Breeding ecology of captive-released and wild Western Burrowing Owls (*Athene cunicularia hypugaea*) in southwestern Manitoba, Canada, 2010-2012

Ecologia reprodutiva de coruja-buraqueira-ocidental (*Athene cunicularia hypugaea*) em estado selvagem e libertada de cativeiro no sudoeste de Manitoba, Canadá, em 2010-2012

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ABSTRACT

Western Burrowing Owl (*Athene cunicularia hypugaea*) populations have shown steady and substantial declines across western Canada in the last 50 years. Many inter-related factors are thought responsible for its rapid decline. A breeding ecology study was initiated in Manitoba to identify threats to wild pairs and to assess a modified reintroduction technique using food supplementation to promote nesting success, recruitment, and survival of captive-released first-year owl pairs to augment the numbers of wild owls. Breeding, foraging and behavioural data of captive-released and wild owls were recorded and compared from 2010-2012. During this period, 14 pairs of captive-released owls and six pairs of wild owls were monitored. Average clutch size for six wild first clutches (8.8 eggs) was higher than for 10 captive-released first clutches (6.5 eggs). Likewise, average replacement clutch size for four wild pairs (6.8 eggs) was higher than that of two captive-released pairs (5.0 eggs). Overall, hatching success for wild owls was 69% and captive-released owls was 60%. All hatched young were raised to fledging age for captive-release and monitored wild nests. During this three-year study, nine of 20 young raised to fledging age by wild pairs were removed from nests to become part of the following seasons' captive breeding group. The captive-release effort resulted in the release of 20 adults and 15 young raised to fledging age over three years; 12 young from captive-release pairs were removed from nests to become part of

the following seasons' captive breeding group. This study demonstrated that this captive-release method was at least partially successful. It remains to be seen if young produced survive over the longer term and contribute to the recovery of this endangered species in Canada.

Keywords: *Athene cunicularia hypugaea*, Breeding Ecology, Endangered Species Recovery Program, Reintroduction

RESUMO

As populações de coruja-buraqueira-ocidental (*Athene cunicularia hypugaea*) registaram declínios constantes e substanciais no oeste do Canadá nos últimos 50 anos. Muitos fatores inter-relacionados são considerados responsáveis por este rápido declínio. Um estudo de ecologia reprodutiva foi iniciado em Manitoba para identificar ameaças a casais selvagens e avaliar uma técnica de reintrodução modificada com recurso a suplementação alimentar para promover o sucesso da nidificação, recrutamento e sobrevivência dos casais de corujas libertados de cativeiro no primeiro ano, para aumentar o número de corujas selvagens. Entre 2010 e 2012 foram registados e comparados dados de reprodução, alimentação e comportamento de corujas selvagens e libertadas de cativeiro. Durante esse período, foram monitorizados 14 casais de corujas libertadas de cativeiro e seis casais de corujas selvagens. O tamanho médio das seis primeiras posturas de casais selvagens (8,8 ovos) foi superior ao das dez primeiras posturas de casais libertados de cativeiro (6,5 ovos). Da mesma forma, o tamanho médio da postura de reposição em quatro casais selvagens (6,8 ovos) foi superior ao de dois casais libertados de cativeiro (5,0 ovos). No geral, o sucesso de eclosão nas corujas selvagens foi de 69% e nas de cativeiro foi de 60%. Todos os juvenis eclodidos foram criados até à idade de emancipação, quer em cativeiro quer nos ninhos selvagens monitorizados. Durante este estudo de três anos, nove dos 20 juvenis criados por casais selvagens foram removidos dos ninhos para integrarem o grupo de reprodução em cativeiro nas estações seguintes. O esforço de reprodução em cativeiro resultou na libertação de 20 adultos e 15 juvenis criados até a idade de emancipação, durante três anos; 12 juvenis de casais libertados de cativeiro foram removidos dos ninhos para integrarem o grupo de reprodução em cativeiro das estações seguintes. Este estudo demonstrou que o método de reprodução em cativeiro foi pelo menos parcialmente bem-sucedido. Resta ver se os juvenis produzidos sobrevivem a longo prazo e contribuem para a recuperação desta espécie ameaçada no Canadá.

Palavras-chave: *Athene cunicularia hypugaea*, ecologia reprodutiva, programa de recuperação de espécies ameaçadas, reintrodução

Introduction

The Western Burrowing Owl (*Athene cunicularia hypugaea*) is a small (19.5-25.0 cm, 150-180 g), ground dwelling owl and the only owl in North America to nest under the ground. In the migratory portion of their range, they rely upon fossorial mammals, such as Richardson Ground Squirrels (*Urocitellus richardsonii*), Black-tailed Prairie Dogs (*Cynomys ludovicianus*), American Badgers (*Taxidea taxus*), and Red Foxes (*Vulpes vulpes*) to excavate burrows which the owls use for nesting. The Burrowing Owl was

designated as an Endangered species under the Canadian Federal Species at Risk Act (SARA) in 2003, and its status was confirmed as Endangered upon re-assessment in April 2006 by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) due to severe and ongoing population declines (Environment Canada 2012).

The furthest eastern extent of the Burrowing Owl range in Canada is in Manitoba. In recent decades, the species range has contracted from southeastern Manitoba near Winnipeg to the southwestern corner of the province (De Smet 1992, 2003). Overall, the Burrowing Owl population in Canada has declined by approximately 63% since the early 1970's and the breeding range has contracted substantially along its northern extremes, but particularly in its western and eastern extent (B.C. and Manitoba) (Environment Canada 2012).

In Manitoba, Burrowing Owls formerly occurred as far north as Dauphin and east of Beausejour. They regularly nested near Winnipeg until the 1980s (De Smet 1997, 2003). In recent years, their range in Manitoba has contracted to the southwestern corner of the province with very few reports outside of this area. No single factor has been identified as causing the decline of the Burrowing Owl in Manitoba or elsewhere in Canada; however, multiple, inter-related factors are thought to be responsible for its major decline. The ultimate cause for Burrowing Owl declines is likely related to habitat loss and degradation. Housing and farming expansion, road development and energy exploration have eliminated much suitable habitat for Burrowing Owls throughout its nesting, migratory, and winter range. Habitat changes and fragmentation have also allowed predators to move into areas where they once were not as common (Environment Canada 2012). Other factors include the decline in fossorial mammals like badgers and prairie dogs, the use of agricultural pesticide which reduce prey availability, migration path and use of wintering grounds. Migration and winter mortality is difficult to assess for long-distance migrants with low nest-site fidelity. As a result, Burrowing Owl migration has not been thoroughly studied at present. In recent years (2013-present), small geolocators and PTT satellite transmitters have been deployed on select owls in western USA states, and Alberta and Saskatchewan in Canada to track migrations. The migration of owls from Manitoba has not been examined.

Reintroductions of Burrowing Owls in Manitoba conducted from 1987-1996 included releases of both young owls (owls born in that season) and one-year old owls (hatched the previous nesting season) obtained from the Owl Research and Rehabilitation Foundation in Ontario, and young transplanted from Saskatchewan, and North Dakota (De Smet 1992, 1997). Owls were held in pens and released after seven days using a soft-release technique. Hard-releases were employed during only one year and were found to be largely unsuccessful. Reintroductions in Manitoba were part of a larger monitoring and recovery effort which examined the factors affecting nesting success and survival, nest and territory re-occupancy, return rates, and movements of banded adults and juveniles (De Smet 1997). Reintroductions were discontinued in 1996 due to poor overall return rates of owls to Manitoba after migration, but limited monitoring and management efforts for the species were continued. From 1997-2006, few Burrowing Owls were observed and it was believed to be on the verge of extirpation from Manitoba until a nesting population inexplicably rebounded in 2006.

Work under this project assessed the feasibility of a modified reintroduction method in Manitoba using recent successful release and food supplementation techniques employed elsewhere in Canada (Wellicome 2000, Poulin et al. 2006, Mitchell 2008, Mitchell et al. 2011) to promote nesting success, recruitment, survival, and return rates of Burrowing Owls in Manitoba.

Figure 1 - Release and nesting sites for captive-released Western Burrowing Owls (*Athene cunicularia hypugaea*) in southwestern Manitoba (2010 to 2012). Broomhill = Reintroduction sites 2010-2012; Pierson and Lyleton = Reintroduction only 2010; Medora and Deloraine = Reintroduction only 2012.

Figura 1 - Locais de libertação e de nidificação de coruja-buraqueira-ocidental (*Athene cunicularia hypugaea*) no sudoeste de Manitoba (2010 a 2012). Broomhill (Laranja) = Locais de reintrodução em 2010-2012; Pierson e Lyleton = Reintrodução apenas em 2010; Medora e Deloraine = Reintrodução apenas em 2012.

Figure 2 - Release pens for captive-released Western Burrowing Owls (*Athene cunicularia hypugaea*) in southwestern Manitoba, Canada, 2010-2012.

Figura 2 - Gaiolas de libertação de corujas-buraqueiras-ocidentais (*Athene cunicularia hypugaea*) provenientes de reprodução em cativeiro no sudoeste de Manitoba, Canadá, em 2010-2012.

Methods

We collected data on the current breeding ecology for both captive-released and wild owls in Manitoba. Data collected included nest initiation, clutch size, hatching and fledging success, adult and juvenile mortality rates on the breeding grounds, and natal and post-breeding dispersal timing and rates. In this study, nesting or nest establishment was defined as clutch initiation (one egg observed in the nest). Fledging age of nestlings (35-42 days after hatching) was determined based on their abilities for sustained flight (greater than 30 m). Nesting success was defined as nests fledging at least one young. "Captive-released" Burrowing Owls were either captive-hatched (i.e., from breeding adults in captivity) or wild-hatched juvenile (i.e., from breeding adults in the wild) owls that were then held in captivity for one winter, paired for nesting, and transferred to release pens (Fig. 2) in the study area in mid-May.

Release site selection

Five sites were selected on private land for the reintroduction of Burrowing Owl pairs and individuals in southwestern Manitoba between 2010 and 2012 (Fig. 1). All release sites were pastureland (native and tame) and were grazed by cattle throughout the late spring and summer months. Sites were selected based on proximity to recent Burrowing Owl observations and nests in recent seasons (2006-2009) and availability of suitable habitat for Burrowing Owls (i.e., open pasture, no trees or shrubs and land with ample ground squirrel populations or burrows). Permission for property access, to release owls, and to observe wild owls throughout the nesting season was granted from all landowners.

Artificial Nest Burrow Installation and Soft Release of Owls

In mid-May of each season, 2.4 m x 2.4 m x 2.4 m tall release pens were set up at release sites. Pens were constructed of a wooden frame with chicken wire (outside) and mesh/bird netting (inside) (Fig. 2). Pens were fenced off with a small section of electric fencing so that cattle would not rub against the pens. Anchor ropes were also added in 2011 and 2012 to further secure the pens from extreme winds and storms. Each pen was equipped with an artificial nest burrow (ANB), 60 cm high wooden post for perching, and a Reconyx wildlife camera that recorded activities at the nest entrance 24 hrs per day (Fig. 3). ANBs used at release sites consisted of a 2.5-3 m length of 15 cm dia, corrugated weeping tile leading to a 19-l plastic bucket that served as the nest chamber. A large section of chicken wire was attached below and around the sides of the nest bucket to protect against potential fossorial predators. Two additional buckets were placed above the main nesting bucket to permit easier access to the nest chamber (Fig. 4). A perching post was installed inside the pen at the entrance to the nest burrow, and access to the nesting bucket (nest chamber) was 1 m outside the enclosure. An adaptation to Poulin et al.'s (2006) design was the addition of a 61 cm long section of 50 mm dia PVC piping that extended from the top bucket down into the nesting bucket (Fig. 5), allowing access to the nest chamber for regular observations of egg-laying and hatching through a fiber optic cable and camera (Peeper 2.0, Sandpiper Industries, California).

A soft-release technique was used to house paired owls until a partial clutch was observed (Poulin et al. 2006, Mitchell et al. 2011). To encourage nest success and reduce potential for nest abandonment pairs were held in pens until at least three

Figure 3 - Artificial Western Burrowing Owls (*Athene cunicularia hypugaea*) nest burrow entrance and fence post for roosting inside pen.

Figura 3 - Entrada de ninho artificial para coruja-buraqueira (*Athene cunicularia hypugaea*) e poste para poiso dentro da gaiola.

Figure 4 - Three-bucket artificial nest burrow for Western Burrowing Owls (*Athene cunicularia hypugaea*) allowed for easier access to the nest chamber, via a removable bucket system located outside the enclosure (adapted from Poulin et al. 2006).

Figura 4 - Ninho artificial para coruja-buraqueira (*Athene cunicularia hypugaea*) composto por três baldes, permitindo acesso mais fácil à câmara de nidificação através do sistema de remoção do balde localizado no exterior da gaiola (adaptado de Poulin et al. 2006).

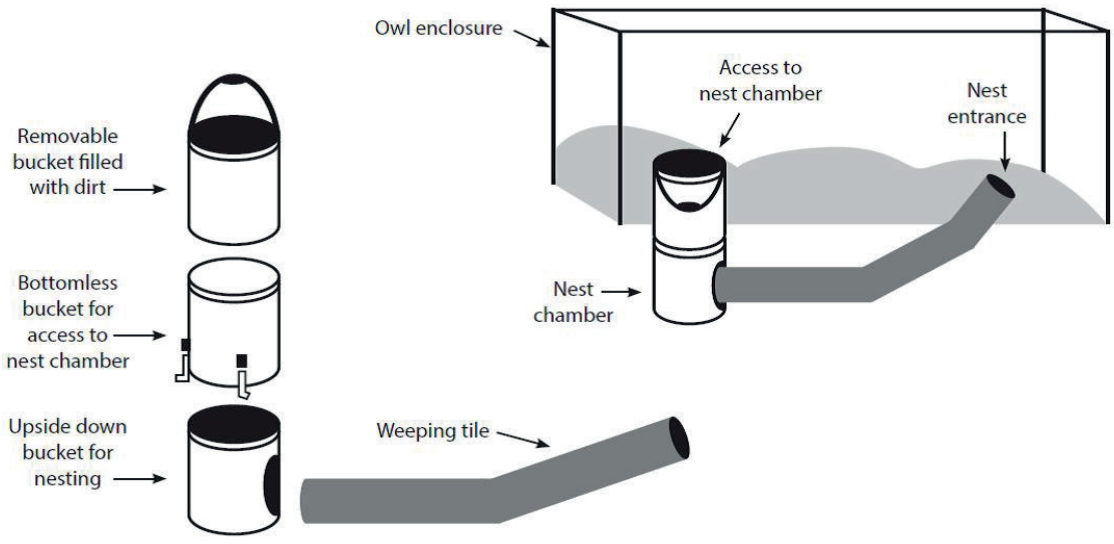

Figure 5 - PVC piping inserted in the top of the third bucket allowed for access to the Western Burrowing Owls (*Athene cunicularia hypugaea*)nest chamber with a fiber optic camera.

Figura 5 - Tubos de PVC inseridos no topo do terceiro balde, permitido acesso à câmara de nidificação da coruja-buraqueira (*Athene cunicularia hypugaea*), através de uma câmara de fibra ótica.

eggs were laid in nests (Poulin et al. 2006). If a nest was not established within six weeks or if a later nest failed (replacement clutches occasionally occurred with early nest failures), owls were recaptured and returned to the Assiniboine Park Zoo for overwintering. A few unpaired owls were also released (2011 & 2012 only) utilizing soft-release techniques (generally released after they had been in the pens for 10 days). Pairs were provided with three frozen-thawed house mice daily. This daily ration was reduced to two mice per pair after the pens were removed to encourage adult owls to forage for food. Adult owl foraging activities were monitored after release daily through personal observations and by reviewing camera images every four days. Once all young emerged from the burrow (generally between 10 and 14 days old) food supplementation was stopped. [Note: from the 2013 season onward, supplemental feeding was continued until the young were seven weeks of age.]

Founding population of Burrowing Owls for Reintroduction

The founding population consisted of hatch-year juveniles from 2009 which included four wild-hatched juvenile owls removed from two larger family groups in southwestern Manitoba (two females and two males); two captive-hatched juvenile owls produced by a non-releasable pair from the Assiniboine Park Zoo (one female and one male); and four captive-hatched juvenile owls from the Alberta Birds of Prey Centre in Coaldale, Alberta (two females and two males). Founding owls were transferred to release sites in mid-May, placed in release pens, and paired for nesting. Owls were intermixed and paired according to where they originated (i.e., Manitoba wild, Birds

Table 1 - Nesting results for captive-released Western Burrowing Owls (*Athene cunicularia hypugaea*) in southwestern Manitoba, Canada, 2010-2012.

Tabela 1 - Resultados da nidificação de casais de coruja-buraqueira-ocidental (*Athene cunicularia hypugaea*) provenientes de cativeiro no sudoeste de Manitoba, Canadá, em 2010-2012.

[1]Based on no. of eggs and young observed in successful nests.

	2010	2011	2012
No. of adult pairs	5	5	4
No. of individuals adults released	0	3	3
No. of first clutches	3	3	4
No. of failed first clutches	2	2	1
No. of replacement clutches	0	2	1
No. of failed replacement clutches	0	1	0
Mean clutch size (first clutch, n=10)	6.6 (n=3, 5-8 eggs)	6.6 (n=3, 6-7 eggs)	6.25 (n=4, 4-8 eggs)
Mean clutch size (replacement clutches, n=3)	0	4 (n=2, 4 eggs each)	6 (n=1, 6 eggs)
Total no. of eggs (first and replacement clutches)	20	28	31
A: No. of eggs (only from nests that hatched eggs)	7	11	27
B: Total no. of hatchlings	2	6	19
% Hatching success[1] (B/A x 100)	29%	55%	70%
No. of hatchlings reaching fledging age	2	6	19
No. of fledgling age young removed for overwintering and later captive-release	1	3	8
No. of fledglings released	1	3	11

of Prey Centre (AB), or Assiniboine Park Zoo (MB)) to avoid breeding related owls. All founding owls were released if they fledged at least one young.

Results

Summary of Captive-released Burrowing Owl Reproduction (2010-2012)

Over the three study years, 14 pairs of captive-released owls and six single males were placed in release pens. Ten of 14 pairs successfully initiated a first clutch (71%); seven of ten pairs (70%) successfully fledged young (including two replacement clutches). Of 13 total nests produced by captive-released pairs (10 first and three replacement clutches), six failed. Failures were caused by flooding of the burrow (4 nests), abandonment (1 nest), and a probable predation attempt resulting in the death of the female (1 nest). Excluding one first clutch that was abandoned soon after the release (with only one egg), average clutch size for first clutches during this study averaged 6.5

(n=9, range 5-8 eggs). Replacement clutches were smaller, averaging 5.0 eggs (n=3, range 4-6 eggs). Including all 13 first and replacement clutches, seven clutches were successful (54%) fledging a total of 27 young (3.86 young/successful nest). Overall, 60% (27 of 45) of eggs that were laid hatched. Nestling survival (post-hatching to fledging age; n=27) was 100%. Nests in 2012 were the most successful with 19 hatchlings from 27 eggs (70%), including one particularly successful pair that hatched and raised all 8 of their eggs/young to fledging age. One of 19 young in 2012 was preyed upon six weeks after hatching at the burrow entrance by a Great Horned Owl (*Bubo virginianus*) (the only known instance of predation of a young prior to dispersal at the release site during this study). Young were of fledging age at 5-6 weeks of age so predation after 6 weeks of age did not affect estimates of fledging success. Twenty adults and 15 fledglings were released and dispersed from the release sites during the three-year study period. An additional 12 juveniles were removed from nests to become part of the captive breeding group the following season (Table 1).

Summary of Wild Burrowing Owl Reproduction (2010-2012)

Of eight wild pairs located during 2010-2012, two pairs (six young) were excluded from the monitored pairs as they were located too late in the nesting season to assess breeding ecology (after young had already fledged). For the six monitored pairs, overall clutch size for first and replacement clutches combined was 8.0 eggs/nest, ranging from 8.8 for six first clutches to 6.8 for four replacement clutches. Only two of the six monitored wild pairs were successful with a first clutch, but all four pairs where nests failed produced a replacement clutch and two of these raised young to fledging age. Twenty of 29 eggs in successful wild nests hatched (69%); all 20 young survived to fledging age. Four of 10 monitored nests (40%) and four of six monitored pairs (67%) successfully raised young to fledging age. Nine of these 20 young were removed from nests in 2010 and 2011 to diversify the gene pool of the captive-released breeding population in the next season (Table 2).

Discussion

Clutch Size, Nesting, and Hatching Success (Captive-released and Wild Burrowing Owls)

During this study, the average clutch size for wild first clutches (8.9 eggs) was higher than for captive-released first clutches (6.5 eggs). Part of this difference may be attributed to the fact that wild pairs initiated first clutches much earlier (April 28-May 15) than captive-released owls (May 24- June 10). Wellicome (2000) found that wild Burrowing Owls show a seasonal decline in clutch size as earlier initiated clutches are generally larger than those laid later in the season. The difference in clutch sizes of first clutches (8.9 and 6.5 eggs) versus replacement clutches (6.8 and 5.0 eggs) in the present study also reflects that later clutches are generally smaller.

Hatching success in this study was defined as the number of young that hatched from eggs in either a first clutch or replacement clutch. Hatching success for wild owl nests was higher in 2010 and 2011 (68% and 71%) relative to more variable captive-released nest success (22% in 2010, 55% in 2011, and 70% in 2012). Overall, hatching success for wild owls was 69% (2010 and 2011) and captive-released owls was 60% (2010- 2012). Mitchell (2008) saw a similar hatching success rate of 57% in her 2005 and 2006 study in B.C. when reintroducing captive-bred pairs through a soft-release technique. During the course of this study, conditions in 2012 were the most suitable for breeding Burrowing Owls, with lower rainfall during the nesting period reducing damp or wet conditions in the burrow. All captive-released pairs were

Table 2 - Nesting results for wild Western Burrowing Owls (*Athene cunicularia hypugaea*) in southwestern Manitoba, Canada, 2010-2012.

Tabela 2 - Resultados da nidificação de casais de coruja-buraqueira-ocidental (*Athene cunicularia hypugaea*) selvagens no sudoeste de Manitoba, Canadá, em 2010-2012.

[1]Only confirmed eggs in all nests. Cartwright (2010) and Elgin (2011) eggs were not counted as pairs/young were found later in the season.

	2010	2011	2012
No. of adult pairs	5	3	0
No. of individual/additional adults observed	2	4	4
No. of first clutches	5	3	0
No. of monitored first clutches	4	2	0
No. of failed first clutches	2	2	0
No. of replacement clutches	2	2	0
No. of failed replacement clutches	1	1	0
Mean clutch size (first clutches, n=6)*	8.8 (n=4, 8-11 eggs)	9.0 (n=2, 9eggs each)	0
Mean clutch size (replacement clutches, n=4)	6.5 (n=2, 6-7 eggs)	7.0 (n=2, 7eggs each)	0
Total no. of eggs (first & replacement clutches)[1]	48	32	0
A: No. of eggs (only from nests that hatched eggs)	22	7	0
B: Total no. of hatchlings	15	5	0
% Hatching success (B/A x 100)	68%	71%	0
No. hatchlings reaching fledging age	15	5	0
No. of fledgling aged young removed for overwintering and later captive-release.	6	3	0
No. of fledglings released	9	2	0

provided with the same supplemental diet in all three seasons for the same duration (up until all young emerged from the burrow). Male captive-released owls in 2011 and 2012 were observed to be well-adapted hunters bringing back a variety of prey items daily to nest burrows. In 2011, there was an increase in frog and toad populations, which benefited both wild and captive-released pairs (noted in pellet dissection remains). This increased food and more suitable nesting conditions may explain the increase in hatching success for captive-released pairs in 2011 and 2012.

The greatest cause of first clutch failure for both captive-released and wild owls during this study was nest flooding due to heavy rainfall. Seven of nine first clutches failed from flooding (7 of 18 nests, 39%) and two from unknown abandonments (2 of 18 nests, 11%). Seven replacement clutches were established (4 wild and 3 captive-released) and three of these failed from either flooding

(n=1) or predation (n=2). Catlin & Rosenberg (2008) noted that resident Burrowing Owls in California were able to replace a clutch quickly after a nest failure and could have up to three or four replacement clutches in a season, generally with smaller clutch sizes produced after each failure. During this study, most pairs where first clutches failed produced replacement clutches within 10 days. Multiple breeding attempts in a single season are common among many birds, however, replacement clutches had not been observed for Burrowing Owls in Manitoba prior to this study (K. De Smet, pers. comm.).

Overall, 12 of 23 monitored Burrowing Owl nests from 2010-2012 failed (52%); failures were attributed to two main factors, flooding (35%) and predation (9%), with the remainder as unknown caused abandonments (9%). Both captive-released and wild owls responded to nest failures by producing a smaller replacement clutch.

Fledging Success

All hatched young were raised to fledging age for captive-released and monitored wild nests during this study. Nests near Cartwright and Elgin were found later in the season (post-fledging) and hatching and fledging success could not be assessed and they were excluded from the nesting analysis. However, with that said, considerably higher fledging rates were documented in this study for captive-released owls than the 1987-1996 Manitoba reintroduction program and similar efforts in Saskatchewan and B.C (De Smet 1997, Poulin et al. 2006, Mitchell 2008).

One explanation for the high fledging rate in this study may be due to our reducing brood sizes prior to fledging. Removal of young from larger families meant that the remaining hatchlings would likely have greater access to prey resulting in increased body condition and survival prior to migration. It also meant that adults had fewer nestlings to care for, thus their hunting activities would be less taxing, potentially increasing their overall fitness.

Emerging threats

Heavy rainfall combined with elevated groundwater levels resulted in extensive flooding of both natural and artificial nest burrows during 2010 and 2011 and the loss of five captive-released nests and three wild nests. Due to the small number of Burrowing Owl occurrences throughout the last two decades it is not possible to measure significance (statistically) of the impact of rainfall on Burrowing Owl numbers. However, the impact of historical precipitation rates on owl occurrences in Manitoba, personal observations from this study, and the 1987-1996 study, and an important study by Fisher et al. (2015), provide evidence that in times of increased precipitation, Burrowing Owls do not fare as well as during drier periods. De Smet (1997) speculated that increased summer rainfall in the early to mid-1990s was a major factor in the sudden decline in productivity and nesting number of Burrowing Owls in southwestern Manitoba. He believed food shortages, nest abandonments, and other factors may have been the major reasons why Burrowing Owl nests were lost or produced few young during that period. This study documented that prolonged wet periods contributing to a higher than normal water table combined with high event rainfall occurrences can have a significant negative effect on Burrowing Owl nesting success through flooding of a large number of nests. The end result of poor overall nesting success is often reduced return rates of nesting adults to the study area in subsequent years.

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