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Research Paper

Evaluating captive-release strategies for the Western Burrowing Owl (*Athene cunicularia hypugaea*)

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ABSTRACT. Quantitatively evaluating and monitoring augmentation efforts are critical for conservation success. We formally evaluated the success of two Western Burrowing Owl (*Athene cunicularia hypugaea*) population augmentation programs in Manitoba and British Columbia by assessing survival of breeding adults, fledging success, and return rates of fledglings. Manitoba's head-starting program holds hatching year (HY) owls taken from the nests of previous captive-released pairs over winter. After being overwintered in human care, the HY owls are released in pairs as second year (SY) owls. British Columbia has a breeding and release program where owls are bred in facilities; their offspring are then held over winter, paired and soft-released in the spring. Both programs soft-release SY pairs that lay clutches in situ and young are referred to as "wild-hatched owls." We investigated both individual owl and release site characteristics in relation to our success metrics. In Manitoba, breeding season survival averaged 81%, but no factors investigated had a significant effect on survival. In British Columbia, wild-hatched owls returned more than captive released owls ($p < 0.001$). Determining the causes behind captive-released owls' reduced rate of return should be a priority for both recovery programs. Fewer owls returned to release sites with more surrounding cropland. Releases should be prioritized at sites with low percentages of cropland. Interestingly, individuals who returned from migration to form pairs and breed had significantly higher reproductive success than captive-released pairs, suggesting effects of survivor-bias or mate choice. By analyzing post-monitoring data, we have identified opportunities for conservation managers to implement modifications to future release protocols.

Évaluation de stratégies de lâcher de Chevêches des terriers (*Athene cunicularia hypugaea*)

RÉSUMÉ. L'évaluation quantitative et le suivi des efforts destinés à repeupler sont essentiels à la réussite de la conservation. Nous avons évalué le succès de deux programmes d'accroissement de population de Chevêches des terriers (*Athene cunicularia hypugaea*) au Manitoba et en Colombie-Britannique, en déterminant la survie des adultes reproducteurs, le succès des jeunes à l'envol et le taux de retour des jeunes. Le programme du Manitoba conserve pendant l'hiver les jeunes de l'année (HY) prélevés de nids de couples précédemment relâchés de captivité. Après avoir passé l'hiver sous surveillance humaine, les chevêches de l'année sont relâchées en couple en tant qu'individus de deuxième année (SY). La Colombie-Britannique dispose d'un programme d'accouplement et de lâcher dans le cadre duquel les chevêches sont élevées dans des installations; les jeunes produits sont ensuite gardés pendant l'hiver, appariés et relâchés au printemps. Ces deux programmes mettent en liberté des couples SY qui pondent in situ et les jeunes issus de ces couples sont reconnus comme « chevêches nées à l'état sauvage ». Nous avons examiné les caractéristiques des chevêches et des sites de lâcher en relation avec nos mesures du succès. Au Manitoba, le taux de survie pendant la saison de nidification était de 81 % en moyenne et aucun des facteurs étudiés n'a eu d'effet significatif sur la survie. En Colombie-Britannique, les chevêches nées à l'état sauvage sont revenues aux sites de lâcher plus souvent que les chevêches relâchées de captivité ($p < 0,001$). La détermination des causes expliquant le taux de retour réduit des chevêches relâchées de captivité devrait être une priorité pour les deux programmes de rétablissement. Moins de chevêches sont retournées sur les sites de lâcher qui comportaient plus de terres cultivées aux environs. Les lâchers devraient être effectués en priorité sur des sites ayant un faible pourcentage de terres cultivées. Il est intéressant de noter que les individus qui sont revenus de leur migration pour former des couples et se reproduire ont eu un succès de reproduction significativement plus élevé que les couples relâchés de captivité, ce qui laisse entrevoir que des effets liés au biais du survivant ou au choix du partenaire existent. En analysant les données de suivi post-lâchers, nous avons déterminé de possibles modifications à introduire dans les futurs protocoles de relâchement par les gestionnaires de la conservation.

Key Words: *Athene cunicularia; endangered species; population augmentation*

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INTRODUCTION

Migratory birds face numerous threats on their journeys because of increased anthropogenic development, habitat degradation and loss, and climate change (Bairlein 2016, Hutchins et al. 2018). The protection of these species presents unique challenges because population abundance is influenced by the conditions of multiple geographical regions at different times of the year (Martin et al. 2007, Runge et al. 2015). Population reinforcement is a useful tool for species recovery that uses a range of breeding and release techniques (Byers et al. 2013). Population reinforcement and subsequent post-release monitoring of migratory species are especially challenging because migratory behavior may be influenced by a complex interaction of the environment, genetics, and physiology, all of which natural selection may act upon during multiple generations of conservation breeding (Burnside et al. 2017, Couzin 2018).

There are numerous high-profile conservation success stories (e.g., the golden lion tamarin [*Leontopithecus rosalia*; Kierulff et al. 2012]) that highlight the importance of these reinforcement programs. However, many recovery program failures in the 1980s prompted the rapid expansion of the field of reintroduction biology, with an emphasis on a more rigorous scientific approach (Seddon et al. 2007, Armstrong and Seddon 2008). Management plans to facilitate conservation success include decisions regarding release site and release methods (e.g., "soft" release in which animals are acclimated and provided food supplementation after release, or "hard" releases in which these supports are not provided), and individual traits at release (such as age and body condition; Canessa et al. 2016). These decisions often have to be made with little prior information, and are later improved upon with information garnered from post-release monitoring (Keith et al. 2011, Canessa et al. 2016). The success of reintroduction or reinforcement efforts can be improved by strategically altering management decisions on the basis of monitoring data.

The Western Burrowing Owl (*Athene cunicularia hypugaea*) is a migratory sub-species of the Burrowing Owl (*Athene cunicularia*). Western Burrowing Owls breed in western Canada and the northwestern United States in the spring and summer months and overwinter in Mexico and the southwestern United States (Committee on the Status of Endangered Wildlife in Canada [COSEWIC] 2017). Canadian populations of Burrowing Owls have experienced population declines in all four provinces where breeding populations exist (Manitoba [MB], Saskatchewan [SK], Alberta [AB], and British Columbia [BC]; COSEWIC 2017). Currently, most individuals exist in AB and SK, with severe population declines at the sub-species' eastern and western range limits (MB and BC; COSEWIC 2017).

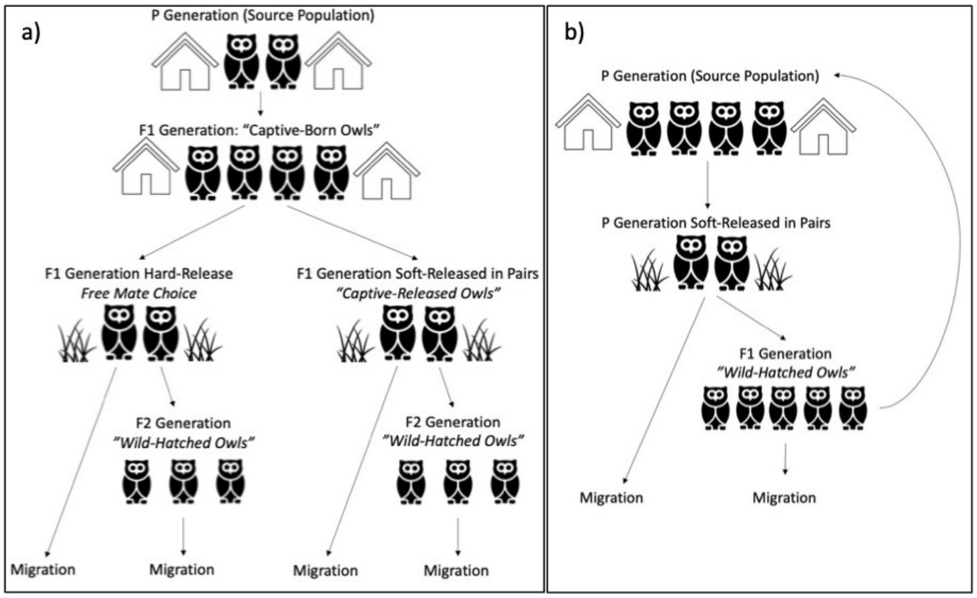
Declines of Burrowing Owls in MB prompted conservation biologists to attempt population augmentation efforts in the province in 1987 (De Smet 1992). However, the program had no returns of young or adults from the release sites in subsequent seasons and low return rates of wild pairs. Thus, the program was discontinued and the species was considered extirpated from the province (COSEWIC 2017). However, 35 wild pairs were observed in Manitoba from 2006 to 2009, initiating current recovery efforts (Froese and Duncan 2021). In 2010, the Manitoba Burrowing Owl Recovery Program (MBORP) was formed to augment the population in Manitoba and continues to the present day. The program has seen one released owl return (in 2011). Only sporadic sightings of individual wild owls have been reported in MB since the start of the program (A. Froese, *personal observations* 2021). In BC, Burrowing Owls were extirpated in the 1980s, prompting initial reintroduction efforts in the Nicola Valley (Leupin and Low 2001) and South Okanagan (Dyer 1989). Ultimately, both programs were discontinued because of low population numbers. In 1990, the Burrowing Owl Recovery Program was started, and it began releasing owls in 1992 from two breeding facilities in BC. As the program increased in scale by incorporating a third breeding facility, more returns were detected over time. The program has seen 359 owls return since its inception. In 2012, 25 wild individuals were observed, but the population is not considered self-sustaining (COSEWIC 2017).

Breeding and release strategies are different in each province (Fig. 1). In MB, a head-starting strategy is employed to increase hatching year (HY) owls' survival via overwintering in managed care. Founding owls are taken from wild nests in Manitoba, the Assiniboine Park Zoo, and the Alberta Birds of Prey Centre as HY owls (Froese and Duncan 2021). These owls are raised in human care and released as second year (SY) birds. SY owls are paired for release via soft-release pens where they mate and produce a clutch in the wild. A variable proportion of owlets are taken from nests of released birds each year, overwintered, and then are paired to breed and released the next year as SY owls (Froese and Duncan 2021). MB releases approximately 20 owls annually. In contrast, BC has developed a captive breeding program (L. Meads, A. Mitchell, and M. Mackintosh, *unpublished manuscript*). A population of owls was established in captivity; these owls are not released but are bred in human care. The captive owls' offspring are held over winter and then are paired and released in the wild as SY owls via soft-release pens. These owls are referred to as captive-released. Their offspring are referred to as wild-hatched. BC releases up to 100 captive-released owls each year.

We investigated success using breeding season survival, return from migration, and reproduction. Our objectives were to (1) identify predictors of successful reproduction (measured by clutch size and number of offspring fledged) in captive-released Burrowing Owls in both MB and BC, (2) compare reproduction between groups of Burrowing Owls (between captive-released owls in BC and MB and between returning owls and captive-released owls within BC), (3) identify predictors of breeding season survival for captive-released Burrowing Owls and their offspring in MB, and (4) identify predictors of return to Canadian breeding grounds for captive-released Burrowing Owls and their offspring in BC. Breeding season survival was investigated only in MB because of reliable data collection on the fates of each owl throughout the breeding season, whereas recruitment was investigated only in BC because of the increasing numbers of returns observed and recorded in recent years.

We examined multiple hypotheses to explain variation in our success metrics (reproduction in both provinces, survival in MB, and return in BC). Body mass may be particularly important for Burrowing Owls, because low body mass is known to have negative effects on survival and productivity (Wellicome 2000, Rosenberg and Haley 2004, Wellicome et al. 2013). Therefore, we predicted larger body mass would result in higher success. Animals in managed breeding and in unfamiliar environments after release

Fig. 1. a) Breeding and release cycle of the Burrowing Owl Conservation Society of British Columbia. A source population is bred ex situ, where they spend their entire lifespan. Their offspring are held overwinter ex situ, and are referred to as captive-born owls. Captive-born owls are released in situ in pairs as second year owls (SY) via soft-release pens. Captive-born owls are captive-released owls. Some captive-born owls are hard-released as singles. Captive-released owls mate in situ; their offspring are defined as wild-hatched owls. Both captive-released and wild-hatched owls then migrate. b) Breeding and release cycle of the Manitoba Burrowing Owl Recovery Program. Hatching year (HY) owls are taken from wild nests or facilities and held over winter ex situ. They are released in situ via soft-release pens as SY owls, thus defined as captive-released owls. Captive-released owls mate in situ; their offspring are defined as wild-hatched owls. Some wild-hatched owls migrate, whereas others are taken ex situ to be released the next year.



may experience lower reproduction (Tavecchia et al. 2009, Milot et al. 2012), thus we predicted that owls who have returned from migration to form pairs and breed would have higher clutch sizes and fledge more offspring than newly-released owls. Additionally, because owls are paired and released using the same technique in both provinces, we predicted that there would be no difference in reproduction between programs. For the BC program specifically, we hypothesized that the origin of owls (captive-released or wild-hatched [captive-released offspring]) would influence the number of returns.

Identifying suitable release sites is particularly important for the success of reintroduction or reinforcement programs, because poor habitat quality has been shown to negatively impact released animals (Cheyne 2006). Burrowing Owls are threatened by the loss of grassland habitat, inclement weather events, and vehicular collisions (Environment Canada 2012). Thus, these environmental factors should be taken into consideration when choosing suitable release sites for Burrowing Owls. Burrowing Owls select burrows in coarse, sandy soil rather than finer, clay soils; thus soil texture may be used as a proxy for habitat quality at release sites (MacCracken et al. 1985, Stevens et al. 2011). Therefore, we predicted that non-native vegetation structure, insufficient soil quality, and close proximity to roads would inhibit the success of Burrowing Owls in both provinces. High precipitation can flood burrows (Fisher et al. 2015); thus we predicted that years with high precipitation would result in lower success.

METHODS

Data collection

All data on MB Burrowing Owls were collected by MBORP from 2010 to 2020. All data on BC Burrowing Owls were collected by the Burrowing Owl Conservation Society of BC (BOCSBC) from 1992 to 2019. For both programs, SY owls are weighed and then paired for release. Soft-release pens are constructed at the release sites and allow the owls to acclimate to the environment, mate, and start to raise a brood before release. Pens are provided with artificial nest burrows, consisting of a weeping tile leading to a plastic bucket buried underground for nesting (Froese and Duncan 2021). Owls are paired on the basis of pedigree data to avoid inbreeding and maximize genetic diversity. Occasionally, single owls are hard-released when there is not a suitable mate available. A hard-release immediately releases the animal into the wild with no intermediate step (Batson et al. 2015). Supplemental food is provided until owlets are fledged. Both MB and BC band their owls for identification before release using aluminum and color bands. Both programs recorded clutch sizes and number of offspring fledged for as many pairs as possible; in BC these data were collected from 2015 onward.

In MB, mortalities after release are recorded by the recovery team. We define mortality as confirmed mortalities (wherein the mortality event was witnessed or evidence of a mortality event was recovered) as well as instances in which an owl disappeared from the release site and a mortality event is suspected by the recovery team, but without physical evidence of such event. In BC, returning owls were recorded and identified by the recovery team. Returning pairs included any owls that returned from migration to breed (wild owls, captive-released owls, and wild-hatched owls [captive-released offspring]), as well as pairs composed of a returning owl and a captive-released owl that was hard-released that year.

Landscape data were collected for each release site by using ArcGIS 10.7 (Environmental Systems Research Institute [ESRI] 2019). A 4.2 km² buffer was created around each release site, representing Burrowing Owls' maximum home range size (Haug and Oliphant 1990, Stevens et al. 2011). The government of Canada's Land Use 2010 map was used to collect land use types (Agriculture and Agri-Food Canada 2015) and the World Soils Harmonized World Soil Database - Texture (FAO/IIASA/ISRIC/ISSCAS/JRC 2012) map was used to collect soil textures at each site. The nearest road was visually discerned using an ESRI base layer; it was determined to be a paved or unpaved road by using the most recent satellite imagery available, and the distance from the release site to the road was measured by using the measurement function in ArcGIS. May to September precipitation (referred to as "precipitation" from here forward) was collected from ClimateWNA for each site per year (Wang et al. 2016).

Statistical analysis

All analyses were performed in R version 4.0.5 (R Core Team 2021). All models were evaluated for multicollinearity by using variance inflation factors (VIFs; package performance; Lüdecke et al. 2021). Predictors were considered to have multicollinearity at a threshold of VIF > 3. All models were run by using the package glmmTMB (Brooks et al. 2017). Model diagnostics were performed by using the dHARMA package (Hartig 2020). All numerical predictors were centered and scaled. Robust mark-recapture data were not collected for survival or returns; thus we used simple return rates to provide an index of first-year survival and philopatry but recognize that this index can be biased by annual variation in re-sighting efforts.

Manitoba: survival models

Generalized linear mixed effect models (GLMMs) were used to evaluate the relationship between survival and several variables. Survival was coded as 0 (did not survive the breeding season) or 1 (survived the breeding season) for each individual. Because of the binary distribution of the response variable, all models with a response variable coded as 1/0 used the binomial family function. The first model was created to assess captive-released owls, and included mass, sex, and release method (hard or soft) as fixed effects. Year and individual ID were included as random effects.

For wild-hatched owls, mass, fledged brood size, and proportion of the brood removed were included as fixed effects, whereas year was included as a random effect. Proportion of the brood removed represents the proportion of owlets removed from a brood for brood reduction and head-starting purposes.

For the environmental models, all owls were included (both captive-released and wild-hatched). Individuals were pooled by release site for each year to account for the variation in the number of owls released at each site. The response variable for this model was the number of owls that survived at each site in a given year. The number of owls released at each site was used as an offset term, so the number survived was proportional to the number released in the model. Each fixed effect (precipitation [MPS], soil texture, distance to nearest road, road type, percent cropland, and percent grassland) was run as a single predictor with the random effect of year because of the small sample size (n = 24).

Manitoba: reproduction models

GLMMs and generalized linear models (GLMs) were used to evaluate the relationship between reproductive parameters (clutch size and number of offspring fledged) and several variables. For clutch size, pair characteristics (female mass and re-nest) were evaluated in a single model by using a zero-inflated Poisson GLMM (n = 45 pairs). Year was included as a random effect. Release site characteristics (percent cropland, percent grassland, precipitation, soil texture, distance to nearest road, and road type) were evaluated as single predictors because of the small sample size (n = 20 total clutches per site per year). Each model contained a release site characteristic and an offset term for the number of pairs released, using a negative binomial GLM. Year was not included in this analysis because the model would not converge with year as a random effect.

For the number of offspring fledged, individual predictors (female mass and re-nest) were evaluated in a single model by using a negative binomial GLM (n = 45 pairs). A re-nest was when a pair tried, unsuccessfully, to nest and then made a second nesting attempt. Clutch size was included as a fixed effect. Release site characteristics were evaluated as predictors of offspring fledged by using negative binomial GLMs (n = 20 total number of offspring fledged per site per year). The total clutch size at each release site in a given year was included as an offset term in each model. Year was not included in this analysis because the model would not converge with year as a random effect.

British Columbia: return from migration models

GLMMs were used to evaluate the relationship between return from migration and several variables. Data were included from 2004 to 2007 and 2014 to 2018. These are years in which sampling success for identifying returning owls was high (> 40% of returning owls identified; Table A1.1). The first model evaluated captive-released individuals, who were all adults at release and time of measurements. Fixed effects included were mass, sex, and release method (hard- or soft-released). The second model evaluated wild-hatched individuals, which were all HY owls at the time of measurement. Fixed effects included were mass and fledged brood size. The last model included both captive-released and wild-hatched individuals in order to evaluate the effects of origin (either captive-released or wild-hatched) on returns. Year was included as a random effect for all models, except for captive-released, in which the model failed to converge with the inclusion of a random effect. The binary response variable was coded as 0 (not observed) or 1 (observed and returned) for all aforementioned models.

For the environmental model, both captive-released and wild-hatched owls were included. Individuals were pooled by release site for each year to account for the variation in the number of owls released at each site. The response variable for this model was the number of owls that returned at each site in a given year. Fixed effects were MPS, soil texture, distance to nearest road, road type, percent cropland, and percent grassland. The number of owls released at each site was used as an offset term, so the number returned was proportional to the number released in the model. Year was included as a random effect.

British Columbia: reproduction models

GLMMs and GLMs were used to evaluate the relationship between reproductive parameters (clutch size and number of offspring fledged) and several variables. Each predictor was run in a separate model to avoid overfitting because of small sample sizes. For clutch size, female mass was evaluated by using zero-inflated Poisson GLMMs with year as a random effect (n = 31 individuals). Release site characteristics (percent cropland, percent grassland, precipitation, soil texture, distance to nearest road, and road type) were evaluated as predictors of total clutch size by using negative binomial GLMMs (n = 30 total clutches per site per year). Year was included as a random effect. The number of pairs released at a site was used as an offset term, so the total clutch size at a site in a given year was proportional to the number of pairs released at a site in a given year.

For the number of offspring fledged, the sample size was too small to reliably evaluate the effects of female mass (n = 15 individuals) while taking into account variation that may be explained by other effects (clutch size and year). Release site characteristics (percent cropland, percent grassland, precipitation, soil texture, distance to nearest road, and road type) were evaluated as predictors of number of offspring fledged by using negative binomial GLMs. Pairs were pooled by their release site. Clutch size was included as a fixed effect. Because of the small sample size, random effects could not be included (n = 19 total number of offspring fledged per site per year).

Comparing reproduction between groups

Median clutch size and number of offspring fledged were compared between captive-released owls from each program (MBORP and BOCSBC) by using a Wilcox-signed rank test. Within BC, median clutch size and number of offspring fledged were compared between captive-released and returning owls using a Wilcox-signed rank test.

RESULTS

Sampling

Between 2010 and 2020, MBORP released 114 owls, 92 of which survived from release to initiate fall migration (81% survival). During this 10-year time period, 145 chicks were hatched; 67 were taken into human care for head-starting and 78 were released in the wild. Of the 78 wild-hatched owls released, eight wild-hatched owls perished pre-fledging and eight post-fledging mortalities were recorded (90% post-fledging survival).

From 1992 to 2018, BOCSBC released 1704 captive owls that produced 2543 wild-hatched owls. In total (captive-released and wild-hatched), 359 owls are known to have returned to BC breeding grounds after migration (8% return). From 2004 to 2007 and 2014 to 2018, 774 owls were released and 2076 were hatched; 212 returned from migration (10% return); however, only 130 of these were identified by their bands (60% identification) and included in the analysis.

Release site characteristics

There were seven release sites in MB. The sites were predominantly surrounded by cropland (an average of 54% cropland across all sites) and contained two soil textures (silt loam [less drainage] and sandy loam [more drainage]). The distance to nearest road ranged from 202 m to 853 m (Table A1.2). Between 2010 and 2019, precipitation ranged from 263 mm to 558 mm. There were 16 release sites in BC. The sites were dominated by grassland (an average of 73% grassland across all sites) and contained two soil textures (clay loam [less drainage] and loam [more drainage]). The distance to nearest road ranged from 16 m to 4948 m (Table A1.3). Between 2004–2007 and 2014–2018, precipitation ranged from 45 mm to 262 mm.

Manitoba

For captive-released owls, the release method had a weak effect on survival, with soft-released individuals experiencing higher survival than hard-released individuals (94.8% vs. 78.6% survival; ß = -0.986 ± 0.635, p = 0.120; Table 1). Models for wild-hatched owls and release site characteristics did not exert a strong effect on survival (Table A1.4). Pairs that re-nested fledged one fewer offspring on average than those that did not (ß = -0.517 ± 0.262, p = 0.048; Table A1.5). Models evaluating individual characteristics for clutch size did not yield strong results (Table A1.6). Release site characteristics did not influence clutch size or number of offspring fledged (Table A1.7).

Table 1. All relevant models pertaining to conservation success for Manitoba Burrowing Owl Recovery Program (MBORP) Burrowing Owls. The model indicates the response variable.

Model	Variable	Estimate	Std. error	p-value
Survival captive-released, n = 122 individuals	Mass	-0.2355	0.2539	0.354
	Sex	-0.3386	0.5202	0.515
	Release method	-0.9861	0.6350	0.120
Number of offspring fledged n = 45 breeding pairs	Female Mass	0.1120	0.1019	0.240
	Re-nest	-0.5044	0.2779	0.070
	Clutch size	0.2877	0.1599	0.072
	Year	0.0143	0.1018	0.889

British Columbia

For captive-released individuals, there was very strong evidence that body mass has an effect on survival. Individuals with a higher mass were more likely to return than those with a lower mass (ß = 0.901 ± 0.327, p = 0.006; Fig. 2, Table 2). Sex exerted a weak effect on return, with male owls returning more than female owls (7 males vs. 4 females, ß = 0.843 ± 0.686, p = 0.219). For wild-hatched individuals, there was moderate evidence that larger mass also resulted in more returns (ß = 0.223 ± 0.132, p = 0.092). There was very strong evidence that origin had a positive effect on return,

Fig. 2. a) Return from migration in relation to mass in captive-released Burrowing Owls in British Columbia ($p = 0.006$). Owls with a greater mass were more likely to return from migration. The blue line represents the regression line and the shaded gray area represents 95% confidence intervals. b) Mean return from migration compared between captive-released and wild-hatched Burrowing Owls from the British Columbia recovery program ($p < 0.001$). More wild-hatched owls returned than captive-released owls. The error bars represent 95% confidence intervals. c) The number of returning owls proportional to the number of owls released in relation to percent cropland at release sites in British Columbia ($p = 0.049$). Fewer owls returned from areas with more cropland. The blue line represents the regression line and the shaded gray area represents 95% confidence intervals.

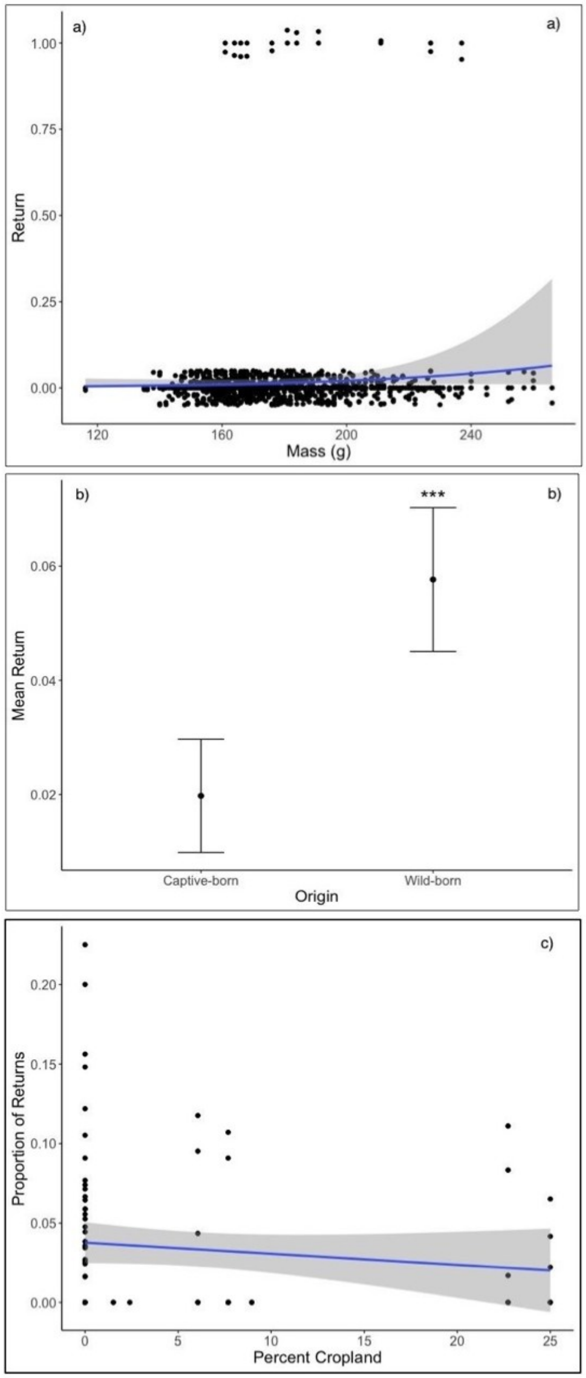


Table 2. All models pertaining to return for Burrowing Owl Conservation Society of BC (BOSCBC) Burrowing Owls. Bolded values represent p-values less than 0.05.

Model	Variable	Estimate	Std. error	p-value
Captive-released	Mass	**0.9006**	**0.3267**	**0.006****
n = 627 individuals	Sex	0.8429	0.6860	0.219
	Release method	-0.2618	0.6206	0.673
Wild-hatched	Mass	0.2216	0.1315	0.092
n = 1125 individuals	Brood size	-0.0829	0.1279	0.517
Origin (captive-released and wild-hatched) n = 2077 individuals	Origin	**1.0465**	**0.2893**	**< 0.001*****
Environmental release site	Percent cropland	**-0.2929**	**0.1492**	**0.049***
characteristics	Percent grassland	-0.2553	0.1877	0.174
n = 81 sites per year	MSP[a]	-0.1543	0.2184	0.480
	Soil texture	-0.2477	0.2805	0.377
	Road type	-0.0092	0.2150	0.965
	Distance to nearest road	0.0749	0.3159	0.813

[a] May to September precipitation.

with wild-hatched owls more likely to return than captive-released owls (ß = 1.047 ± 0.289, p < 0.001; Fig. 2). Percent surrounding cropland strongly affected the number of returns, with less cropland resulting in more returns (ß = -0.293 ± 0.149, p = 0.049; Fig. 2). See Table A1.8 for all model results. For reproduction, soil texture was the only release site characteristic to have a moderate influence on the number of offspring fledged (ß = -0.9831 ± 0.583, p = 0.091). Pairs at release sites with clay loam soil fledged more offspring than those at sites with loam soil (2.21 offspring/pair vs. 1.43 offspring/pair). Female mass and release characteristics did not exert a strong effect on clutch size (Table A1.9)

Comparing reproduction between groups

Captive-released owls in MB had a mean clutch size of 6.07 ± 0.43 eggs/pair and mean number of offspring fledged/pair of 2.67 ± 0.37. Captive released-owls in BC had a mean clutch size of 5.88 ± 0.40 eggs/pair and mean number of offspring fledged per pair of 2.02 ± 0.40. Returning owls in BC had a mean clutch size of 7.70 ± 0.31 eggs/pair and fledged 4.22 ± 0.40 offspring/pair (Table 3). Captive-released owls in MB fledged more young than captive-released owls in BC (p < 0.050) but there was no evidence of higher clutch sizes (p = 0.748). Related, captive-released owls in BC had higher instances of fledging zero young compared to captive-released owls in MB (50% vs. 33%, respectively). Returning owls in BC had larger clutch sizes (p < 0.001) and fledged more young (p < 0.001) than captive-released owls.

DISCUSSION

Manitoba

Survival of captive-released Burrowing Owls in MB from release to initiation of migration (approximately five months) was 81%. Mitchell et al. (2011) reported 70% survival of soft-released owls in BC, and Poulin et al. (2006) reported 81% survival for captive-released Burrowing Owls in SK. Wild owls were found to have 96% survival (Poulin et al. 2006). Thus, MBORP captive-released owls seem to have similar, or higher, survival rates than owls in other release programs in Canada; however, captive-released owls may have lower survival than wild owls in general. Post-fledging juvenile (wild-hatched) survival was 90% in MB, which is much higher than what was reported in BC (65%; Mitchell 2008) and for a population of SK Burrowing Owls (58%; Todd et al. 2003). Management strategies such as more frequent supplemental feeding or more intensive management in the MB program may be the cause of these higher survival rates over the breeding season.

We also found that Burrowing Owls from MBORP fledged significantly more offspring than owls from BOCSBC, despite there being no significant difference in clutch size between the programs. Owls in BC had higher instances of fledging zero young compared to MB, largely because of nest abandonments. Both recovery programs have observed this behavior wherein paired owls initiate a clutch but then abandon it after the soft release pen is opened or removed. MBORP staff will typically relocate and re-pair unsuccessful owls, increasing the number of successful pairs in their program. MBORP has also extended the length of time spent in soft-release pens in some years, decreasing the chances of abandoning a clutch (Mitchell et al. 2011). These appear to be good management strategies to increase reproduction, and are possible because of the small number of pairs (~10) that are monitored annually compared to the BC program (~50).

British Columbia

BC has seen increasing numbers of returning Burrowing Owls over the last five years. For both captive-released and wild-hatched owls, body mass influenced return from migration, such that heavier owls had a higher return rate than lighter owls. Migration incurs a great energetic cost (Bowlin et al. 2005, Weber 2009); thus it is not surprising that owls with a larger body mass are more successful at migrating (Kelsey and Bairlein 2019). Lower recruitment of smaller owls may also be indicative of survival on overwintering grounds. If owls in better condition are more likely to survive over winter, it is also more likely they will return to

Table 3. Comparison of clutch size (mean ± SE) and number of offspring fledged (mean ± SE) among populations of Burrowing Owls in British Columbia (BC) and Manitoba (MB).

Population	Clutch size (eggs/pair)	Offspring fledged (young/pair)
MBORP[a] *Captive-released owls*	6.07 ± 0.43	2.67 ± 0.37
BOBCS[b] *Captive-released owls*	5.88 ± 0.40	2.02 ± 0.40
BC *Returning owls*	7.70 ± 0.31	4.22 ± 0.40

[a] Manitoba Burrowing Owl Recovery Programs.
[b] Burrowing Owl Conservation Society of British Columbia.

Canadian breeding grounds. High overwintering mortality has been noted as a threat to Burrowing Owls (Environment Canada 2012, Wellicome et al. 2014). Releasing owls in the best possible body condition may facilitate overwintering success and supports the continued use of supplemental feeding to facilitate recruitment.

We also found that high percentages of cropland surrounding release sites negatively influenced return from migration. Historically, it was thought the conversion of grassland habitat to agriculture was a primary driver in the decline of Burrowing Owls in Canada, with 80% of grassland habitats converted to agricultural use by 1987 in the Prairie Provinces (WWFC 1987). However, the effect of vegetation types on Burrowing Owl persistence is highly contentious. Some studies have found that Burrowing Owls select nests in grasslands and avoid cropland (Clayton and Schmutz 1999, Poulin et al. 2005), whereas others have found that owls chose to nest closer to crop fields than expected by chance (Rich 1986, Belthoff and King 2002). In AB and SK, owls fledged more young in areas with more cropland, not less (Scobie et al. 2020). To the best of our knowledge, no studies have evaluated the effects of cropland on Burrowing Owl survival directly; however, we found that there was no apparent effect of vegetation type on survival of captive-released owls in MB. Grassland conversion has slowed in recent years, and thus there is little quantitative evidence of negative effects of cropland on Burrowing Owl fitness (Scobie et al. 2020). BC is not a part of the Great Plains ecosystem and has been understudied regarding environmental factors contributing to Burrowing Owl declines. However, grassland habitat is also being lost in BC, but perhaps different types than in other provinces (e.g., orchards and vineyards; Leupin 2004). When land is converted, the type of land use may significantly influence how Burrowing Owls are affected (e.g., differences in prey availability; Moulton et al. 2006). More research is needed to discern the relationship between cropland and Burrowing Owl productivity and survival in BC. Nonetheless, evidence from our study suggests that new release sites in BC should be chosen where there is minimal surrounding cropland. This recommendation may not be applicable to Burrowing Owl recovery programs in prairie ecosystems, as in MB there was no apparent effect of cropland on owl survival.

Origin was a significant and strong predictor of return from migration. Burrowing Owls hatched in the wild (wild-hatched) had a higher return rate than those held in captivity and then released (captive-released). This has been observed in previous work (Mitchell et al. 2011; L. Meads, A. Mitchell, and M. Mackintosh, *unpublished manuscript*), but this is the first study to validate origin as a statistically significant predictor of return. Migration is a complex phenomenon that involves the interaction between behavioral, environmental, and genetic components (Shuter et al. 2011, Couzin 2018). Thus, a number of factors could influence these results, including factors related to parental teaching of skills. It is possible that captive-released owls have lower survival than wild-hatched owls during migration because they did not learn adequate predator avoidance or foraging skills during their developmental period while in human care (Carrate and Tella 2016, Swaisgood et al. 2018). Burnside et al. (2017) found that captive-bred Asian houbaras (*Chlamydotis macqueenii*) initiated migration later and wintered closer to breeding grounds than wild conspecifics. Whereas many behaviors are likely to be innate in Burrowing Owls, similar to other migratory birds, other behaviors could be learned and practiced before migration and contribute to an individual's success (Shuter et al. 2011). Determining the causes behind captive-released owls' reduced rate of return success in general and compared to wild-hatched owls should be a priority for both recovery programs.

Within BC, we found that returning Burrowing Owls had significantly higher clutch sizes and fledged significantly more young than captive-released owls. There are two hypotheses that may explain these differences. The first is survivor bias; animals that might be in poorer condition and be less reproductively successful may not have survived migration (Harrison et al. 2011, Festa-Bianchet 2019). The remainder of animals that have migrated back to breed are more likely to have higher reproductive success. An explicit comparison of body condition between captive-released and returning owls would be needed to evaluate this hypothesis but unfortunately these data are not available. The second hypothesis is mate choice. All the subsets of owls included in the returning group (wild, captive-released, wild-hatched, and hard-released) had free mate choice. Captive-released owls are paired to maximize genetic diversity, but there is evidence that this strategy may not guarantee genetic or behavioral compatibility (Ballou et al. 2010, Asa et al. 2011). These incompatibilities can lead to poor reproductive success, an outcome counter to the goals of captive breeding programs (Asa et al. 2011, Ihle et al. 2015, Schulte-Hostedde and Mastromonaco 2015).

Data limitations

In MB, statistical power was reduced in analyses for investigating the effect of release site characteristics on both survival and reproduction by pooling Burrowing Owls by site and year to account for the unequal number of owls released per site. However, this method eliminated the possibility of one frequently-used site dictating trends in the data and thus resulted in the most representative analysis of the data. Future research in MB should focus on release site characteristics with a priori hypotheses that results in an experimental design that lends itself to more robust analyses. In BC, statistical power was also reduced in analyses investigating the effect of release site characteristics on reproduction via small sample sizes by using the same method described above. Soil texture had a strong but non-significant effect on reproduction in BC, and thus this factor may warrant further research. For analyses investigating returns in BC, not all returning owls were able to be identified by their bands, and thus some data were not captured in our analysis. It is unclear how this may have influenced results, but the discrepancy was partially accounted for by limiting data included in the analysis to years with better sampling success, which still provided a robust sample size. Although some analyses were limited by using observational data, we were still able to identify significant trends influencing the success of population reinforcement efforts of the Burrowing Owl.

Conclusions

Using data from post-release monitoring, we evaluated conservation success in two Burrowing Owl population reinforcement programs using three metrics: survival, return from migration, and reproduction. MB captive-released owls are surviving the breeding season well, and saw higher fledging success than their counterparts in BC. However, individual or release site characteristics did not influence survival or reproduction in MB. In BC, we were able to perform a novel analysis on predictors of return from migration because of the relatively high number of returns recorded by the recovery team. Both individual and release site characteristics were found to influence return from migration. BC and MB use different conservation strategies that may influence outcomes; however, each program comes with vastly different challenges because of their geographic differences. Conservation of species using population reinforcement may be different for each species, and even the same species in different habitats. A critical element of success in these programs is the collection of data that can be used to gain insights on how the program can improve over time. Our study has identified opportunities to implement adaptive management (such as releasing owls at sites with less cropland in BC) informed by data garnered by post-release monitoring. Evaluating and monitoring population reinforcement efforts are critical.

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APPENDIX

Table A1.1: Number of returns of Burrowing Owls seen in each year in British Columbia (BC) compared with positive identifications. Return refers to returning to release sites within BC after migration. Years were designated to have a "high" or "low" sampling success, based off on percent identified (>40% was considered "high").

Release Year	Number of Owls Released	Return Year	Seen	Positive Identifications	Percent Identified	Sampling Success
2001	71	2002	7	0	0.0	Low
2002	46	2003	8	1	12.5	Low
2003	29	2004	9	2	22.2	Low
2004	53	2005	10	5	50.0	High
2005	81	2006	15	13	86.7	High
2006	91	2007	18	16	88.9	High
2007	120	2008	16	7	43.8	High
2008	116	2009	15	0	0.0	Low
2009	103	2010	23	2	8.7	Low
2010	99	2011	19	2	10.5	Low
2011	89	2012	21	0	0.0	Low
2012	81	2013	15	0	0.0	Low
2013	84	2014	17	0	0.0	Low
2014	100	2015	50	25	50.0	High
2015	67	2016	40	28	70.0	High
2016	53	2017	27	19	70.4	High
2017	96	2018	30	12	40.0	High
2018	113	2019	6	5	83.6	High

Table A1.2: Environmental characteristics for 16 release sites for captive-released Burrowing Owls in British Columbia.

Release Site	Percent Cropland	Percent Grassland	Soil Texture	Distance to Nearest Road (m)	Road Type
Beresford	0	72.93	Clay loam	625	Unpaved
Badger Flats	0	97.6	Loam	3546	Paved
Chutters	25.0	69.53	Clay loam	16	Unpaved
Deleeuws	7.69	50.77	Loam	156	Unpaved
East Chopaka	0	94.35	Loam	4948	Paved
Elkink	0	76.12	Loam	1321	Paved
Guichons	0	74.8	Clay loam	726	Paved
Haughtons	6.06	42.42	Clay loam	222	Paved
Hamilton	0	70.77	Clay loam	2811	Paved
Lac Du Bois	0	96.95	Loam	289	Unpaved
Napier Lake	8.96	56.72	Clay loam	355	Paved
Penticton Indian Band	1.52	62.88	Loam	1122	Unpaved
Quilchena	22.73	71.97	Clay loam	198	Paved
Sage and Sparrow	0	98.4	Loam	4465	Paved
White Lake	2.4	43.2	Loam	222	Paved
Upper Nicola Band	0	98.44	Clay loam	1519	Paved

Table A1.3: Environmental characteristics for seven release sites for captive-released Burrowing Owls in Manitoba.

Site	Percent Cropland	Percent Grassland	Soil Texture	Distance to Nearest Road (m)	Road Type
164	58.14	24.81	Silt loam	318	Unpaved
Broomhill	23.62	65.35	Silt loam	282	Paved
Coulter	32.03	60.94	Sandy loam	852	Unpaved
Deloraine	92.68	5.69	Sandy loam	713	Unpaved
Medora	48.85	21.37	Sandy loam	202	Paved
Pierson	45.16	39.52	Sandy loam	259	Unpaved
Treesbank	84.21	9.02	Silt loam	639	Unpaved

Table A1.4: All weak models pertaining to survival for Manitoba Burrowing Owl Recovery Program (MBORP) Burrowing Owls. Environmental release site characteristics were run in separate models due to sample size.

Model	Variable	Estimate	Std. Error	p-value
Wild-Hatched n = 69 individuals	Mass	0.1418	0.5112	0.782
	Brood Size	0.4557	0.4855	0.348
	Proportion of Brood Removed	-0.2853	0.5036	0.571
Environmental Release Site Characteristics *(Single Predictors)* n = 24 sites per year	Distance to Nearest Road	-0.0846	0.0904	0.349
	Percent Grassland	-0.0479	0.0609	0.431
	Percent Cropland	0.0511	0.0651	0.432
	Precipitation	0.0354	0.0555	0.524
	Soil Texture	0.0809	0.1309	0.537
	Road Type	-0.0503	0.1131	0.657

Table A1.5: Relevant models pertaining to conservation success for Manitoba Burrowing Owl Recovery Program (MBORP) Burrowing Owls. The model indicates the response variable.

Model	Variable	Estimate	Std. Error	p-value
Survival: *Captive-Released* n = 122 individuals	Mass	-0.2355	0.2539	0.354
	Sex	-0.3386	0.5202	0.515
	Release Method	-0.9861	0.6350	0.120
Number of Offspring Fledged n = 45 breeding pairs	Female Mass	0.1200	0.0918	0.193
	Re-nest	**-0.5234**	**0.2612**	**0.045 ***
	Clutch Size	0.2811	0.1544	0.067

Table A1.6: All weak models pertaining to clutch size for Manitoba Burrowing Owl Recovery Program (MBORP) Burrowing Owls. Environmental release site characteristics were run in separate models due to sample size.

Model	Variable	Estimate	Std. Error	p-value
Breeding Pair Characteristics n = 45 breeding pairs	Female Mass	0.0842	0.0648	0.194
	Re-nest	0.1208	0.1500	0.421
Environmental Release Site Characteristics *(Single Predictors)* n = 20 sites per year	Distance to Nearest Road	0.1180	0.0882	0.181
	Percent Grassland	-0.0738	0.0817	0.366
	Percent Cropland	0.0881	0.0825	0.285
	Precipitation	0.0478	0.0846	0.572
	Soil Texture	-0.1417	0.1753	0.419
	Road Type	-0.0459	0.1677	0.785

Table A1.7: Environmental release site characteristics models pertaining to number of offspring fledged for breeding pairs of Burrowing Owls in the Manitoba Burrowing Owl Recovery Program (MBORP). Environmental release site characteristics were run in separate models due to sample size.

Model	Variable	Estimate	Std. Error	p-value
Environmental Release Site Characteristics *(Single Predictors)* n = 20 sites per year	Distance to Nearest Road	0.0444	0.1418	0.754
	Percent Grassland	-0.0779	0.1341	0.561
	Percent Cropland	0.0852	0.1333	0.523
	Precipitation	-0.0898	0.1248	0.472
	Soil Texture	-0.0447	0.2924	0.879
	Road Type	-0.3188	0.0972	0.230

Table A1.8: All models pertaining to return for Burrowing Owl Conservation Society of BC (BOSCBC) Burrowing Owls. Bolded values represent p-values less than 0.05.

Model	Variable	Estimate	Std. Error	p-value
Captive-Released n = 627 individuals	**Mass**	**0.9006**	**0.3267**	**0.006 ****
	Sex	0.8429	0.6860	0.219
	Release Method	-0.2618	0.6206	0.673
Wild-Hatched n = 1125 individuals	Mass	0.2216	0.1315	0.092
	Brood Size	-0.0829	0.1279	0.517
Origin *(Captive-Released & Wild-Hatched)* n = 2077 individuals	**Origin**	**1.0465**	**0.2893**	**< 0.001 *****
Environmental Release Site Characteristics n = 81 sites per year	**Percent Cropland**	**-0.2929**	**0.1492**	**0.049 ***
	Percent Grassland	-0.2553	0.1877	0.174
	Precipitation	-0.1543	0.2184	0.480
	Soil Texture	-0.2477	0.2805	0.377
	Road Type	-0.0092	0.2150	0.965
	Distance to Nearest Road	0.0749	0.3159	0.813

Table A1.9: All weak models pertaining to clutch size for Burrowing Owl Conservation Society of BC (BOCSBC) Burrowing Owls. Variables were run in separate models due to sample size.

Model	Variable	Estimate	Std. Error	p-value
Breeding Pair Characteristics n = 31 individuals	Female Mass	0.0074	0.0044	0.092
Environmental Release Site Characteristics *(Single Predictors)* n = 30 sites per year	Distance to Nearest Road	0.3528	0.1807	0.051
	Percent Grassland	0.1532	0.0974	0.116
	Percent Cropland	0.1255	0.0942	0.183
	MSP[a]	-0.0588	0.0816	0.471
	Soil Texture	-0.1321	0.2125	0.534
	Road Type	0.0124	0.0904	0.891