



Research Papers

Pre-Migratory Movements by Juvenile Burrowing Owls in a Patchy Landscape

Déplacements pré-migratoires de jeunes Chevêches des terriers dans un paysage fragmenté

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ABSTRACT. Dispersal is a fundamental aspect of population dynamics, and can have direct implications on processes such as the colonization of habitat patches. Pre-migratory movements, landscape fragmentation, and body condition have all been hypothesized as key factors influencing dispersal in birds, but little direct evidence exists to support these ideas. We used radio-telemetry and supplementary feeding to test if body condition or landscape pattern influenced pre-migratory movements of juvenile Burrowing Owls (*Athene cunicularia*) in a fragmented landscape. We categorized grassland patches as either large (≥ 95 ha) or small and isolated (≤ 58 ha and ≥ 1.5 km to next nearest grassland patch), and young owls were either provided supplemental food as nestlings or not. Owlets receiving supplemental food and residing in large grassland patches moved a greater maximum distance from their nest than similarly fed owlets residing in small patches (large = 1605 ± 443 m; small = 373 ± 148 m). In contrast, non-supplemented owlets from large and small patches did not differ in their maximum distance moved from the nest (large = 745 ± 307 m; small 555 ± 286 m). Only two of 32 individuals from small patches moved >800 m, whereas ten of 23 owlets from large patches moved >800 m. In addition, owlets from large patches continued to move farther and farther from their nest before migration, whereas owlets in small, isolated patches ultimately moved <400 m from their nests before migration, despite having initiated dispersal in a manner similar to owlets from large patches. Our results, along with evidence we synthesize from previous studies, suggest that juvenile Burrowing Owls in small patches are unwilling or unable to cross the cropland matrix of a fragmented landscape.

RÉSUMÉ. La dispersion est un élément fondamental de la dynamique des populations et peut avoir des répercussions directes sur des processus comme la colonisation d'habitats. Les déplacements pré-migratoires, la fragmentation du paysage et la condition physique ont tous déjà été considérés comme des éléments clés pouvant influencer sur la dispersion des oiseaux, mais il existe peu de données pour attester de ceci. Nous avons utilisé la radio-télémetrie et le nourrissage artificiel afin de vérifier si la condition physique et la structure du paysage influencent sur les déplacements pré-migratoires de jeunes Chevêches des terriers (*Athene cunicularia*) dans un paysage fragmenté. Nous avons classé les parcelles de prairies comme étant grandes (≥ 95 ha) ou petites et isolées (≤ 58 ha and $\geq 1,5$ km de la parcelle la plus proche), et les chevêches au nid ont reçu, ou non, de la nourriture. Les chevêches nourries et provenant de grandes parcelles se sont déplacées de leur nid sur une distance maximale plus grande que les chevêches nourries provenant de petites parcelles (grandes = 1605 ± 443 m; petites = 373 ± 148 m). À l'opposé, les distances maximales parcourues par les chevêches non nourries provenant de grandes ou de petites parcelles n'ont pas différencié (grandes = 745 ± 307 m; petites = 555 ± 286 m). Seulement 2 des 32 chevêches provenant de petites parcelles se sont déplacées sur >800 m, tandis que 10 des 23 chevêches provenant de grandes parcelles l'ont fait. De plus, les chevêches provenant de grandes parcelles se sont éloignées de plus en plus de leur

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nid avant la migration, tandis que celles provenant de parcelles petites et isolées se sont finalement déplacées sur <400 m de leur nid avant la migration, même si elles avaient amorcé leur dispersion de la même façon que les chevêches provenant de grandes parcelles. Nos résultats, en parallèle aux résultats obtenus dans les études antérieures, montrent la réticence ou l'incapacité qu'ont les jeunes Chevêches des terriers nés dans de petites parcelles à franchir la matrice cultivée dans un paysage fragmenté.

Key Words: *Athene cunicularia*; Burrowing Owl; habitat fragmentation; natal dispersal; post-fledging dispersal; pre-migratory dispersal; supplemental food

INTRODUCTION

Many factors influence whether an animal chooses to disperse and how far individuals move before settling. Individual attributes such as age, sex, or body condition and extrinsic factors such as local food availability or competition are common correlates of the propensity of animals to disperse. More recently, metapopulation theory (Turchin 1998) has stressed the importance of landscape pattern as a factor influencing dispersal. When areas of suitable habitat are isolated from one another, dispersal tends to be delayed or restricted (Mader 1984, Merrimam et al. 1989, Baur and Baur 1990, Opdam 1990, Lens and Dhondt 1994). Reductions in dispersal can have consequences for metapopulation persistence if suitable but isolated habitat fragments are not recolonized after subpopulations go extinct.

Much of what is known about dispersal in birds comes from resident species. In general, natal dispersal is more extensive than breeding dispersal, females disperse greater distances than males, and birds move away from areas with fewer resources or greater competition (Greenwood and Harvey 1982). Individuals in better body condition may be more likely to disperse from natal areas, whereas adults in better body condition and with successful past reproduction at a site tend not to disperse (Bayne and Hobson 2002, Barbraud et al. 2003). The understanding of dispersal in migratory birds is more limited, although many of the same patterns appear to hold (Pärt 1990). However, because migratory birds leave their natal and breeding territories each year and cross vast expanses of unsuitable habitat, some authors have suggested that dispersal in migrants may be less limited by landscape pattern than it is for residents (Ambuel and Temple 1983). If landscape pattern does not influence migrant dispersal, then occurrence within

habitat patches and size of subpopulations should not be correlated with isolation of habitat. In contrast, many studies have found effects of isolation on migratory bird occurrence or abundance, implying that ability to migrate may not be correlated with dispersal ability (Villard et al. 1995).

One explanation for the discrepancy between long-distance migratory and short-distance dispersal ability is that the first stage of dispersal by migrants occurs as exploratory movements during late summer. Such movements are thought to be important in identifying potential breeding sites for use in subsequent years (Pärt 1990, Morton 1991, 1992, Morton et al. 1991, Belthoff and Dufty 1998, Dufty and Belthoff 2000). If landscape pattern reduces exploratory movements of migrants, then isolated yet otherwise suitable habitat patches may remain vacant in future years because birds were not able to find the suitable patches when they were looking for them. Despite the potential importance of pre-migratory movement as a factor influencing metapopulation persistence of migrants in patchy landscapes, few tests of the relative importance of landscape pattern, individual attributes, local extrinsic factors, and their interactions have been conducted.

The Burrowing Owl (*Athene cunicularia*) is a small migratory raptor that nests in grasslands of western North America. At the species' northern range edge in western Canada, Burrowing Owls are rare and declining (Wellicome and Holroyd 2001). It has been suggested that loss or degradation of suitable grassland habitat has contributed to this decline, yet unoccupied sites still exist in seemingly suitable grassland habitat. Thus, limits to dispersal may play a role in limiting habitat occupancy and, ultimately, population size. Pre-migratory movements of juvenile Burrowing Owls in large tracts of grassland

occur in a slow but incremental fashion away from their original nest site, with juveniles using several satellite burrows before migration (Clayton and Schmutz 1999, King and Belthoff 2001). These movements presumably result in juvenile owls gaining knowledge of the natal landscape before migration, and may aid in decision making about locations they might return to in subsequent breeding seasons. If pre-migratory movement provides a benefit to Burrowing Owls in identifying potential territories for future breeding, then we hypothesized that the maximum distance moved by juvenile owls before migration would be greater in large and contiguous habitats than in small and isolated patches. A secondary prediction of this hypothesis is that individuals in better body condition would be more likely to make such movements as they are more likely to have sufficient reserves to allow for migration and pre-migratory exploration (Barbraud et al. 2003).

Alternatively, Burrowing Owls may not be moving before migration to gain information about the landscape around them. Competition for resources during the post-fledging period can be intense for Burrowing Owls given the potential for a large number of siblings in any given nest (Todd and Skilnick 2003). Inter-sibling competition for food may result in some individuals being forced from the natal area simply to gain sufficient food reserves to prepare for migration (Barbraud et al. 2003). If this is the case, then the movement of Burrowing Owls should be best described by the level of competition. Thus, individuals with fewer siblings should be less likely to move assuming that lack of food was not the reason for fewer young being produced in the first place. A secondary prediction of this hypothesis is that individuals in poorer condition should be the ones forced from the natal area if remaining in areas of familiarity is beneficial (Weatherhead and Forbes 1994).

METHODS

To test our hypotheses, we conducted a radio-telemetry study in the moist mixed-grassland ecoregion of southern Saskatchewan, Canada. The study area lies on the Regina Plain, and is roughly bound by the cities of Moose Jaw (50°34'N, 105°17'W), Regina (50°25'N, 104°39'W), and Weyburn (49°40'N, 103°52'W). Land in this region is primarily under dry-land cultivation for cereal production. Less than 7% native grassland remains,

and remnant patches are small and fragmented (Riemer et al. 1997, Gauthier et al. 2002). Roads dissect the landscape in a grid pattern and parcels of common habitat often exist as quarter sections (800 m x 800 m; 64 ha) of pasture or crop. Native grassland vegetation in the area includes blue gramma grass (*Bouteloua gracilis*), northern wheat grass (*Agropyron dasystachym*), western wheat grass (*A. smithii*), spear grass (*Stipa comata*), and June grass (*Koeleria cristata*).

We defined patches of grassland as either being small and isolated or large and contiguous, based on the size of the patch and the degree to which it was isolated from the next closest patch of grassland. A grassland patch was deemed small and isolated if it was a quarter-section or smaller (≤ 64 ha) and was separated on all sides by at least a 1.5 km width of non-grassland (e.g., crop). The average size of small and isolated patches was 13 ha (1–58 ha). Average distance to the next patch of grassland was 2400 m and ranged from 1500 m to 6000 m. We defined a patch as large and contiguous if the total area of grassland was greater than one quarter section (64 ha), but because of ranching practices, grasslands patches that were larger than a quarter-section tended to be substantially so. We had one large patch of 95 ha (most of two quarter sections), and the rest of the sites were next to, or part of, thousands of hectares of contiguous grassland. The Burrowing Owls we included in this study nested in large and small patches scattered across the more than 10 000 km² study area.

The movement of individual owls was recorded through radio-telemetry using 4–6 g transmitters ($\leq 5\%$ of body mass). Transmitters were attached 35 to 40 days after hatch on owls weighing >120 g. Using these mass criteria meant that the oldest owls in the brood were more likely to be selected for transmitter attachment. Necklace-style transmitters were used ($n = 95$) in all 4 years; some backpack-style transmitters ($n = 11$) were used in 1999 and 2000. Only four (three in small patches, one in a large patch) of the owls included in our analysis wore backpack-style transmitters, and this likely had little if any impact on the results of the study. In 1997 and 1998, we randomly selected one of the oldest chicks in each nest, and in 1999 and 2000, we randomly selected one of the oldest male and female chicks from each nest. Sex was not included in our analyses because it was perfectly correlated with year (all unknowns occurred in 1997 and 1998).

We tracked radio-tagged owls using a portable receiver (Wildlife Materials Inc.) and either a two-element Yagi antenna or an omni-directional, vehicle roof-mounted antenna. We determined the status and diurnal location of each radio-tagged owl every 2–3 d until radio failure, death, or migration. We tried not to flush owls when tracking them to minimize impacts on their behavior. Whenever possible, the position of radio-tagged birds was determined from a distance using binoculars or a spotting scope. Global positioning system (GPS) readings and measurements were taken later, once the owl had moved to a different location. When transmitter signals could not be detected from the ground, aerial searches were conducted from a single-engine Cessna 172 aircraft, equipped with strut-mounted radio-tracking equipment. We assumed juveniles migrated when transmitter signals were permanently lost beginning in early September.

To maximize variation in body condition of juvenile owls, we supplemented 33 nests with food (Wellicome 2005). Supplementation consisted of nesting pairs receiving 255 g of dead lab mice every 3 d during the nestling period. Supplemental food was provided beginning when the eggs were within a few days of hatching, and ending 41 d after hatch. Six of the ten nests in 1997 were provided supplemental food; 12 of the 18 in 1999, five of the ten in 1999, and four of the six nests in 2000 received this extra food. In total, ten of the 20 nests in large patches and 17 of the 24 nests in small patches received supplemental food.

Appropriate permits for these activities were obtained from Saskatchewan Environment, the Canadian Federal Bird Banding Office, and the University of Regina President's Committee on Animal Care.

Data Analysis

To test whether landscape pattern or feeding treatment influenced the maximum distance moved (log-transformed) over the entire pre-migratory period, we compared five preselected mixed-effects models (Rabe-Hesketh and Everitt 2004) using Akaike's Information Criterion corrected for small sample size (AIC_c). Mixed models are a form of generalized linear model appropriate when movement of individuals is correlated (i.e., brothers and sisters in 1999 and 2000). Random effects

account for lack of independence caused by correlation of residuals within individuals moving from the same nest. The total residual error in the response variables was partitioned into a nest-specific component along with the residual error within nests. In other words, a random intercept was calculated for each nest location that accounted for the lack of independence between individuals that were hatched from the same nest. Year was also included as a random effect, which allows model predictions to be generalized outside the specific years of study. AIC_c allows the fit of two or more models to be compared based on the log-likelihood of each model, with penalty terms applied. The penalty term is applied based on the number of parameters so that more complex models need to have substantially better fit than simpler models with fewer predictors to be selected as the most likely model in a candidate set.

The five models that we considered in our candidate set were: 1) feeding treatment (surrogate for body condition); 2) landscape pattern; 3) brood size; 4) feeding treatment*landscape pattern; and 5) brood size*landscape pattern. If pre-migratory movement was dependent on individual body condition, then we predicted that birds that had been fed would be more likely to move simply because they were in better condition than non-fed birds. However, good body condition may be insufficient to offset risks of moving across poor-quality habitat, such that landscape pattern might interact with body condition, with good condition individuals in large patches more likely to move. Although feeding owl nestlings did result in better body condition at fledging (Wellicome 2000), greater movement does not necessarily mean that birds are moving because they are in better condition. Feeding owls results in greater individual survival of chicks within broods, such that food-supplemented birds with transmitters may actually have greater competition for food, particularly when the extra food provided in the supplementation is removed. Reduced food per individual could result in greater movement away from the nest in food-supplemented birds, simply to avoid competitive effects from siblings. Therefore, we tested whether the number of siblings at fledging was the best predictor of pre-migratory movement. We also tested whether brood size at the time of fledging interacted with landscape pattern, as there may be a trade-off between the risks of moving across poor-quality habitat in the hopes of finding better food resources and competition for known resources around the nest site.

Although the absolute distance moved from the nest is a key component to pre-migratory movement, we were also interested in whether the pattern of movement away from the nest over time differed with landscape pattern for the same reasons described above. To compare the distances fed and unfed owls from large and small patches moved from their nest through the duration of the pre-migratory period, we divided observations of radio-tagged individuals into 10-d age intervals, and determined the maximum distance that an individual bird was located from its nest burrow during that interval. The maximum distance within each time interval was derived from two to four locations per bird. This interval approach was used to better ascribe the extent of the exploratory movements. That is, if an owl moved a large distance on one day but then moved back closer to the nest in subsequent days, then our method would still capture these large, potentially exploratory movements.

To determine the factors associated with the maximum distance owls moved from their nest over time, we repeated our mixed effects modeling with the following models: 1) feeding treatment*time; 2) brood size*time; 3) landscape pattern*time; 4) feeding treatment*landscape pattern*time; and 5) brood size*landscape pattern*time. Both patch size and feeding treatment were treated as categorical variables whereas time was a continuous variable. In these models, we did not include year or nestID as random effects because of model convergence problems. Instead, we included a random slope for individuals (Rabe-Hesketh and Everitt 2004). A random slope model estimates a unique slope in terms of the distance moved per unit time and averages these values across all individuals to derive a slope estimate that accounts for the different patterns of movement among individuals, rather than assuming that all individuals move the same way over time.

All models were developed using Stata® statistical software (version 9.2; StataCorp, College Station, Texas). Summary statistics are reported as means \pm 1 SE unless otherwise reported.

RESULTS

From 1997 through 2000, we affixed 106 transmitters onto owls from 78 different nests. Approximately half these birds died during the post-

fledging period (Todd et al. 2003), leaving 55 birds (1997, $n = 10$; 1998, $n = 18$; 1999, $n = 17$; 2000, $n = 10$) with complete data sets from nest departure to migration. On average, radio-tagged juvenile owls first left their nests 53.3 ± 1.4 d after hatching, migrated 108.1 ± 1.6 d after hatching (27 September ± 1.2 d), and used 5.3 ± 0.4 satellite burrows (primarily badger (*Taxidea taxus*) burrows) before migrating. We found juveniles using the same burrows for 1–19 consecutive sightings. Given that telemetry observations were made once every 2–3 d, some juveniles could have been using the same satellite burrow for up to 38 consecutive days.

The model that best predicted maximum distance moved was landscape pattern*feeding treatment. This model had a weight of 0.51, with twice as much support as the other models in the candidate set (Table 1a). Of the owls that were fed, those in large patches moved farther from the nest before migration (1605 ± 443 m; median = 1200 m) than those in small patches (373 ± 148 m; median = 180 m). Of the owls that were not fed, those in larger patches moved an average of 745 ± 307 m (median = 306 m), whereas those in small patches moved an average of 555 ± 286 m (median = 270 m). Only 6% (two of 32) of juveniles in small patches moved >800 m (the length of a quarter section), whereas 43% (ten of 23) of juveniles in large patches moved >800 m.

The pattern of owl movements away from the nest over time was best described by the model landscape pattern*time, which had an Akaike weight of 0.70 (Table 1b). Owls from both small and large patches began leaving their nests between 50 and 59 d of age, but juvenile owls from large patches continued to move farther and farther away, and were over 1 km from their nest by the time they migrated. Until 50 d, the increase in the maximum distance moved was minor and similar for owls from small and large patches. However, after 50 d, the maximum distance moved increased rapidly over time for owls from large patches, but reached a plateau for owls in small patches (Fig. 1). Juvenile owls from small, isolated patches effectively stopped moving away from their nests at about 70 to 79 d of age, and remained <400 m from their nest until they migrated. The two models feeding treatment*landscape pattern*time and brood size*landscape pattern*time both had low but similar Akaike weights (0.13 and 0.11, respectively).

Table 1. Akaike's Information Criterion for five models in candidate set. Results are shown for (a) maximum distance moved over the duration of the study, and (b) the maximum distance moved per 10-d interval before migration. Akaike weights are scaled between 0 and 1, with higher weights indicating greater support. Parameter estimates are also reported for the model selected as having the best fit. The response variable of distance moved was ln-transformed before analysis. A constant of 1 was added to the distance moved per unit time before transformation because of the presence of zeros. Landscape pattern was a dummy variable coded 0 for large, 1 for small. Feeding treatment was a dummy variable coded 0 for fed, 1 for unfed. Time was a continuous variable ranging from 1 to 11, with each increment representing a 10-d interval relative to hatching date.

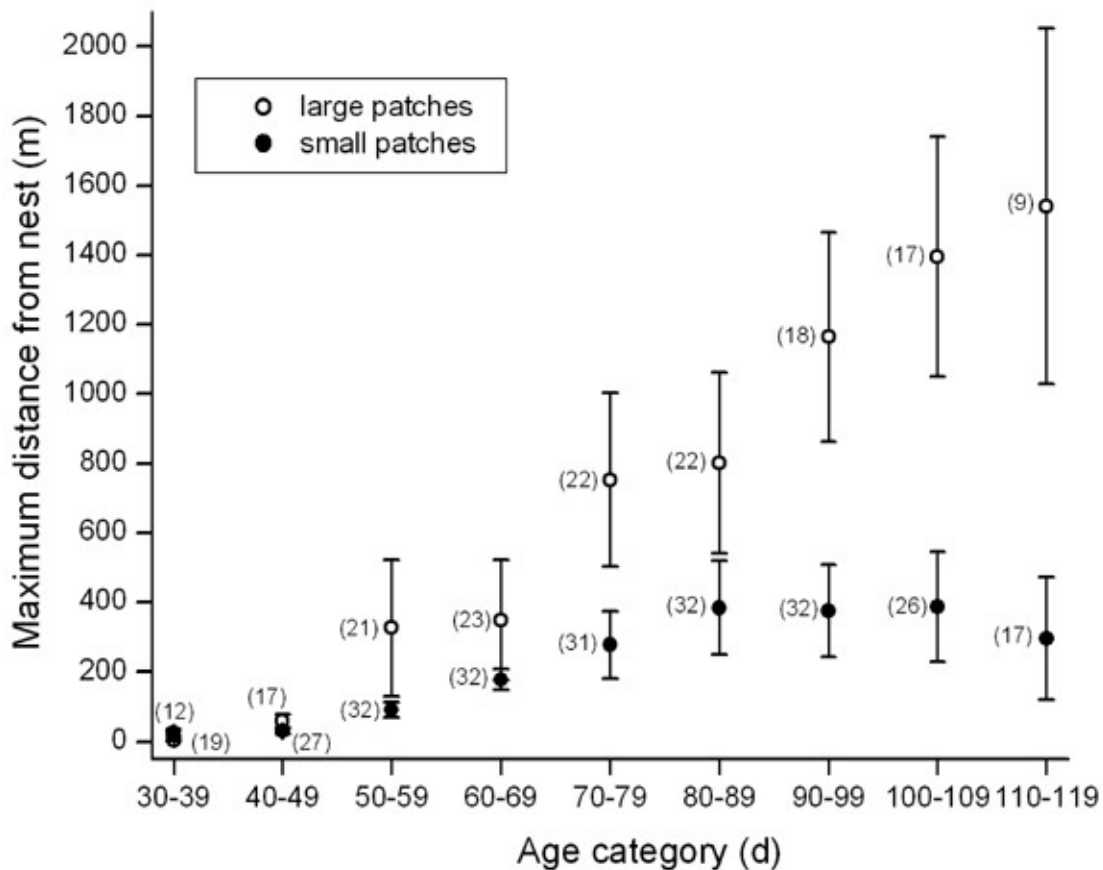
MODEL	AIC	AKAIKE WEIGHT
(a) Models predicting maximum distance moved before migration		
Feeding Treatment (FT)	186.5	0.004
Siblings (S)	183.7	0.01
Landscape Pattern (LP)	178	0.25
FT*LP	176.6	0.51
FT*S	178.2	0.23
Ln (maximum distance) = 6.82+(-1.55*LP)+(-0.90*FT)+(1.40*LP*FT)		
(b) Models predicting maximum distance moved per 10-d time interval		
T * S	1727.9	0.05
T * LP	1722.6	0.7
T * FT * LP	1726.3	0.11
T * FT * S	1725.9	0.13
Ln (maximum distance) = 0.88+(0.69*LP)+(0.66*T)+(-0.25*LP*T)		

DISCUSSION

Our results support the hypothesis that pre-migratory movement is beneficial for juvenile owls. We found little support for the idea that Burrowing Owl movement away from the nest before migration is forced by competition with conspecifics. Juvenile Burrowing Owls in contiguous tracts of grassland that were in good body condition moved about three times further from their natal burrows than did

juveniles from small, isolated prairie fragments. These results are consistent with other studies that have described dispersal behavior of Burrowing Owls, but not specifically in relation to landscape pattern or body condition (Table 2). Davies and Restani (2006) found juvenile Burrowing Owls inhabiting black-tailed prairie dog (*Cynomys ludovicianus*) colonies in western North Dakota, where available burrows are clustered together, dispersed a maximum of 0.3 km, and averaged only

Fig. 1. The maximum distance juvenile Burrowing Owls were found from their nest within 10-d age categories. Means \pm SE were derived from repeated measures of 55 individuals (sample sizes in parentheses).



0.1 km maximum distance from the natal nest before migrating. In Canada, black-tailed prairie dog distribution is naturally limited to a small area of southwestern Saskatchewan. Thus, Burrowing Owls across the Canadian prairies predominantly nest in ground squirrel (*Spermophilus* spp.) and badger burrows that are widely distributed within intact portions of the grasslands (Wellcome and Holroyd 2001). Clayton and Schmutz (1999) found juvenile Burrowing Owls from a fragmented landscape in Saskatchewan moved an average of

only 0.55 ± 0.16 km ($n = 12$). In contrast, Clayton and Schmutz (1999) recorded juvenile Burrowing Owls from the open rangelands of Alberta dispersing an average of 5.47 ± 1.73 km ($n = 10$). King and Belthoff (2001) found that juvenile Burrowing Owls using badger burrows in the Snake River Birds of Prey National Conservation Area moved an average of 2.1 ± 0.9 km ($n = 13$) from nest burrows before migration. Combined, these results strongly suggest that landscape pattern influences the pre-migratory movement patterns of

juvenile Burrowing Owls. Unfortunately, the configuration of the landscape in our study area precluded us from differentiating between the effects of patch size and patch isolation separately.

The influence of body condition on movement patterns of Burrowing Owls is less clear. The maximum distance moved was greater by individuals that were fed in large patches, but it was lower for fed individuals in small patches. However, there was no evidence to suggest that body condition influenced the timing of movements. This contrasts with the predictive model of dispersal for juvenile screech-owls (*Otus kennicottii* Elliot and *O. asio* L.) developed by Belthoff and Dufty (1998). They suggested that corticosterone, an adrenal glucocorticoid known to stimulate locomotor and foraging activity, increases in blood plasma before dispersal. Increases in corticosterone were predicted to occur through events such as decreases in parental provisioning or increases in sibling aggression. The model further predicts that individuals in good condition would be the first to disperse when their corticosterone levels hit some threshold, and that individuals in poorer condition would continue to forage on the natal area and initiate dispersal later. Importantly, however, this model also predicts that birds in poor condition may also move early because, at low food levels, a bird either leaves or starves. Because we did not measure individual body condition in this study, we cannot address whether this explains the observed movements of any of the unfed birds.

Landscape or functional connectivity is a concept that has been used to describe the degree to which the landscape either facilitates or impedes animal movement among habitat patches (Taylor et al. 1993, Tischendorf and Fahrig 2000). The factors that affect functional connectivity for Burrowing Owls in prairie habitat remain unclear. An animal's perceptual range undoubtedly plays an important role in determining functional connectivity, as it defines the range of information upon which movement decisions are based (Lima and Zollner 1996). The relatively short stature of grassland habitats and low variability in terrain may constrain the perceptual range of juvenile Burrowing Owls to sizes that are relatively small compared with other birds their size. A small perceptual range may preclude juvenile Burrowing Owls from dispersing far from their nest in small patches because they are unable to identify whether suitable resources exist beyond the natal patch. Although more detailed

work is required, our results suggest that the perceptual range of Burrowing Owls could be less than 1.5 km, as this is the minimum distance individuals in small patches would have to travel in a single move to traverse crop fields and make it to the next available grassland.

Satellite burrows appear to be a critical resource for juvenile Burrowing Owls, facilitating their pre-migratory movements (Clayton and Schmutz 1999, King and Belthoff 2001). Throughout their range in North America, Burrowing Owls use the abandoned burrows of fossorial mammals, such as ground squirrels, badgers, and prairie dogs (*Cynomys* spp.), for nesting and roosting (Wellicome and Holroyd 2001). Burrows in crop fields tend to be rare or ephemeral because of ploughing practices (Poulin et al. 2005). Only once during this study did we find a radio-tagged juvenile roosting in an area without burrows. On the few occasions we did find juveniles in ploughed fields, they were always located at burrows. King and Belthoff's (2001) finding that each individual owl used an average (\pm SE) of 5.1 ± 1.2 satellite burrows was similar to ours (5.3 ± 0.4 burrows). Dispersing juveniles rely heavily on a number of different burrows throughout the pre-migratory period, highlighting the importance of burrow availability during this stage.

The consequences of reduced dispersal by Burrowing Owls in fragmented prairie landscapes remain unknown. At the individual level, small, isolated patches may make juvenile Burrowing Owls more susceptible to predation or perhaps starvation if siblings compete for food resources. Accordingly, there was a tendency in our study population toward higher survival in large patches, although this difference was not statistically significant (Todd et al. 2003). At the population level, disruption of pre-migratory movements in juvenile Burrowing Owls may reduce recolonization of suitable but unoccupied habitat. The effects of dispersal restrictions on metapopulation persistence are poorly understood, but Warnock (1996) found that habitat fragmentation was negatively correlated with patch persistence of Burrowing Owls in Saskatchewan. This suggests that dispersing owls may be less likely to locate small, isolated, but otherwise suitable habitat patches. We speculate that pre-migratory juvenile movements may be critical for the colonization of empty habitat patches. Juvenile Burrowing Owls in this study had approximately 10 weeks to gain information on potential breeding sites between fledging and fall

Table 2. A comparison of studies reporting mean maximum distances juvenile Burrowing Owls moved from their nest before migration.

Study	<i>n</i>	Region	Patch Size	Mean maximum distance from nest (m)	General description of study area
Clayton and Schmutz (1999)	10	Alberta	large	5470	open ranchland, <20% cultivated
King and Belthoff (2001)	13	Idaho	large	2100	196 000-ha conservation area
This study	23	Saskatchewan	large	1056	Thousands of hectares of grassland
Clayton and Schmutz (1999)	12	Saskatchewan	small	550	agricultural land, >90% crops
Davies and Restani (2006)	29	North Dakota	small	96	35 ha prairie dog colonies
This study	32	Saskatchewan	small	374	patches of <58 ha

migration. In contrast, the average time between spring arrival and clutch initiation in Saskatchewan averages only 2 weeks (Wellicome 2000). For animals at the northern edge of their range, such as Burrowing Owls in Saskatchewan, the relatively short breeding season may preclude extensive exploration for suitable territories during spring, thus reducing the probability that small, isolated patches are located. Understanding whether birds decide on potential breeding sites before leaving for migration is very poorly understood and is an interesting area for further study.

CONCLUSION

In summary, habitat fragmentation plays an important role in the movement patterns of juvenile Burrowing Owls. Our results, along with evidence we synthesize from previous studies, suggest that juvenile Burrowing Owls in small patches are restricted from making large pre-migratory movements. Owls in small grassland patches are apparently unwilling to cross—or unable to find suitable conditions within—the matrix of a fragmented landscape, and thus remain relatively

close to their natal burrow until migration. If there are negative consequences from this modified behavior, then altered pre-migratory movements may be a mechanism to help explain why owl persistence is low in fragmented landscapes within North America, and may in part explain the overall Burrowing Owl population decline.

Responses to this article can be read online at:
<http://www.ace-eco.org/vol2/iss2/art4/responses/>

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