al*., 2016, 2018). The more open habitat structure created by mowing is analogous to the native grasslands and squirrels probably benefit from improved predator detection.

From our short-term data from radio-tracking squirrels for the first 90 days post-release, we found that squirrels released at sites with no clay survived better than those released at sites where the soils contained clay. Clay soil was also the most powerful predictor of dispersal, with squirrels released on clay soils settling farther from the release site. Yet, average movement was the same for squirrels released on clay and no-clay soils, indicating that clay soils induced directed travel away from the release site, i.e., dispersal. The most plausible explanation is that high clay content thwarts burrow establishment because clay soils are less friable; thus, when translocated squirrels are released on these soils, they reject the site and travel in search of more suitable soils for digging. Our long-term data obtained from trapping circa 1 year post-release similarly establish primacy for soil characteristics governing establishment of CAGS at the release site, with geological formation ranking first among the factors predicting long-term persistence. Squirrels released onto metavolcanic rock were much more likely to persist than those released onto hard-packed alluvial geologic layers. Metavolcanic rock is characterized by less compacted, more friable soils with less clay content than alluvial layers in the study area (Bowman, 1973). This finding may be an outcome of higher dispersal rates from alluvial soils, higher mortality rates on alluvial soils, or a combination of both.

Table 1. Models predicting survival and movement of collared squirrels for 90 days post-release (left) and factors examined for their influence on survival, linear distance and average movement (right)

Model	K	-Log likelihood	AIC_c	Δ_i	w_i	Evidence ratio
Models predicting survival (N = 93)						
Treatment	3	301.6	609.5	0	0.16	1
Treatment, sex	4	300.6	609.6	0.10	0.15	1.1
Treatment, sex, soil [no clay]	5	299.9	610.5	1.00	0.10	1.6
Treatment, soil [no clay]	4	301.1	610.8	1.26	0.08	1.9
Sex	3	303.4	611.0	1.46	0.08	2.1
Sex, soil [no clay]	4	302.3	611.0	1.48	0.08	2.1
Treatment, geology	4	301.3	611.2	1.66	0.07	2.3
Treatment, sex, translocation	5	300.3	611.4	1.91	0.06	2.6
Treatment, translocation	4	301.5	611.5	1.96	0.06	2.7
Treatment, sex, geology	5	300.4	611.5	1.97	0.06	2.7
Treatment, sex, weight	5	300.4	611.5	1.98	0.06	2.7
Treatment, source	4	300.4	611.5	1.98	0.06	2.7
Models predicting linear distance (N = 49)						
Soil	3	95.2	193.4	0	0.36	1
Null	2	93.3	194.7	1.24	0.19	1.9
Soil, sex, weight, sex × weight	6	90.5	195.0	1.61	0.16	2.2
Soil, translocation	4	93.2	195.1	1.71	0.15	2.4
Soil, geology	4	93.1	195.4	1.93	0.14	2.6
Models predicting average movement (N = 68)						
Sex, year, translocation	5	113.5	240.3	0	0.58	1
Sex, year	4	115.0	241.0	0.67	0.42	1.4

Parameter	Weighted estimate	Unc. SE	Lower 85% CI	Upper 85% CI	Sum of weights
Models predicting survival (N = 93)					
Intercept	3.871	0.203	3.58	4.17	
Treatment [mow]	0.175	0.200	−0.12	0.46	**0.85**
Treatment [auger]	0.249	0.178	−0.01	0.51	
Treatment [control]	−0.423	0.176	−0.68	−0.17	
Sex [female]	−0.207	0.132	−0.40	−0.02	**0.57**
Soil [no clay]	−0.260	0.239	−0.61	0.09	0.25
Geology [alluvial]	0.087	0.129	−0.10	0.27	0.13
Translocation [initial]	0.073	0.128	−0.11	0.26	0.12
Weight	−0.081	0.133	−0.27	0.11	0.06
Source [RJER]	−0.378	0.436	−1.01	0.25	0.06
Source [NASNI]	−0.454	0.380	−1.01	0.10	
Source [Pine Valley]	0.832	0.684	−0.16	1.82	
Models predicting linear settlement distance (N = 49)					
Intercept	4.518	0.454	3.85	5.18	
Soil [no clay]	−0.764	0.407	−1.36	−0.17	**0.81**
Sex [female]	−0.161	0.247	−0.52	0.20	0.16
Weight	−0.630	0.337	−1.12	−0.14	0.16
Sex × weight	−0.777	0.337	−1.27	−0.28	0.16
Translocation [initial]	−0.202	0.254	−0.57	0.17	0.15
Geology [alluvial]	−0.169	0.259	−0.55	0.21	0.14
Models predicting average movement (N = 68)					
Intercept	2.885	0.170	2.64	3.13	
Sex [female]	0.427	0.176	0.17	0.68	**1.00**
Year [2011]	1.469	0.385	0.91	2.03	**1.00**
Year [2012]	−0.277	0.222	−0.60	0.05	
Year [2013]	−1.192	0.376	−1.74	−0.64	
Translocation [initial]	−0.445	0.260	−0.82	−0.07	0.58

Sum of weights in bold indicate model-averaged parameters we consider influential (confidence interval does not contain zero and sum of weights >0.5).

Similarly, soils influence habitat associations (Lohr *et al.*, 2013) or burrow structure (Laundré & Reynolds, 1993) in other burrowing mammals, suggesting that soils should more often be incorporated into habitat suitability models for burrowing species (Hennessy *et al.*, 2018). Taken together, these findings strongly indicate that soils that support burrow excavation are more suitable for ground squirrels and will promote establishment of translocated or naturally dispersing squirrels.

Long-distance post-release dispersal is one of the greatest challenges facing translocation programs (Armstrong & Seddon, 2008). Greater dispersal distances are often associated with greater cumulative risk as animals expose themselves to predators, climatic extremes, conspecific conflict, and may suffer reduced foraging opportunities. Thus, many methods have been developed to dampen dispersal and anchor animals at the release site (Stamps & Swaisgood, 2007; Le Gouar, Mihoub & Sarrazin, 2012; Swaisgood & Ruiz-Miranda, In press). As a best practice, we adopted several tactics known to reduce post-release dispersal in other species, including on-site acclimation, supplementation, provision of resources such as cover refuge from predators, and

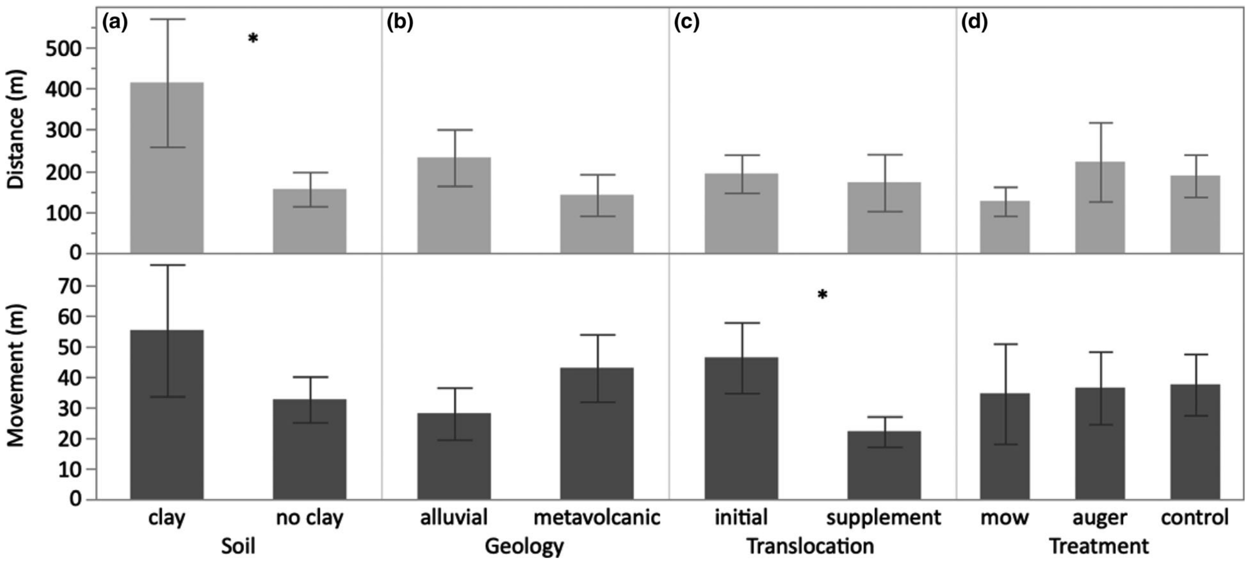

Figure 2 Above: Total mean linear distance moved between release and settlement (dispersal) as a function of (a) Soil type, (b) Geological formation, (c) Translocation type (d) and experimental Treatment. Below: The mean average distance moved between consecutive GPS locations as a function of (a) Soil type, (b) Geological formation, (c) Translocation type (d) and experimental Treatment. Asterisk (*) denotes significant differences.

Table 2. Models predicting squirrel persistence based on trap monitoring the following year, after the first breeding season post-release (left) and influential factors that explain squirrel persistence based on trap monitoring the following year, after the first breeding season post-release (right)

Model	K	-Log likelihood	AIC_c	Δ_i	w_i	Evidence ratio	Parameter	Weighted estimate	Unc. SE	Lower 85% CI	Upper 85% CI	Sum of weights
Models predicting spring trap results for translocated squirrels only (*N* = 566)							Models predicting spring trap results for translocated squirrels only (*N* = 566)					
Geology, sex, geology × sex, translocation	6	145.3	300.7	0	0.34	1	Intercept	−2.888	0.307	−3.33	−2.45	
Geology, sex, geology × sex, translocation, site	7	144.8	301.8	1.06	0.2	1.7	Geology [alluvial]	−0.506	0.291	−0.93	−0.09	**1**
Geology, sex, geology × sex, year	6	144.9	302.0	1.24	0.19	1.9	Sex [female]	0.498	0.292	0.08	0.92	**0.86**
Geology, translocation	4	148.3	302.6	1.87	0.14	2.5	Translocation [initial]	−0.381	0.165	−0.62	−0.14	**0.81**
Geology, sex, translocation	5	147.3	302.7	1.92	0.13	2.6	Geology [alluvial] × Sex [female]	0.478	0.284	0.07	0.89	**0.73**
							Site [Jamul]	0.213	0.222	−0.11	0.53	0.20
							Year [2012]	−0.622	0.269	−1.01	−0.23	0.19
							Year [2013]	0.035	0.215	−0.28	0.34	0.19

Sum of weights in bold indicate model-averaged parameters we consider influential (confidence interval does not contain zero and sum of weights >0.5).

creating socially familiar release groups. Despite these efforts, our data reveal that if managers choose to release CAGS on sites with clay content in the soil, they may risk long-distance dispersal that compromises conservation objectives.

We also found that initial translocations, releasing CAGS at sites without a resident population of squirrels, were less successful in terms of long-term persistence than supplemental translocations, releasing squirrels at the same site in subsequent years. This finding is consistent with the idea of

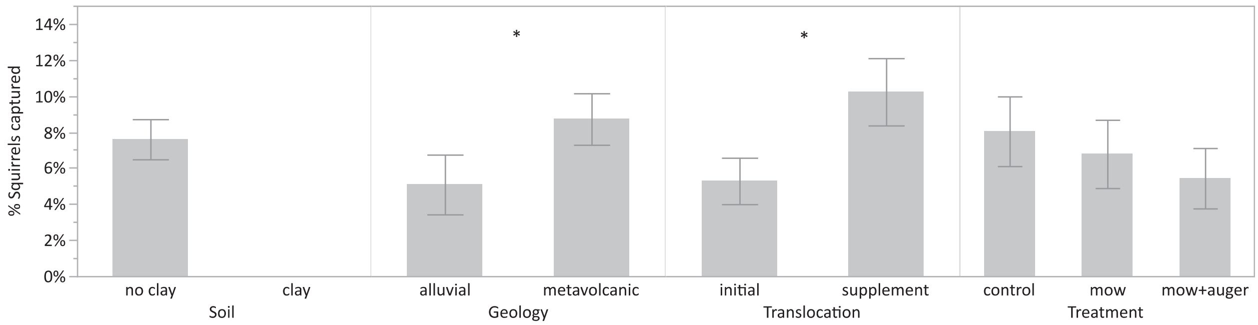

Figure 3 The percentage of translocated squirrels captured on plots the following year post-release differed as a function of soil, geologic parent material, translocation type, and vegetation treatment. Despite the large effect size, clay vs. no clay comparison failed to reach significance due to small N resulting from abandonment by all squirrels within 1 year of release for the two clay sites and discontinuation of translocations conducted on sites with clay thereafter. Values are not estimates of the number of surviving squirrels but are instead minimum percent of translocated squirrels remaining at the site and captured during 5 days of trapping effort.

conspecific attraction, which posits that animals prefer to settle near conspecifics and/or derive socially mediated fitness benefits from living near conspecifics (Reed & Dobson, 1993). Thus, it may be easier to establish CAGS at sites that already have squirrels present, but in insufficient numbers, than to establish CAGS in areas where they have been locally extirpated, though competition with resident squirrels could negatively impact releasees.

An important and perhaps surprising lesson involves the difficulties encountered in successfully translocating this species. As a pest species, one might assume that CAGS are robust and behaviorally flexible enough to endure the challenges of translocation, yet this and other studies have been characterized by very low survival rates. Mortality was greater than 80% among our control-translocated squirrels within 90 days of release and 60% among squirrels released into plots where the vegetation was experimentally reduced. Only by releasing a relatively large number of squirrels and conducting supplemental translocations were we able to establish more long-term persistence. By contrast, very similar translocation methods yielded much higher 90-day survival rates in the endangered Stephens' kangaroo rat *Dipodomys stephensi*, where approximately 40–75% survived 3 months depending on the translocation tactic employed (Shier & Swaisgood, 2012).

Conservation implications

Our experimental management approach to developing translocation protocols for CAGS yielded a number of important findings that can guide decisions by managers and policy makers. Most important, managers should understand the limitations on where CAGS can be re-established. When protecting and restoring grassland ecosystems for mitigation and conservation purposes, managers need to consider how easily key wildlife species can also be re-established. Our data suggest that for CAGS it is critical to consider soil texture, and that at least rough approximations of soil type are readily available in spatially explicit online databases. Informed release site selection can therefore promote more cost-effective rewilding (*sensu* Pettorelli *et al*., 2018) and help managers create ecological systems that will be more sustainable with less intervention (Pesendorfer *et al*., 2018).

Vegetation management is a more malleable managerial challenge, and our findings suggest that with some effort sites with unsuitable non-native vegetation can be altered to create more favorable habitat for native wildlife, and in some cases help restore native plant life as well (Antonsen & Olsson, 2005). Altering vegetation structure through burning, grazing or mowing (the best method varies with context) is a relatively simple means of managing non-native grassland habitat (Stromberg *et al*., 2007; D'Antonio *et al*., 2010) for native species such as CAGS, and thus is a reasonable tool for enhancing historical components in predominantly novel ecosystems (Corlett, 2015). Many California grasslands can be classified as novel ecosystems with novel combinations of species and altered ecosystem function due to intensive human land-use patterns. Our approach is not intended to restore the original ecological community, but to take a mostly novel ecosystem and increase its value for native plant and animal conservation, that is make it more of a hybrid ecosystem containing both novel and historical components (Hobbs, Higgs & Harris, 2009). A mowing regime alone may increase native plant cover in grasslands (Antonsen & Olsson, 2005), while the addition of squirrels in sufficient numbers – through their foraging and digging activities – may create a more open habitat favored by other native wildlife and provide burrows used as refuges for a number of species. Thus, a CAGS translocation program is part of a grassland rewilding program, where rewilding is defined as "the reorganisation of biota and ecosystem processes to set an identified social–ecological system on a preferred trajectory, leading to the self-sustaining provision of ecosystem services with minimal ongoing management" (Pettorelli *et al*., 2018).

We anticipate that a primary use of our CAGS translocation protocol will be the creation of burrow habitat for burrowing owls on protected, targeted sites, with beneficial effects for other native and at-risk wildlife. Managers working in primarily non-native grasslands that characterize much of the western United States might best leverage our findings by identifying target sites where owl occupancy is desired, and – if squirrels are absent – vegetation management is feasible or already in place. Translocation of key common wildlife, such as CAGS, can be an additional tool to perform ecological services through the creation of burrow systems, the alteration of vegetation structure through foraging activities (Hennessy *et al*., 2016), or other desired ecosystem effects such as seed dispersal (Pesendorfer *et al*., 2018).

By applying and further developing best-practice principles, such as those recommended in the IUCN (2013) guidelines, we have been able to solve a previously intractable species translocation program. Translocation practitioners face a sometimes-bewildering set of alternatives when deciding what tactics can be tested in a given translocation and what tactics or recommendations need to be implemented with the hope that they will improve outcomes. Our CAGS translocations were more successful than previous attempts, and these differences may be partially attributed to untested actions we took, including ensuring social familiarity in the release group, releasing large number of animals, minimizing stress, providing on-site acclimation, creating cover habitat for predator evasion at the release site, and other efforts. We sacrificed knowledge on the impacts of these variables so that we could hold them constant while we manipulated and evaluated other variables. From these tested variables, we learned that supplementation is more effective than releases into areas without residents, and that soils and vegetation structure are especially important post-release habitat determinants of success. These lessons are therefore broadly generalizable: (1) the important decision-making involved in determining what to manipulate, measure and test, or implement in a more controlled fashion; (2) the need for translocation practitioners to think more deeply about the concept of habitat suitability and to manipulate habitat variables to achieve a better understanding of habitat (not too long ago more than half of all habitat evaluations in translocations were based on subjective impression alone (Wolf, Garland & Griffith, 1998); and (3) habitat comprised of mostly invasive plant species can be made more suitable for native wildlife by altering the structure but not composition of the habitat.

The methods for translocating CAGS we have developed promise to make translocation of this common but ecologically important species an easier, more effective, and more routine conservation action in the future, and provide important lessons for other species translocation programs.

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Supporting information

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

Table S1. Description of explanatory variables analyzed with regard to translocation outcome.

Table S2. Sample sizes, experimental treatments, and other details for translocated California ground squirrels.

Table S3. Outcomes for collared translocated California ground squirrels.

Figure S1. Map of southern San Diego County showing one of three source sites (blue) and release sites (red).

Figure S2. (a) Experimental treatments and habitat enhancement for experimental replicates (plots) receiving translocated California ground squirrels. Each plot was divided into three habitat treatments: mow, mow + auger, and untreated control. Acclimation cages (circles) were placed along the periphery of each treatment. All plot treatments received the addition of cover in the form of brush piles, stumps and logs in 2012 and 2013. (b) Trap lines transected the plot along the border between treatments and through the middle of each treatment, extending 40 m outside of the plot.