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Research Paper

Influence of vegetation on the nocturnal foraging behaviors and vertebrate prey capture by endangered Burrowing Owls

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ABSTRACT. Restrictions in technology have limited past habitat selection studies for many species to the home-range level, as a finer-scale understanding was often not possible. Consequently, these studies may not identify the true mechanism driving habitat selection patterns, which may influence how such results are applied in conservation. We used GPS dataloggers with digital video recorders to identify foraging modes and locations in which endangered Burrowing Owls (*Athene cucularia*) captured prey. We measured the coarse and fine-scale characteristics of vegetation at locations in which owls searched for, versus where they caught, vertebrate prey. Most prey items were caught using hover-hunting. Burrowing Owls searched for, and caught, vertebrate prey in all cover types, but were more likely to kill prey in areas with sparse and less dense vegetative cover. Management strategies designed to increase Burrowing Owl foraging success in the Canadian prairies should try to ensure a mosaic of vegetation heights across cover types.

Influence de la végétation sur la recherche nocturne de nourriture et la capture de proies vertébrées par la Chevêche des terriers, espèce en voie de disparition

RÉSUMÉ. Pour de nombreuses espèces, les études antérieures sur la sélection de l'habitat ont été limitées à l'échelle du domaine vital en raison des restrictions technologiques de l'époque, et la compréhension à une échelle plus fine n'était souvent pas possible. Par conséquent, ces études ne cernent sans doute pas le mécanisme véritable derrière les tendances dans la sélection de l'habitat, influençant peut-être du coup la façon avec laquelle ces résultats sont transposés en actions de conservation. Nous avons utilisé des géolocalisateurs (GPS) et des caméras numériques afin de déterminer les techniques qu'adoptaient la Chevêche des terriers (*Athene cucularia*), une espèce en voie de disparition, pour capturer ses proies et d'identifier les sites de capture. Nous avons mesuré les caractéristiques fines et grossières de la végétation aux sites ayant servi à la recherche pour les comparer à celles des sites dans lesquels les proies vertébrées ont été capturées. La majorité des proies ont été attrapées lors de vols stationnaires. Les chevêches ont cherché et attrapé leurs proies vertébrées dans tous les types de couvert végétal, mais étaient plus susceptibles d'en tuer aux endroits où la végétation était clairsemée et moins dense. Les stratégies d'aménagement destinées à augmenter le succès d'alimentation de la Chevêche des terriers dans les Prairies canadiennes devraient viser la présence d'une mosaïque de végétation de hauteurs différentes dans les divers types de couvert végétal.

Key Words: *Burrowing Owl*; *foraging ecology*; *movement path*; *prey accessibility*; *prey acquisition*; *vegetation*

INTRODUCTION

Studies of avian habitat selection tend to identify the environmental conditions in which individuals of a species place their territories or home ranges relative to environmental conditions available to the entire population (2nd order selection; Johnson 1980). More recently, studies have begun monitoring the movement of individuals to understand the use of habitat components within the home range (sensu 3rd order selection; Johnson 1980). Combined with better remote sensing information on environmental conditions, 3rd order studies have improved our understanding of what individuals select (use more than available) versus avoid (use less than available). However, the behaviors that underlie 3rd order selection remain elusive for most animals (Rousseau et al. 2010), particularly nocturnal species. In general, 3rd order habitat selection studies use resource selection functions to infer the importance of habitat elements based on whether they are selected or avoided, with little understanding of the behavior in which the animal is actually engaged.

Foraging success is a good predictor of reproductive success and/or survival, particularly for raptors (Bechard 1982, Korpimäki and Wiehn 1998, Wellicome 2000). Thus, understanding the habitat elements associated with successful prey acquisition relative to other behaviors is crucial to interpreting habitat selection and its implications for fitness. To understand where foraging occurs in an animal's home range relative to other behaviors requires highly accurate spatial locations and detailed assessments of the environmental conditions in which individuals search for, attempt to capture, and ultimately acquire prey.

The Burrowing Owl (*Athene cucularia*) is a fossorial owl associated with grassland ecosystems in prairie Canada. The reproductive success of Burrowing Owls is limited by the abundance and/or availability of small mammal prey (Wellicome 2000, Poulin and Todd 2006). Sissons (2003) studied nocturnal habitat selection by Burrowing Owls in native grasslands and concluded that Burrowing Owls 'select' for areas with higher prey density because nocturnal locations (obtained via triangulation

using VHF telemetry) had higher Robel pole scores than random points. Higher Robel scores indicate taller and denser vegetation, which has been correlated with increased abundance of small mammals (Sissons et al. 2001, Poulin 2003, Sissons 2003, Hennin 2010). However, foraging studies of numerous diurnal raptors have visually observed exact kill sites and found prey tends to be captured in areas with lower vegetation density or plant cover (Wakely 1978, Bechard 1982, Chipman et al. 2008) presumably because prey may be easier to capture in such areas. Knowing what conditions are important for successful Burrowing Owl foraging is important because Canadian government recovery plans call for efforts to create better foraging habitat for the species (COSEWIC 2006). It has been hypothesized that prey abundance and/or availability may have decreased over time for owls (Environment Canada 2012) because of conversion of native grassland to cropland. Attempts to create better foraging habitat are occurring. However, the degree to which prey capture varies among land-cover types and is influenced by vegetation structure is not well understood.

Our objective was to determine how meso- and microscale predictors of vegetation structure influenced where Burrowing Owls looked for and captured prey. Specifically, we tested if Burrowing Owls show differential selection for particular land-cover types based on the average height and density of the vegetation within cover types, and/or whether they select for local vegetation conditions within broad cover types in which the abundance or availability of prey is presumably highest. Based on Sissons' (2003) study, we predicted Burrowing Owls should hunt in areas in which the vegetation is taller and denser if prey abundance is the primary determinant of where owls hunt. However, the conditions that improve habitat quality for small mammals may reduce the ability of many raptors to acquire that prey. Thus, an alternative hypothesis is that owls hunt in areas in which vegetation conditions are most conducive to prey capture rather than areas in which prey are most abundant. Specifically, we tested whether micro- and mesoscale variations in vegetation structure influenced where nocturnally foraging Burrowing Owls travelled, searched for, and captured prey, relative to random locations. We predicted Burrowing Owls would fly over areas of tall dense vegetation in which prey were more abundant in an effort to find locations in which they could more easily capture prey, i.e., local areas with short, sparse vegetation. We also compared whether points in which Burrowing Owls initiated a hunting behavior (hovering) differed from areas in which a prey capture occurred to determine if vegetation structure influenced foraging success.

METHODS

The study area extended approximately from the towns of Hanna and Medicine Hat, Alberta, to the towns of Kindersley, Maple Creek, and Weyburn, Saskatchewan. The study area is dominated by the mixed-grassland ecoregion. Land use consists primarily of cattle ranching in Alberta and agriculture in Saskatchewan. Where native grass is present, it is dominated by needle and thread (*Stipa comata*), wheatgrasses (*Agropyron* sp.), blue grama (*Bouteloua gracilis*), and junegrass (*Koeleria macrantha*). Agriculture consists of wheat types, oilseeds, coarse grains, and pulse crops. Tame grass within the home ranges of the Burrowing Owls in this study consisted entirely of crested wheatgrass (*Agropyron pectiniforme*).

Monitoring foraging paths

We studied the crepuscular/nocturnal foraging behavior of male Burrowing Owls in June and July, 2009 and 2010. Nocturnal foraging paths were measured using GPS dataloggers, which recorded locations at an interval of 1 fix per 2 seconds from 21:00 to 07:00. The datalogger records a three-dimensional location, i.e., latitude, longitude, and altitude, speed, angle of two-dimensional movement, and degree of precision. Accuracy of the logger is high, with 95% of locations falling within 4.2 m when recorded for 24 hours in a fixed position (Dell'arricia et al. 2010).

We captured males when their respective broods were between 7 and 20 days posthatch. Males were trapped at nests or known roosts using bow-nets or one-way-door, walk-in traps (Winchell 1999). Once caught, males were weighed and given an aluminum Fish and Wildlife band and datalogger. Dataloggers were attached as a backpack using half-weave Teflon ribbon. Teflon was secured to the datalogger with lightweight packing tape containing a tear-proof, fiberglass cross-weave. Males were returned to their nest burrows once dataloggers were attached. Owls were captured a second time, approximately 3-4 days later, to remove the datalogger and retrieve spatial data. Occasionally, owls forcibly removed the dataloggers; some of these units were recovered fortuitously, or through searches, near nests or roost burrows.

Determining foraging success

To determine if prey were captured, we concurrently positioned digital video recorders (DVRs) > 50 m from each nest burrow. A security-style DVR powered by four 6-volt, deep-cycle marine batteries ran two infrared, waterproof security cameras. One camera was placed on the ground at the burrow mouth, opposite the mound, which permitted an unobstructed view of delivered prey. We placed a second camera approximately 1 meter from the burrow, filming 'over-the-shoulder' of the first camera. This camera functioned as a backup in case an accurate identification could not be made on the first camera and to detect prey deliveries occurring off the mound. Although the presence of cameras at the nest caused some owls to initially react with alarm, all owls returned prey the same evening cameras were placed. We did not attempt to quantify potential differences in prey return rates between filmed and nonfilmed nests because it is not possible to determine nocturnal prey delivery rates without infrared recording equipment. We assumed cameras affected each foraging male equally. The DVR records a date and time stamp on the screen, which was synchronized with the time on the datalogger.

The DVR footage recorded the time of all prey deliveries as the dataloggers recorded owl movement. For each recorded delivery, we used a GIS program (ArcMap) to evaluate the movement data of the male prior to each prey delivery. The first step was to determine if the prey delivery recorded on video was made by the male. We then examined the movement path prior to the delivery of prey. Specifically, we looked for clusters of points that preceded a direct flight to the nest that led to a prey delivery, hereafter termed capture cluster. The location within the cluster immediately preceding flight was considered the capture site, i.e., we assumed that the last point in the cluster was where the prey was actually killed. Prey items we suspected the male transferred to the female off-camera were included if the male returned to the nest but did not appear on camera, and the female flew out of view for < 15 seconds and returned with prey. We assumed the female did not have time to catch that prey and thus attributed the capture to the

male. Deliveries occurring when the male was not present at the nest were not included, nor were those preceded by the male's presence at a known roost. Males routinely cache prey in roost burrows (Poulin et al. 2005), and as such, these deliveries may have been cache retrievals, not prey captures.

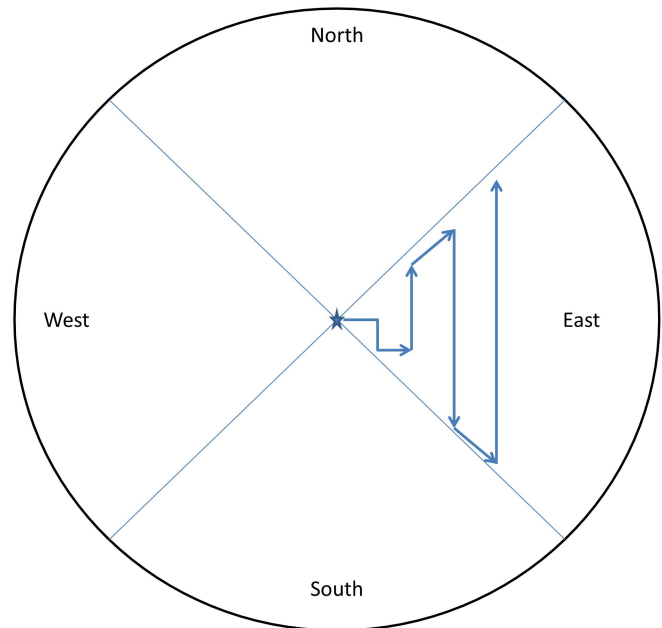
We identified each prey item to species from the DVR footage. When we could not identify prey to species, it was assigned to broader categories, such as 'mouse' or 'small mammal' or in a very small number of cases, 'vertebrate.' All of these deliveries were included in the analysis because we were confident the item was not an invertebrate. Approximately 95% of the prey returned to the nest are vertebrates by biomass (Poulin and Todd 2006); thus vertebrates comprise the overwhelming majority of the calories provided to the brood. Further, Burrowing Owls often catch insects on the wing making identification of the prey capture site impossible. For these reasons, vertebrate captures and their locations are the sole focus of this study.

Evaluating vegetation conditions along the foraging path

We visited all capture sites for each owl that we identified during the field season. We also visited a minimum of 10 randomly selected fly and 10 hover points per owl. At fly points, owls were moving in a relatively straight line at a constant speed. We assumed owls were searching for prey while flying. Vegetation at hover locations were sampled by randomly selecting one point within the cluster of points in which owls moved at slow speeds and maintained a relatively constant altitude. Hover points did not result in prey being delivered to the nest however. Finally, we sampled locations that were randomly generated within a 3.2-km radius of each owl's nest because this was the most distant location at which we recorded an owl from its nest. Although the total number of random points within each owl's home range differed among owls, the number of random points for an individual owl equaled its total number of used, i.e., hover, flight, and capture, points. We navigated to each location using a handheld GPS accurate to < 5 meters.

At each location, we took a Robel pole measurement to estimate a visual obstruction index based on the height and density of the vegetation (Robel 1970). Measurements were taken in the four cardinal directions and averaged. The Robel pole was marked in 5 cm intervals, and we recorded the highest interval that was obstructed. To estimate how vegetation might obstruct an owl's ability to view small mammal prey from above, we also measured the percentage of exposed ground (hereafter PEG) within a 5 m radius of each location. Measurements consisted of a visual approximation of the percent area of exposed ground in each of the four cardinal directions and were averaged for each point (Fig. 1). Exposed ground includes bare soil and ground covered by lichens because lichens offers no structural concealment for small mammals. Robel scores were weakly correlated with PEG measurements (Spearman's rho = -0.35, $p < 0.001$). We contend that Robel scores better describe visibility on an angle, whereas PEG may provide a better measurement of what is viewed from directly above. We conducted vegetation measurements within two weeks of recording each owl's movement patterns. No harvesting of crops or haying occurred during the time the position was recorded and the vegetation data collected. Grazing may have occurred but could not be quantified.

Fig. 1. Percent exposed ground (PEG) sampling method. The star in the center represents the sample location. The PEG was estimated by looking straight down and walking a path in each quadrant, as indicated by the arrows. The PEG was sampled in the four cardinal directions and averaged for the location. Circle radius is 5 m.

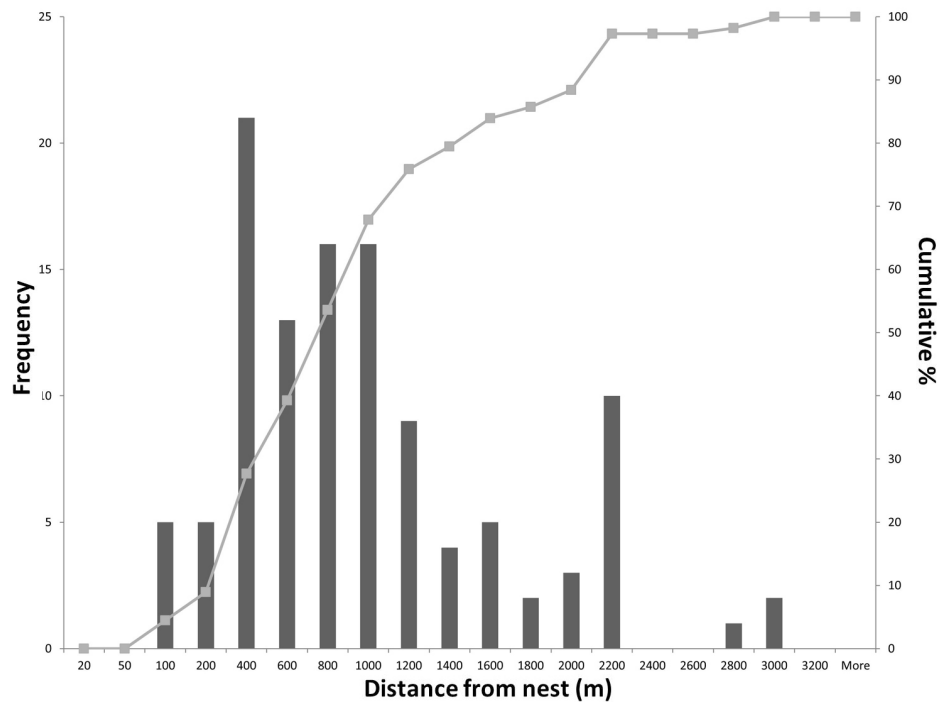


Statistical analysis

We used a mixed-effects, multinomial logistic regression in Stata 11.2 using the GLLAMM procedure (Skrondal and Rabe-Hesketh 2004) to determine if local vegetation conditions and/or land-cover types differed between random, capture, fly, and hover points. Multinomial logistic regression is a generalization of logistic regression that allows for more than two discrete outcomes. In other words, the model predicts the probability of the different possible outcomes of three or more categories relative to the same set of predictor variables. The baseline or reference condition for our comparisons was random points to which we compared the vegetation conditions at capture, hover, and fly points.

We then compared four sets of predictor variables to determine which model best described the observed differences in capture, hover, fly, and random points. We compared the relative fit of the four models using Akaike's Information Criteria adjusted for small sample size (AICc) and Bayesian Information Criteria (BIC). Bayesian Information Criteria is similar to Akaike's Information Criteria, but is more conservative when assessing improvements in model fit because it applies a more severe penalty for more parameters. Model 1 described the microscale vegetation using average Robel scores (hereafter ROBEL) and PEG as predictors. Model 2 was the mesoscale description of vegetation using five land-cover classes, i.e., native grass, tame grass, stubble,

Fig. 2. Distance of capture sites to the nest. The boxed line represents the cumulative percentage of captures at each distance bin.



wetland, and agricultural crop. Native grass was treated as the reference condition for the model. Model 3 was the additive effect of land cover and microscale vegetation measured at the point level. Model 4 was an interactive model, which included the multiplicative effect of land cover and PEG, as well as land cover and ROBEL. Our rationale for estimating the interactive model was that owls might be more likely to select areas with relatively shorter and less dense vegetation within land-cover types that were on average taller or more dense, i.e., agricultural crops, whereas in land-cover types with vegetation that was on average short and sparse, there may have been no need to discriminate. Ninety-five percent confidence intervals for the relative risk ratio for each behavioral comparison were used to determine statistical significance.

In all models, the individual owl was treated as a random effect. This approach was intended to account for the lack of independence in observations, variation in each owl's foraging strategy, available land-cover configuration, and the differences in number of locations available for each owl (Larsen et al. 2000, Gilles et al. 2006).

RESULTS

We put dataloggers on 18 males and identified 112 vertebrate prey captures (mean = 6.2; range = 1-14). Over 78% of captures were the result of hover hunting (Fig. 2) and most captures occurred in native grass, followed by cropland, stubble, tame grass, and wetlands (Table 1). The average distance-to-nest for all capture sites was 895 m (SD 662). Just under half of all captures (47%)

occurred at > 800 m from the nest, and 17% of captures occurred at > 1600 m from the nest. Fewer than 10% of captures occurred at < 200 m from the nest (Fig. 2). A total of 91 capture sites were identified in the field and had local vegetation sampled.

Table 1. Summary of vertebrate prey captures for each land-cover type by Burrowing Owls (*Athene cunicularia*) in Alberta and Saskatchewan, 2009-2010. "Small mammal" refers to an item that was positively identified as a small mammal, but could not be categorized further. "Unknown" deliveries were identified as vertebrates, but could not be categorized further.

Cover Type	Vertebrate Prey Types					Total
	Vole	Mouse	Small Mammal	Anuran	Unknown	
Native Grass	12	8	8	8	1	37
Wetland	0	0	1	1	0	2
Tame Grass	1	3	0	0	0	4
Tame Hay	0	0	1	0	0	1
Cropland	1	28	1	1	0	31
Stubble	1	20	6	0	2	29
Roadways	0	6	0	2	0	8
Total	15	65	17	12	3	112

In native grass, owls captured a greater diversity of prey types (Table 1), and this land-cover type was the main source of voles (80%) and amphibians (75%). Mice dominated captures in stubble and cropland. Over half of all captures (58%) were confirmed as mice, followed by unidentified small mammals (15%), voles (13%), amphibians (11%), and unidentified vertebrates (3%). Confirmed species identification was possible for 32 prey items and consisted of 15 deer mice, 9 meadow voles, 5 northern-grasshopper mice, 2 sagebrush voles, and 1 olive-backed pocket mouse. Further, 10 anuran deliveries were confirmed but identification of species was not possible.

Which model provided a better fit depended on the selection criterion used (Table 1). Akaike's Information Criteria for small sample size suggested that model 3 (land-cover type + local vegetation: $\chi^2 = 79.4$, $df = 18$, $P < 0.001$, pseudo $r^2 = 0.024$) was slightly better supported than model 1 (local vegetation only: $\chi^2 = 55.6$, $df = 6$, $P < 0.001$, pseudo $r^2 = 0.017$). Model 2 (land cover alone: $\chi^2 = 33.4$, $df = 12$, $P = 0.001$, pseudo $r^2 = 0.010$), and model 4 (interactive effect of land cover and local vegetation: $\chi^2 = 144.9$, $df = 42$, $P < 0.001$, pseudo $r^2 = 0.044$) had little support based on either criterion. Based on BIC, the strongest support was for model 1, local vegetation only.

Based on model 2 (land-cover type only; Table 2), the number of capture points in a particular land-cover class was significantly different than expected based on the frequency of random points in each land-cover class. Hover points were also significantly different from random. However, the patterns were inconsistent because fewer capture points occurred than expected in tame grass relative to the number of random points. In contrast, there were more hover points in tame grass than expected based on the availability of random points. There was some evidence that capture and hover points were less likely to occur than expected relative to random points or points over which owls flew in cropland. However, this pattern was weak. There was no significant difference between fly versus random, capture versus fly, and capture versus hover.

Table 2. Comparisons of model fit based on Akaike's Information Criteria adjusted for small sample size (AICc) and Bayesian Information Criteria (BIC) for each of the four models considered.

Model	K	AICc	Δ AICc	AICcWt	BIC	Δ BIC	BIC Wt
Local vegetation	10	3239.9	3.3	0.13	3287.1	0	1
Land cover	16	3276.0	39.3	0	3353.1	67.6	0
Local vegetation + Land cover	22	3236.6	0	0.68	3350.9	59.8	0
Local vegetation * Land cover	46	3239.1	2.5	0.19	3460.6	187.2	0

Based on Kruskal-Wallis tests, there was a significant difference in ROBEL ($\chi^2 = 324.4$, $df = 4$, $P < 0.001$) and PEG ($\chi^2 = 474.3$, $df = 4$, $P < 0.001$) between land-cover types. The main difference in ROBEL was that it was higher in cropland than all other land-cover types. Percentage of exposed ground (PEG) was lower in native grassland and wetlands, intermediate in agriculture, and higher in tame grass and stubble (Table 3).

We quantified ROBEL and PEG values at 91 locations in which prey were acquired, 263 hover locations, 271 fly locations, and 857 random locations. We identified 13 capture sites after the field season, and 8 captures occurred on roads and thus had no vegetative score. Based on model 1, capture and hover locations typically had lower ROBEL and higher PEG scores than random or flying points (Tables 4 and 5). The statistical significance of these comparisons varied depending on whether or not we controlled for land cover (Table 6).

DISCUSSION

When using high-energy foraging strategies, Burrowing Owls alternated between periods of direct, swift flights and stationary hovering. Foraging theory for a pause-travel forager suggests that an animal will initiate travel after hovering to distance itself from the previously searched location (Andersson 1981). Our data suggest the Burrowing Owl may also fly over habitat patches in which vegetative structure makes prey detection or capture less likely. Fly locations had higher ROBEL and lower PEG scores than capture or hover locations, suggesting that dense cover is not optimal habitat for Burrowing Owl hunting. Vegetation at capture and hover locations was similar, which suggests that owls engage in hovering when the vegetative structure increases prey detection and possibility of capture. This does not imply that prey presence always results in a capture; rather the patterns suggest that Burrowing Owls hover over suitable patches and wait for prey detection, rather than hovering after prey is detected, although the latter may occur as well.

Burrowing Owls flew, hovered, and captured prey in most of the land-cover types. However, within each cover type there was no evidence of an interaction between PEG scores and land-cover type, suggesting that Burrowing Owls search for local areas that optimize detection and capture of prey relative to the surrounding vegetative conditions rather than foraging in cover types in which PEG scores were lowest. Given that the average owl must travel several kilometers, regardless of the land-cover type, prior to capturing prey (Marsh et al. 2014), this strategy of searching for local sites that offer relatively higher prey accessibility may optimize a foraging owl's chances of detecting and capturing spatially unpredictable prey in all cover types rather than focused hunting in grasslands exclusively.

Sissons (2003) concluded that Burrowing Owl foraging locations were more likely to have higher Robel pole scores when compared with random locations in native grass and attributed this selection to increased prey abundance. His average random Robel score, which included all land-cover types in his study area, was 4.5 cm, and the average 'foraging' Robel score was 6.4 cm. The average Robel scores for random points and used points in native grass in our study were 10 cm and 5 cm, respectively. Native uplands, which equate to native grass in our study, dominated Sissons' study area. It is possible that the uplands in Sisson's study were grazed to the extent that prey were present only in taller remnant patches of grass, requiring the owls to forage where small mammals were present, rather than available. However, previous work on owl habitat selection relied on VHF technology, which may have been of insufficient spatial accuracy to identify actual locations, and which precludes determining the owl's behavior at each point. This means that much of the spatial information measured in past studies perhaps recorded behaviors other than successful foraging.

Table 3. Selection index for various behavioral comparisons within each land-cover class (1 means the proportion of used points is the same as what was available). Results are based on model 2, i.e., land cover not controlling for local vegetation. The second behavior in each comparison is the reference condition. In curved brackets is the ratio of points in each behavior class, e.g., 26 captures versus 349 randoms. In squared brackets is the total cell contribution in χ^2 units for that behavioral comparison to the overall chi-square value for that comparison. Larger values have a greater difference in observed than expected.

Behavioral comparison	Cropland	Stubble	Native Grass	Tame Grass	Wetland	Total Chi-square
Capture vs. Random	0.70 (26:349) [5.0]	1.55 (23:140) [0.3]	1.19 (35:278) [1.7]	0.67 (2:28) [9.3]	0.76 (5:62) [0.4]	$\chi^2 = 16.6$ $P = 0.002$
Fly vs. Random	1.09 (120:349) [0.6]	1.17 (52:140) [1.0]	0.85 (75:278) [1.5]	0.90 (8:28) [0.1]	0.82 (16:62) [0.5]	$\chi^2 = 3.7$ $P = 0.45$
Hover vs. Random	0.79 (85:349) [3.7]	1.05 (45:140) [0.1]	1.04 (89:278) [0.1]	2.91 (25:28) [16.6]	1.00 (19:62) [0.0]	$\chi^2 = 20.4$ $P < 0.001$
Capture vs. Fly	0.65 (26:120) [4.2]	1.32 (23:52) [1.2]	1.39 (35:75) [2.6]	0.75 (2:8) [0.1]	0.93 (5:16) [0.0]	$\chi^2 = 8.2$ $P = 0.09$
Capture vs. Hover	1.13 (26:85) [0.3]	0.68 (23:45) [2.3]	0.88 (35:89) [0.4]	4.32 (2:25) [4.7]	1.31 (5:19) [0.3]	$\chi^2 = 8.1$ $P = 0.09$
Hover vs. Fly	0.73 (85:120) [5.0]	0.89 (45:52) [0.3]	1.22 (89:75) [1.7]	3.22 (25:8) [9.3]	1.22 (19:16) [0.4]	$\chi^2 = 16.6$ $P = 0.002$

Table 4. Mean \pm 1 standard deviation for ROBEL and percent exposed ground (PEG) for each land-cover class. Numbers in brackets are the range.

Land-cover Variable	ROBEL	PEG	n
Cropland	20.5 \pm 23.4 (0 – 100)	43.8 \pm 23.2 (0 – 90)	580
Stubble	2.4 \pm 5.6 (0 – 59)	69.2 \pm 25.3 (4 – 100)	260
Native Grassland	3.2 \pm 5.7 (0 – 54)	24.8 \pm 16.6 (0 – 85)	477
Tame Grassland	5.2 \pm 10.0 (0 – 66)	56.1 \pm 18.1 (0 – 93)	63
Wetland	4.2 \pm 6.2 (0 – 38)	34.1 \pm 18.8 (0 – 95)	102

Table 5. Mean \pm 1 standard deviation for ROBEL and percent exposed ground (PEG) for each behavior class. Numbers in brackets are the range.

Behavior	ROBEL	PEG	n
Random	11.5 \pm 18.8 (0 – 100)	39.3 \pm 26.0 (0 – 100)	857
Capture	5.4 \pm 9.7 (0 – 53)	47.4 \pm 24.7 (6 – 96)	91
Flying	11.4 \pm 19.2 (0 – 95)	43.4 \pm 26.2 (0 – 100)	271
Hovering	5.3 \pm 11.9 (0 – 70)	47.7 \pm 26.5 (0 – 100)	263

Although our results offer new insights into Burrowing Owl foraging patterns, they do little to explain the decline in Burrowing Owl populations in western Canada. Owls catch prey in both native and nonnative cover types, proportional to each cover type's availability with the exception of stubble (Marsh et al. 2014). However, stubble is not targeted simply because this cover type contains the highest average PEG scores. Burrowing Owls still caught prey in areas with higher PEG and lower ROBEL scores than random locations. Thus, even in a sparsely vegetated cover type, i.e., in patches with sparser vegetative conditions than average, prey are searched for and captured. Heterogeneity across the landscape may be more important than the presence or absence of any specific cover type.

Based on our results, it is difficult to conclude that any cover type negatively affects Burrowing Owl reproductive success by precluding successful foraging. However, mature cropland was not an available cover type in this study because most crops did not reach maturation until later in the summer after we stopped monitoring owl movement. Therefore, it remains unknown whether tall crops negatively affect foraging Burrowing Owls. Mature cropland may be particularly obstructive and therefore detrimental to foraging Burrowing Owls later in the breeding season, especially for juveniles. However, most chicks die from starvation within the first 20 days of the nestling stage, which suggests that changes in crop structure later in the season are not the primary reason for low fledging success (Wellicome 2000). It is possible that mature cropland forces Burrowing Owls, particularly inexperienced juveniles, to forage more extensively in areas lacking obstructive vegetation, such as roadways, increasing the risk of anthropogenic mortality. However, Todd et al. (2003) and Shyry (2005) concluded that most juvenile mortality results from avian predation, with starvation and anthropogenic causes contributing relatively little.

Table 6. Risk rate ratios (RRR, where 1 indicates no difference) for ROBEL and percent exposed ground (PEG) between different behavioral comparisons. Bolded risk rate ratios have 95% confidence intervals that do not include 1.

Behavioral comparison	Local vegetation variable	RRR	RRR
		Local vegetation model	Local vegetation + Land cover model
Capture vs. Random	ROBEL	0.975 (0.955-0.995)	0.983 (0.961-1.006)
	PEG	1.008 (1.000-1.016)	1.012 (1.000-1.023)
Flying vs. Random	ROBEL	1.002 (0.995-1.010)	1.000 (0.991 – 1.009)
	PEG	1.007 (1.001 – 1.012)	1.005 (0.998 – 1.012)
Hovering vs. Random	ROBEL	0.975 (0.962 – 0.987)	0.978 (0.965 – 0.992)
	PEG	1.009 (1.003 – 1.014)	1.013 (1.006 – 1.021)
Capture vs. Fly	ROBEL	0.973 (0.952 – 0.994)	0.983 (0.961 – 1.007)
	PEG	1.002 (0.992 – 1.0111)	1.007 (0.994 – 1.019)
Capture vs. Hover	ROBEL	1.000 (0.978 – 1.024)	1.006 (0.980 – 1.032)
	PEG	1.000 (0.991 – 1.009)	0.999 (0.987 – 1.012)
Hover vs. Fly	ROBEL	0.972 (0.959 – 0.986)	0.978 (0.962 – 0.994)
	PEG	1.002 (0.995 – 1.009)	1.008 (0.999 – 1.017)

Management implications

A grazing regime that encourages small-scale heterogeneity of grass heights may be beneficial to Burrowing Owls. Although owls seem to search for areas in which vegetation is sparse, transforming an entire pasture of native or tame grass to sparse-grass conditions through intensive grazing would decimate small mammal numbers. Edge et al. (1995) found a 50% decline in vole populations after large-scale mowing, which was intended to mimic intense grazing. Conversely, too little grazing in native or tame pastures could also be detrimental to Burrowing Owls, because the height and density of vegetation may prevent owls from accessing abundant prey. Altering stocking rates of cattle to benefit Burrowing Owls will be complex however because the degree of management may vary between years depending on grassland productivity.

Altering the structure of cropland early in the nestling stage may not need to take place to allow successful foraging by adult owls. However, once mature, cropland is more likely to impede foraging. Land management that creates small areas in which vegetation is either removed or trampled could be beneficial. Many farmers leave fields as fallow every third or fourth season to allow nutrient recovery and to conserve water. We propose that instead of leaving an entire quarter section fallow, it may be possible to alternate crop and stubble within the quarter section each year. This would allow the benefits incurred from fallowing, but at a larger scale permit the same amount of crop to be planted annually. In an alternating crop-stubble scenario, a foraging owl would not have to travel far to bypass cropland in favour of stubble. Additionally, such a scenario would not likely require additional management, such as trampling. What effect such a configuration would have on small mammal populations and other animals is unknown and warrants further study. Likewise, associated costs and benefits to farmers also need to be examined.

Recent conservation efforts in Alberta and Saskatchewan include converting cropland to native grass. The efficacy of this effort

with respect to increasing the foraging success of Burrowing Owls is not clear, because Burrowing Owls are as, or more, successful at catching prey in cropland or stubble as they are in native grass during the middle of the breeding season. Conservation efforts aimed at improving successful foraging may be more easily implemented and more effective, by ensuring each cover type offers sufficient prey accessibility. However, providing access to mature cropland requires landowner participation, as well as continuous effort and possible financial compensation. If crops become so obstructive that Burrowing Owls cannot detect or access prey later in the season, increasing the amount and variation in native grass structure could benefit the owls by providing a more consistent foraging resource.

Responses to this article can be read online at:
<http://www.ace-eco.org/issues/responses.php/640>

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