

Research article

Learning and hunting success of burrowing owls (*Athene cunicularia*) during pre-release live-prey training in the Manitoba burrowing owl recovery programme

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Abstract

Reintroduction biology is a new and expanding discipline for which experimental study is critical to progress. Training methods were evaluated for live-prey capture as part of a breeding and reintroduction project for the burrowing owl (*Athene cunicularia*), an iconic prairie species endangered throughout Canada. Handling of owls prior to training sessions had a negative effect on the proportion of mice depredated. Owl experience exerted a measurable effect on depredation, suggesting that there is a learned component to hunting behaviour; however, this effect was not statistically significant. Mouse colour and owl sex had no effect on depredation. Overall, the proportion of mice depredated was low, probably because the training session environment presented additional challenges to the owls that would not occur in nature. In response to these findings, changes were made to training protocols the following year and, anecdotally, these changes resulted in a marked increase in the proportion of mice depredated.

Introduction

Reintroduction biology seeks to develop and apply best practices for the breeding and reintroduction of species into areas of their historical range, in an effort to establish self-sustaining populations and contribute to the restoration of natural biodiversity (Seddon et al. 2007). However, a small, fragmented, and largely retrospective literature has been an obstacle to progress in the field and there is a need for experimental studies to improve outcomes for reintroduced animals (Seddon et al. 2007).

The few studies on the reintroduction of predatory animals support live-prey training prior to release, but these studies have focused on mammal reintroductions (Miller et al. 1998;

Biggins et al. 1999; Mathews et al. 2005; Houser et al. 2011). There is almost nothing in the literature about the effect of live-prey training on predatory birds; to our knowledge, only one paper considers the question of effect and none evaluate potential strategies and procedures for such training (Fajardo 2000). We employed two live-prey training procedures for captive over-wintered burrowing owls (*Athene cunicularia*) to evaluate the effects of handling stress on the owls' ability to depredate a live domesticated mouse (*Mus musculus*). We also retrospectively analysed three years of training data to evaluate if burrowing owls learned from the training sessions, if they demonstrated a preference for mouse colour, and if hunting success differed between owl sexes.

The burrowing owl is Endangered throughout Canada, but was once a familiar summer resident of the Canadian prairies

(COSEWIC 2006). Its native range extends from Canada and the western United States to Florida, Mexico, and Central and South America. Canadian burrowing owls are migratory, overwintering in California, Arizona, New Mexico, Texas, Louisiana and Florida (Sheffield 1997). In Canada, the population has shown steep and steady declines in all western provinces and especially in the northwestern and northeastern extent of their range in British Columbia and Manitoba (COSEWIC 2006; Environment Canada 2012). Several factors are thought to be responsible for the declines, including critical loss and fragmentation of grassland habitat, vehicle collisions, increased predation, decreased prey, and the loss of burrowing mammals, and therefore burrows, in the owls' home range (Sheffield 1992; de Smet 1997; Dechant et al. 2002; COSEWIC 2006; Environment Canada 2012). In 2004, widespread surveys detected no burrowing owls in Manitoba, although local landowners continue to report occasional sightings of the rare bird; since 2010, five to 10 burrowing owls have been reported each year (Environment Canada 2012).

Environment Canada's Recovery Strategy for the burrowing owl outlines a goal of re-establishing the species population in Manitoba to the 1993 historical distribution of 23 breeding pairs (Environment Canada 2012). Since 2010, the Manitoba Burrowing Owl Recovery Programme (MBORP) has managed a breeding and reintroduction project, which aims to reverse the ongoing decline of burrowing owls in Manitoba through reintroduction, research, education and landowner stewardship. In addition to Manitoba, burrowing owl reintroduction programmes are active in British Columbia and Alberta, and historically in several American states. This study evaluates live-prey training procedures for burrowing owls in order to make evidence-based recommendations for conservation efforts.

Although burrowing owls breed together in loose colonies, they are solitary hunters. Burrowing owls hunt a wide range of invertebrates (grasshoppers, crickets, beetles, moths, butterflies, dragonflies and caterpillars), amphibians (frogs, toads and salamanders), reptiles (snakes, lizards and turtles), mammals (mice, voles, shrews, bats, ground squirrels and young rabbits), and smaller birds (songbirds and ducklings) (Froese 2016). Dissected pellets collected around Manitoba burrowing owl nests showed a high biomass of vertebrate species (83–99%) (Froese 2016). Young owls begin to play and hunt invertebrates near their natal burrow between 2 and 6 weeks of age, and fledge at 35–42 days (Environment Canada 2012; Froese 2016). At study sites in Manitoba, migration occurs in late fall (October), when young of the year (YOY) are 8 to 9 weeks old (Froese 2016).

Burrowing owls have a short lifespan (1–9 years) and a high reproductive rate with clutch sizes ranging from 7–13 eggs (Martin 1973; Environment Canada 2012). As expected in a species with this life history, post-fledging pre-migratory survival has a strong influence on population size, and starvation is an important mortality factor in fledging and dispersing burrowing owls (Dechant et al. 2002; Todd et al. 2003). Starvation is also an important mortality factor in rehabilitated owls released from captive environments (Fajardo 2000).

Other important contributors to fledgling and dispersing burrowing owl mortality include depredation and anthropogenic influences (Todd et al. 2003). Post-fledging mortality tends to be high. Between 1998 and 2000, a burrowing owl population in Saskatchewan experienced a mortality rate of 45% for fledgling birds in the 3-month post-fledging period. Mortality over the same period in 1997 however was 0%, which was likely influenced by an unusually high abundance of voles (*Microtus spp.*) that year (Todd et al. 2003).

The MBORP breeding and reintroduction programme focuses on reducing first-year mortality and increasing recruitment in southwestern Manitoba by overwintering some owls in a

captive environment and releasing them the following spring. Overwintering occurs at the Assiniboine Park Zoo (APZ) in Winnipeg, Manitoba, as part of a collaborative effort. Owls are paired in soft-release enclosures in early May when the owls reach sexual maturity at around 11 months of age (Froese 2016).

Materials and methods

Animal husbandry

All methodological procedures were approved by the APZ's Research Ethics Review Committee, which follows the guidelines of the Canadian Council on Animal Care (CCAC 2003).

The MBORP founding population consisted of four wild young from two nests in southwestern Manitoba in 2010. Due to the high mortality observed for burrowing owls during fledging and first migration, a YOY head-start and breeding programme was developed (De Smet 1997; Froese 2016). From July to October, fledgling burrowing owls were transferred from field sites in southwestern Manitoba to an overwintering facility at APZ in Winnipeg. In May, the overwintered owls were paired by sex and soft-released for breeding at MBORP's field sites in southwest Manitoba. These field sites represent natural burrowing owl habitat; however, the environment provided for breeding is artificial, including predator-proof fencing around the burrows and supplemental feeding. From July to October, fledgling owls from this breeding programme were transferred to the overwintering facility at APZ. In addition to fledgling owls, adult owls from the breeding programme were selected for overwintering if they failed to migrate, if they failed to raise a successful nest that summer, or if they lost their mate due to a mortality event. Burrowing owls that raised successful nests and retained their mates were presumed more likely to demonstrate site fidelity and return the following spring than owls that did not (De Smet 1997).

From 2014–2016, owls were individually weighed and transferred to a specific enclosure for the live-prey training session. In 2017, procedures were revised to reduce presumed handling stress on the owls. A cross-over trial was initiated in 2017 to determine if the updated procedures resulted in greater hunting success in the sessions. A cross-over trial is a longitudinal study in which the subjects receive a sequence of different exposures.

Overwintered owls were generally grouped according to sex and clutch. The selection criteria for housing owls in groups evolved over time, and by 2016 the following procedure was established: same-sex siblings were housed together, and if a parent was overwintered, it was housed together with its same-sex offspring. Adult male owls without same-sex offspring were housed alone. Adult female owls without same-sex offspring were housed in adult female groups or alone.

Housing consisted of indoor wire mesh pens measuring 1.85–3.02 m long, 1.08–1.22 m wide, and 2.49 m high. These pens contained a simple arrangement of perching branches and artificial burrows or tunnels (6" weeping tile cut into 0.9–1.2 m sections) and plastic hides (19" 5 l buckets with a 6" diameter hole cut out of the side). Male and female owls were housed on opposite sides of the building with a visual barrier between them, and daylight hours were controlled to ensure owls did not prematurely lay eggs prior to transfer to the reintroduction sites. Owls not in a training session were offered one or two previously frozen thawed mice daily, throughout their time in this captive setting.

Live mice were housed and cared for according to CCAC guidelines (CCAC 2003). Updated animal care protocols were applied to the mice in 2017. Mice were housed in social groups and provided with suitable enrichment items. They were provided with deep bedding (wood shavings), shelter (cardboard), had access to food and water at all times, and were checked by animal care staff every 24 hours.

Table 1. Summary of burrowing owls that participated in live-prey training in 2014–2016, 2017 and 2018.

2014–2016 owls			
Summers hunting	M owls	F owls	Total (n)
0	8	5	13
1	4	3	7
2	2	3	5
3	0	5	5
4	0	2	2
Total owls (n)	14	18	32
2017 owls			
	M owls	F owls	Total (n)
Group 1	4	3	7
Group 2	4	4	8
Total owls	8	7	15
2018 owls			
Summers hunting	M owls	F owls	Total (n)
0	4	1	5
1	4	1	5
>1	2	2	4
Total owls (n)	10	4	14

Live crickets were fed supplemental to the owls' diet in 2014–2016 and 2018. To avoid possible interference with the cross-over trial, crickets were not fed in 2017.

Training protocol

Live-prey training sessions were conducted in March, April and May of 2014–2016. A group of one to three owls was removed from its enclosure and each owl was individually weighed in a lightweight cloth bag and placed in a training enclosure. If the housed group was larger than three owls (i.e., 4), then two owls were selected to participate in the training session, and the remaining two owls participated in the next session.

A training session lasted 3 days and occurred in a separate training enclosure in the same building where the owls were overwintered. The training enclosures were similar to the overwinter enclosures in materials, dimensions and furnishings. A clear colourless plastic container (60 cm long, 40 cm wide, and 35 cm high) was placed on the floor of the training enclosure and live mice were placed in the container. Mice could not escape from the container. One mouse was placed in the container for each owl in the enclosure. During a training session, no food was offered to the owls other than the live mice.

A zookeeper monitored the owls and mice every 24 hours. If a mouse was depredated, it was replaced with a live mouse. At the end of the training session, all owls were weighed again and returned to their home enclosures. Owls were weighed before and after each training session to ensure that no individual owl lost an unacceptable amount of body condition (greater than 20% body weight) as a result of the session.

The following data were recorded daily: owl identification number, owl sex, the number and colour of mice placed in the container, and the number and colour of mice depredated. Mouse colours were categorised as: white, brown, grey, brownish grey, black, buff, brown/white spotted, black/white spotted, grey/white spotted, and buff/white spotted. Owl weights were recorded prior to each training session (on Day 0) and at the end of each training session (on Day 3).

In 2017, the training protocol was modified to reduce suspected handling stress on the owls. A cross-over trial was performed to compare the new training protocol to the methods used in 2014–2016. A RECONYX RM45 RapidFire camera (USA) was placed outside the owl enclosures during training sessions to monitor hunting behavior. The camera recorded activity 24 hours per day.

In 2017, burrowing owls were selected for overwintering according to the same criteria as in 2014–2016. The owls (n=15) were divided randomly into four groups: Group 1 males (n=4), Group 1 females (n=3), Group 2 males (n=4), and Group 2 females (n=4) (Table 1). Owls were housed together in enclosures containing between one and three owls, and according to the same criteria as in 2014–2016. Cloth sheets between enclosures acted as a visual barrier between neighbors. As in 2014–2016, owls housed together were trained together. Space constraints prevented individual housing of owls.

In the updated training protocol (Treatment A of the cross-over study), owls were trained in their home enclosure instead of moving them to a training enclosure. Owls were weighed 72 hours (Day -3) prior to the training session. This schedule was designed to allow owls to recover from presumed handling stress prior to their training session. On Day 0, training began when live mice were placed in the clear plastic training container within the enclosure. The owls were re-weighed at the end of the training session (Day 3). Data collection and all other procedures were the same as in 2014–2016.

Treatment B of the cross-over study applied the methods used in 2014–2016. Owls were weighed in a lightweight cloth bag on Day 0 of the training session and moved to a new enclosure for training. The clear plastic container holding live mice was placed in the enclosure. The owls were re-weighed at the end of the training session (Day 3). A period of 72 hours was observed between the two consecutive treatment trials (from A to B or from B to A) where all owls received only dead mice.

No fewer than two mice were placed in a training container. Thus, if a single owl was trained, two mice were present and when more than one owl was trained in the session, the number of mice equalled the number of owls present. Mice in the training container were provided with wood shavings as bedding (depth=3 cm) and a cardboard shelter (16 cm long, 10 cm wide, 2 cm high). Food and water were available at all times. A zookeeper checked mice every 24 hours. The maximum number of days a mouse was housed inside the prey container was three. If a mouse was not depredated in 3 days, it was returned to its original holding enclosure for at least 24 hours.

In 2018, the live-prey training protocol was updated to reflect the findings of the 2017 data analysis. Owls (n=14) remained in their original enclosures and were not moved, handled, or weighed throughout the 4-week live-prey training period. During this period, owls had access to at least two (1 mouse per owl, or 2 mice if there was only 1 owl in the enclosure) live mice each day. If an owl did not depredate a live mouse within 2 days, a previously frozen thawed dead mouse was offered on the third day. Mice were placed in a live-prey container, which remained in each of the owls' home cages. In response to the 2017 camera trap images, new live-prey containers were employed in 2018. These containers were made from tan-brown opaque plastic instead of clear colourless, and were larger (105 cm long, 48 cm wide, and 43

cm high) than those used in 2014–2016 (60 cm long, 40 cm wide, and 35 cm high). Owl and mouse husbandry and welfare practices were otherwise the same as in 2017.

Statistical analysis

Statistical analysis was performed with the statistical software R (R Core Team 2017) and the package runjags (Denwood 2016). The data contained a large number of 0s (instances where no mouse was depredated) and as a result, standard maximum likelihood statistical methods were not possible. Consequently, Bayesian models were used to analyse the data.

The cross-over trial was analysed using a Bayesian logistic model to estimate the effects of treatment (A=2017 protocol, or B=2014–2016 protocol), sequence of treatments (A then B vs. B then A), time period (whether trial took place first or second for that owl group, regardless of treatment), owl group (a random effect to account for each owl group experiencing multiple trials), and day of trial (a random effect to account for data being collected on multiple days for each owl group and trial combination) on the binary response variable of mouse eaten (in no trial was >1 mouse eaten). Vague priors were used for all parameters and three chains run. Chains showed good mixing and a Gelman-Rubin statistic of 1.00 for all parameters indicated convergence was reached.

For the retrospective analysis of data from 2014–2016, a logistic Bayesian model was again used to consider the effect of experience (number of summers hunting) and sex on hunting success (probability of catching a mouse), while incorporating repeated measures terms for days within sessions and multiple sessions per owl group. Simulated data generated from the final model fit were compared to the observed data to confirm model fit was appropriate and convergence confirmed using the Gelman-Ruben statistic. For those trials in which a mouse was taken, a second similar Bayesian analysis was run that considered the effect of mouse colour on probability of depredation. Change in owl mass was analysed using a standard linear model with starting mass as a covariate and experience, coded as none (YOY) or some experience (owls ≥ 2 years old), as a predictive factor.

Results

Cross-over study (2017)

There was a significant effect of treatment on owl hunting success. Owls that were not handled for 72 hours prior to their training session (Treatment A) were more likely to depredate live mice than owls that were weighed and moved to a new enclosure on Day 0 of their training session (Treatment B) ($P<0.001$; Figure 1).

A significant sequence effect was also present. While Group 2 owls ate no mice in Treatment B, Group 1 owls did eat some mice in Treatment B. Group 2 owls did eat mice during Treatment A, but they did not eat as many mice as the Group 1 owls. In short, Group 2 owls experienced handling and transport to a new enclosure on Day 0 of their first training session, and these owls depredated fewer mice than Group 1 owls across both treatment sessions (Figure 1).

Day within the training session had an effect (Bayesian, $P<0.001$). Owls in Treatment A (2017 protocol) of the cross-over study were most likely to depredate a mouse on Day 2 of the training session, and least likely on Day 1 (Figure 2). There was no significant period effect during the cross-over study (Bayesian, $0.1<P<0.2$).

During the course of the 2017 cross-over study, it was discovered that one of the male Group 2 owls was blind in one eye. To ensure this did not affect results by diminishing the Group 2's overall performance, the analysis was re-run with this owl removed. This marginally increased the mean for CO Group 2 in period 2 and reduced the significance of the sequence effect in

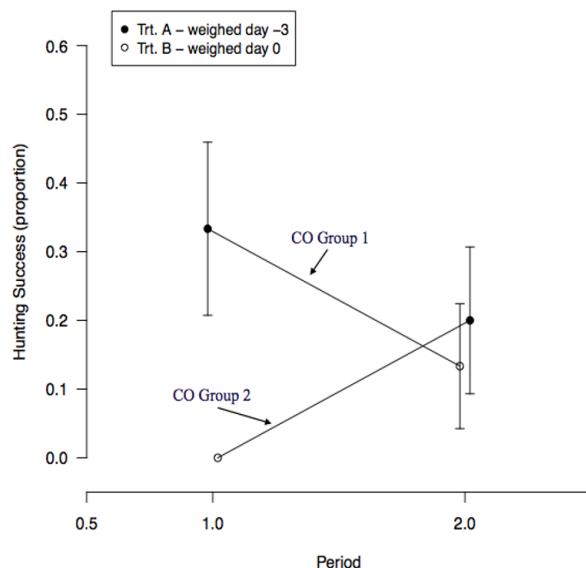


Figure 1. Hunting success as measured by proportion of mice depredated over the course of two training sessions. Owls not handled for 72 hours prior to their training session (Treatment A) depredated more live mice than owls that were weighed and moved to a new enclosure on Day 0 of their training session (Treatment B) (Bayesian, $P<0.01$).

the study, but did not eliminate the significance or change the overall conclusions.

The 2017 camera images revealed many instances of owls pacing around the clear plastic containers and looking in at the mice, and few instances of owls pouncing or performing other behaviours inside the mouse containers.

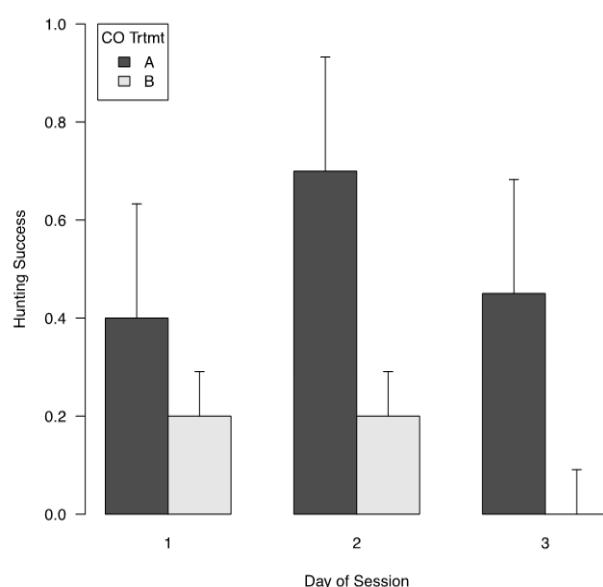


Figure 2. Significant day effect for hunting success in 2017 cross-over study (based on Bayesian model analysis for effect of day within session, $P<0.001$).

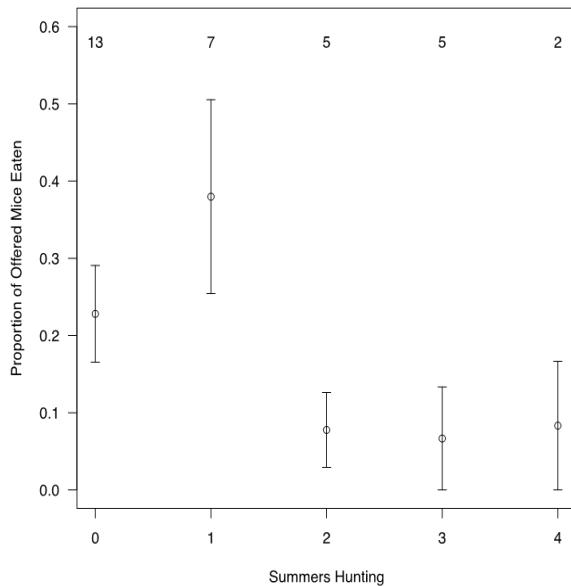


Figure 3. Mean proportion of mice offered and depredated by owl groups for each level of experience. Numbers at top of plot area indicate sample size for each experience level. Thus, while clearly not statistically significant, there is some suggestion that owls with a full summer of natural hunting experience (2 years old) have improved hunting success. Greater sample sizes will be needed to adequately test this hypothesis.

Retrospective study (2014–2016)

Retrospective analysis of data from 2014–2016 assessed whether owls were more likely to depredate mice as they gained more experience from training. Owls appeared to be least likely to depredate a mouse during the first session of the season, and most likely to depredate a mouse during the fourth session. However, high variance and low sample size meant this effect was not statistically significant (Table 2). Similarly, some indication for training effect was seen in 2017, because Group 1 was more effective in Treatment B than Group 2 (Figure 1).

Owls with natural hunting experience (2 years old, with one full summer hunting in wild) may perform better in training sessions than owls with minimal natural hunting experience (YOY; Figure 3). However, the effect was not statistically significant in the Bayesian analysis and thus further data are needed to adequately test this apparent trend. Similarly, there was no significant difference in weight change during the training sessions for owls with hunting experience (≥ 2 years old) compared to YOY, although variance in weight change notably decreased with increasing experience.

Table 2. Data from 2014–2016 showing the mean proportion of mice depredated on Sessions 1, 2 and 3 of the overwintering period, and the associated standard deviations. Variance in the data was sufficiently high that session sequence (1–4) did not exert a statistically significant training effect (Bayesian, $P>0.4$).

Session no.	Mean proportion of mice eaten	Mice eaten	Mice offered
1	0.20±0.38	22	108
2	0.25±0.38	26	111
3	0.33±0.38	26	78

Table 3. Data from 2014–2016 showing the mean proportion of mice depredated on days one to three of each training session, and the associated standard deviation. Variance in the data was sufficiently high that day of session (1–3) did not exert a statistically significant effect (Bayesian, $P>0.2$).

Day of session	Mean proportion of mice eaten	Mice eaten	Mice offered
1	0.10±0.23	10	101
2	0.29±0.41	30	101
3	0.36±0.43	34	95

The proportion of mice depredated in 2014–2016 was greatest on Day 3, and smallest on Day 1, but variance was high and thus this effect was not statistically significant (Table 3).

Owls did not appear to show any preference for mouse colour. There was also no evidence for sex bias during live-prey training sessions; mouse depredation was equally likely by female and male owls (Bayesian, $P>0.5$).

Response (2018)

In 2018, the live-prey training protocol was updated to reflect the findings of the 2017 data analysis. Moving and handling of owls was eliminated during the live-prey training period. Larger tan-brown opaque plastic live-prey containers were used in response to the 2017 camera-trap observations of owls pacing and peering in at the mice through the clear plastic. These changes appear to have resulted in a marked increase in the proportion of mice depredated (Table 4). Differences between conditions in 2014–2016 vs. 2018 preclude statistical comparison but anecdotally, mean proportion of mice depredated has increased using the new protocol.

Discussion

Although overall depredation rates were low, owl handling, treatment sequence, day of session, and owl experience all exerted measurable effects on depredation rate. Mouse colour and owl sex had no effect.

Owl handling had a negative effect on the proportion of mice depredated by owls in the 2017 training sessions. Owls that were not handled for 72 hours prior to their session were more likely to depredate live mice than owls that were weighed and moved to a new enclosure on Day 0 (Figure 1). When owls were caught

Table 4. Data from 2014–2016 and 2018 showing the mean proportion of mice depredated over all training sessions, and the associated standard deviations.

Year	Mean proportion of mice eaten	Mice eaten	Mice offered
2014–2016	0.25±0.36	74	297
2018	0.78±0.49	131	168

and handled, they responded with alarm chatter vocalisations, mydriasis (dilated pupils), tachypnea (elevated respiratory rate), open-mouth breathing, ‘fluffing up’, and episodes of ‘playing dead’. These observations are consistent with a behavioural and physiological stress response. Although similar in design, the new environment of the separate training enclosure may have exerted an effect on the owls in addition to the handling.

Sequence of treatment also had an effect. Group 2 owls experienced handling and transport to a new enclosure on Day 0 of their first training session, and these owls depredated fewer mice than Group 1 across both treatments (Figure 1). The poor performance of Group 2 owls in Session 2 (Treatment A) may have been due to residual stress from Session 1 (Treatment B). Group 1 owls may have performed better than Group 2 owls because, despite recent handling and a new enclosure, the training (live mice, plastic container) was at least familiar to them. A similar effect was seen in the 2014–2016 data, in that owls tended to depredate more mice in subsequent training sessions throughout the season. Further study is necessary to establish whether a true effect of artificial (training) experience on hunting success exists for burrowing owls in captivity, although it seems likely that it does.

In both the 2014–2016 and the 2017 data sets, owls were less likely to depredate a mouse on Day 1 of the training session than on Day 3. In 2014–2016, handling stress prior to each training session likely affected the owls’ ability to hunt, with the greatest effect observed on the day of handling. Increasing hunger may also have increased the owls’ interest in hunting as the session continued. In the 2017 cross-over study, while only half of the owls were handled on Day 0 of each training session, the alarm chatter of handled owls may have negatively impacted the other owls and reduced their hunting activity on Day 0.

Retrospective analysis of data from 2014–2016 assessed whether the owls were more likely to depredate mice as they gained more experience in the training sessions. With subsequent training sessions, an increased probability of mouse depredation was evident, but it was not statistically significant (Table 3). As demonstrated by the 2017 cross-over trial, handling may have contributed to low overall depredation rates in 2014–2016.

However, it may be that the clear plastic mouse containers were the biggest obstacle to the owls’ hunting success across all of the sessions. Camera-trap images showed many instances of owls pacing around the clear plastic containers and looking in at the mice, and few instances of owls pouncing or performing other behaviours inside the mouse containers. Prey training sessions should be better designed to mimic natural conditions. Additionally, a better parameter for measuring hunting success and learning behaviour could be time-to-event, rather than mouse depredated versus not.

In response to the 2017 data analysis, the live-prey training protocol was updated in 2018 to eliminate owl handling during live-prey training. Additionally, larger live-prey containers constructed from tan-brown opaque plastic were used and these changes probably contributed to the dramatic, albeit anecdotal, increase in proportion of mice depredated that year, by preventing the owls from looking in at the mice through the clear plastic walls of the container, and forcing them to perch on or in the containers to see the mice (Table 3). Due to numerous uncontrolled variables (different owls, animal care staff, weather patterns, cleaning schedules and training schedules), these results should be interpreted cautiously.

Although all mouse-related activity probably contributed to the physical fitness and problem-solving ability of the owls upon their release, more research is needed to evaluate the effect live-prey training has on post-release survival. Owls with two or more full summers of adult hunting experience in the wild performed

no better in the sessions than owls with less experience (Figure 3). However, the sample size for owls with more experience was small, and these were also individuals that had failed to successfully raise a clutch or had failed to migrate for at least two consecutive seasons. It may be these individuals were maladapted to the programme generally. Where sample size was larger – for owls with one full summer of adult hunting experience – hunting success was greater than in the YOY with less experience, although still not statistically significant (Figure 3). Given what is known about other predatory species (Miller et al. 1992; Biggins et al. 1999; Fajardo et al. 2000; Mathews et al. 2005; Houser et al. 2011), it seems likely that hunting success does have some experiential learning component in owls, and that prey training prior to release has the potential to improve post-release survival. A study of barn owls (*Tyto alba*) in Spain appears to support this hypothesis. Survival and mortality patterns were analysed in captive-bred and released owls and wild owls released after rehabilitation from injury. Compared to local wild populations, the released owls experienced greater mortality due to starvation. This effect was observed regardless of release method, but owls released following live-prey training had a significantly higher rate of survival (Fajardo et al. 2000).

Mitchell (2008) found that type of release method was the most significant contributor to low survival of captive-bred burrowing owls in British Columbia. A soft-release method, in which owls were confined to a predator-proof enclosure for their first two weeks at the release site, resulted in higher survival than a hard-release, in which owls were released after 12–24 hours in a burrow (no enclosure). Supplemental food was provided for both the hard and the soft-released owls, and wild prey items were proportionally similar in captive-released and wild burrowing owl pellets, suggesting that prey identification in burrowing owls is largely innate (Mitchell 2008). This idea is supported by the present study, in which mouse colour did not appear to influence depredation. Given the wide range of taxa that burrowing owls are known to consume, this result is unsurprising. How closely a species, such as *Mus musculus*, resembles its wild small mammal counterpart is likely of little consequence to the prey training. Rather than the ability to recognise prey, the owl’s ability to swiftly capture and kill is probably the more important aspect of prey-training.

Although Mitchell (2008) found that the proportion of supplemental food consumed relative to other diet items did not differ between captive-released and wild supplemented owls, hard-released birds did rely more on supplemental food for the first 15 days of release than the soft-released birds after release from their enclosures (33% vs. 14% pellet biomass). Because this study compared proportion of prey categories in the diet and did not assess quantity of prey consumed or body condition of the owls, it is unclear if the captive-released burrowing owls were as successful as the wild owls at acquiring prey. Further study is clearly needed to evaluate how prey training affects post release body condition and pre-migration survival in burrowing owls.

Estimating survival post-migration is a complicated matter. Wild burrowing owls have high first-year mortality and low first migration return rates. Of 538 banded young from natural nests in Manitoba in 1987–1996, only 3.5% returned (De Smet 1997). By eliminating the first-year potential for high mortality, and releasing owls with breeding success and increased maturity and fitness, MBORP has hoped to establish site fidelity and more burrowing owl returns post-release. Burrowing owls in breeding and reintroduction programmes in Manitoba and British Columbia have shown very low return rates, and it is unknown whether this is due primarily to post-migration mortality, or to low site fidelity. In British Columbia, young hatched in the wild from captive-bred released owls seem to return at a higher rate than the captive-

bred released owls (Lauren Meads, pers. comm. 2019). The overwintering of YOY burrowing owls in Manitoba has an unknown affect on their migration instinct. Further research is clearly needed to establish what is happening to released Manitoba burrowing owls after leaving their nest-sites for migration.

Lastly, live mice are likely a suitable training item for female and male burrowing owls alike. Female burrowing owls stay close to the nest until their young fledge, hunting primarily invertebrate species while males hunt farther from the nest and prey upon a greater proportion of vertebrates. Males provide for the family group; consequently, a female burrowing owl selects her mate according to his demonstrated hunting skills (Martin 1973; Froese 2016). Nevertheless, there was no evidence for a sex-bias in hunting success during the live-prey training sessions.

A high biomass of vertebrate species (83–99%) has been found in pellets collected around burrowing owl nests in Manitoba, but invertebrate prey items are also recognised as an important dietary component (Froese 2016). With the exception of the 2017 cross-over trial, live invertebrate prey (crickets) were made available to the captive burrowing owls throughout the overwintering period. Given the high biomass of vertebrate prey in Manitoba burrowing owl pellets, vertebrate species such as mice are likely beneficial to live-prey training. In some regions and institutions however, the use of live-prey is prohibited. The use of strictly invertebrate live-prey is recommended in such cases.

Conclusions

This study showed that handling can negatively impact hunting success during live-prey training of burrowing owls. The data suggest there is an experiential learning component to hunting of live-prey; however, the effect was not statistically significant due to a low overall number of depredation events. The artificial constraints of the training system (clear plastic containers) may have been the biggest obstacle to hunting success during the sessions. When planning live-prey training, every effort should be made to mimic natural conditions. Whenever possible, survival and/or body condition scoring of released individuals should be the metric used to evaluate the success of programme interventions.

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